

Advancing tree water deficit as a physiological indicator of drought stress

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Summary

Forests act as large terrestrial carbon sinks that buffer the effects of anthropogenic climate change. Under ongoing climate change, however, they are increasingly exposed to drought events that threaten tree vitality and the stability of ecosystem services. Assessing these impacts requires indicators that continuously capture tree drought stress and can be linked to ecosystem-scale analyses and process-based modeling.

High-resolution dendrometers may be particularly valuable in this context because they provide continuous, relatively easy-to-apply observations of stem-radius dynamics. From these measurements, tree water deficit (TWD) can be derived as the deviation of the current stem radius from its previously reached maximum, reflecting shrinkage associated with water loss from elastic stem tissues. Conceptually, TWD captures the depletion and replenishment of internal tree water stores when transpiration and water uptake are imbalanced, thereby providing a tree-level signal of internal water dynamics. However, its physiological interpretation, functional relevance, and representation in process-based models remain insufficiently constrained.

This thesis aims to advance the use of TWD as a physiologically interpretable and model-compatible signal of drought stress. Three research questions are addressed, each evaluated in a specific study: (1) Does dendrometer-derived TWD reflect key physiological indicators of tree drought stress during severe dehydration and recovery? (2) Can normalized TWD serve as a common hydraulic stress axis for interpreting functional drought responses? (3) Can TWD be represented in a parsimonious modeling framework compatible with ecosystem-scale simulations?

The first study investigates the physiological basis of TWD in a controlled drought experiment with *Pinus sylvestris* (Scots pine) and *Larix decidua* (European larch) saplings. Progressive drought was monitored with dendrometers and complemented by measurements of midday water potential (ψ) and stomatal conductance (g_s). During dehydration, TWD was strongly related to ψ and g_s , allowing the identification of TWD thresholds associated with the onset of drought stress and potential tissue damage. Trees that were rewetted after severe drought showed incomplete TWD recovery, which may indicate hydraulic or cellular damage and provide information on recovery potential. However, this incomplete recovery also led to a temporary decoupling among TWD, ψ , and g_s . In addition, the study identifies suitable TWD normalization as a key challenge for developing transferable, field-applicable monitoring approaches, while persistent overnight TWD emerges as a directly applicable drought-stress signal.

The second study tests whether normalized daily minimum TWD (TWD_{min,norm}) can provide a common functional drought-stress axis. It synthesizes three controlled drought experiments on saplings of *Pinus sylvestris*, *Picea abies* (Norway spruce), and *Pseudotsuga menziesii* (Douglas-fir), in which dendrometers were combined with continuous whole-tree shoot and root gas

exchange measurements. Across the three conifer species and experimental setups, daily tree-level net carbon balance declined consistently with increasing $\text{TWD}_{\text{min,norm}}$ and shifted from net carbon uptake to net carbon loss at approximately $\text{TWD}_{\text{min,norm}} = 0.20$ [0.13–0.31]. Species-specific thresholds occurred within a narrow $\text{TWD}_{\text{min,norm}}$ range, indicating that normalized TWD can identify functionally comparable drought-stress levels. However, g_s and transpiration dynamics were less consistently described by $\text{TWD}_{\text{min,norm}}$, likely because they are also shaped by atmospheric demand and short-term water availability, which differed among experiments. These results indicate that dendrometer-derived TWD can, after appropriate normalization, serve as a transferable drought-stress metric, particularly for tree-level carbon balance.

The third study translates TWD into a model-compatible representation of internal tree water dynamics. It introduces the newly developed *Tree Water Imbalance and Storage Tracker* (TWIST), a parsimonious, diagnostic module that simulates volume-based TWD from transpiration and soil water availability. TWIST also derives relative tree water content (RWC_{tree}) from TWD and an estimate of internal water storage as an interpretable proxy for internal dehydration. Coupled to the process-based ecosystem model LandscapeDNDC and evaluated against dendrometer-derived TWD at a Czech *Fagus sylvatica* (European beech) forest site, TWIST broadly reproduced observed daily and seasonal dynamics, including diurnal depletion–replenishment cycles, reduced nocturnal rehydration under declining soil moisture, and progressive deficit accumulation during drought. By generating TWD and RWC_{tree} as diagnostic model outputs, TWIST links dendrometer-derived drought information to stand-level forest simulations.

Altogether, this thesis demonstrates that TWD contains physiologically meaningful information at several complementary levels. First, as an integrative signal of tree water uptake and loss, TWD provides a simplified and model-compatible framework for quantifying tree dehydration. Second, temporal TWD patterns can help distinguish phases of drought stress: low stress when daily TWD is fully replenished overnight, functional limitations in growth, gas exchange, and carbon gain associated with persistent pre-dawn TWD, and potentially damaging stress when increasing pre-dawn TWD coincides with diminishing daily TWD cycles. Third, appropriately normalized TWD may provide a transferable drought-stress axis for comparing stress levels across contexts and supporting threshold-based evaluations of drought impacts on trees.

While challenges remain, particularly regarding robust normalization beyond experimental conditions, the transferability of experimental relationships, and moving beyond the current diagnostic role of simulated TWD, this thesis outlines how increasingly available dendrometer measurements can improve tree-level drought monitoring. TWIST further enables a comparison between simulations and dendrometer-based observations and may help improve the representation of drought-stress dynamics in models. In this way, TWD provides a starting point for linking tree-level dendrometer measurements to ecosystem-scale analyses and may help improve assessments and projections of forest responses to increasing drought stress.

Zusammenfassung

Wälder sind große terrestrische Kohlenstoffsinken und schwächen dadurch die Auswirkungen des anthropogenen Klimawandels ab. Im Zuge des fortschreitenden Klimawandels sind sie jedoch zunehmend Dürreereignissen ausgesetzt, die die Vitalität von Bäumen und die Stabilität von Ökosystemleistungen bedrohen. Um diese Auswirkungen bewerten zu können, werden Indikatoren benötigt, die kontinuierlich Trockenstress bei Bäumen erfassen und mit Analysen auf Ökosystemebene sowie mit prozessbasierten Modellen verknüpft werden können.

Hochauflösende Dendrometer können in diesem Zusammenhang besonders wertvoll sein, da sie kontinuierliche und vergleichsweise einfache Messungen von Veränderungen des Stammradius ermöglichen. Aus diesen Messungen kann das Baum-Wasser-Defizit (tree water deficit; TWD) als Abweichung des aktuellen Stammradius vom zuvor erreichten Maximum berechnet werden. Es spiegelt eine Schrumpfung wider, die durch den Verlust von Wasser aus elastischen Stammgeweben hervorgerufen wird. Konzeptionell erfasst TWD damit die Entleerung und Wiederauffüllung interner Baumwasserspeicher, wenn Transpiration und Wasseraufnahme aus dem Boden nicht im Gleichgewicht sind. Die physiologische Bedeutung und funktionelle Aussagekraft von TWD sind jedoch noch unzureichend geklärt, ebenso wie die Darstellung von TWD in prozessbasierten Modellen.

Ziel dieser Dissertation ist es, TWD als physiologisch interpretierbares und modellkompatibles Signal für Trockenstress weiterzuentwickeln. Dazu werden drei Forschungsfragen behandelt, die jeweils in einer eigenen Studie untersucht werden: (1) Spiegelt dendrometerbasiertes TWD zentrale physiologische Trockenstresseindikatoren bei Bäumen während starker Austrocknung und anschließender Erholung wider? (2) Kann normalisiertes TWD als gemeinsame hydraulische Stressachse zur Interpretation funktioneller Trockenheitsreaktionen dienen? (3) Kann TWD auf vereinfachte Weise in Modelle integriert und mit Simulationen auf Ökosystemebene verbunden werden?

In der ersten Studie wird die physiologische Grundlage von TWD in einem kontrollierten Dürreexperiment mit Setzlingen von *Pinus sylvestris* (Waldkiefer) und *Larix decidua* (Europäische Lärche) untersucht. Neben Dendrometermessungen wurden Messungen des mittäglichen Wasserpotenzials (ψ) sowie der stomatären Leitfähigkeit (g_s) durchgeführt. Die Studie zeigt enge Zusammenhänge zwischen TWD, ψ und g_s während der Austrocknung und leitet TWD-Schwellenwerte für den Beginn von Trockenstress und potenzieller Gewebeschädigung ab. Bäume, die nach starker Dürre erneut bewässert wurden, zeigten eine unvollständige Erholung des TWD, was auf hydraulische oder zelluläre Schäden hinweisen und Aufschluss über das Erholungspotenzial geben kann. Diese unvollständige Erholung führte jedoch auch zu einer vorübergehenden Entkopplung der Beziehungen zwischen TWD, ψ und g_s . Zudem identifiziert die Studie eine

geeignete Normalisierung von TWD als zentrale Herausforderung für übertragbare, praxisnahe Monitoringansätze, während über Nacht verbleibendes TWD als direkt anwendbares Trockenstresssignal herausgearbeitet wird.

In der zweiten Studie wird geprüft, ob das normalisierte tägliche Minimum von TWD ($\text{TWD}_{\text{min,norm}}$) als gemeinsame funktionelle Trockenstressachse dienen kann. Dafür wurden drei kontrollierte Dürreexperimente an Setzlingen von *Pinus sylvestris*, *Picea abies* (Gemeine Fichte) und *Pseudotsuga menziesii* (Douglasie) zusammengeführt, in denen Dendrometermessungen mit kontinuierlich erfasstem Gaswechsel von Trieben und Wurzeln der Bäume kombiniert wurden. Trotz der Unterschiede zwischen den drei Nadelbaumarten und den experimentellen Aufbauten nahm die tägliche Netto-Kohlenstoffbilanz auf Baumebene mit zunehmendem $\text{TWD}_{\text{min,norm}}$ konsistent ab und wechselte bei ungefähr $\text{TWD}_{\text{min,norm}} = 0.20$ [0.13–0.31] von einer Netto-Kohlenstoffaufnahme zu einem Netto-Kohlenstoffverlust. Artspezifische Schwellenwerte lagen innerhalb eines vergleichsweise engen $\text{TWD}_{\text{min,norm}}$ -Bereichs, was darauf hindeutet, dass normalisiertes TWD vergleichbare Trockenstressniveaus identifizieren kann. g_s - und Transpirationsdynamiken wurden durch $\text{TWD}_{\text{min,norm}}$ jedoch weniger konsistent beschrieben, vermutlich weil sie auch stark auf atmosphärischen Wasserbedarf und kurzfristige Wasserverfügbarkeit reagieren, die sich zwischen den Experimenten unterschieden. Diese Ergebnisse deuten darauf hin, dass dendrometerbasiertes TWD bei geeigneter Normalisierung als übertragbare Trockenstressmetrik dienen kann, insbesondere für die Kohlenstoffbilanz auf Baumebene.

In der dritten Studie wird TWD in eine modellkompatible Darstellung interner Baumwasserdynamiken überführt. Dazu wird der neu entwickelte *Tree Water Imbalance and Storage Tracker* (TWIST) eingeführt, ein bewusst einfaches, diagnostisches Modul, das volumenbasiertes TWD aus Transpiration und Bodenwasserverfügbarkeit simuliert. TWIST leitet außerdem den relativen Wassergehalt von Bäumen (RWC_{tree}) aus TWD und einer Schätzung des internen Wasserspeichers ab, wodurch ein interpretierbarer Indikator für interne Dehydrierung entsteht. Gekoppelt an das prozessbasierte Ökosystemmodell LandscapeDNDC wurde TWIST anhand von dendrometerbasiertem TWD an einem tschechischen Rotbuchenwaldstandort (*Fagus sylvatica*) evaluiert. Dabei konnte es die beobachteten TWD-Dynamiken weitgehend reproduzieren, darunter tägliche Entleerungs- und Wiederauffüllungszyklen, eine verringerte nächtliche Rehydrierung bei abnehmender Bodenfeuchte sowie die fortschreitende Akkumulation von TWD während saisonaler Dürreperioden. Durch die Ausgabe von TWD und RWC_{tree} als diagnostische Modellgrößen verknüpft TWIST dendrometerbasierte Trockenheitsinformationen mit Waldsimulationen auf Bestandsebene.

Zusammengenommen zeigt diese Dissertation, dass TWD physiologisch relevante Informationen auf mehreren komplementären Ebenen enthält. Erstens bietet TWD als integratives Signal des Ungleichgewichts zwischen Wasseraufnahme und Wasserverlust einen vereinfachten und modellkompatiblen Rahmen zur Quantifizierung des hydraulischen Zustands eines Baumes.

Zweitens können zeitliche TWD-Muster helfen, verschiedene Phasen von Trockenstress zu unterscheiden: geringer Stress, wenn das tägliche TWD über Nacht vollständig wieder aufgefüllt wird; funktionelle Einschränkungen von Wachstum, Gaswechsel und Kohlenstoffassimilation, wenn TWD über Nacht nicht mehr vollständig ausgeglichen wird; sowie potenziell schädigender Stress, wenn TWD insgesamt akkumuliert, während die täglichen TWD-Zyklen abnehmen. Drittens kann normalisiertes TWD eine übertragbare Trockenstressachse bieten, um Stressniveaus über verschiedene Kontexte hinweg zu vergleichen und TWD-Schwellenwerte zur Bewertung der Dürreauswirkungen auf Bäume einzusetzen.

Offen bleiben insbesondere Fragen zur robusten Normalisierung von TWD außerhalb experimenteller Bedingungen, zur Übertragbarkeit experimenteller Zusammenhänge und zur Weiterentwicklung von simuliertem TWD über die derzeitige diagnostische Rolle hinaus. Gleichzeitig zeigt diese Dissertation Wege auf, wie zunehmend verfügbare Dendrometermessungen das Monitoring einzelner Bäume verbessern können. TWIST ermöglicht zudem einen direkteren Vergleich zwischen Simulationen und dendrometerbasierten Beobachtungen und kann dabei helfen, Dynamiken von Trockenstress in Modellen besser abzubilden. Damit bietet TWD einen Ansatzpunkt, um baumbezogene Messungen mit Modellsimulationen und Analysen auf Ökosystemebene zu verbinden und die Auswirkungen des im Klimawandel zunehmenden Trockenstresses auf Wälder besser zu erfassen und modellbasiert abzuschätzen.

List of Publications

The content and structure of the included publications have been preserved in their original form. Chapter 2 is presented as accepted by the journal, prior to typesetting. Chapters 3 and 4 are included as submitted to the journal.

Chapter 2

Ziegler Y, Grote R, Alongi F, Knüver T, Ruehr NK. 2024. Capturing drought stress signals: The potential of dendrometers for monitoring tree water status. *Tree Physiology*, Volume 44, Issue 12, tpae140, DOI: 10.1093/treephys/tpae140.

Credit statement: Y.Z., N.K.R., and R.G. designed the experiment. Y.Z., supported by F.A. and T.K., performed the measurements. Y.Z. analyzed the data and wrote the manuscript, with input and approval from all authors.

Chapter 3

Ziegler Y, Alongi F, Knüver T, Rehschuh R, Zeppan JK, Ruehr NK. 2026. Tree water deficit reveals a drought-induced carbon balance transition across three coniferous species. *In review*.

Credit statement: Y.Z. conceptualized the synthesis design and, supported by J.K.Z., re-analyzed all data. F.A., T.K., and R.R., supported by N.K.R., conducted the underlying experiments. Y.Z. wrote the manuscript, with input and approval from all authors.

Chapter 4

Ziegler Y, Labenski P, Thurner M, Krejza J, Šigut L, Ruehr NK, Grote R. 2026. TWIST: A diagnostic framework for representing tree water deficit dynamics in process-based forest models. *In review / preprint*. DOI: 10.64898/2026.06.15.732331.

Accompanied by the software publication: **Ziegler Y**, Ruehr NK, Grote R. 2026. TWIST: Tree Water Imbalance and Storage Tracker (TWIST) module (v2.0). *Zenodo*, DOI: 10.5281/zenodo.19692465.

Credit statement: Y.Z., supported by N.K.R. and R.G., developed and evaluated TWIST. Y.Z., P.L., and R.G. contributed to the setup of the LandscapeDNDC site. J.K. and L.Š. provided observational data. Y.Z. wrote the manuscript, with input and approval from all authors.

During my PhD project, I also contributed to the following publications and research outputs, which were not included as separate chapters in this thesis but did contribute to the interpretation of the results.

- Giese M, **Ziegler Y**, Ruehr NK. 2024. CaviTools: Automated processing of xylem cavitation and optical dendrometry image sequences (1.1). *Zenodo*, DOI: 10.5281/zenodo.13328771.
- Alongi F, Knüver T, McAdam SAM, **Ziegler Y**, Gast A, Ruehr NK. 2026. Drought-induced delays in stem hydraulic development shape gas exchange and growth recovery in Douglas fir. *Plant Physiology*, Volume 200, Issue 3, kiaf654, DOI: 10.1093/plphys/kiaf654.
- Zeppan JK, Hülsmann L, Knüver T, **Ziegler Y**, Ruehr NK. 2026. Water Availability and Hydraulic Strategies Control Leaf Thermoregulation and Damage During Heat Stress and Recovery in Temperate Tree Species. *Plant, Cell & Environment* 0: 1–15. DOI: 10.1111/pce.70605.
- Thurner M, Grote R, Labenski P, **Ziegler Y**, Ruehr NK. The many ways to model drought-induced tree mortality – A call for considering tree water storage and integrating hydraulic damage mechanisms and legacy effects. *In preparation*.
- Giardina F, Ahmed MA, Bachofen C, Baldocchi D, Baur MJ, Bloom C, Bortolami G, Bose AK, Bouda M, Brodribb T, Byrne MP, Cheng X, Couvreur V, Deluigi J, Di Bert S, Duddek P, Floriancic MG, Fu Z, Gessler A, Grondin A, Grossiord C, Helpap P, Hildebrandt A, Huang H, Jansen S, Javaux M, Kahmen A, Koehler T, Konings AG, Kroll J, Labenski P, Lehmann MM, Lehmann P, Martinetti S, Mencuccini M, Meusburger K, McCormick E, Or D, Orth R, Peters RL, Piovano D, Rao MP, Rigling A, Rouholahnejad Freund E, Ruehr N, Sabot M, Schoch J, Seeburger P, Stoll F, Tardieu F, Trugman AT, Vanderborght J, Verhoef A, Wang-Erlandsson L, Wankmüller FJP, Werner C, Wolf S, Zarebanadkouki M, Zeng Y, Zhan C, **Ziegler Y**, Carminati A. Connecting plant–water interactions across scales: historical discrepancies and emergent convergences. *In preparation*.

List of Abbreviations and Symbols

General

A_{net}	Net assimilation rate
C	Carbon
C_{net}	Tree-level net carbon balance ($A_{\text{net}} + R_{\text{root}}$)
CO ₂	Carbon dioxide
DBH	Diameter at breast height
DoE	Day of experiment
E	Transpiration rate
ET	Evapotranspiration
g_s	Stomatal conductance
GPP	Gross primary productivity
NSC	Non-structural carbohydrates
PAR	Photosynthetically active radiation
PLC	Percentage loss of hydraulic conductivity
P_{12}, P_{50}, P_{88}	Water potentials at 12 %, 50 %, and 88 % loss of hydraulic conductivity
R^2	Coefficient of determination
RMSE	Root mean square error
R_{root}	Root respiratory carbon loss rate
RWC	Relative water content
SE	Standard error
SD	Standard deviation
SWC	Soil water content
T_{air}	Air temperature
VPD	Vapor pressure deficit
ψ	Water potential
ψ_{g5}, ψ_{g50}	Water potentials corresponding to 5 % and 50 % of maximum stomatal conductance

Tree water deficit

d	Stem diameter
d_{max}	Previously reached maximum stem diameter

MDS	Maximum daily shrinkage
MDS _{q99}	99th percentile of MDS; used for normalization in Chapter 4
MDS _{ref}	Reference MDS; used for normalization in Chapter 3
TWD	Tree water deficit ($d_{\max} - d$)
TWD _{g5} , TWD _{g50}	TWD thresholds corresponding to 5 % and 50 % of maximum stomatal conductance
TWD _{max} (Chapter 2)	Maximum observed TWD around tree death; used for normalization
TWD _{max} (Chapters 3–4)	Daily maximum tree water deficit
TWD _{min}	Daily minimum tree water deficit
TWD _{norm}	Normalized tree water deficit
TWD _{min,norm}	Normalized daily minimum tree water deficit

TWIST module

F_E	Transpiration separation factor; controls the fraction of current transpiration demand compensated by water uptake within a time step
F_{TWD}	TWD reduction factor; controls the fraction of the existing tree water deficit replenished within a time step
F_θ	Relative soil-water limitation threshold; value of θ_{rel} below which water uptake is additionally limited
f_{drought}	Drought limitation function for soil water uptake
LandscapeDNDC	Process-based ecosystem model coupled with TWIST
MDWL _{q99}	99th percentile of maximum daily water loss; volume-based analogue of MDS _{q99} used to normalize TWD _{sim}
m_{sapwood}	Dry-weight sapwood mass
RWC _{tree}	Relative tree water content simulated by TWIST
U	Soil water uptake
U_E	Component of water uptake compensating current transpiration demand
U_{TWD}	Component of water uptake replenishing previously accumulated TWD _{sim}
W	Estimated maximum available internal tree water storage
ρ_{dry}	Oven-dried wood density
ρ_{sat}	Fully saturated wood density
θ_{rel}	Relative soil water content; scaled from 1 at field capacity to 0 at wilting point
TWD _{sim}	Volume-based tree water deficit simulated by TWIST
TWIST	Tree Water Imbalance and Storage Tracker

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1 INTRODUCTION

1.1 Forests at the interface of climate change

Across the globe, anthropogenic climate change is increasing temperatures and altering hydro-climatic conditions. As a result, climate extremes are increasing in frequency, duration, and intensity (Spinoni et al., 2018; IPCC, 2021; Suarez-Gutierrez et al., 2023; Tripathy et al., 2023). These changes expose terrestrial ecosystems to more stressful environmental conditions, with drought and heat representing two major constraints on ecosystem functioning (Gazol et al., 2025; Chen et al., 2025).

Forests play a key role in the terrestrial biosphere. They cover approximately one-third of the global land surface and act as an important carbon sink, removing a substantial fraction of anthropogenic CO₂ emissions from the atmosphere (Pan et al., 2011; Friedlingstein et al., 2022; Pan et al., 2024). Beyond carbon sequestration, forests support biodiversity and provide a wide range of ecosystem services, including water regulation, wood provision, and cultural and recreational values (Mori et al., 2017; Allen et al., 2025). Consequently, the capacity of forests to maintain their ecological functions is important for both climate mitigation and the provision of ecosystem services.

At the same time, forests are affected by the environmental changes they help to buffer. Water limitation can reduce primary productivity (Frank et al., 2015; Sippel et al., 2018; Green et al., 2019), limit tree growth (Bose et al., 2025; Etzold et al., 2026), and increase the risk of functional damage and mortality (Allen et al., 2010; Schuldt et al., 2020; Senf et al., 2020; International Tree Mortality Network, 2025). Heat stress, often co-occurring with drought (Werner et al., 2025), can further amplify declines in forest functioning and increase damage. Moreover, forests are increasingly exposed to natural disturbance agents, including wildfires, windstorms, pathogens, and insect outbreaks (Seidl et al., 2017; Forzieri et al., 2021), and face anthropogenic pressures such as deforestation (Curtis et al., 2018).

These responses can contribute to longer-term changes in tree performance and forest structure (McDowell et al., 2020; Müller and Bahn, 2022; Pretzsch et al., 2022), which remain a major source of uncertainty. While immediate reductions in gas exchange during drought are relatively well investigated, the persistence of drought legacy effects remains less well understood (Ruehr et al.,

2019; Kannenberg et al., 2020; Kannenberg et al., 2022). This uncertainty limits projections of whether forests will maintain their role as carbon sinks under future climate regimes, particularly because ecosystem models still struggle to represent drought-induced damage, recovery dynamics, and mortality processes (Hartmann et al., 2018; Bugmann et al., 2019). Against this background, this thesis focuses primarily on drought effects and on the detection and quantification of tree water status as a key indicator of forest stress and recovery.

1.2 Tree water relations and physiological drought responses

Understanding forest responses to climate extremes requires an understanding of the physiological mechanisms by which individual trees regulate water loss, carbon uptake, and hydraulic function. These processes are not independent: stomatal regulation, carbon assimilation, growth, and hydraulic safety are tightly coupled through tree water relations (Venturas et al., 2017; Torres-Ruiz et al., 2024).

Trees lose water via transpiration and gain it from the soil. Water is taken up by roots and transported through the xylem along the soil–plant–atmosphere continuum (Dixon, 1915; Tyree and Zimmermann, 2002). This transport is driven by gradients in water potential, a measure of the energy status of water and thus water availability (Steppe, 2018). The resulting water flux is further modulated by the hydraulic conductance of pathway tissues (Tyree and Zimmermann, 2002; Mencuccini et al., 2019) and by internal tree water storage and hydraulic capacitance (Meinzer et al., 2009; Salomón et al., 2017; Preisler et al., 2022). When water availability decreases, driven by soil drying or increasing atmospheric demand, tree water potentials decline, thereby increasing xylem tension and the risk of hydraulic dysfunction (Tyree and Sperry, 1989; Choat et al., 2012).

Stomata directly link tree water and carbon fluxes (Farquhar and Sharkey, 1982). They allow CO₂ to diffuse into the leaf for photosynthetic carbon assimilation, but they also expose the tree to water loss through transpiration. This coupling creates a fundamental trade-off: trees can maintain carbon gain when stomata remain open, but doing so increases water loss, which can intensify hydraulic stress (Choat et al., 2012; Sperry et al., 2017), with atmospheric demand acting as an amplifying factor. Tree responses to drought stress thus reflect a balance between maintaining productivity and reducing the risk of excessive dehydration (Sperry et al., 2017).

A short-term response to declining water availability is stomatal closure (Buckley, 2019). This reduces stomatal conductance, thereby limiting transpiration and slowing the rate of water potential decline. However, stomatal closure also reduces photosynthesis while respiratory processes continue, shifting the net carbon balance towards lower carbon gain and, under severe or prolonged stress, potentially net carbon loss (Flexas, 2002). Species differ in how tightly they regulate stomata during drought, ranging from more conservative water-saving behavior to less

conservative strategies that sustain gas exchange longer but may increase hydraulic risk (Tardieu and Simonneau, 1998; Klein, 2014). Even when stomata are closed, residual water losses cannot be fully avoided (Blackman et al., 2019; Duursma et al., 2019), driven by minimal stomatal and cuticular conductance and atmospheric demand (Garen and Michaletz, 2025). Thus, under prolonged drought, the progression towards critical dehydration depends on stomatal regulation, internal water storage, atmospheric demand, and exposure time (Burlett et al., 2025).

If drought intensifies, hydraulic and cellular damage can occur. Increasing xylem tension can cause embolism, reducing hydraulic conductivity and impairing water supply to living tissues (Tyree and Sperry, 1989). Hydraulic vulnerability is commonly described by thresholds such as P_{50} , the water potential at which 50% of xylem conductivity is lost, providing a comparative measure of species drought sensitivity (Choat et al., 2012). Dehydration can also affect living tissues through turgor loss and, at more extreme stress, cellular injury or collapse (Mantova et al., 2022). Overall, tree mortality may result from interacting mechanisms including hydraulic failure, carbon starvation, impaired repair processes, and biotic stress interactions (Hartmann et al., 2018; McDowell et al., 2022).

Drought recovery is not simply the reversal of drought stress. It depends on whether stress caused only reversible changes or irreversible damage. Following stress release, leaf water potentials can often recover quickly as plant water status is restored through still-functional hydraulic pathways. After a mild drought, stomatal conductance and photosynthetic enzyme activity can also recover rapidly. However, severe drought may lead to xylem embolism and a reduced overall hydraulic conductance, and gas exchange may remain constrained by hydraulic limitations or impaired photosynthetic metabolism (Ruehr et al., 2019; Rehschuh et al., 2020). Although some plants may be able to actively refill embolized xylem conduits under specific conditions (Ogasa et al., 2019; Souden et al., 2020), embolized conduits often remain nonfunctional (Arend et al., 2022; Gauthey et al., 2022), introducing the need to form new xylem to restore hydraulic capacity (Ruehr et al., 2019; Alongi et al., 2026). Recovery thus depends on the coordination between turgor restoration, xylem repair or replacement, and the availability and allocation of non-structural carbohydrate reserves (Ruehr et al., 2019; Peters et al., 2021; Mantova et al., 2021). Because repair and regrowth are carbon-demanding while carbon uptake is often reduced during early recovery, these coupled hydraulic and carbon constraints can prolong drought effects beyond the drought period itself and contribute to legacy effects in forest carbon and water cycling (Ruehr et al., 2019; Kannenberg et al., 2020; Kannenberg et al., 2022; Müller and Bahn, 2022).

Together, these processes highlight several key variables and processes for assessing tree drought responses, including plant water potential, hydraulic conductance and capacitance, stomatal conductance and transpiration, photosynthetic carbon assimilation and respiration, non-structural carbohydrate reserves, and hydraulic damage or recovery state. However, many of

these variables are difficult to observe across large numbers of trees, making drought monitoring of trees a central challenge.

1.3 The challenge of monitoring physiological drought stress

Drought stress can be monitored using approaches that differ in spatial scale, temporal resolution, how directly they reflect tree water status, and practical feasibility. At the environmental level, drought is commonly characterized through precipitation deficits, soil water availability, atmospheric demand, or drought indices that integrate meteorological variables over time (Seneviratne et al., 2010; Spinoni et al., 2018). These metrics are essential for describing drought exposure and comparing drought intensity across regions and years. However, they characterize external environmental conditions rather than the physiological stress experienced by trees, which also depends on species identity, hydraulic traits, tree size, rooting depth, soil structure, microclimate, and internal water storage.

Ecosystem-scale approaches provide important information on forest carbon and water dynamics. Eddy covariance measurements quantify net ecosystem CO_2 and H_2O exchange (Baldocchi, 2003). Remote sensing further extends drought monitoring through microwave-derived proxies of canopy water content, such as vegetation optical depth (Konings et al., 2019), and optical vegetation indices related to canopy greenness, water content, and pigment status (Bloom et al., 2025). These approaches are essential for upscaling, but they integrate multiple sources and processes. Eddy covariance reflects the combined contributions of canopy and understory gas exchange, soil respiration, and evaporation. Remote-sensing signals are affected by canopy structure, species composition, phenology, and spatial heterogeneity. Optical vegetation indices can capture broad seasonal or monthly trends in tree water stress but may miss short-term dynamics (Bloom et al., 2025). Thus, while being valuable, these approaches do not directly isolate the internal water status of individual trees (Konings et al., 2019; Restrepo-Acevedo et al., 2026).

At smaller scales, gas exchange and water flux measurements enable more direct insights into tree function. Sap flow sensors provide continuous and tree-specific information on xylem water transport and can be used to infer tree water use or transpiration (Steppe et al., 2010; Steppe et al., 2015; Poyatos et al., 2021). However, estimating whole-tree water use requires method-specific calibration and assumptions about sapwood area and radial sap flow profiles. Leaf-level measurements of stomatal conductance, transpiration, and photosynthesis directly quantify the water–carbon trade-off (Farquhar and Sharkey, 1982; Buckley, 2019). However, they remain sensitive to short-term variation in light, vapor pressure deficit, and temperature, and their application in trees is often constrained by crown access and limited spatial replication.

To assess physiological drought stress more directly, environmental drivers and functional

measurements need to be linked to variables that describe the actual water status of trees. As outlined in the previous section, water potential provides a physiologically meaningful reference for tree water status and hydraulic stress (Steppe, 2018; Novick et al., 2022). Pressure chamber measurements provide valuable reference observations, but they are discrete, labor-intensive, and require excision of leaves or twigs (Rodriguez-Dominguez et al., 2022; Restrepo-Acevedo et al., 2026). Continuous measurements of water potential can be obtained using psychrometers or microtensiometers, which can resolve temporal dynamics that pressure chamber measurements miss. Recent field applications show that microtensiometers can capture subdaily dynamics of stem and soil water potential (Haberstroh et al., 2025b; Cachinero-Vivar and Pérez-Priego, 2026; Magh et al., 2026). However, such measurements remain technically demanding. Psychrometers require careful calibration and thermal protection and can be problematic in resin-rich gymnosperms (Martinez et al., 2011; Restrepo-Acevedo et al., 2026), while microtensiometers depend on stable sensor–xylem contact and careful installation. Their broader deployment can be limited by species-specific anatomy, stem size, bark properties, signal drift, and uncertainty outside validated measurement ranges (Magh et al., 2026; Restrepo-Acevedo et al., 2026).

Taken together, existing approaches allow drought responses to be assessed from ecosystems to leaves and from environmental exposure to physiological tree function. Yet they also highlight a methodological gap: the need for continuous tree-level indicators closely linked to plant water status and internal water storage dynamics across many individuals. Although microtensiometers are beginning to close part of this gap, their technical requirements still limit broad deployment. This motivates the parallel development of complementary approaches, including dendrometer-based monitoring of stem diameter changes, from which tree water deficit dynamics can be derived (Zweifel et al., 2021a).

1.4 Tree water deficit as an indicator of physiological drought stress

1.4.1 Dendrometer measurements and derivation of tree water deficit

Modern dendrometers provide a continuous, non-destructive method for observing tree-level stem-diameter dynamics at micrometer resolution (Zweifel and Häslar, 2001; King et al., 2013; De Swaef et al., 2015). Two common sensor types are point dendrometers, which record local changes in stem radius, and band dendrometers, which record changes in stem circumference. In both types, stem expansion or shrinkage is mechanically transmitted to a displacement transducer and converted into an electrical signal proportional to the displacement; for example, potentiometer-based instruments convert the motion of a sliding contact into a change in electrical resistance and, consequently, in output voltage. Measurement uncertainty arises from temperature sensitivity and thermal expansion of the frame or electronics, sensor hysteresis or friction, mounting stability, bark properties, and contact pressure. The resulting measurements

contain both irreversible growth and reversible water-related changes in stem size (Zweifel et al., 2016), making dendrometers useful for studying tree growth as well as tree water dynamics (Steppe et al., 2015; Dietrich et al., 2018; Sevanto, 2025).

The separation of growth and water-related shrinkage is commonly based on the zero-growth concept (Zweifel et al., 2016). This concept assumes that irreversible radial growth occurs only when the stem exceeds its previously reached maximum size, whereas deviations below this maximum are interpreted as reversible tree water deficit (TWD). Thus, TWD is defined as stem shrinkage, usually expressed in μm , and calculated as the difference between the previously reached maximum and the current stem radius. The underlying assumption is that, once tissues have lost enough water to cause measurable shrinkage, turgor is too low to allow cell division and expansion. This is a simplification because the exact turgor thresholds for growth limitations may vary among tissues, species, and environmental conditions. Nevertheless, the zero-growth concept provides a practical, widely used first-order approximation for separating growth from reversible diameter changes and deriving TWD from dendrometer records (Knüsel et al., 2021; Zweifel et al., 2021a; Salomón et al., 2022).

As an alternative to classical dendrometry on stems or branches, optical dendrometers have recently been developed to quantify reversible shrinkage dynamics in organs such as petioles or needles (Bourbia and Brodribb, 2023; Bourbia et al., 2025). These approaches can reduce the confounding influence of radial growth and provide complementary information on plant water status that is conceptually related to stem-derived TWD.

1.4.2 Physiological interpretation of tree water deficit

Physiologically, TWD accumulates when transpiration temporarily exceeds water uptake, thereby withdrawing water from internal storage tissues (Zweifel et al., 2001; Steppe et al., 2006). This adds a radial storage component to the vertical soil–plant–atmosphere water pathway: in addition to water taken up from the soil and transported through the xylem, water can move between elastic living tissues and the xylem along water potential gradients (Steppe et al., 2006; Meinzer et al., 2009; Preisler et al., 2022). As cells lose water, they lose turgor and volume, resulting in shrinkage of elasticity-dependent tissues (Steppe et al., 2006; Peters et al., 2021). Stem diameter variations are therefore closely linked to changes in stem water content (De Schepper et al., 2012) and can be interpreted as a signal of the imbalance between water loss and uptake (Zweifel et al., 2005; De Swaef et al., 2015). However, dendrometer-derived TWD remains a proxy for tree water status rather than a direct measurement of absolute changes in internal water content (Restrepo-Acevedo et al., 2026).

TWD has been increasingly explored as a measure of physiological drought stress. Its dynamics are sensitive to soil water availability and atmospheric demand (King et al., 2013; Dunkleberger et al., 2023; Oberhuber et al., 2023; Salomón et al., 2024), while species-specific hydraulic

strategies and storage properties further modulate how water deficits develop and how they are expressed in stem shrinkage (Sánchez-Costa et al., 2015; Martinetti et al., 2025). Several studies have reported relationships between TWD and water potential, suggesting that dendrometer observations can provide information on hydraulic stress and may support continuous estimates of tree water status (Cochard et al., 2001; Drew et al., 2011; Dietrich et al., 2018; Lauriks et al., 2022). Recent work combining dendrometers with continuous microtensiometer measurements further supports the potential of linking TWD to stem water potential dynamics in mature forest trees (Cachinero-Vivar and Pérez-Priego, 2026; Magh et al., 2026).

1.4.3 Functional interpretation and normalization

For drought impact assessment, the value of TWD depends not only on whether it reflects tree water status, but also on whether it can be linked to functional responses. Because TWD reflects changes in tissue hydration and is related to water potential, it provides a plausible link to drought-induced changes in gas exchange, growth, and hydraulic risk. First experimental studies suggest that dendrometer-derived shrinkage dynamics may help identify critical drought thresholds, including mortality risk (Lamacque et al., 2020; Andriantelomanana et al., 2024). However, the physiological meaning, transferability, and stability of such thresholds remain uncertain, particularly across species, drought intensities, and post-drought recovery. Likewise, direct links between TWD and functional variables such as stomatal conductance, transpiration, photosynthetic carbon assimilation, and respiration are currently not well established. Establishing these links would allow TWD to be interpreted not only as a water-status proxy but also as an indicator of physiological transitions along the drought-stress continuum.

A central limitation is that TWD-based relationships are not necessarily universal. This is particularly problematic when absolute TWD amplitudes are compared across individuals, species, or sites, because stem shrinkage depends not only on drought stress intensity but also on tree size and age, bark and xylem anatomy, rooting depths, tissue elasticity, microclimate, and sensor position (De Swaef et al., 2015; Andriantelomanana et al., 2024). Normalization is therefore a key requirement for moving from tree- and installation-specific dendrometer signals to transferable TWD drought-stress metrics. Existing approaches normalize TWD relative to reference shrinkage amplitudes, such as the maximum observed TWD (Dietrich et al., 2018; Andriantelomanana et al., 2024) or daily shrinkage metrics (Peters et al., 2025). However, which reference best preserves physiological meaning while enabling comparison across trees, species, and sites remains unresolved.

Beyond its monitoring potential, TWD may also serve as a useful entry point for improved process-based drought stress modeling, as discussed in the following section.

1.5 Towards improved modeling of tree water status

Process-based ecosystem models are essential for scaling physiological drought responses from individual trees to stands and for exploring drought impacts under environmental conditions that exceed current observations. In recent years, plant hydraulic schemes have increasingly been incorporated into such models to improve the representation of plant water stress and drought responses (Paschalis et al., 2024). One example is LandscapeDNDC, a process-based ecosystem model developed to simulate coupled carbon, water, and nitrogen fluxes among vegetation, soil, and the atmosphere (Grote et al., 2011a; Haas et al., 2013). Nadal-Sala et al. (2024) incorporated tree hydraulic processes into LandscapeDNDC, thereby enabling the simulation of soil and plant water potentials and stomatal regulation of transpiration, following Eller et al. (2020). Nevertheless, in LandscapeDNDC and process-based models more generally, representations of drought legacy effects, hydraulic damage, recovery, and mortality remain limited or highly uncertain (Hartmann et al., 2018).

One reason is that many model formulations still focus primarily on soil water availability, water potential, or loss of hydraulic conductivity, whereas internal tree water pools and their depletion are rarely represented (Martinez-Vilalta et al., 2019). This is important because internal water storage buffers short-term imbalances between transpiration and water uptake, and affects the progression from reversible water deficit to hydraulic or cellular damage (Salomón et al., 2017; Preisler et al., 2022; Mantova et al., 2022). Detailed hydraulic models, such as SurEau and SurEau-Ecos (Cochard et al., 2021; Ruffault et al., 2022), can represent multiple water storage compartments and detailed water flows between them, while hydrodynamic or hydraulically enhanced vegetation models, including FETCH4, ED2-Hydro, ORCHIDEE-CAN-NHA, FATES-HYDRO, and LPJ-GUESS, increasingly resolve plant water transport, water-potential dynamics, and in some cases tissue water storage (Missik et al., 2025; Xu et al., 2016; Yao et al., 2022; Xu et al., 2023; Meyer et al., 2025). However, detailed hydraulic representations often require extensive parameterization, which makes broader application and empirical constraint difficult. Moreover, when drought impacts or drought-induced mortality are represented, they are often linked to water potential or conductivity loss thresholds rather than to explicit declines in internal water content (e.g., Yao et al., 2022; Ruffault et al., 2022; Xu et al., 2023; Meyer et al., 2025).

In this context, TWD is potentially useful because it provides both an observable signal and a conceptual representation of imbalances between water loss, water uptake, and internal storage. This dual role is important because useful model variables need to be simple enough for practical implementation while retaining physiological meaning and, ideally, being constrainable by observations. TWD may therefore provide a complementary entry point for model development and evaluation. Existing models of stem diameter variation have provided important mechanistic insight into dendrometer signals (Sevanto, 2001; Zweifel et al., 2005; Steppe et al., 2006), but they were primarily designed for signal interpretation rather than for integration into ecosystem models.

This leaves a need to better connect dendrometer observations with model representations of internal water storage, drought stress, and recovery.

Together, these perspectives position TWD as a promising yet underdeveloped link between continuous tree-level observations, physiological drought responses, and process-based representations of tree water status.

1.6 Research gaps and objectives

Despite the increasing use of dendrometer-derived TWD as an indicator of drought stress, several key uncertainties remain. First, the physiological relationships between TWD, water potential, and stomatal conductance remain insufficiently explored, particularly under severe drought, hydraulic damage, and post-drought recovery. Second, it remains unclear whether normalized TWD can serve as a comparable hydraulic stress axis for explaining functional drought responses in tree-level water and carbon dynamics. Third, TWD is rarely represented in process-based modeling frameworks, limiting the use of dendrometer data to evaluate and improve model representations of drought stress and to link tree-level water status to ecosystem-scale assessments.

The overarching question of this thesis is: How can tree water deficit be advanced as a continuous, physiologically interpretable, and model-compatible signal to assess drought stress, internal tree water status, and functional limitations across species, study systems, and spatial scales?

To address this question, three objectives are pursued:

1. **Physiological basis:** Test whether TWD reflects key physiological indicators of tree drought stress during severe drought and recovery.
2. **Functional interpretation:** Evaluate whether normalized TWD can serve as a common hydraulic stress axis for functional drought responses across contrasting experimental contexts.
3. **Process-based modeling:** Develop and evaluate a model-compatible diagnostic representation of TWD and relative tree water content.

1.7 Thesis structure

This thesis follows a stepwise approach that moves from establishing the physiological basis of TWD to its functional interpretation and finally to process-based modeling. Chapters 2–4 each present a publication addressing one of the three objectives outlined above, while Chapter 5

synthesizes the findings and discusses the potential, limitations, and future development of TWD. The individual publications address the following topics:

Chapter 2: TWD during severe drought and recovery

A controlled greenhouse experiment with *Pinus sylvestris* and *Larix decidua* saplings is used to investigate how dendrometer-derived TWD relates to water potential and stomatal conductance. By exposing trees to progressive drought and rewatering, with lethal dehydration reached in a subset of individuals, this chapter tests whether TWD captures key phases of hydraulic stress and whether these relationships remain stable during recovery.

Chapter 3: TWD as a common hydraulic stress axis

Drought experiments across three conifer species, *Pinus sylvestris*, *Picea abies*, and *Pseudotsuga menziesii*, are synthesized to evaluate whether normalized daily minimum TWD can serve as a common hydraulic stress axis. Using dendrometers in combination with whole-tree gas exchange measurements, this chapter examines how tree-level net carbon balance, stomatal conductance, and transpiration change along this TWD-based stress gradient, including the transition from net carbon uptake to net carbon loss.

Chapter 4: Development of a TWD model framework

The newly developed TWIST module is presented and evaluated. It simulates TWD and relative tree water content based on transpiration, relative soil water availability, and an estimate of internal tree water storage. By coupling TWIST with the LandscapeDNDC ecosystem model and comparing simulated TWD dynamics with dendrometer observations, this chapter explores how TWD can be represented as a model-compatible diagnostic of internal tree water status.

2 CAPTURING DROUGHT STRESS SIGNALS: THE POTENTIAL OF DENDROMETERS FOR MONITORING TREE WATER STATUS

This chapter has been published as:

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Abstract

The severity of droughts is expected to increase with climate change, leading to more frequent tree mortality and a decline in forest ecosystem services. Consequently, there is an urgent need for monitoring networks to provide early warnings of drought impacts on forests. Dendrometers capturing stem diameter variations may offer a simple and relatively low-cost opportunity. However, the links between stem shrinkage, a direct expression of tree water deficit (TWD), and hydraulic stress are not well understood thus far. In this study, we exposed two widespread conifers *Pinus sylvestris* and *Larix decidua* to lethal dehydration by withholding water and closely monitored TWD, midday water potential (ψ), and midday stomatal conductance (g_s) under controlled greenhouse conditions. We found strong relationships between the three variables throughout the dehydration process, particularly suggesting the potential for continuous ψ predictions and stomatal closure assessments. However, the relationships decoupled during recovery from severe drought. We also identified TWD thresholds that signal the onset of drought stress and tissue damage, providing insights into stress impacts and recovery potential. While

these findings are promising, challenges remain in practically transferring them to field set-ups by suitable TWD normalization. Importantly, we observed that midday g_s was drastically reduced when TWD persisted overnight, providing a directly applicable drought stress signal that does not require normalization. In conclusion, while challenges remain, our results highlight the potential of dendrometers for monitoring tree water dynamics. Implementing dendrometer networks could support the development of early-warning metrics for drought impacts, enabling large-scale monitoring in diverse settings, such as urban areas and forest ecosystems.

2.1 Introduction

The frequency and severity of droughts are expected to increase with climate change (Spinoni et al., 2018, Suarez-Gutierrez et al., 2023), resulting in global tree damage and mortality (Allen et al., 2010, Senf et al., 2020, Yi et al., 2022), negatively affecting the carbon balance and ecosystem functioning (Choat et al., 2018). Water limitation immediately affects tree carbon sequestration through species-specific water control mechanisms. Regulation of stomatal conductance (g_s) reduces water loss at the expense of net photosynthesis (A_{net}). Severe droughts affect the hydraulic system of trees, resulting in poorly understood long-term legacy effects (Müller and Bahn, 2022) and having lasting impacts on plant functionality and forest structures (Pretzsch et al., 2022).

Understanding the progressive impacts during and after drought enables adaptive measures. Monitoring tree physiological responses offers valuable information on species sensitivity and dependence on site properties, supporting management strategies such as selecting less susceptible species and timely irrigation in urban settings. However, appropriate techniques for operational tree water status monitoring are still not widely applied (Novick et al., 2022).

Usually, water potential (ψ) is measured to assess levels of drought stress. Generally, ψ gradients, primarily driven by soil water availability, leaf-level transpiration and cohesion forces (cohesion-tension theory, Dixon, 1915), govern the water transport in vascular plants. Parameters such as ψ at which 50% of hydraulic conductivity is lost (P_{50}) provide insights into tree species' susceptibility to hydraulic damage (Choat et al., 2012). However, notable limitations exist: Traditional pressure chamber measurements for ψ are complex (Rodriguez-Dominguez et al., 2022) and destructive sampling from tree canopies is necessary. Though valuable for stress indication, they are not continuous, and simultaneously monitoring multiple individuals requires substantial logistic effort. Thermocouple psychrometers provide continuous measurements but are complex, temperature-sensitive, and not universally applicable, especially for resin-rich gymnosperms (Martinez et al., 2011, Novick et al., 2022).

Therefore, identifying mechanisms for continuous tree drought stress evaluation can vastly improve forest monitoring. A promising candidate is tree water deficit (TWD; Zweifel, 2015,

Steppe, 2018, Salomón et al., 2022), derived from stem diameter variations monitored by dendrometers capturing μm -scales, which are already widely applied (e.g., TreeNet; Zweifel et al., 2021a), cost-efficient and non-destructive. TWD represents the decrease between actual and recorded maximum stem diameter (Zweifel, 2016, Knüsel et al., 2021). It is sensitive to environmental conditions like vapor pressure deficit (VPD) and soil water content (SWC) (Zweifel et al., 2005, Sánchez-Costa et al., 2015, Dunkleberger et al., 2023, Oberhuber et al., 2023), water storage capacity of cell tissues (De Swaef et al., 2015), and water use traits such as stomatal regulation (Drew et al., 2011, Liu et al., 2023). During the day, trees typically transpire more water than they can take up due to limitations in whole plant conductance or soil water availability, resulting in the mobilization of internal water reservoirs. On top of apoplastic water release (Mantova et al., 2022), symplastic water release from living elastic tissues (Knipfer et al., 2019), such as bark and phloem, results in turgor loss, reduction of cell volume, and subsequent stem shrinkage (Zweifel et al., 2001, De Swaef et al., 2015, Steppe et al., 2015). While xylem shrinkage is often neglected, it can also contribute to reversible water release, largely depending on living cells within the xylem matrix (Skelton, 2020, Oberhuber et al., 2023). With ample soil water, internal storage pools replenish at night, allowing stem diameter recovery or even a new maximum (Zweifel et al., 2021b). However, during periods of extended water limitation, growth is assumed to stop due to cell turgor losses inhibiting cell division and expansion (Zweifel, 2016, Krejza et al., 2022), while TWD accumulates, making it an indirect indicator of drought stress.

TWD is closely related to ψ (Cochard et al., 2001, Steppe et al., 2006, Drew et al., 2011, Peters et al., 2021, Lauriks et al., 2022), potentially enabling continuous ψ predictions (Dietrich et al., 2018) and stress monitoring. Additionally, TWD correlates with gas exchange, and TWD thresholds for plant mortality can be determined (Lamacque et al., 2020, Andriantelomanana et al., 2024). Knowledge of tree sensitivity thresholds can leverage existing data series, offering insights into the severity of past and current droughts.

However, the relations between TWD and physiological parameters have been evaluated within a limited range of species and drought-stress conditions, constraining their practical applicability. Most studies investigate mild drought conditions, excluding the impact of irreversible drought damage (Cochard et al., 2001, Drew et al., 2011, Dietrich et al., 2018). Under severe drought, dynamics might change as embolism events irreversibly release additional water from inelastic xylem conduits (Knipfer et al., 2019, Skelton, 2020) and trigger the collapse of elastic cells (Mantova et al., 2022, Andriantelomanana et al., 2024). Understanding the ψ -TWD relationship during this critical phase is essential to indicate long-term damage (Vergeynst et al., 2015). Furthermore, correlations of TWD with gas fluxes are of interest but have received even less investigation than those with ψ . While ψ indicates the degree of drought stress and the current risk of irreversible damage, g_s represents plant functioning and possible carbon assimilation. Lastly, the impacts of stress release on the relationship between TWD and physiological parameters

are currently unknown. Depending on drought severity, recovery pace varies among different physiological processes, with gas exchange parameters requiring more time compared to ψ (Ruehr et al., 2019, Rehschuh et al., 2020). If TWD recovery timing (Lamacque et al., 2020) does not match that of ψ and g_s relationships decouple. Moreover, understanding how post-stress recovery dynamics affect susceptibility to future droughts is crucial to assessing forest functioning in a changing climate (Ruehr et al., 2019, Kannenberg et al., 2020).

Here we conducted a greenhouse study and exposed seedlings of two coniferous species, *Pinus sylvestris* and *Larix decidua*, to complete dehydration and variable rewetting. We chose the species due to their ecological relevance (Obojes et al., 2024) and their different strategies regarding water use, namely anisohydric vs. isohydric behavior (Oberhuber et al., 2015). The experiment allowed us to analyze the relationships of TWD to midday ψ and g_s during drought progression and how stress release modifies these relationships. Specifically, we targeted the questions (1) How are TWD and ψ related during lethal drought progression? (2) Does the relationship between TWD and ψ change during recovery (after re-watering)? (3) How is TWD related to gas exchange during drought and recovery? and (4) Can we derive early-warning metrics on tree drought stress intensities based on TWD?

2.2 Materials and Methods

2.2.1 Experimental setup

We conducted an experimental study in an environmentally controlled greenhouse facility at the KIT-Campus Alpin in Garmisch-Partenkirchen (708 m a.s.l., 47°28'32.9' N, 11°3'44.2' E) in June to August 2023. Three-year-old Scots pine (*Pinus sylvestris* L.) and European larch (*Larix decidua* Mill.) seedlings ($n = 24$ per species) were obtained from a local tree nursery in Gunzenhausen, Germany, in March 2023 and planted in individual 5.7 L pots containing an organic clay substrate and perlite at a ratio of 5 : 1 supplemented with 6 g of slow-release fertilizer (Osmocote 5 8-9M, Micromax Premium; ICL Specialty Fertilizers, Geldermalsen, Netherlands). On average, *P. sylvestris* seedlings were 79.3 ± 3.2 cm high and had a stem diameter of 15.5 ± 0.7 mm. For *L. decidua*, corresponding values were 79.0 ± 2.9 cm and 12.2 ± 0.7 mm, respectively.

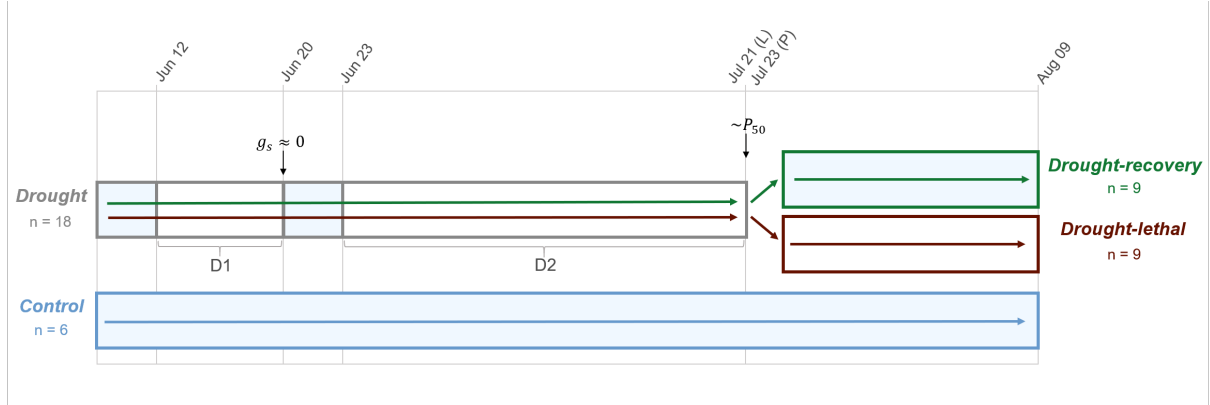


Figure 2.1: Overview of the experimental design. Shown are the drought and recovery cycles for *L. decidua* (L) and *P. sylvestris* seedlings that were randomly assigned to a control ($n = 6$ per species) or drought treatment ($n = 18$ per species). We irrigated the trees to field capacity or withheld irrigation as depicted. In the first drought D1, we induced mild stress and re-watered all drought-trees once stomatal conductance approached $g_s \approx 0$. In the more extended drought D2, we aimed at inducing severe stress. Once water potentials (ψ) reached values representing hydraulic conductance losses of about 50% (P_{50}), we separated the drought treatment into a drought–recovery ($n = 9$ per species) which was re-watered and a drought–lethal treatment ($n = 9$ per species) which further dehydrated until tree death.

We placed the seedlings inside the greenhouse compartment to acclimate to the new conditions three weeks before the experiment started and watered them to field capacity (twice a day 100 ml + individual watering if necessary). At the experiment start, the trees were assigned randomly to a control ($n = 6$ per species) or drought treatment ($n = 18$ per species) as depicted in Fig. 2.1. The drought treatment included more trees to allow frequent sampling. The control trees further received water, while irrigation in the drought treatment was stopped during two drought phases and resumed during recovery. All drought-treated trees were first exposed to a nine-day drought period (D1). After a three-day recovery phase, a second and more extended drought cycle followed (D2) until ψ ranged around the determined P_{50} values (see Tab. 2.1 a), which took 28 days for *L. decidua* and 30 days for *P. sylvestris*. Then the drought treatment trees were equally and randomly distributed either to a drought–lethal or a drought–recovery treatment. To observe the full range of dehydration, the drought–lethal trees were further dehydrated until tree death occurred. In contrast, seedlings in the drought–recovery treatment were re-watered to investigate how the recovery potential after hydraulic damage occurrence develops.

Temperature and humidity (CS215, Campbell Scientific Inc., Logan, Utah, USA), as well as photosynthetic active radiation (PAR; PQS 1, Kipp & Zonen, Delft, The Netherlands), were continuously measured half-hourly to verify stable conditions. Daytime air temperature was $23 \pm 2^\circ\text{C}$ (mean $\pm$ SD), daytime VPD $1.0 \pm 0.3 \text{ kPa}$ (Fig. S2.6), and ambient light conditions in the greenhouse were supplemented by LED grow lamps (LED-KE 400 VSP, DHLicht, Wuelfrath,

Germany) to ensure a constant PAR of $600 \pm 100 \frac{\mu\text{mol}}{\text{s}\cdot\text{m}^2}$ for 15 hours a day. Trees were supplied with water using an automated irrigation drip system, and soil water content (SWC; UMS Water Content Sensor 10HS, ten-minute frequency; logger CR1000, Campbell Scientific, Inc. USA) was recorded for ten trees per species (control $n = 2$, drought–recovery $n = 4$, drought–lethal $n = 4$).

2.2.2 Non-continuous measurements

Water potential

Midday water potential (ψ) was measured frequently between once a day and once a week, depending on the experimental phase with a pressure chamber (Model 600D, PMS Instruments, Oregon, USA; Scholander et al., 1965). In the case of *L. decidua*, we sampled small twigs, and for *P. sylvestris*, we utilized needle fascicles to save plant material and maximize the number of possible measurements. For *P. sylvestris* twigs were sampled only in the drought–lethal treatment during the last phase of dehydration, wherein ψ reached low values and needles were too desiccated to provide a trustful base for measurements. We measured ψ until values of < -7 MPa were reached. Based on our vulnerability curves (Fig. S2.7), we considered the trees dead at this stage. Daily means presented in the results section include a minimum sample size of three for the drought and two for the control treatments, with higher sample sizes for most days.

Leaf gas exchange

Midday leaf gas exchange, including stomatal conductance g_s ($\text{mmol m}^{-2} \text{s}^{-1}$), transpiration E ($\text{mmol m}^{-2} \text{s}^{-1}$) and net photosynthesis A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$), was measured using the portable LI-COR 6800 system (LI-COR Biosciences, Lincoln, Nebraska, USA) on ten specific days on the same needle cohorts for each species, covering different stages in the drought–recovery cycles (control $n = 3$, drought–recovery $n = 3 - 5$, drought–lethal $n = 3 - 5$). In the case of *P. sylvestris*, ten needles were formed to a flat surface and enclosed in a leaf cuvette (2 cm^2). In the case of *L. decidua*, we enclosed one needle fascicle. Ambient cuvette parameters were kept constant, including a photosynthetic photon flux density of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, a CO_2 concentration of 410 ppm , a 10000 rpm fan speed, air temperature of 25°C and relative humidity of 50% . Due to stable VPD during the experiment (Fig. S2.6), g_s and E dynamics did not differ substantially (Fig. S2.8), so transpiration is not individually discussed in this work.

Vulnerability curves

We conducted Cavitron measurements (Cochard, 2002) on the control seedlings ($n = 4$ per species) after the experiment. Stem samples were cut and directly re-cut under water, wrapped in cling film, enclosed in a cooling bag and transported to a laboratory at the University Innsbruck. Prior measurements, we completely removed the bark underwater, and samples were re-cut again

on both ends to a length of 28 cm to fit into a custom-build rotor placed in a centrifuge (Sorvall RC-5; Thermo Fisher Scientific, Waltham, MA, USA) following the methods from Beikircher et al. (2010). We determined the percentage loss of conductance (PLC) by measuring the decrease in hydraulic conductivity while we reduced step-wise the rotational speed to increase the xylem pressure. PLC was calculated as

$$\text{PLC} = 100 \cdot \frac{1 - k_t}{k_i}, \quad (2.2.1)$$

where k_i is the initial hydraulic conductance and k_t is the hydraulic conductance at the respective xylem pressure.

2.2.3 Dendrometer measurements

A total number of 13 trees per species (control $n = 3$, drought–recovery $n = 5$, drought–lethal $n = 5$) were equipped with dendrometers (Ecomatik Diameter Dendrometers, Type DD-S and DD-S1, ten-minute frequency, 1.5 μm resolution) to capture relative variations in stem diameter. Before the sensor installation (Fig. S2.9), we removed the most outer dead layers of the bark and measured the initial stem diameters per tree with a calliper to calculate absolute diameter changes from the dendrometer records.

One of the *P. sylvestris* drought–recovery trees equipped with a dendrometer showed an unexpectedly weak TWD–recovery after the final rewetting. As we cannot exclude a secondary pathogen infestation we excluded this seedling from further analysis.

2.2.4 Tree water deficit

We derived the tree water deficit (TWD) from the continuous high-resolution stem diameter variations as follows:

$$\text{TWD} = d_{\max} - d, \quad (2.2.2)$$

where d is the current absolute stem diameter and $d_{\max}$ is the maximum diameter measured for an individual tree in the past, which sets the theoretical maximum diameter under conditions of fully hydrated tissues. We apply the zero-growth concept, assuming that growth cannot occur during periods of stem contraction (Zweifel, 2016, Dietrich et al., 2018). In addition, we calculated a normalized TWD for treatment means:

$$\text{TWD}_{\text{norm}} = \frac{\text{TWD}}{\text{TWD}_{\max}}, \quad (2.2.3)$$

where $\text{TWD}_{\max}$ is the highest TWD occurring for drought–lethal trees at the end of the experiment.

2.2.5 Statistical analyses

We performed data processing, visualization and statistical analysis with the programming language R, version 4.2.2 (R Core Team, 2022). The significance of treatment and species differences was evaluated using a linear mixed model likelihood ratio test (*'lme'* package; Bates et al., 2015). All results presented are treatment means with standard error (SE). To derive the matching TWD with midday ψ and g_s in the shown relationships, we averaged the TWD of all dendrometer-equipped trees between 1 and 4 pm on the corresponding days (midday TWD). Besides, we derived pre-dawn TWD, averaged from 3 to 4 am. Note that the g_s and ψ treatment means also include measurements on trees not equipped with dendrometers to reduce destructive harvest per tree. Data for individual trees is depicted in the supplementary material (Fig. S2.10). Regression fits were produced with the *nls()* function, and the 95% confidence intervals for all regression parameters and regression curves were estimated via bootstrapping. For the relation between TWD_{norm} and ψ , we used the following sigmoidal regression:

$$\text{TWD}_{\text{norm}}(\psi) = \frac{A}{1 + e^{-b \cdot (\psi + c)}}, \quad (2.2.4)$$

where e is the Euler function and the parameters A , b , and c determine the asymptotic behavior, steepness, and inflection point (indicating 50% of water depletion). While in the literature, this approach is usually applied (e.g. Dietrich et al., 2018), its inversion is mathematically complex, particularly at the assumed plateaus where multiple ψ values belong to the same TWD, which hinders ψ retrieval directly from TWD measurements. Therefore, in a second approach, we reversed axes, separated $\text{TWD}_{\text{norm}}-\psi$ data into three "slope groups" and fitted linear curves ($\psi(\text{TWD}_{\text{norm}}) = a \cdot \text{TWD}_{\text{norm}} + C$). We defined the cross-sections of the regression lines as thresholds for phase changes. For the relationship between g_s and TWD_{norm} , we chose an exponential approach:

$$g_s(\text{TWD}_{\text{norm}}) = a \cdot e^{-b \cdot \text{TWD}_{\text{norm}}} + C, \quad (2.2.5)$$

where the parameter a defines the vertical scaling, b the bending, and C and the vertical offset of the function. Equation 2.2.5 was further used to retrieve thresholds for stomatal closure, in expression the TWD_{norm} at g_s equaling 5% and 50% (TWD_{g5} , TWD_{g50}) of the g_s control mean. Similarly, ψ_{g5} and ψ_{g50} (equaling the concept of G_{c50} in Peters et al. (2023)) thresholds were retrieved from sigmoidal $g_s-\psi$ relationships ($g_{\text{norm}}(\psi) = 1/(1 + \exp(-a \cdot (\psi + b)))$).

The software package *'fitplc'* (Duursma and Choat, 2017) was applied to create vulnerability curves from the Cavitron measurements. We used sigmoidal regressions and determined ψ values introducing a PLC of 12%, 50% and 88% (P_{12} , P_{50} , P_{88}), which function as key hydraulic thresholds (Urli et al., 2013, Dorji et al., 2024).

2.3 Results

2.3.1 Vulnerability to drought

The hydraulic vulnerability curves of both species, *L. decidua* and *P. sylvestris*, indicate similar P_{50} values of -3.16 and -3.11 MPa (Tab. 2.1 a) and thus comparable drought susceptibility, which is in agreement with ranges determined for mature trees in Peters et al. (2023). However, the curve for *L. decidua* is steeper, corresponding to a faster rate of conductance loss per decrease of ψ (Fig. S2.7). Besides, in the case of *P. sylvestris* ψ values corresponding to halfway and fully closed stomata (ψ_{g50} , ψ_{g5}) are higher, and the slope of the response curve at ψ_{g50} - a measure for isohydricity (Peters et al., 2023) - is steeper, indicating a stricter stomatal control (Tab. 2.1 b, Fig. S2.11).

Table 2.1: Water potentials of vulnerability curve and stomatal closure thresholds for seedlings of *L. decidua* and *P. sylvestris*. (a) ψ at 12 %, 50 % and 88 % (P_{12} , P_{50} , P_{88}) Percentage Loss of Conductance (PLC) and the according 95% confidence interval in brackets according to Fig. S2.7. (b) ψ at g_s of 5% and 50% relative to control means (ψ_{g5} , ψ_{g50}) and the according 95% confidence interval in brackets according to Fig. S2.11.

	Species	<i>L. decidua</i>	<i>P. sylvestris</i>
(a)	P_{12} [MPa]	-2.74 (-2.34 / -3.06)	-2.52 (-2.32 / -2.66)
	P_{50} [MPa]	-3.16 (-3.00 / -3.24)	-3.11 (-3.04 / -3.17)
	P_{88} [MPa]	-3.47 (-3.35 / -3.63)	-3.58 (-3.45 / -3.70)
(b)	ψ_{g5} [MPa]	-1.87 (-1.58 / -2.23)	-1.33 (-0.91 / -1.57)
	ψ_{g50} [MPa]	-1.06 (-0.62 / -1.24)	-0.82 (-0.72 / -0.88)

2.3.2 Tree water status during drought recovery cycles

Changes in SWC affected both ψ and TWD (Fig. 2.2, Tab.2.2). During D1, ψ exhibited a slight yet significant decrease compared to control conditions ($P \leq 0.01$). Concurrently, stem diameter variations displayed increased diurnal amplitudes, particularly pronounced in *L. decidua*. By the end of D1, TWD did not fully vanish during night-time and started to accumulate. After stress release, TWD and ψ both returned to control levels. In the more prolonged drought period D2, ψ levels reached -3.0 ± 0.2 MPa and -2.7 ± 0.2 MPa for *L. decidua* and *P. sylvestris*, respectively. Initially, TWD exhibited an increased diurnal cycle again, but after approximately two weeks, stem shrinkage continued without any diameter expansion during the night. By the end of D2, TWD levels reached 1.3 ± 0.1 mm for *L. decidua* and 1.6 ± 0.2 mm for *P. sylvestris*, translating to a relative shrinkage of 12.5 ± 0.6 % and 10.5 ± 1.0 % and a TWD_{norm} of 0.76 and 0.73. Upon rewetting, plants of the drought–recovery treatment showed an instantaneous recovery of ψ . In contrast, TWD decreased rapidly after stress release but did not fully return to control values

($P < 0.01$). For *L. decidua*, approximately $85 \pm 3\%$ of the diameter shrinkage was reversed within one day, while for *P. sylvestris*, this value was $80 \pm 2\%$. Subsequently, both species resumed daily stem diameter variations gradually decreasing TWD. Ultimately, TWD returned to the control values after 8 days for *L. decidua* and after 9 days for *P. sylvestris*.

Table 2.2: Water status and gas exchange variables during a drought and recovery experiment conducted on potted seedlings of *L. decidua* (L) and *P. sylvestris* (P) under controlled conditions. Depicted are water potential (ψ), tree water deficit (TWD), soil water content (SWC), stomatal conductance (g_s) and net photosynthesis (A_{net}). The values correspond to Fig. 2.2 and 2.4 and indicate the mean $\pm$ SE of the control treatment across the experiment, as well as treatment means $\pm$ SE of the drought treatment at the end of the first and second drought phase (D1 and D2) and of the drought-lethal treatment at the end of the experiment. The last two columns correspond to the period re-watered trees required to fully recover to pre-stress levels after D1 and D2, respectively.

Parameter	Species	Mean control	End D1	End D2	End drought-lethal	recovery D1 [days]	recovery D2 [days]
ψ [MPa]	L	1.1 ± 0.02	1.2 ± 0.1	3.0 ± 0.2	7.0 ± 0	<3	<1
	P	0.6 ± 0.02	1.0 ± 0.1	2.7 ± 0.2	6.5 ± 0.5	<3	<1
TWD [mm]	L	0.01 ± 0.0002	0.3 ± 0.03	1.3 ± 0.1	1.8 ± 0.1	0	8 ± 1
	P	0.04 ± 0.0002	0.2 ± 0.04	1.6 ± 0.2	2.1 ± 0.2	0	9 ± 1
TWD [%]	L	0.1 ± 0.001	2.7 ± 0.2	12.5 ± 0.6	16.4 ± 0.4		
	P	0.2 ± 0.001	1.3 ± 0.2	10.5 ± 1.0	14.3 ± 0.8		
SWC [%]	L	33.6 ± 0.3	18.9 ± 1.8	2.8 ± 0.6	0.1 ± 0.1	0	0
	P	33.5 ± 0.2	17.8 ± 1.6	1.9 ± 0.7	0.2 ± 0.2	0	0
g_s [$\frac{mmol}{m^2 s}$]	L	104 ± 7	12 ± 1	3 ± 0.4	3 ± 2	<3	20 ± 3
	P	76 ± 5	10 ± 3	3 ± 0.3	3 ± 0.5	<3	10 ± 3
A_{net} [$\frac{\mu mol}{m^2 s}$]	L	5.4 ± 0.3	1.9 ± 0.2	0.0 ± 0.04	-0.1 ± 0.03	<3	12 ± 3
	P	6.0 ± 0.3	1.3 ± 0.3	0.0 ± 0.04	-0.1 ± 0.05	<3	6 ± 3

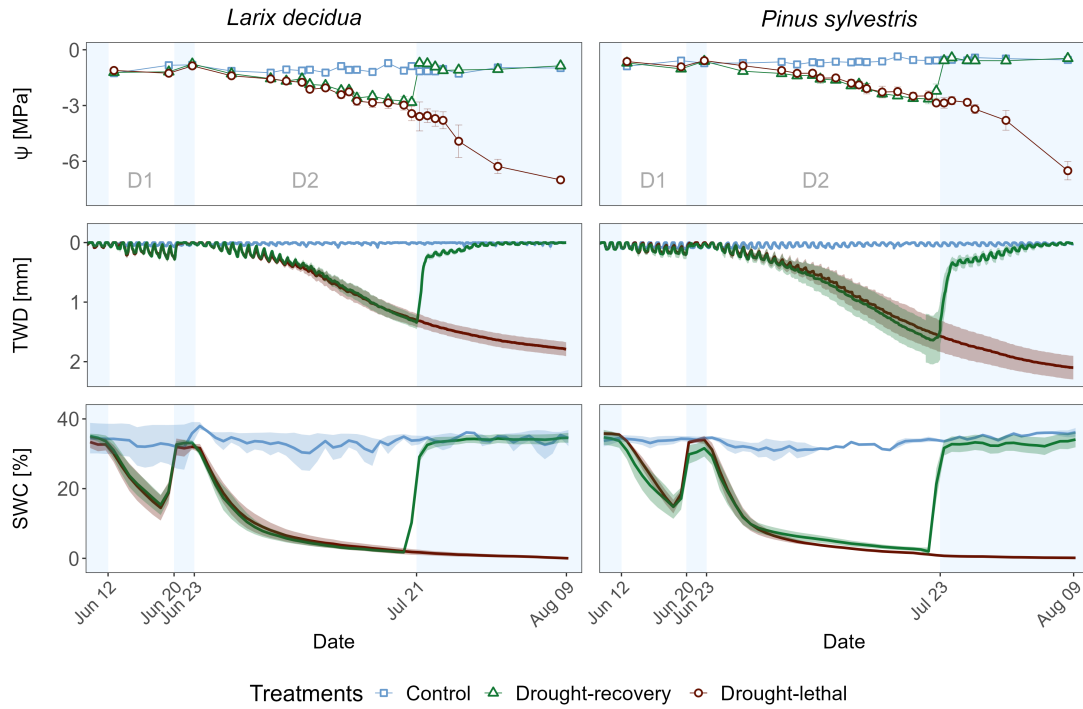


Figure 2.2: Temporal dynamics of water relations during a drought and recovery experiment conducted on potted seedlings (*L. decidua*, *P. sylvestris*) under controlled conditions. Depicted are water potential (ψ), tree water deficit (TWD) and soil water content (SWC) as treatment means $\pm$ SE. White areas illustrate phases of drought (D1 and D2), blue areas indicate recovery phases. In the final recovery phase, the drought treatment was split equally and only drought-recovery seedlings were re-watered, while drought-lethal trees were fully dehydrated.

2.3.3 Relationship between TWD and ψ

We found a strong relationship between TWD and ψ persisting across all drought conditions until lethal dehydration in both *L. decidua* and *P. sylvestris*. It can be effectively characterized by a single species-specific sigmoidal fit (Fig. 2.3 a, b; pseudo- R^2 of 0.97 for both species). To better assess the possibility of using TWD as a predictor for ψ we replotted the data with reversed axes (Fig. 2.3 c, d) and found three distinct phases. Phase (I) shows an initial decrease in ψ with a low TWD response, (II) a steep linear relation indicating decreasing ψ with increasing TWD, and (III) a less pronounced increase in TWD with further decreasing ψ . The first change of phases occurs at a normalized TWD of 0.02 for *L. decidua* and 0.04 for *P. sylvestris*, respectively, with corresponding ψ close to ψ_{g50} (ψ at $g_s = 50\%$ of control). The second shift appears at a TWD_{norm} of 0.74 and 0.81, corresponding to ψ values of -3.0 MPa and -2.9 MPa (in between P₁₂ and P₅₀). The R^2 is lowest with 0.64 in phase (I) for *L. decidua*, while in all other cases R^2 is ≥ 0.88 for both species.

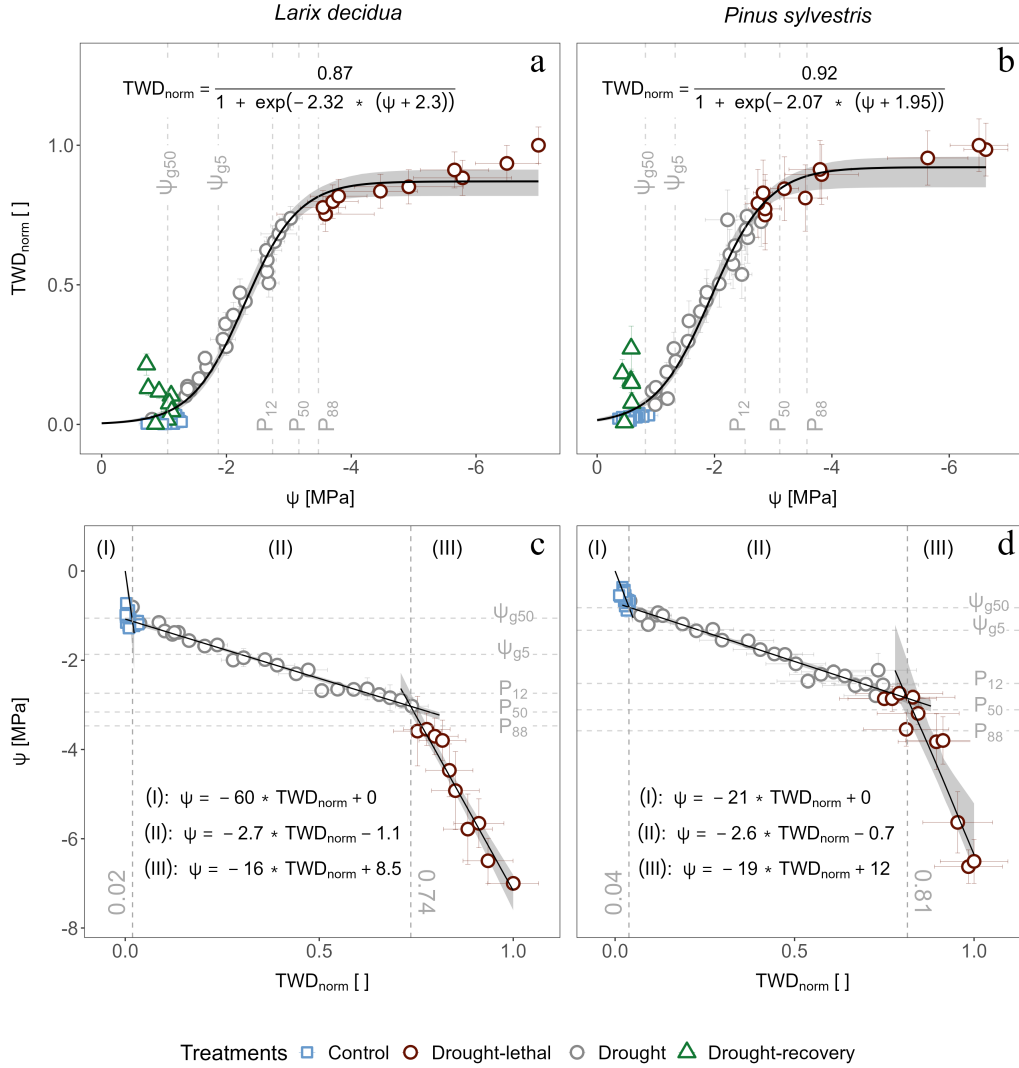


Figure 2.3: Relationship between midday water potential (ψ) and normalized tree water deficit (TWD_{norm}) during a drought and recovery experiment conducted on potted seedlings (*L. decidua*, *P. sylvestris*) under controlled conditions. In the upper row (a, b), we applied a sigmoidal fit with ψ as the predictor variable. In the bottom row (c, d), we reversed axes and split the data into three distinct phases with linear regressions (excluding the drought–recovery treatment). Data are treatment means $\pm$ SE. The TWD was derived from measurements between 1 – 4 pm corresponding to the ψ measurements. Normalized TWD was derived relative to the largest averaged TWD in the drought–lethal trees. Shaded areas depict the 95% confidence intervals of the fitted regressions.

However, the responses of the drought–recovery treatment (green triangles in Fig. 2.3 a, b) could not adequately be represented by the ψ -TWD relationship as observed during continuous drought development. Upon rewetting after D2, immediate recovered ψ values correspond to

TWD persisting at levels higher than anticipated by the sigmoidal fit. In contrast, rewetting after D1 did not exhibit such prolonged effects on TWD.

Taking a closer look at species-specific TWD- ψ responses, we found slight differences in timing and depletion rates. Specifically, TWD accumulates at lower ψ levels for *L. decidua* compared to *P. sylvestris*. The point at which 50% of water is depleted (c parameter in the sigmoidal fit) occurred significantly later for *L. decidua* compared to *P. sylvestris*: -2.3 ± 0.1 MPa versus -2.0 ± 0.1 MPa ($P < 0.01$). Additionally, *L. decidua* exhibited a higher shrinkage rate per MPa ψ (b parameter in the sigmoidal fit, $P < 0.01$).

2.3.4 Leaf gas exchange during drought–recovery cycles

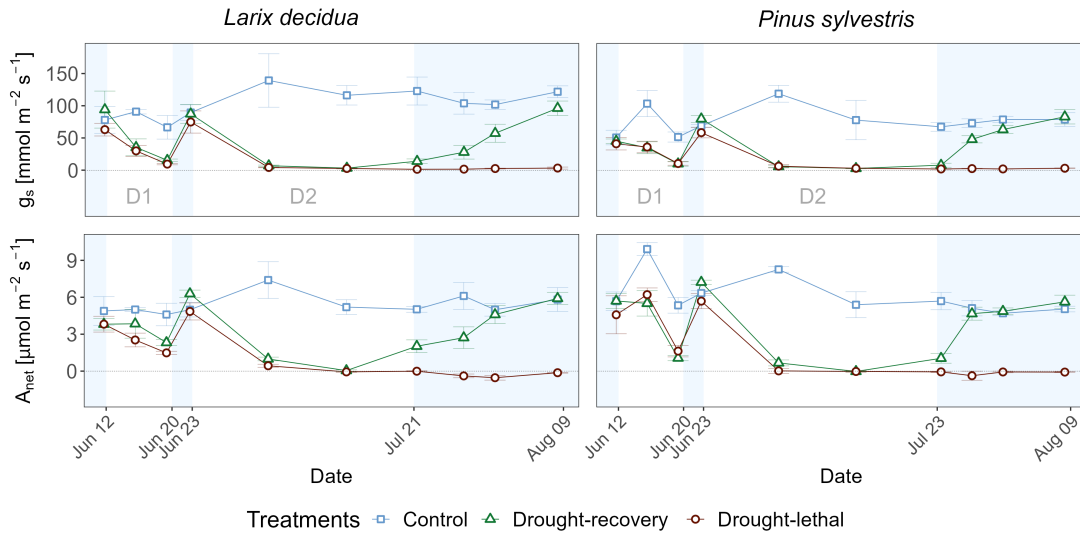


Figure 2.4: Temporal dynamics of leaf gas exchange in the course of a drought and recovery experiment conducted on potted seedlings (*L. decidua*, *P. sylvestris*) under controlled conditions. Depicted are stomatal conductance (g_s) and net photosynthesis (A_{net}) as treatment means $\pm$ SE. White areas illustrate phases of drought (D1 and D2), blue areas indicate recovery phases. In the final recovery phase, the drought treatment was split equally and only drought–recovery seedlings were re-watered, while drought–lethal trees were fully dehydrated.

Leaf gas exchange was highly sensitive to both drought and rewetting conditions (Fig. 2.4, Tab.2.2). At the end of D1, ψ reached 1.2 ± 0.1 MPa for *L. decidua* and 1.0 ± 0.1 MPa for *P. sylvestris*. Accordingly, g_s was reduced significantly ($P < 0.01$) to 11.5% and 13.3% of control values, respectively, while A_{net} dropped to 35.2% and 21.7%. The ψ_{g5} of full stomatal closure was reached in the first half of D2. During the remaining drought period, g_s remained at its minimum and A_{net} approached zero. Leaf gas exchange fluxes quickly returned to control values after D1 but required time for full recovery following D2 (Tab.2). In particular, g_s recovery after D2 took approximately 20 ± 3 days for *L. decidua* and 10 ± 3 days for *P. sylvestris*. Similarly,

the recovery period for A_{net} was approximately 12 ± 3 in *L. decidua* and 6 ± 3 days *P. sylvestris*. Hence, the gas exchange of *P. sylvestris* tended to recover faster compared to *L. decidua*, with g_s recovering generally slower than A_{net} in both species.

2.3.5 Relationship between TWD and g_s

We found a strong exponential relationship between g_s and both the midday (Fig. 2.5 a,b) and pre-dawn TWD (Fig. 2.5 c,d) during dehydration. Corresponding pseudo- R^2 values are 0.87 in both cases for *L. decidua* and 0.77 and 0.81 for midday and pre-dawn TWD, respectively, for *P. sylvestris*. Small increases in TWD resulted in drastic decreases in gas exchange, which appeared more pronounced for pre-dawn than for midday TWD, highlighting the sensitivity of g_s to water deficit. While midday TWD allows estimations of partial stomatal closure, the pre-dawn TWD signal provided a clearer response at full stomatal closure, indicated by a phase shift at $TWD > 0$. In more detail, at a midday TWD_{norm} of 0.06 for *L. decidua* and 0.08 for *P. sylvestris* 50% stomatal closure was reached (md-TWD $_{g50}$), shortly after the first shift in the TWD- ψ relation and in a range where pre-dawn TWD is still 0. Stomatal closure became apparent at midday TWD values of 0.23 and 0.25 for *L. decidua* and *P. sylvestris*, respectively, corresponding to pre-dawn TWD values of only 0.02 and 0.07 (md- and pd-TWD $_{g5}$).

Due to different recovery behaviors of TWD and g_s , the drought-recovery treatment following the final rewetting was slightly outside the expectation of the exponential curves for both species. However, we found species-specific differences. For *L. decidua*, g_s during drought-recovery was partly lower than anticipated by the regression curve due to a delayed gas exchange recovery. Conversely, for *P. sylvestris*, g_s deviated from the curve with values higher than expected, indicating a delay in TWD recovery. While the recovery of g_s and TWD showed similar trends, it differed in timing. g_s exhibited a gradual recovery, whereas TWD initially showed a rapid response followed by a gradual decrease.

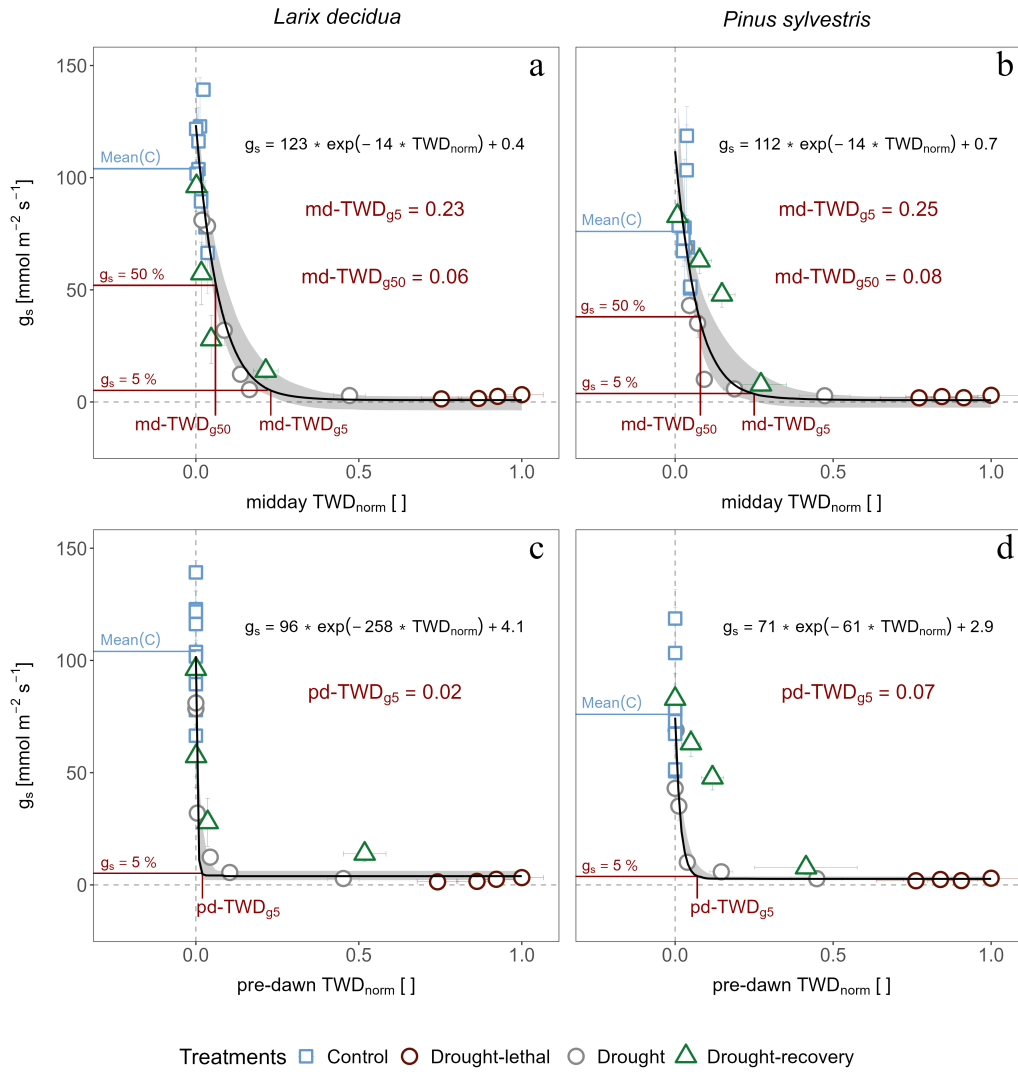


Figure 2.5: Relationship between midday leaf-level stomatal conductance (g_s) and normalized tree water deficit (TWD_{norm}) during a drought and recovery experiment conducted on potted seedlings (*L. decidua*, *P. sylvestris*) under controlled conditions. In (a, b), g_s is related to midday (md) TWD, derived from measurements between 1 – 4 pm, corresponding to the g_s measurements. In (c, d), g_s is related to pre-dawn (pd) TWD, derived from measurements between 3 – 4 am. We applied exponential fits (black) neglecting the drought-recovery data points with the shaded area indicating the 95% confidence interval of the curve. Additionally, the TWD_{norm} at g_s equaling 5% (a-d; TWD_{g5}) and 50% (a-b; TWD_{g50} ; red lines) of the control mean (Mean(C); blue lines) was determined. Data are treatment means $\pm$ SE. Normalized TWD was derived relative to the largest averaged TWD in the drought-lethal trees.

2.4 Discussion

Our data confirm strong relationships between ψ and TWD, as well as g_s and TWD. However, these relationships became unstable during recovery after severe drought. While dendrometer-based TWD measurements show promise for predicting ψ (Dietrich et al., 2018) and can serve as a drought stress indicator, caution is required when including periods of drought recovery in the analysis.

2.4.1 How does TWD develop with decreasing ψ ?

The relationship between TWD and ψ was robust for both investigated tree species, including severe and lethal drought stress, but not during the recovery phase after D2 (see section 2.4.2). Both species showed similar TWD patterns, supporting previous studies indicating minor differences in drought susceptibility (Dulamsuren et al., 2019, Feng et al., 2021). Nevertheless, we found species-specific disparities. *L. decidua* exhibited a weaker stomatal control (Peters et al., 2023) and responded more anisohydric than *P. sylvestris* (Oberhuber et al., 2015). Additionally, *L. decidua* demonstrated a greater rate of shrinkage per ψ decrease during dehydration, aligning with expectations of high transpiration rates even under dry conditions (Leštianska et al., 2020).

We observed shifts in the TWD- ψ relationship with increasing water shortage, representable by either a single sigmoidal curve or distinct linear fits. Sigmoidal regressions were proposed by Dietrich et al. (2018) and the authors expect a saturation of TWD at the lowest ψ they have measured (about -2.5 MPa for *L. decidua* and -1.8 MPa for *P. sylvestris*). In contrast, our data suggest that TWD has not reached half its maximum at this ψ . Besides an overall high correlation, the sigmoidal fit fails to capture the development under the lowest ψ levels for our data. After expected tree death, as suggested by ψ measurements, it seems that the remaining water availability in elastic tissues did not lead to an asymptotic TWD saturation but a continued shrinkage, as demonstrated in phase III (Fig. 2.3 c,d) and supported by similar findings of Andriantelomanana et al. (2024) for *Populus tremula*. This also induces difficulties selecting TWD_{max} , which is crucial for normalization of the TWD signal (See section 2.4.4). Linear TWD- ψ relationships were also found for the tropical species *Callitris intratropica* (Drew et al., 2011) and the temperate species *Juglans regia* (Cochard et al., 2001), *Picea abies* and *Larix decidua* (Oberhuber et al., 2015). However, none of these studies captured severe drought stress and slope shifts in the TWD- ψ relationship were consequently not present. Overall, the linear approach appears more realistic and applicable. While the sigmoidal method requires a complex inversion for ψ retrievals, the linear procedure allows direct predictions. Although defining additional inclination points may be a practical limitation, these inclination points could serve as valuable stress-severity thresholds. However, caution is required when extending regression curves beyond their calibrated range. For instance, Vergeynst et al. (2015) suggest

extrapolating a single linear ψ -TWD regression fit for continuous ψ determination. With a slope change appearing at the onset of hydraulic damage, as our data suggest, such an extrapolation will lead to errors under severe drought stress (here in phase (III)). Also, predicting ψ under near-zero TWD is difficult despite a linear correlation, while in phases (II) and (III), TWD becomes a better predictor as dehydration accumulates.

We propose that the two slope changes in the TWD- ψ relationship (Fig. 2.3 (c,d)) can serve as thresholds for the onset of initial drought stress and the loss of instant recovery potential. While often a subsequent release of water from elastic and inelastic tissues during dehydration is proposed, Lauriks et al. (2022) suggest an overlapping, and Andriantelomanana et al. (2024) a fully simultaneous succession. Our results support partially overlapped water release from elastic and inelastic tissues and distinct phases indicating different drought severity and recovery potential. For phase (I), we hypothesize a parallel release of apoplastic and symplastic water with apparent but low volume loss. At this stage, the TWD vanishes at night, indicating no soil water limitation. The shift to phase (II) seems to be triggered by stomatal closure, as it occurs around ψ_{g50} . Further dehydration results in complete stomatal closure within the phase. Here, accumulation of TWD due to water release purely stems from elastic tissues, leading to the highest depletion rate. In contrast to the observation of Andriantelomanana et al. (2024), our data suggest no water release from inelastic tissues until the end of the phase according to the determined vulnerability curves and measured ψ . We assume that the second shift in slope corresponds to the onset of hydraulic damages as it occurs between P_{12} and P_{50} . In Phase (III), P_{88} is accompanied by less rapid but nonetheless persistent shrinkage, indicating further release of symplastic water, joined by water release from embolized xylem conduits. Mantova et al. (2022) argue that cavitation events trigger the collapse of living cells, i.e. cell necrosis due to mechanical or oxidative stress. In particular, the loss of meristematic cells is critical since they play a crucial role in the survival and recovery of trees. While embolized xylem conduits are lost, secondary growth building new xylem can improve conductance. However, this requires surviving meristematic cells with a functional water supply (Mantova et al., 2022). Water released by xylem embolism may be used to sustain hydration of elastic tissues (Skelton, 2020), and hence delaying cell collapse (Knipfer et al., 2019, Lamacque et al., 2020). Further shrinkage in phase (III) suggests increasing PLC and meristematic cell loss, leading to longer recovery after stress release. At a certain threshold, the recovery potential may be lost completely, resulting in tree death (Lamacque et al., 2020, Andriantelomanana et al., 2024).

2.4.2 Is the relationship between TWD and ψ impacted by stress release?

Since physiological processes recover at different rates after severe drought (Ruehr et al., 2019, Rehschuh et al., 2020), we expected a changed TWD- ψ relationship during recovery. While the severe drought phase D2 caused changes, the mild drought conditions in D1 had negligible impact.

During D1, the highest occurring TWD was within the early part of phase (II), and stress release led to an instantaneous recovery of all physiological parameters, shifting the TWD- ψ relationship back to its initial stage. In contrast, at the end of D2, *P. sylvestris* trees were within the latter part of phase (II) and *L. decidua* trees in the early part of phase (III). Despite the rapid increase of ψ to levels similar to controls, TWD did not fully recover for several days in both species. Interestingly, the diameter increase showed similarities to a capacitor recharge curve, and further investigations might enable valuable insights into tree-water relations from TWD recovery, such as capacitance determination. In the TWD- ψ relationship, we observed a recovery hysteresis effect. The drought–recovery treatment deviated from the curve (Fig. 2.3 a,b) but gradually approached it again while TWD recovered back to control values. Hence, during this phase, the relationship does not hold. The distinct recovery behavior after D1 and D2 further supports our argument that the trees lose their potential for instantaneous recovery at the shift from phase (II) to phase (III).

However, whether the incompletely recovered stem diameter after rewetting still indicates a water deficit is arguable. By definition, TWD is greater zero if the current diameter is smaller than the maximum diameter in the past (see Eq. 2.2.2). On the other hand, TWD is supposed to reflect the condition where elastic tissues are not fully hydrated and, consequently, not at their maximum volume. The sharp diameter increase after stress release stopped after approximately one day without full recovery to pre-stress conditions, eventually caused by an impairment of the xylem-phloem connection increasing radial resistance (Steppe et al., 2006, Salomón et al., 2017). Another explanation might be the collapse of elastic cells, which can not rehydrate afterwards (Lamacque et al., 2020, Fortunel et al., 2023). In this case, the disparity in diameter observed one day after stress release would indicate accumulated cell damage rather than a persistent water deficit.

Thus, the incomplete recovery of stem diameter after stress release may be a proxy for assessing cell damage and, consequently, recovery potential or even mortality risk. Previous studies have identified specific thresholds for TWD beyond which mortality occurs. *Lavandula* seedlings perished once they reached a stem shrinkage of approximately 21% (Lamacque et al., 2020), while *Populus tremula* seedlings succumbed at values ranging from 7% to 12%, depending on growth conditions (Andriantelomanana et al., 2024). In our study, the maximum stem shrinkage reached during D2 was $12.5 \pm 0.6\%$ for *L. decidua* and $10.5 \pm 1.0\%$ for *P. sylvestris*. Although none of the trees died, they all required a prolonged recovery time and can be supposed to have experienced damaged tissue. In *L. decidua*, 85% of the diameter shrinkage reversed after stress release, which may indicate that roughly 15% of living parenchyma or meristematic cells were irreversibly damaged. For *P. sylvestris* this value corresponds to 20%. Despite higher ψ_{min} values before rewetting compared to *L. decidua* and similar P_{50} , *P. sylvestris* exhibited higher tissue damage susceptibility. Notably, damage was not directly quantified in this study, and the

exact cause of the incomplete diameter recovery is debatable. Further investigations of partial TWD recovery upon various stress levels and TWD thresholds for mortality may yield promising metrics enabling drought damage predictions, especially if they include in-situ embolism and cell collapse quantification.

2.4.3 How are TWD and gas exchange related?

The exponential decline of g_s with increasing TWD is consistent with findings from two *Lavandula* species (Lamacque et al., 2020). While the initial decrease in ψ does not directly limit g_s (Rehseh et al., 2020), the first increase in TWD already signified drought stress, triggering partial stomatal closure and subsequent declines in gas exchange. Once TWD did not fully recover during the night, leading to a pre-dawn TWD greater than 0, stomata were closed or nearly closed the following midday - a stress signal directly applicable to field conditions. However, a direct quantitative prediction of g_s appears challenging due to the sensitive response between g_s and TWD. Alternatively, TWD could be used to estimate ψ , facilitating a more straightforward prediction of the gas exchange rates with hydraulic models (Anderegg et al., 2017, Eller et al., 2018). Besides quantifying g_s relations, correlations between TWD and transpiration might reveal interesting insights, especially if one considers canopy-level transpiration as a measure of whole tree water loss under variable VPD (Peters et al., 2023).

Upon stress release after D2, we observed hysteresis effects in the g_s -TWD relationships due to asynchronous TWD and gas exchange recovery. The restoration of pre-stress levels seems to depend on tissue damage and recovery strategies. In general, the recovery of stomatal conductance is complex and relies on species-specific factors such as genotype, abscisic acid concentration, hydraulic resistance, and transpiration rates (Buckley, 2019). In the case of *L. decidua*, a higher percentage of shrinkage was reversed directly after stress release, resulting in a slightly faster TWD recovery. *P. sylvestris* showed less immediate TWD recovery but a faster recovery in g_s and the carbon assimilation rate A_{net} . This differential recovery may indicate distinct priorities, with *P. sylvestris* emphasizing gas exchange recovery. In contrast to D2, the mild drought D1 did not exhibit changes in the g_s -TWD relationship, aligning with the observation that gas exchange only requires prolonged recovery after hydraulic impairments occurred (Skelton et al., 2017).

The thresholds at which stomata close in response to increasing TWD are likely species-specific (Lamacque et al., 2020, Andriantelomanana et al., 2024) and reflect individual water-use strategies. Trees rely on internal water reservoirs during drought, resulting in varying degrees of stomatal closure depending on the species' tendency to limit water loss. However, in our study, both *L. decidua* and *P. sylvestris* exhibited nearly identical g_s -TWD relationships, despite differences in water use strategies (Oberhuber et al., 2015, Martín-Gómez et al., 2023) and different ψ_{g50} and ψ_{g5} values. Consequently, stomatal closure developed at similar TWD thresholds. These thresholds likely depend on stomatal density, leaf traits, and the possibility of reducing internal

conductivity by non-stomatal effects. For example, *Lavandula* species fully close stomata at a stem shrinkage of $\approx 5\%$ (Lamacque et al., 2020), while in our case md-TWD_{g5} translates to values of approximately 2% for *L. decidua*, and 1.7% for *P. sylvestris*, indicating a more sensitive stomatal response. *Populus tremula* reacts even faster, with full stomatal closure reported at the onset of midday TWD accumulation (Andriantelomanana et al., 2024). Investigating such responses offers a promising approach to assessing water-use strategies. Besides, TWD thresholds for stomatal closure could serve as warning signals in field conditions. Practically, monitoring the occurrence of pre-dawn TWD might be a simple and directly applicable measure to predict stomatal closure. Applying midday TWD_{g50} and TWD_{g5} appears to provide more detailed insights into the degree of stomatal opening. However, transferring these thresholds (and ψ -TWD relations) requires normalization of TWD signals, a challenge still limiting practical use.

2.4.4 The challenge of normalizing TWD

A significant challenge in applying TWD relationships in field conditions is the normalization with TWD_{max}, especially when lethal conditions are not captured by measurements. In our study, we defined TWD_{max} as the mean maximum TWD of drought-lethal trees at the end of the experiment. However, post-mortem shrinkage complicates this choice, as defining TWD_{max} at a different time would alter thresholds and relationship functions. Additionally, transferring TWD_{max} to different tree sizes and environmental conditions requires careful consideration, given that tissue shrinkage depends on factors such as bark-to-xylem ratio, wood density, elastic modulus, and growth conditions (Andriantelomanana et al., 2024). For instance, *P. sylvestris* exhibited greater absolute shrinkage than *L. decidua*, but the latter showed a larger relative shrinkage (Tab. 2.2), possibly indicating more water storage in elastic cells, supported by a thicker bark and a lower bark-to-xylem ratio (0.48 vs. 0.25; Fig. S2.12). Future research should aim for a more stable and transferable normalization, e.g. by differentiating between bark and xylem shrinkage, or by experimenting with different normalization variables such as maximum daily shrinkage (Peters et al., 2023).

2.4.5 Conclusions

Dendrometer-derived TWD provides direct insights into the water dynamics of individual trees by enabling continuous ψ determination, the assessment of stomatal closure, and the application of tree drought stress thresholds. However, the normalization of the TWD data remains a challenge and affects transferability. Additionally, recovery phases following severe droughts can alter the TWD relationships to ψ and g_s . On the positive side, the incomplete diameter recovery after stress release provides an opportunity to quantify drought-induced damage and estimate recovery times. Dendrometer networks, capable of collecting data from numerous trees, allow the evaluation of tree functionality at larger scales. These networks could serve as early warning

systems, detecting initial drought onset as well as severe drought conditions. A persisting TWD not refilled during the night is a clear drought stress signal, accompanied by drastically reduced midday leaf gas exchange. Further TWD accumulation can then hint towards critical damage to tree functionality and, ultimately, the risk of tree mortality. Identifying susceptible species and locations could guide mitigation efforts and appropriate management actions. Applications extend to urban environments for tree watering practices and forest ecosystems to support comprehensive monitoring efforts.

Acknowledgments

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2.5 Supplementary Material for Chapter 2

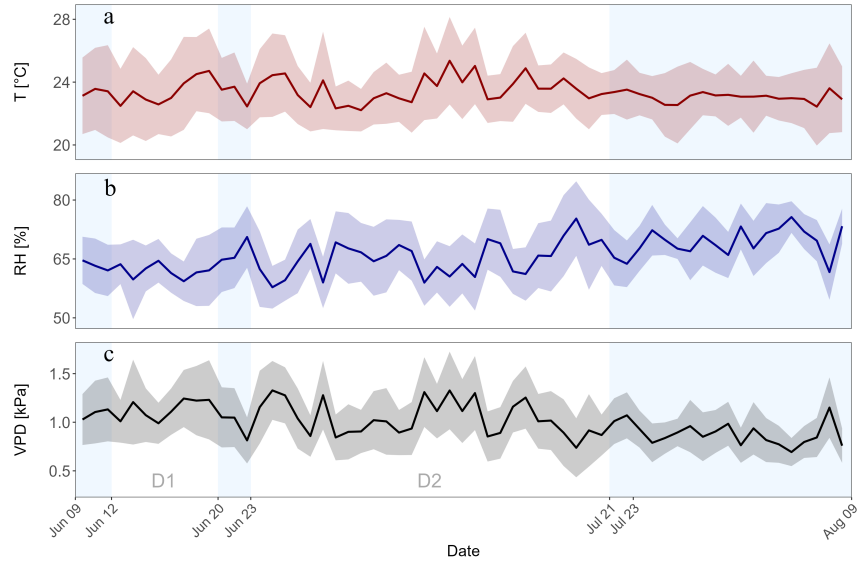


Figure S2.6: Temporal dynamics of meteorological variables in the course of a drought and recovery experiment conducted on potted seedlings (*L. decidua*, *P. sylvestris*) under controlled conditions. Depicted are temperature (T; a), relative humidity (RH; b), and vapour pressure deficit (VPD; c) as daily means $\pm$ SD. White areas illustrate phases of drought (D1 and D2), and blue areas indicate recovery phases.

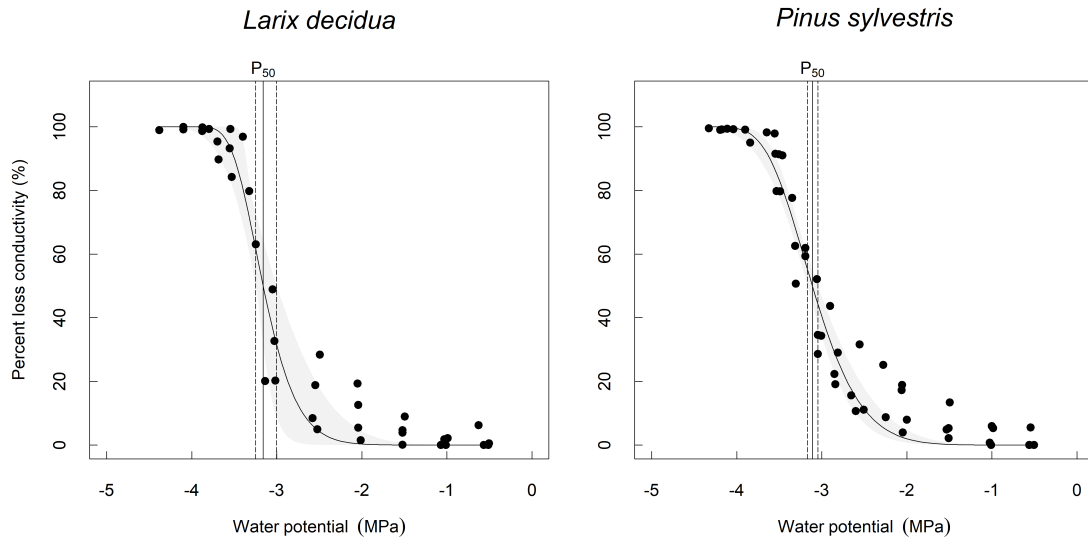


Figure S2.7: Vulnerability curves as determined with Cavitron measurements on $n = 4$ seedlings of *L. decidua* and *P. sylvestris*. Dots indicate individual measurements. The shaded area corresponds to the 95% confidence interval of the sigmoidal regression. The water potentials at which 50% of conductivity is lost (P_{50}) are depicted as vertical lines.

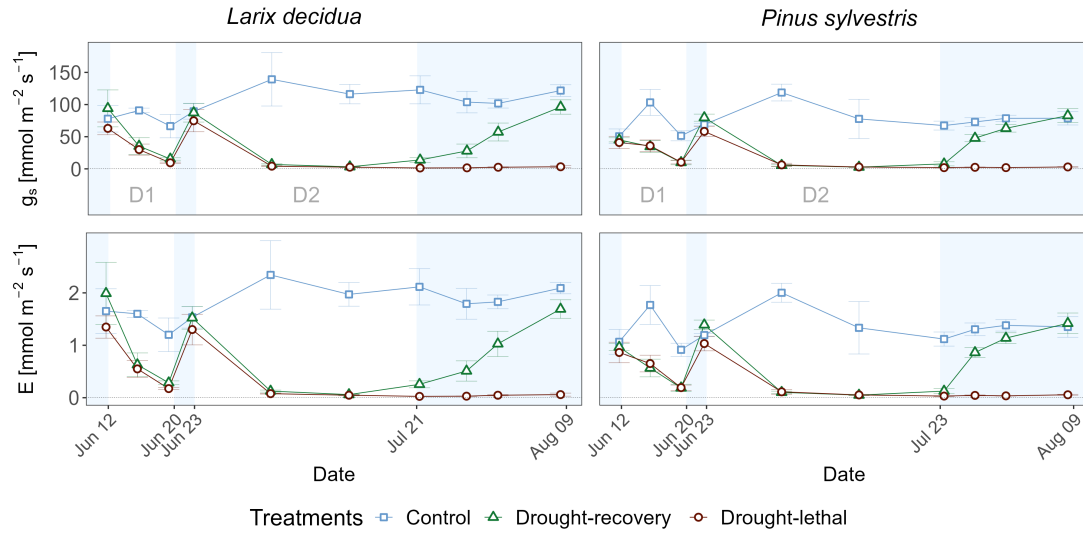


Figure S2.8: A comparison of stomatal conductance (g_s) and transpiration (E) revealed no substantial differences in temporal dynamics. Data are depicted as treatment means $\pm$ SE. White areas illustrate phases of drought (D1 and D2), blue areas indicate recovery phases. In the final recovery phase, the drought treatment was split equally and only drought-recovery seedlings were re-watered, while drought-lethal trees were fully dehydrated.



Figure S2.9: Exemplary dendrometer setup.

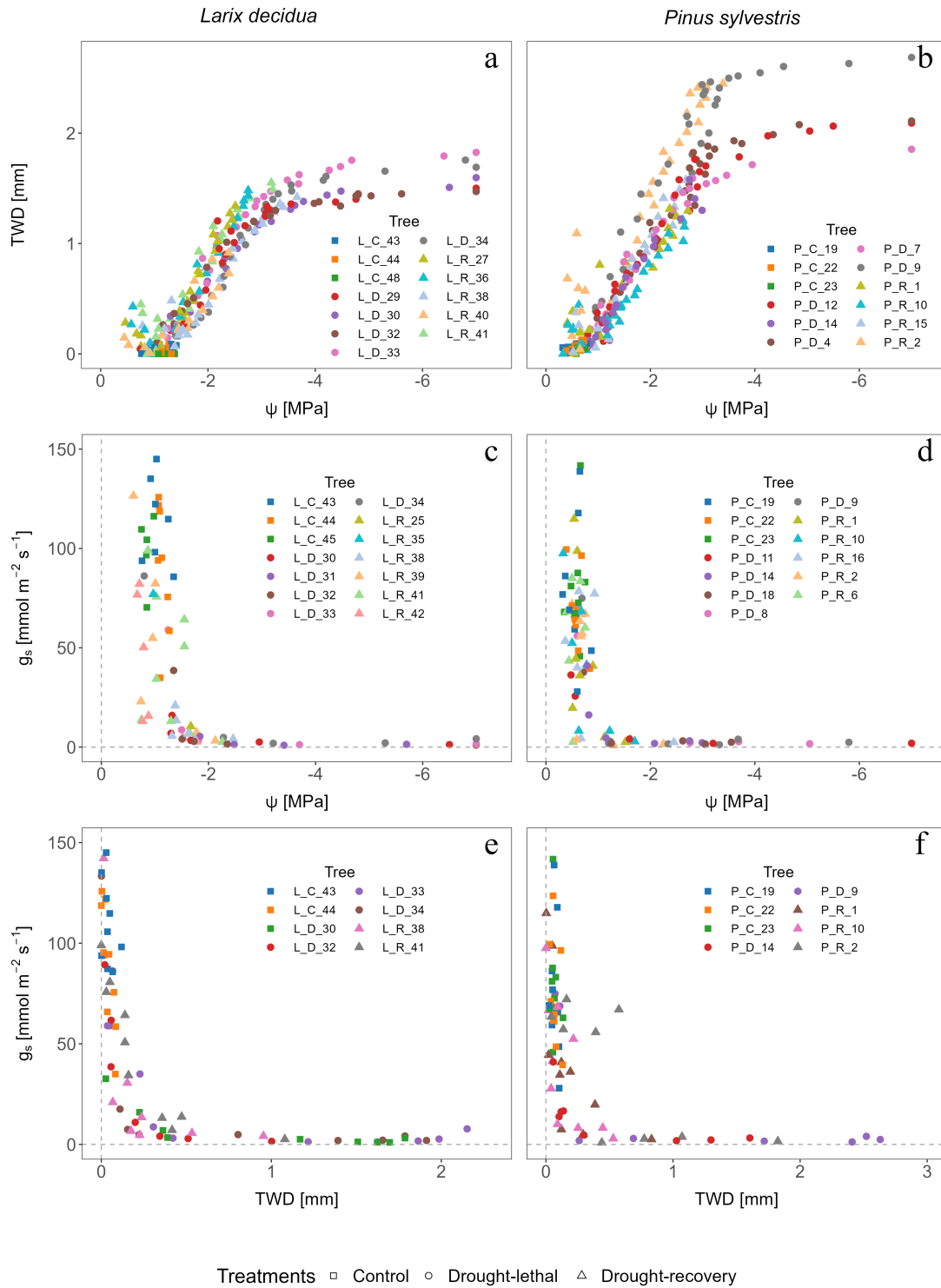


Figure S2.10: Midday water potential (ψ), midday stomatal conductance (g_s), and tree water deficit (TWD), with each dot corresponding to measurements taken from the same tree on the same day. For the first g_s measurement (June 12), the corresponding ψ was taken from the following day. TWD values were averaged between 1-4 pm. Please note that the treatment means presented in the main manuscript (Fig. 3 and 4) also include additional measurements not shown here, specifically from trees where not all variables were measured simultaneously.

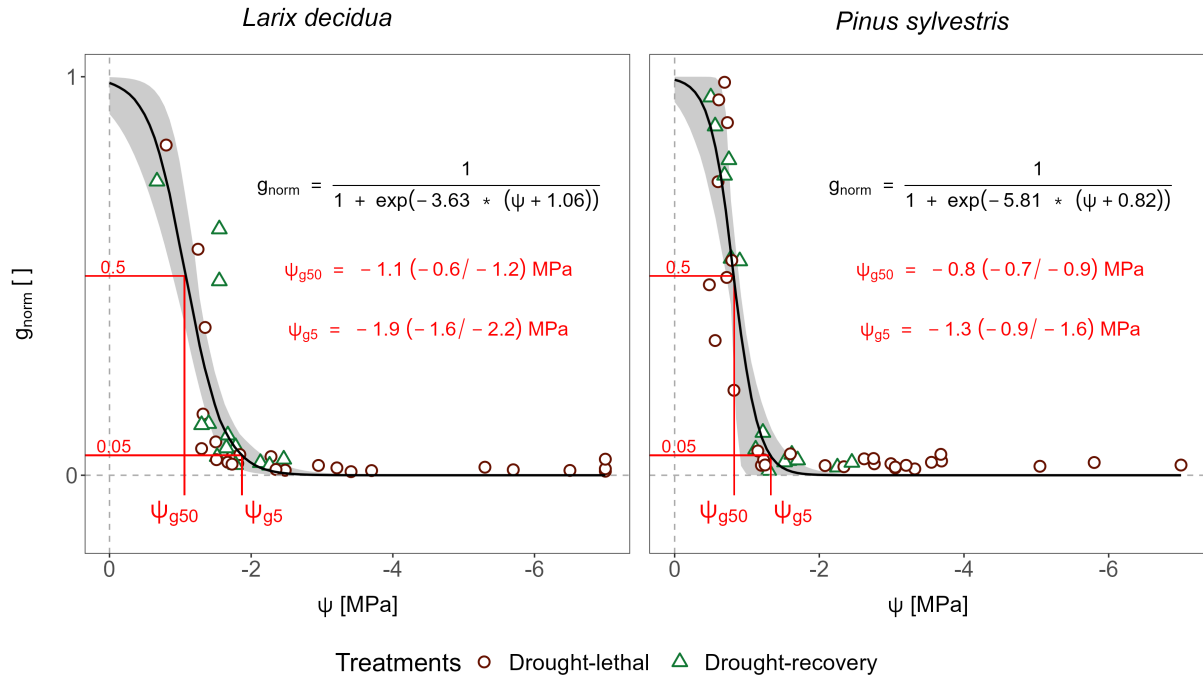


Figure S2.11: Determination of ψ_{g50} and ψ_{g5} — the midday water potentials (ψ) at which midday stomatal conductance (g_s) reaches 50% and 5% of the control mean — for *L. decidua* and *P. sylvestris*. Dots represent individual measurements, including only drought-lethal trees and drought-recovery trees prior to the final re-wetting (For all treatments, see Fig. S2.10 (c,d)). Stomatal conductance (g_s) was normalized against the control mean (g_{norm}) and paired with ψ values measured on the same tree. A sigmoidal fit (black line) was applied, with the 95% confidence interval indicated by shaded areas.

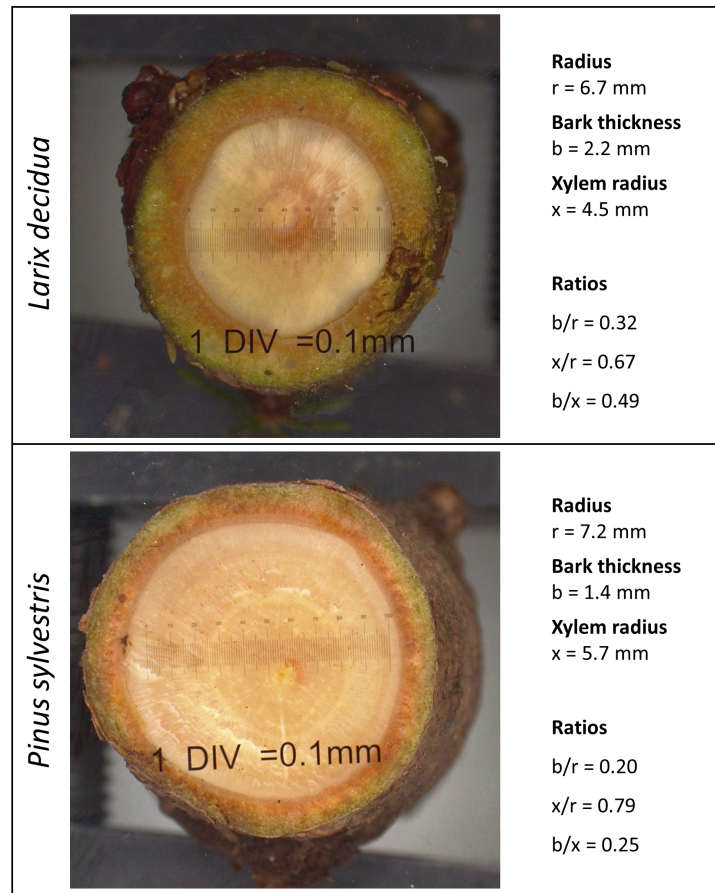


Figure S2.12: Cross-section images of a fully hydrated *L. decidua* and *P. sylvestris* stem, used to determine total stem radius (r), xylem radius (x), and bark thickness (b). Additionally, we calculated the proportion of bark and xylem on the radius (b/r and x/r , respectively) and the bark-to-xylem ratio (b/x).

3 TREE WATER DEFICIT REVEALS A DROUGHT-INDUCED CARBON BALANCE TRANSITION ACROSS THREE CONIFEROUS SPECIES

This chapter has been submitted as:

Ziegler Y, Alongi F, Knüver T, Rehschuh R, Zeppan JK, Ruehr NK. 2026. Tree water deficit reveals a drought-induced carbon balance transition across three coniferous species. *In review*.

Abstract

Drought increasingly threatens the forest carbon (C) sink, highlighting the need to understand how hydraulic stress interacts with C dynamics. We synthesized three drought experiments on *Pinus sylvestris*, *Picea abies*, and *Pseudotsuga menziesii* seedlings, combining whole-tree root and shoot chambers with dendrometer measurements, to test whether tree-level net C balance (sum of net shoot assimilation and root respiratory C losses) and gas-exchange responses can be described along a normalized daily minimum tree water deficit ($TWD_{\min, \text{norm}}$) axis derived from stem shrinkage. Across species and drought pathways, daily C balance declined consistently with increasing $TWD_{\min, \text{norm}}$ and crossed from net C uptake to net C loss at $TWD_{\min, \text{norm}} = 0.20$ [0.13–0.31]. Species-specific thresholds fell within a narrow $TWD_{\min, \text{norm}}$ range, whereas water-potential equivalents diverged, indicating no common water-potential threshold. Stomatal conductance and transpiration were less consistently described by $TWD_{\min, \text{norm}}$ alone, likely reflecting additional influences of atmospheric demand and short-term water availability. Diurnal analyses showed that the transition emerged gradually through progressive shortening and weakening of daytime C gain, rather than abrupt cessation of assimilation. Together, these findings suggest that

normalized TWD can identify physiologically meaningful C balance thresholds, providing a basis for using dendrometer-based hydraulic monitoring to assess tree-level C dynamics under drought.

3.1 Introduction

Forests act as major global carbon (C) sinks and play a crucial role in regulating the atmospheric C cycle (Pan et al., 2011; Harris et al., 2021; Friedlingstein et al., 2022). At the ecosystem scale, the net C balance reflects the difference between gross C uptake through photosynthesis and total C release through autotrophic and heterotrophic respiration, including understory and soil microbial respiration (Baldocchi, 2003). However, climate change is increasing the frequency, duration, and intensity of drought events (IPCC, 2021; Gebrechorkos et al., 2025), posing a growing threat to the stability of forest C sinks (Allen et al., 2010; Adams et al., 2017; McDowell et al., 2022; Van Der Woude et al., 2023). Intensifying drought stress may even shift forests to C sources in extreme cases (Bréda et al., 2006; McDowell et al., 2008; Anderegg et al., 2013; Rosan et al., 2024; Haberstroh et al., 2025a). Understanding the resilience of forest C sinks under a changing climate is therefore critical for predicting future C dynamics (Anderegg et al., 2015; Adams et al., 2017; McDowell et al., 2022).

Tree-level net C balance (C_{net}), here defined as the sum of net shoot assimilation (A_{net} ; including shoot respiration) and root respiratory C losses (R_{root} ; negative), represents only one component of ecosystem C exchange, but characterizing it is a necessary step toward understanding drought impacts on forests more broadly. During ongoing drought stress, C_{net} is primarily altered through changes in gas exchange. As soil water availability declines, trees progressively reduce stomatal conductance (g_s) to limit transpirational water loss and prevent excessive declines in leaf water potential (ψ) (Sperry et al., 2017; Buckley, 2019). High atmospheric water demand can further intensify drought stress (Grossiord et al., 2020). This stomatal regulation restricts the diffusion of CO_2 into the leaf, thereby constraining photosynthetic C assimilation (Flexas, 2002; Buckley, 2019). With increasing drought severity, additional non-stomatal processes can further constrain photosynthesis, including declines in mesophyll conductance and biochemical limitations of the photosynthetic machinery (Flexas, 2002; Flexas et al., 2012; Dewar et al., 2018). As respiratory C losses continue, even at reduced rates, C_{net} may turn negative when these losses exceed C assimilation under severe stress (Gattmann et al., 2021).

The close mechanistic coupling between water and C dynamics in trees suggests that hydraulic stress may serve as a meaningful predictor of C_{net} . This coupling also extends to drought-induced tree mortality, which can be interpreted in terms of interacting hydraulic failure and C starvation mechanisms (McDowell et al., 2008; Adams et al., 2017). While the relative importance of these mechanisms remains debated (Adams et al., 2017; McDowell et al., 2022), their interaction implies that hydraulic state and C balance should be considered jointly during drought. Identifying

whether changes in C_{net} are linked to simple hydraulic stress metrics could therefore provide new insights into C dynamics during drought.

Despite extensive research on drought physiology, it remains difficult to consistently quantify and compare drought stress (Novick et al., 2022; Restrepo-Acevedo et al., 2026). Drought intensity is often characterized using environmental metrics such as soil moisture or precipitation deficits, yet these indicators do not necessarily reflect the hydraulic state of the tree itself. Water potential provides a more direct measure of plant water status, but varies widely among species due to differences in hydraulic traits and tissue properties (Martinez-Vilalta et al., 2019; Trueba et al., 2019). In addition, measurements of ψ are typically labor-intensive and limited in temporal and spatial coverage (Rodriguez-Dominguez et al., 2022). Continuous sensor-based approaches to capture ψ , such as microtensiometers, can help overcome some of these limitations, but are not yet broadly applicable across large numbers of individuals and experimental contexts (Magh et al., 2026; Restrepo-Acevedo et al., 2026). Investigating alternative continuous measurements of tree water status in parallel may therefore help address this challenge.

High-resolution dendrometer measurements of stem diameter variations provide such a continuous proxy for internal tree water status. These measurements capture reversible stem shrinkage and swelling associated with changes in tissue hydration, thereby reflecting imbalances between transpiration and water supply (Zweifel et al., 2001; Steppe et al., 2006). The resulting tree water deficit (TWD) quantifies stem diameter shrinkage relative to the fully hydrated state, integrates hydraulic stress at the whole-tree level, and provides insight into the progression of drought stress (Zweifel et al., 2016). Because dendrometers are non-destructive and easy to apply, they offer a practical approach for monitoring drought stress in trees (De Swaef et al., 2015; Sevanto, 2025).

Recent work has demonstrated that TWD is closely related to ψ and g_s , linking dendrometer signals to key physiological processes (Dietrich et al., 2018; Ziegler et al., 2024). Progressive accumulation of TWD can also indicate the onset of hydraulic damage and has been associated with thresholds linked to tree mortality risk (Andriantelomanana et al., 2024; Ziegler et al., 2024). More recently, normalized formulations of TWD (TWD_{norm}) have been proposed to enable comparisons of hydraulic stress across individuals and species (Peters et al., 2025).

However, it remains to be tested whether TWD_{norm} can be compared across different contexts, and how well it constrains different physiological processes under changing environmental conditions. In particular, its relationship to C_{net} remains underexplored. Testing how water fluxes and C_{net} change along TWD_{norm} could therefore provide new insights into how drought progression affects tree functioning. Such relationships could substantially enhance the value of dendrometer monitoring by enabling improved tracking and prediction of tree-level C balance.

By synthesizing data from controlled drought experiments on three juvenile conifer species, this study combines continuous dendrometer and whole-tree gas exchange measurements across

contrasting experimental conditions. Reanalyzing these datasets within a common framework allows us to test whether $\text{TWD}_{\text{min,norm}}$ – representing the best-hydrated state of each day – can serve as a continuous indicator of hydraulic state and how it relates to C_{net} and water-related gas exchange during drought. Specifically, we address three questions: (i) Can $\text{TWD}_{\text{min,norm}}$ serve as a common hydraulic stress axis to explain variation in C_{net} , g_s , and transpiration across species and experimental drought pathways? (ii) Does a consistent $\text{TWD}_{\text{min,norm}}$ threshold exist at which C_{net} transitions from net C uptake to net C loss? (iii) How do diurnal gas exchange and C_{net} dynamics progressively change with increasing $\text{TWD}_{\text{min,norm}}$?

3.2 Materials and Methods

This study synthesizes data from three previously published controlled experiments conducted on conifer seedlings, namely (i) a combined heat–drought experiment on *Pinus sylvestris* (Rehseh and Ruehr, 2022; Rehseh et al., 2022), (ii) a short- and long-duration drought experiment on *Picea abies* (Knüver et al., 2025), and (iii) a drought experiment on *Pseudotsuga menziesii* (Alongi et al., 2026).

The original publications addressed experiment-specific questions related to treatment effects on gas exchange, hydraulic damage, and recovery dynamics. In the present synthesis, we reanalyzed a subset of these data within a state-based framework, comparing physiological responses at similar tree hydraulic states, represented by $\text{TWD}_{\text{min,norm}}$, rather than at similar experimental times or within treatment categories. This allowed us to compare gas exchange and C_{net} across species and drought pathways that differed in timing, intensity, and environmental conditions.

3.2.1 Common experimental framework and treatment contrasts

All three experiments were conducted in the same greenhouse facility and shared a common focus on drought stress. The same Tree Flux System and high-resolution stem dendrometers were used in each experiment, ensuring consistent measurement principles and enabling direct comparison across experiments.

While drought stress was imposed in all experiments, the temporal development and intensity of drought differed (Fig. S3.5). In the drought–heat treatment of *P. sylvestris*, daytime air temperature (T_{air}) and vapor pressure deficit (VPD) were deliberately increased by additional heating, resulting in substantially elevated atmospheric demand compared to the control (Fig. S3.6). In contrast, VPD was not actively manipulated in the drought treatments of *P. abies* and *P. menziesii*. For these species, moderate increases in daytime VPD during drought emerged as an indirect consequence of reduced transpiration and thus reduced air humidity inside the chambers.

An overview of experimental designs, treatments, and time periods included in this synthesis is provided in Table 3.1 and the experiment-specific descriptions below. More detailed information

on the individual experimental setups can be found in the respective original publications.

Table 3.1: Overview of the three drought experiments synthesized in this study. The table shows the time periods included in the present analysis, which were aligned with the respective stress phases but excluded recovery periods. Treatment abbreviations are defined in the treatment row and used in subsequent rows. T_{air} and VPD values correspond to daytime means of air temperature and vapor pressure deficit, respectively.

Species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Pseudotsuga menziesii</i>
Tree age	3 years	3 years	3 years
Time	19 Sep to 12 Oct 2018	5 Aug to 20 Aug 2021	7 Jun to 3 Jul 2023
Treatments	Control (C ; n=6) Drought–heat (DH ; n=6)	Control (C ; n=4) Short drought (SD ; n=4) Long drought (LD ; n=4)	Control (C ; n=6) Drought (D ; severe; n=4)
Irrigation	C: Field capacity DH: Reduced*	C: Field capacity SD: None LD: None**	C: Field capacity D: None
T_{air}	C: 26–27 °C DH: 26–40 °C***	C: 25–26 °C SD: 25–26 °C LD: 25–26 °C	C: 24–25 °C D: 24–25 °C
VPD	C: 0.5–1.5 kPa DH: 1.2–5.7 kPa***	C: 1.0–1.3 kPa SD: 1.0–2.4 kPa LD: 2.1–2.5 kPa	C: 1.5–2.1 kPa D: 2.4–2.9 kPa
Reference	Rehsehuh and Ruehr, 2022; Rehsehuh et al., 2022	Knüver et al., 2025; Knüver, 2025	Alongi et al., 2026

* Reduced daily morning irrigation; amount progressively decreased.

** Irrigation stopped, with occasional watering to avoid too fast dehydration.

*** T_{air} and VPD were increased stepwise during the *Pinus sylvestris* drought–heat treatment.

Pinus sylvestris heat–drought experiment

For the heat–drought experiment on *P. sylvestris* (Rehsehuh and Ruehr, 2022; Rehsehuh et al., 2022), gas exchange measurements started in September 2018. The experiment comprised a control, a combined drought–heat treatment, and a separate heat treatment. Because this study synthesizes drought effects, data from the heat-only treatment were excluded from the analysis. Seedlings assigned to the drought–heat treatment had been pre-stressed by reduced irrigation for about 6 weeks prior to chamber measurements. During the experiment, drought stress coincided with a stepwise increase in daytime T_{air} and VPD. Drought–heat seedlings received limited daily irrigation to maintain soil water content values of about $\sim 5\%$, whereas control seedlings were kept close to field capacity.

***Picea abies* short- and long-duration drought experiment**

Gas exchange measurements in the *P. abies* experiment started in August 2021 (Knüver et al., 2025). The experiment comprised a control, a short-drought, and a long-drought treatment. Seedlings in the long-drought treatment had experienced pre-experimental water limitation for about 4 weeks, whereas short-drought trees were well-watered prior to the onset of measurements. During the experiment, irrigation was withheld in drought treatments (with occasional watering to prevent rapid dehydration), while control trees were maintained under well-watered conditions.

Sample sizes used in the present synthesis ($n=4$ per treatment) are in some cases smaller than those reported in the original study. In the short-drought treatment, one individual was excluded because the dendrometer signal was discontinuous and stepwise, indicative of a technical malfunction. In the long-drought treatment, several individuals were excluded because irrigation applied during transfer to the chamber system partially relieved drought stress and interrupted the continuous progression of drought.

***Pseudotsuga menziesii* drought experiment**

The experiment on *P. menziesii* (Alongi et al., 2026) comprised a control, a mild drought treatment, and a severe drought treatment and started in June 2023. In the present synthesis, only the control and severe drought treatment were included, as the mild drought treatment did not induce sustained stem shrinkage. In the severe drought treatment (hereafter referred to as drought), irrigation was completely stopped, while control trees were maintained at field capacity.

3.2.2 Whole-tree gas exchange calculations

Continuous measurements of gas exchange were conducted using customized chambers (Tree Flux System) supplied with air of known CO_2 and H_2O concentrations at constant flow rates. To separate above- and belowground fluxes, each tree was enclosed in two separate chamber compartments: a shoot compartment enclosing the aboveground shoot and a root compartment enclosing the potted root system in C-free substrate. Only one compartment was measured at a time, and all compartments were sampled sequentially in a fixed measurement cycle. Absolute CO_2 and H_2O mole fractions of incoming (supply) and outgoing air (sample) were quantified using infrared gas analyzers, and concentration differences were logged at 10 s resolution during each measurement interval. After chamber equilibration, stable measurements from the end of each interval were averaged to obtain one value per compartment and measurement cycle. The duration of the full measurement cycle differed between experiments, resulting in return intervals per compartment ranging from 40 to 120 minutes.

As a first step, periods of system malfunction were excluded from the raw data. Next, gas-

exchange variables were calculated at their original, experiment-specific measurement time points (Sections 3.2.2–3.2.2). To reduce the influence of isolated non-physiological outliers, a spike replacement procedure was applied separately for each tree and variable. If the absolute deviation of a value from both neighboring observations exceeded a variable- and tree-specific threshold, defined as seven times the median absolute deviation of consecutive jumps, this value was replaced by the mean of the two neighboring observations. This procedure was restricted to isolated single-point anomalies and therefore preserved the overall temporal structure of diurnal flux dynamics. Finally, processed data were aggregated to hourly-interpolated and daily-integrated values (Section 3.2.2).

Transpiration and stomatal conductance

Transpiration rate (E , $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) was calculated for each measurement interval following standard chamber gas exchange theory:

$$E = \frac{\dot{m} (W_{\text{sample}} - W_{\text{supply}})}{(1 - W_{\text{sample}}) A_{\text{leaf}}}, \quad (3.2.1)$$

where $\dot{m}$ is the molar air flow rate (mols^{-1}), W_{sample} and W_{supply} are the water vapor mole fractions (mol mol^{-1}) of outgoing and incoming air, respectively, and A_{leaf} is total leaf area enclosed in the shoot chamber (m^2). Thus, E is expressed per unit leaf area to account for crown size and facilitate comparison among individuals and species.

Stomatal conductance (g_s ; $\text{mol m}^{-2} \text{s}^{-1}$) was derived from leaf-area-normalized E according to:

$$g_s = E \cdot \frac{1 - (W_{\text{leaf}} + W_{\text{sample}}) / 2}{W_{\text{leaf}} - W_{\text{sample}}}, \quad (3.2.2)$$

where W_{leaf} is the water vapor mole fraction inside the leaf, approximated from the saturation vapor pressure at chamber air temperature (assuming leaf temperature to be close to air temperature) and measured atmospheric pressure. This formulation assumes well-mixed air within the shoot chamber and a negligible boundary-layer conductance relative to g_s . Because g_s is derived from whole-shoot chamber E , it represents an apparent shoot-level conductance normalized to leaf area. It may therefore include non-stomatal water-vapor fluxes such as cuticular water loss or potential bark water loss. Periods with relative humidity exceeding 85% were excluded from g_s calculations to avoid occasional water condensation.

Carbon fluxes

Net CO_2 fluxes were calculated independently for the shoot and root compartments using the same approach. For each compartment and measurement interval, the instantaneous C flux (F_C ; $\text{g C m}^{-2} \text{h}^{-1}$) was calculated as:

$$F_C = \left[-\frac{\dot{m}}{A_{\text{leaf}}} (C_{\text{sample}} - C_{\text{supply}}) - F_{\text{H}_2\text{O}} \cdot C_{\text{sample}} \right] \cdot M_C \cdot 3600, \quad (3.2.3)$$

where C_{sample} and C_{supply} are CO_2 mole fractions (mol mol^{-1}) of sample and supply air, $M_C = 12.01 \text{ g mol}^{-1}$ is the molar mass of C, and the factor 3600 converts seconds to hours. $F_{\text{H}_2\text{O}}$ denotes the compartment-specific water vapor flux, calculated analogously to Eq. 3.2.1; for the shoot compartment, $F_{\text{H}_2\text{O}}$ corresponds to E . The $F_{\text{H}_2\text{O}} \cdot C_{\text{sample}}$ term corrects for dilution of CO_2 by water vapor exchange. The aboveground flux represents net shoot assimilation (A_{net}), integrating photosynthetic C uptake and shoot respiratory C release. The belowground flux was interpreted primarily as root respiration (R_{root}), because no C assimilation occurs belowground and trees were grown in C-free substrate, minimizing background soil microbial respiration. By convention, positive values indicate net C uptake, and negative values indicate net C release. Thus, A_{net} can be either positive or negative, depending on whether photosynthetic uptake exceeds shoot respiratory losses, while R_{root} is always negative, as root respiration exclusively releases C. Both A_{net} and R_{root} were normalized to leaf area. While this is standard for shoot gas exchange, it is less conventional for belowground fluxes. Nevertheless, normalizing R_{root} ensures unit consistency with A_{net} , which is required for their direct summation:

$$C_{\text{net}} = A_{\text{net}} + R_{\text{root}}. \quad (3.2.4)$$

The resulting C_{net} ($\text{g C m}^{-2} \text{ h}^{-1}$) expresses tree-level net C balance per unit assimilating leaf area, thereby again reducing differences associated with canopy size. Experiment-specific time series of C_{net} , A_{net} , and R_{root} are provided in Fig. S3.7 to illustrate tree-level net C balance dynamics together with their underlying component fluxes.

For further methodological details regarding the Tree Flux System, see Birami et al. (2020) and Rehschuh et al. (2022).

Temporal integration and interpolation

Variables calculated for the original irregular measurement intervals were processed into two complementary datasets used in subsequent analyses. For subdaily analyses, the time series were harmonized to a common hourly time grid by linear interpolation between consecutive measurement time stamps, providing a consistent basis for comparing diurnal dynamics across experiments despite differing return intervals. For daily analyses, variables were integrated directly over the original irregular time stamps to preserve the native temporal structure and avoid interpolation-induced bias. These daily integrals were calculated using the trapezoidal rule:

$$X_{\text{day}} = \sum_{i=1}^{n-1} \frac{X_i + X_{i+1}}{2} \Delta t_i, \quad (3.2.5)$$

where X_i represents the respective variable (C_{net} , E , or g_s) at time step i and Δt_i is the elapsed time between consecutive measurements. To ensure full daily coverage, artificial data points were added at 00:00 and 23:59, duplicating the first and last measurements of each day. Only days with sufficient temporal coverage and without critical data gaps were retained. Daily C_{net} ($\text{g C m}^{-2} \text{ day}^{-1}$) and daily transpirational water loss ($\text{mol H}_2\text{O m}^{-2} \text{ day}^{-1}$) were obtained by integrating C_{net} and E , respectively.

Stomatal conductance was integrated over time analogously, but since integrated g_s does not represent a physical quantity of mass exchange, daily g_s sums were treated as an index, further normalized to the 95th percentile of daily g_s sums observed under well-hydrated reference conditions, operationally defined by complete nocturnal recovery of TWD. The 95th percentile was used instead of the maximum to reduce sensitivity to isolated high values. Hereafter, this quantity is referred to as the normalized daily g_s index.

3.2.3 Tree water deficit

Stem diameter variations were continuously monitored for each tree in all experiments using high-resolution point dendrometers (DD-S, Ecomatik, $1.5\mu\text{m}$ resolution) mounted at the stem base. Measurement frequencies differed slightly among experiments (10–30 min), and for the present synthesis, all time series were aggregated to hourly values.

To isolate hydraulically driven stem diameter changes from irreversible growth, TWD was derived using the zero-growth concept, which assumes that growth occurs only when stem diameter exceeds its previous maximum (Zweifel et al., 2016). For each time step t , TWD was calculated as the difference between the historical maximum stem diameter (d_{max}) and the current stem diameter (d):

$$\text{TWD}(t) = d_{\text{max}}(t) - d(t). \quad (3.2.6)$$

Hence, positive values of TWD indicate stem shrinkage relative to the last growth-induced maximum and thus a hydraulic water deficit, whereas values approaching zero indicate stem rehydration. Experimental TWD time series for all trees included in this synthesis are shown in Fig. S3.8.

Derivation of daily TWD metrics

For each tree and day, the daily minimum TWD (TWD_{min}) was defined as the lowest TWD value observed between 00:00 and 14:00, representing the best-hydrated state during the daily cycle. The corresponding daily maximum (TWD_{max}) was identified as the highest TWD value occurring after TWD_{min} and before midnight of the same day. In the *P. sylvestris* experiment, early-morning irrigation occasionally disrupted the typical diurnal shrinkage pattern, leading

to delayed TWD maxima the following night. To account for this effect, the search window for $\text{TWD}_{\max}$ in *P. sylvestris* was extended until 05:00 of the following day.

Maximum daily shrinkage (MDS) was calculated as the difference between the daily maximum and minimum TWD.

Normalization of tree water deficit using maximum daily shrinkage

To enable comparison of TWD across species, we normalized TWD following the conceptual approach of Peters et al. (2025). In that framework, normalized TWD is obtained by scaling TWD with a tree-specific maximum shrinkage capacity (MDS_{ref}), defined as the 99th percentile of a multi-year MDS time series. This yields the dimensionless quantity:

$$\text{TWD}_{\text{norm}} = \frac{\text{TWD}}{\text{MDS}_{\text{ref}}}. \quad (3.2.7)$$

In the present greenhouse experiments, dendrometer records covered only short drought periods, and control trees did not experience pronounced water limitation. As a consequence, estimating a stable tree-specific MDS_{ref} within each individual time series was not feasible, because the largest MDS possible (occurring at high transpiration with still sufficient stem rehydration) may not be captured for all individuals. Therefore, we derived a species-level MDS_{ref} by pooling all available trees within each species and calculating the average of the $k = 10$ largest MDS (Fig. S3.9). The choice of k represents a pragmatic compromise between capturing the upper range of observed MDS and avoiding excessive influence from a single extreme value. This approach provides a robust estimate of species-specific maximum shrinkage capacity. We assumed that inter-individual differences in MDS_{ref} were small relative to species-level differences due to identical age, greenhouse preconditioning, and experimental setup, and that drought treatments encompassed conditions sufficient to approach maximal shrinkage capacity. Species-specific values of MDS_{ref} are 0.311 mm for *P. sylvestris*, 0.306 mm for *P. abies* and 0.178 mm for *P. menziesii*.

Thus, our normalization follows the rationale of Peters et al. (2025) but adapts the estimation of MDS_{ref} from a tree-specific, multi-year quantile to a species-level, pooled estimate suitable for short-term experimental droughts.

3.2.4 Aggregation along a hydraulic stress axis

The resulting TWD_{norm} time series shown in Fig. 3.1 revealed that drought trajectories differed strongly among experiments in timing, duration, and maximum severity. Thus, experimental time did not represent comparable physiological states across datasets. We therefore used normalized daily minimum TWD ($\text{TWD}_{\text{min,norm}}$), representing the best-hydrated stem state of each day, as a common hydraulic stress axis for subsequent analyses.

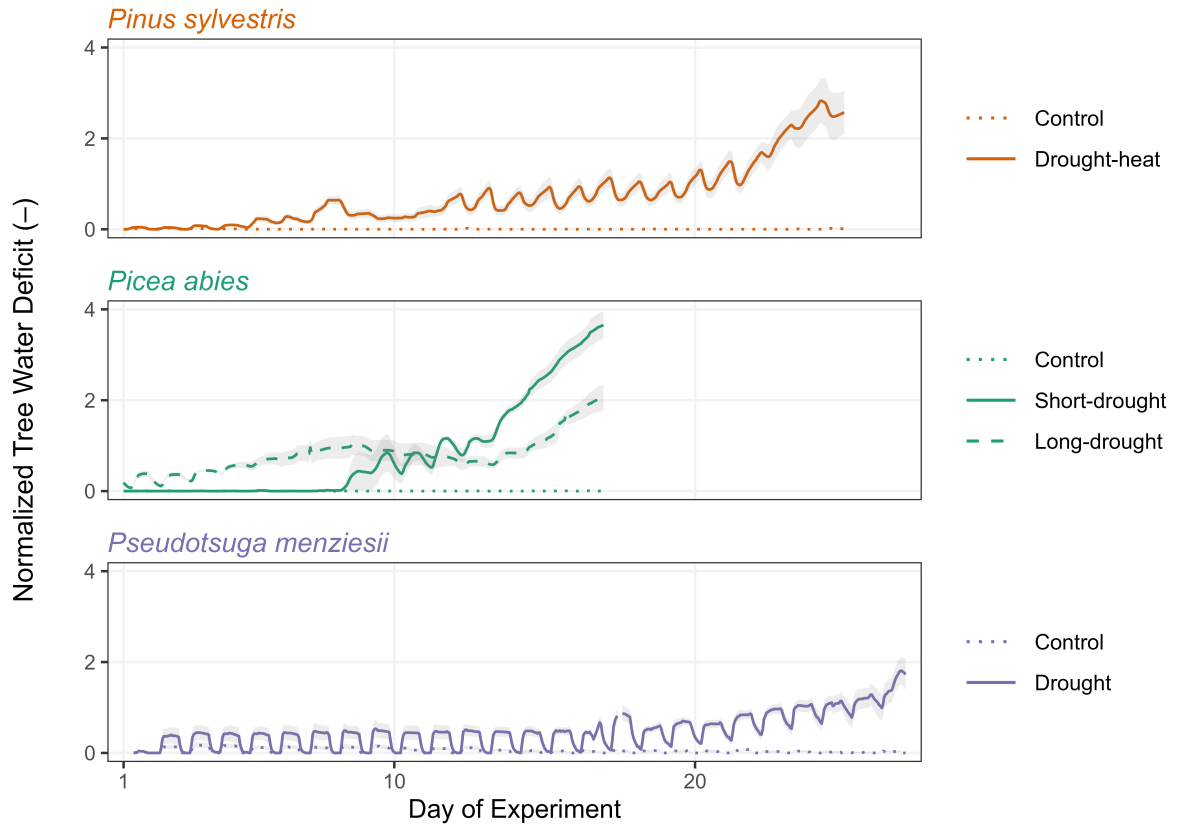


Figure 3.1: Experiment-specific dynamics of normalized tree water deficit (TWD_{norm}). Lines show treatment means, and shaded bands indicate standard errors. The x-axis shows the day of experiment (DoE), with DoE = 1 denoting the first day included in the present synthesis for each experiment.

Table 3.2: Intervals of normalized daily minimum tree water deficit ($\text{TWD}_{\text{min,norm}}$) used for analyses in Figs. 3.2–3.4.

Interval				
1			$\text{TWD}_{\text{min,norm}} =$	0
2	0	<	$\text{TWD}_{\text{min,norm}} \leq$	0.1
3	0.1	<	$\text{TWD}_{\text{min,norm}} \leq$	0.25
4	0.25	<	$\text{TWD}_{\text{min,norm}} \leq$	0.5
5	0.5	<	$\text{TWD}_{\text{min,norm}} \leq$	1
6	1	<	$\text{TWD}_{\text{min,norm}} \leq$	2
7			$\text{TWD}_{\text{min,norm}} >$	2

To analyze the relationship between C_{net} , g_s , and E and hydraulic stress, we assigned both hourly and daily data to one of seven intervals along the $\text{TWD}_{\text{min,norm}}$ axis, as defined in Table 3.2. The intervals are defined with increasing width to capture non-linear changes along the axis and account for data availability. Sample sizes for each interval are listed in Table S3.4.

Within each interval, variables of interest were averaged either at the species level or across species, depending on the analysis. For diurnal analyses, intervals 4–5 and 6–7 were combined to limit the number of panels and avoid redundant information.

3.2.5 Water potential (ψ) measurements and TWD – ψ relationships

Midday leaf water potentials (ψ) were measured periodically in all experiments. For *P. sylvestris* and *P. menziesii*, a Scholander-type pressure chamber was used. In the *P. menziesii* experiment, ψ was measured on pilot trees exposed to the same treatment conditions rather than on chamber trees. In the *P. abies* experiment, ψ was measured using a PsyPro system.

For each measurement day, ψ treatment means were matched with the corresponding treatment-level $\text{TWD}_{\text{min,norm}}$ means. Species-specific linear ψ – $\text{TWD}_{\text{min,norm}}$ relationships were then estimated using ordinary least squares regression (Fig. S3.10). Because ψ cannot be uniquely resolved at $\text{TWD}_{\text{min,norm}} = 0$, only the lowest ψ value at $\text{TWD}_{\text{min,norm}} = 0$ was included in the regression for each species.

3.2.6 Statistical analysis: response curves and uncertainty estimation

Individual trees were treated as biological replicates. Repeated gas-exchange and dendrometer measurements within each tree were treated as repeated observations. To avoid pseudo-replication, data were averaged hierarchically within each $\text{TWD}_{\text{min,norm}}$ interval. First, daily observations were averaged within individual trees, yielding one value per tree and interval. These tree-level interval means were then averaged across trees of the same species to obtain species-level interval means and associated standard errors (SE). In addition, for C_{net} a global mean was calculated per interval by averaging species-level means, thereby assigning equal weight to each species.

Response curves were fitted to the species-level or across-species interval means using an exponential decay model of the form

$$y = a \exp(-bx) + c, \quad (3.2.8)$$

where x denotes $\text{TWD}_{\text{min,norm}}$ and y the respective daily response variable. Model parameters were estimated by non-linear least squares, with non-negative constraints imposed on parameters a and b . For C_{net} , a transition threshold was defined as the $\text{TWD}_{\text{min,norm}}$ value at which the fitted response curve crossed $C_{\text{net}} = 0$.

Uncertainty in fitted response curves and thresholds was quantified using a cluster bootstrap

approach (Efron and Tibshirani, 1994). For each bootstrap replicate, individual trees were resampled with replacement within each species, using the same number of trees as in the original dataset. $\text{TWD}_{\min, \text{norm}}$ interval means were then recomputed, and response curves were refitted. Bootstrap distributions from 5000 replicates were used to derive pointwise 95% confidence intervals (CI) for fitted curves across the stress gradient and percentile-based CIs for thresholds, defined by the 2.5th and 97.5th percentiles.

The species-specific $\text{TWD}-\psi$ relationships were then used to translate $\text{TWD}_{\min, \text{norm}}$ -based C_{net} transition thresholds into corresponding ψ estimates. Here, uncertainty propagation was implemented by Monte Carlo sampling of both $\text{TWD}_{\min, \text{norm}}$ threshold uncertainty and regression parameter uncertainty. $\text{TWD}_{\min, \text{norm}}$ thresholds were sampled from normal distributions parameterized by their bootstrap medians and 95% CIs, while regression parameters were sampled from multivariate normal distributions based on their estimated covariance matrices. This yielded simulated distributions of ψ thresholds, from which 95% CIs were derived.

All data processing, statistical analyses, and graphical visualizations were conducted in R version 4.4.0 (R Core Team, 2022).

3.3 Results

3.3.1 Net carbon balance responses along the $\text{TWD}_{\min, \text{norm}}$ axis

Across species and treatments, daily C_{net} decreased with increasing $\text{TWD}_{\min, \text{norm}}$ and followed an exponential decline as described by the fitted global response curve (Fig. 3.2). The curve crossed zero at $\text{TWD}_{\min, \text{norm}} = 0.20$ [0.13–0.31], defining the transition threshold between positive and negative daily C_{net} .

Species-specific response curves yielded similar $\text{TWD}_{\min, \text{norm}}$ values for the C_{net} transition threshold with overlapping confidence intervals (Table 3.3; Fig. S3.11). This supported the use of a global response curve across species and drought pathways. However, these transition thresholds ranged from 0.13 in *P. menziesii* to 0.24 in *P. abies* and response patterns were not completely identical, indicating that the global relationship should be interpreted as a common response pattern, rather than a fully species-independent relationship.

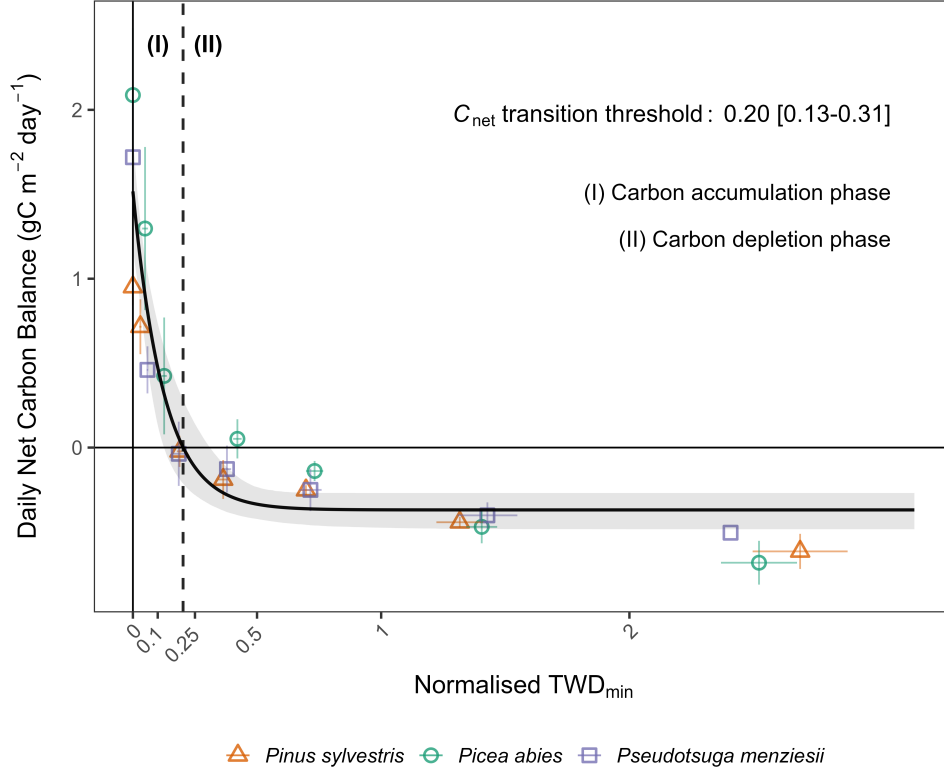


Figure 3.2: Global relationship between daily tree-level net carbon balance (C_{net} ; leaf-area normalized) and normalized daily minimum tree water deficit ($\text{TWD}_{\text{min,norm}}$) across species and treatments. Points represent species-level means, and error bars indicate $\pm\text{SE}$ per $\text{TWD}_{\text{min,norm}}$ interval (see Table 3.2). Positive values indicate net C uptake, whereas negative values indicate net C release. The solid line shows the fitted exponential response across species, and the shaded band indicates the corresponding 95% bootstrap confidence interval. The vertical dashed line marks the estimated C_{net} transition threshold, defined as the $\text{TWD}_{\text{min,norm}}$ value at which fitted C_{net} crossed zero.

Table 3.3: Transition thresholds between positive and negative daily tree-level net C balance. Values are given as normalized daily minimum tree water deficit ($\text{TWD}_{\text{min,norm}}$) medians with 95% confidence intervals and the corresponding midday water potentials (ψ) derived from species-specific $\text{TWD}-\psi$ relationships (Fig. S3.10).

Species	$\text{TWD}_{\text{min,norm}}$ (-)	ψ (MPa)
<i>Pinus sylvestris</i>	0.21 [0.11 – 0.34]	-0.91 [-0.77 – -1.03]
<i>Picea abies</i>	0.24 [0.13 – 0.56]	-1.44 [-1.03 – -1.80]
<i>Pseudotsuga menziesii</i>	0.13 [0.09 – 0.19]	-2.24 [-2.11 – -2.37]
Global	0.20 [0.13 – 0.31]	—

C_{net} was calculated as $A_{\text{net}} + R_{\text{root}}$, and the relationships of these component fluxes to $\text{TWD}_{\text{min,norm}}$ are shown separately in Fig. S3.12. Similarly, A_{net} declined strongly with increasing $\text{TWD}_{\text{min,norm}}$ but remained close to zero at high $\text{TWD}_{\text{min,norm}}$, rather than reaching the clearly negative values observed for C_{net} . The near-zero threshold of A_{net} occurred at a substantially higher $\text{TWD}_{\text{min,norm}}$ than the C_{net} transition threshold, namely at $\text{TWD}_{\text{min,norm}} = 0.66$ [0.40–1.14]. R_{root} rates were highest (most negative) at low $\text{TWD}_{\text{min,norm}}$ and decreased strongly with increasing hydraulic stress, but remained a persistent respiratory C loss across the gradient. Thus, once A_{net} approached low values, remaining root respiratory C losses substantially contributed to the transition of C_{net} below zero.

When $\text{TWD}_{\text{min,norm}}$ -based C_{net} transition thresholds were translated into ψ -equivalents using species-specific $\text{TWD}_{\text{min,norm}}-\psi$ relationships (Fig. S3.10), the corresponding ψ values differed more strongly among species than the $\text{TWD}_{\text{min,norm}}$ thresholds. ψ -equivalent transition values ranged from -0.91 MPa in *P. sylvestris* to -2.24 MPa in *P. menziesii*, with non-overlapping confidence intervals among species (Table 3.3). In other words, while $\text{TWD}_{\text{min,norm}}$ indicated a relatively consistent transition in daily C_{net} across species, this transition did not correspond to a common ψ value.

3.3.2 Stomatal conductance and transpiration responses along the $\text{TWD}_{\text{min,norm}}$ axis

The normalized daily g_s index and daily transpirational water loss both showed steep nonlinear declines with increasing $\text{TWD}_{\text{min,norm}}$ (Fig. 3.3). However, in contrast to the global relationship observed for C_{net} , responses of g_s and E differed more strongly among species, and no common response curve was apparent. At high $\text{TWD}_{\text{min,norm}}$, both variables remained at residual values above zero. While *P. abies* and *P. menziesii* showed comparable patterns and lower residual values, *P. sylvestris* exhibited a slightly higher normalized daily g_s index and substantially higher residual transpiration at high $\text{TWD}_{\text{min,norm}}$, consistent with the distinct drought–heat context of this experiment.

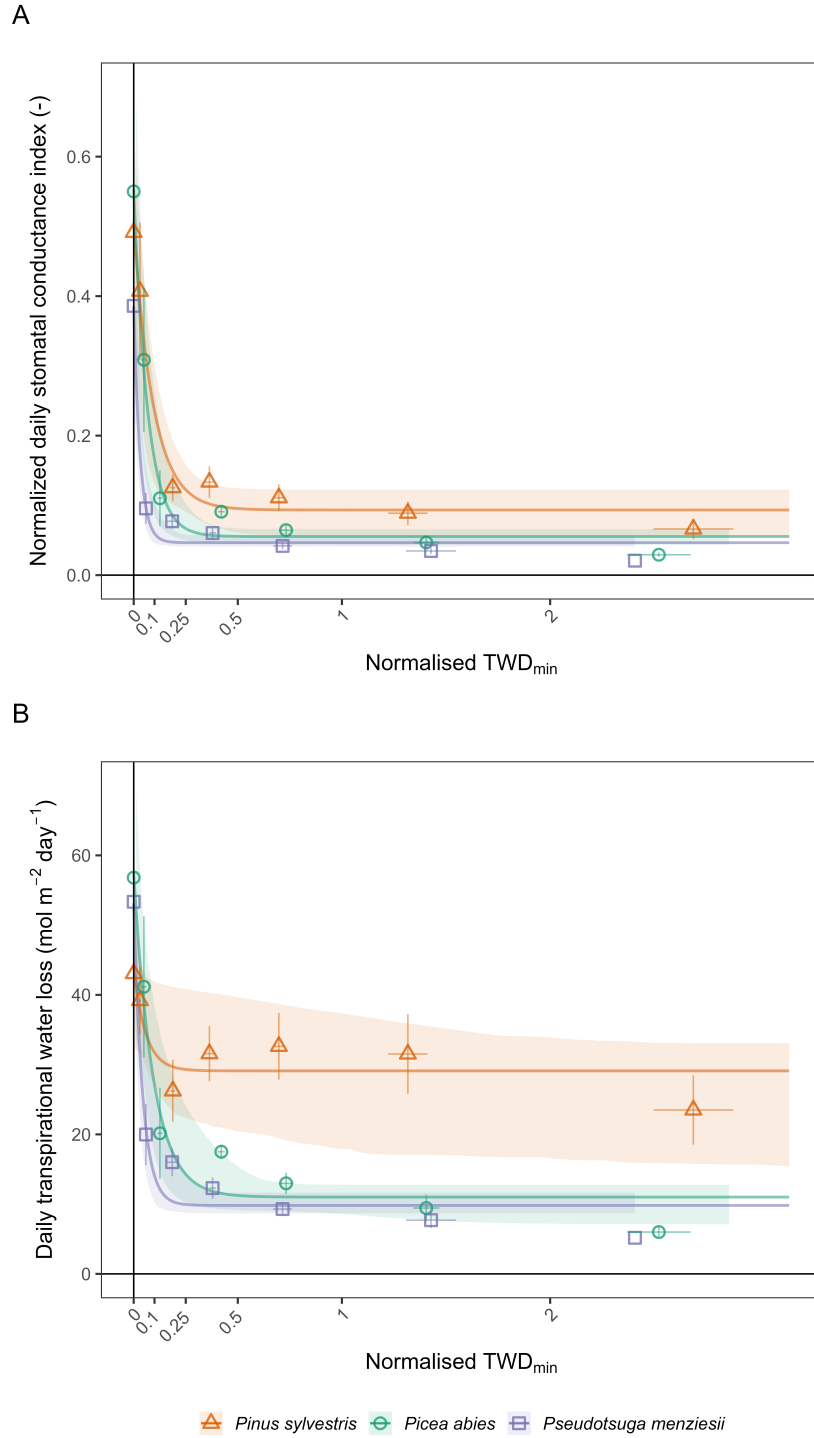


Figure 3.3: Species-specific relationships of (A) the normalized daily stomatal conductance index and (B) daily transpirational water loss with normalized daily minimum tree water deficit ($TWD_{min, norm}$) across treatments. Points represent species-level means, and error bars indicate $\pm SE$ per $TWD_{min, norm}$ interval (see Table 3.2). Lines show species-specific response curves, and shaded bands indicate their 95% bootstrap confidence intervals.

3.3.3 Diurnal dynamics along the $TWD_{min,norm}$ axis

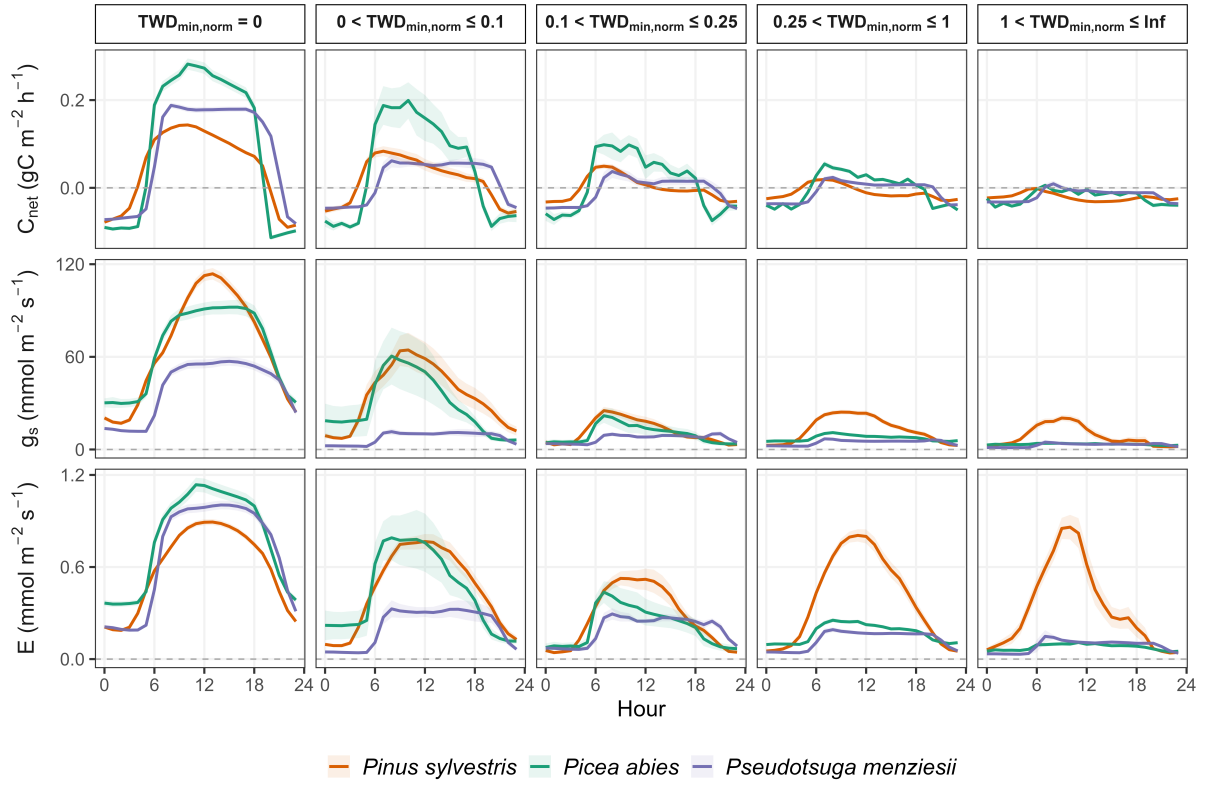


Figure 3.4: Diurnal cycles of (top) net carbon balance (C_{net}), (middle) stomatal conductance (g_s), and (bottom) transpiration (E) across intervals of normalized daily minimum tree water deficit ($TWD_{min,norm}$), representing increasing hydraulic drought stress from left to right. The $TWD_{min,norm}$ intervals correspond to those used in Figs. 3.2-3.3, with intervals 4–5 and 6–7 combined for visualization (see Table 3.2). Lines show species-specific hourly means, and shaded bands indicate $\pm SE$. Dashed horizontal lines indicate zero net carbon balance. Corresponding diurnal cycles of A_{net} , R_{root} , temperature, and VPD are shown in Fig. S3.13; interval statistics are given in Table S3.4

We compared diurnal dynamics of C_{net} , g_s , and E along the same $TWD_{min,norm}$ interval scheme used for the daily response curves above, with intervals 4–5 and 6–7 combined for visualization (Fig. 3.4). Thus, the diurnal cycles represent the subdaily patterns that, after daily integration, underlie the interval means shown in Figs. 3.2 and 3.3. All variables changed progressively along this stress gradient. At low $TWD_{min,norm}$, C_{net} showed a pronounced diurnal pattern and remained positive during most of the daylight period. With increasing $TWD_{min,norm}$, both the magnitude and duration of positive C_{net} declined, until values remained close to or below zero throughout the day at the highest $TWD_{min,norm}$ intervals. The corresponding component fluxes depicted in Fig. S3.13 showed that this pattern was mainly associated with a progressive

reduction in daytime A_{net} , while R_{root} respiration rates also decreased (became less negative), but indicated consistent daily C losses even in the highest $\text{TWD}_{\text{min,norm}}$ interval.

Stomatal conductance declined strongly with increasing $\text{TWD}_{\text{min,norm}}$, with particularly low g_s in *P. menziesii* already at intermediate stress levels. In contrast, *P. sylvestris* maintained slightly higher g_s and substantially higher residual E at high $\text{TWD}_{\text{min,norm}}$ compared with the other two species. This divergence coincided with the stepwise increase in temperature in the *P. sylvestris* drought–heat treatment, which also increased daytime VPD (Fig. S3.13). Hence, with stress progression, gas exchange activity shifted earlier in the day and decreased later in the afternoon.

3.4 Discussion

This synthesis across three experiments suggests that $\text{TWD}_{\text{min,norm}}$ can serve as a common hydraulic stress axis for comparing functional drought responses across species and experimental drought pathways. Along this axis, daily tree-level net C balance showed a consistent nonlinear decline and transitioned from net C uptake to net C loss within a similar $\text{TWD}_{\text{min,norm}}$ range across the three coniferous species. This consistency indicates that normalized TWD may be particularly useful for assessing drought effects on tree-level C balance.

3.4.1 Normalized TWD as a common hydraulic stress axis

Drought progression was expressed in terms of $\text{TWD}_{\text{min,norm}}$, a useful proxy for hydraulic stress as it reflects stem water storage depletion and is associated with declining ψ and tissue dehydration (Zweifel et al., 2016; Dietrich et al., 2018; Ziegler et al., 2024). Our approach aligned experiment-specific physiological drought responses along a common hydraulic stress axis. This alignment was particularly clear for C_{net} , for which common response patterns emerged across species and drought pathways (Fig. 3.2). To understand why C_{net} followed the $\text{TWD}_{\text{min,norm}}$ stress axis relatively consistently, it is necessary to consider how increasing hydraulic stress regulates both C uptake and respiratory C release.

The decline in C_{net} is mechanistically plausible because increasing hydraulic stress constrained gas exchange across all species. The normalized daily g_s index declined strongly with $\text{TWD}_{\text{min,norm}}$ (Fig. 3.3A), indicating progressive stomatal limitation of CO_2 uptake (Flexas, 2002; Buckley, 2019). At the same time, root respiratory C losses became smaller with increasing $\text{TWD}_{\text{min,norm}}$ (Fig. S3.12), consistent with previous chamber-based gas exchange observations in conifer seedlings under progressive drought (Gattmann et al., 2021). However, this reduction in respiratory C release was not sufficient to offset the decline in A_{net} , resulting in an overall decline in C_{net} along the hydraulic stress axis.

Canopy water loss was less consistently described by $\text{TWD}_{\text{min,norm}}$ than C_{net} . In particular,

P. sylvestris maintained higher residual daily transpirational water loss at high $TWD_{\min, \text{norm}}$ than the other species (Fig. 3.3B), coinciding with elevated temperature and VPD (Fig. S3.6) and additionally stimulated by small morning irrigation pulses (Fig. S3.5) in the drought–heat treatment. This divergence indicates that $TWD_{\min, \text{norm}}$ itself does not fully capture water loss dynamics, because transpiration is not only a function of conductance, but also of the leaf-to-atmosphere water vapor gradient. In addition, it seems that the short-term increases in soil water availability fueled transpiration rather than rehydrating internal tissue water deficits.

Despite the substantially higher water loss at high $TWD_{\min, \text{norm}}$ in *P. sylvestris*, its residual normalized daily g_s index remained only slightly elevated compared to the other two species. This elevated g_s signal could reflect temperature-dependent impacts on minimum conductance after stomatal closure, including cuticular and stomatal contributions (Duursma et al., 2019; Garen and Michaletz, 2025), or changes in water vapor viscosity. However, higher residual g_s and water loss in *P. sylvestris* did not translate into higher A_{net} . This suggests that the similar C_{net} responses across species were not determined by stomatal regulation alone, but may also have involved non-stomatal constraints on assimilation, such as reductions in mesophyll conductance and biochemical limitations of the photosynthetic machinery (Flexas, 2002; Flexas et al., 2012; Dewar et al., 2018; Buckley, 2019). Together, these patterns suggest that $TWD_{\min, \text{norm}}$ captured variation in C_{net} more consistently than variation in water loss, which remained influenced by VPD and short-term water availability.

3.4.2 The C_{net} transition threshold and its physiological interpretation

The transition from positive to negative daily C_{net} occurred within a relatively narrow range of $TWD_{\min, \text{norm}}$ across the three species included in this synthesis. When translated into ψ , however, the corresponding ψ -equivalents differed substantially among species (Table 3.3). While ψ -based thresholds depend strongly on hydraulic traits and tissue properties (Martinez-Vilalta et al., 2019; Trueba et al., 2019), this contrast suggests that normalized TWD may help to bridge such species-specific differences.

Importantly, the C_{net} transition occurred at lower $TWD_{\min, \text{norm}}$ than the near-zero threshold of A_{net} . Thus, in order to use TWD as an indicator for the tree C balance, the transition cannot be inferred from shoot assimilation alone. Although root respiratory C losses decreased with increasing hydraulic stress, they remained apparent and therefore contributed to shifting the tree-level C balance below zero. This highlights the value of the Tree Flux System, a custom gas exchange chamber system, which enabled a comprehensive whole-tree perspective on above- and belowground C flux dynamics by combining A_{net} and R_{root} , thereby going beyond typical leaf-level A_{net} measurements.

Interpreting the C_{net} transition threshold physiologically suggests that drought progression involves two distinct phases. In the first *carbon accumulation phase*, incomplete overnight stem

rehydration is reflected by $TWD_{\min, \text{norm}} > 0$, suggesting constrained radial growth according to the zero-growth concept (Zweifel et al., 2016), while C_{net} still remains positive. Thus, C uptake persists while major sinks are reduced, consistent with photosynthesis-growth decoupling (Krejza et al., 2022; Rao et al., 2026), which may lead to an accumulation of non-structural carbohydrates (NSC) (Galvez et al., 2011; Tardieu et al., 2011; Muller et al., 2011). Although the exact timing of growth limitation is difficult to determine (Tardieu et al., 2011; Blackman et al., 2019), the turgor-dependence of cell expansion and division provides a mechanistic basis for drought-induced growth constraints (Lockhart, 1965; Peters et al., 2021; Potkay and Feng, 2023).

Consistent with this interpretation, increasing NSC concentrations during early drought were observed in the *P. menziesii* experiment (Alongi et al., 2026), although comparable measurements were not available for the other experiments analyzed here. Such accumulation may indicate a transient C reserve that could buffer later periods of negative C_{net} and support post-drought recovery, consistent with optimal-storage theory (Stefaniak et al., 2024) and with evidence that depleted stem NSC can impair hydraulic recovery (Tomasella et al., 2021). However, NSC responses to drought are context-dependent and vary among organs, species, drought duration, and drought intensity (Wang and Wang, 2025). Whether NSC accumulation during the early onset of drought primarily reflects a passive consequence of reduced sink demand (Körner, 2003; Potkay et al., 2022) or an actively regulated storage strategy (Wiley and Helliker, 2012; Stefaniak et al., 2024) therefore remains debated.

During the following more critical *carbon depletion phase*, declining A_{net} no longer compensates for remaining respiratory C losses, so that C_{net} becomes negative, indicating severe metabolic constraints. This reliance on NSC reserves to sustain metabolism has been evidenced in the *P. menziesii* experiment, where NSC concentrations declined during continued drought while TWD accumulated (Alongi et al., 2026). At the same time, continued residual transpiration contributes to the depletion of internal water storage (Duursma et al., 2019), potentially resulting in the accumulation of hydraulic and cellular damage (Mantova et al., 2022). Repair and recovery processes then increase C demand, while depleted NSC reserves may limit the capacity of trees to restore physiological function (Ruehr et al., 2019). Combined, these interacting processes can induce long-term drought legacy effects and increase mortality risk (Adams et al., 2017; McDowell et al., 2022), indicating that the $TWD_{\min, \text{norm}}$ -based *carbon depletion phase* provides a useful metric of drought severity and potential constraints on post-drought resilience.

3.4.3 Progressive diurnal changes with increasing $TWD_{\min, \text{norm}}$

The diurnal cycles shown in Fig. 3.4 resolve the daily integrated responses along the $TWD_{\min, \text{norm}}$ axis into their underlying within-day dynamics. A negative daily C_{net} value does not imply that daytime C uptake was absent. Rather, it indicates that periods of positive C_{net} were too short

or too weak to compensate for respiratory C losses over the full 24-h cycle. With increasing $TWD_{\min, \text{norm}}$, the daily C balance shifted through a progressive reduction in both the duration and magnitude of positive C gain. However, only in the most severe stress interval was A_{net} reduced to near-zero values throughout most of the day, whereas at lower stress intervals some photosynthetic assimilation still occurred (Fig. S3.13). Thus, the C_{net} threshold in Fig. 3.2 represents a progressive transition in the integrated daily C balance, not an abrupt loss of photosynthetic activity.

The diurnal g_s patterns extend the findings of Ziegler et al. (2024), who identified pre-dawn $TWD > 0$ as an indicator of drought stress associated with strongly reduced midday g_s . The continuous measurements presented here show that this midday decline is part of a broader shift in the timing and duration of daily gas exchange. With increasing $TWD_{\min, \text{norm}}$, periods of active gas exchange tended to become shorter and, in several cases, more restricted to earlier parts of the day, although this pattern was not equally pronounced across species. The overall reduction in g_s is consistent with increasing hydraulic limitation, whereas stronger afternoon declines likely reflect the additional influence of daytime atmospheric demand (Liu et al., 2024), particularly in the *P. sylvestris* drought–heat experiment (Fig. S3.13).

3.4.4 Limitations and future directions

The present synthesis combines data from experiments that were originally designed to address specific research questions rather than a shared cross-experiment framework. Consequently, treatment conditions differed among experiments, including temperature, VPD, and irrigation protocols, particularly in the *P. sylvestris* heat–drought treatment. At the same time, this heterogeneity provides a stringent test of the proposed stress axis: the relatively consistent C_{net} response along $TWD_{\min, \text{norm}}$ emerged despite such differences, supporting the use of $TWD_{\min, \text{norm}}$ as a practical cross-experiment stress coordinate.

Additional uncertainty arises from methodological aspects of the analysis. The normalization of TWD remains an active area of research, and it is not yet fully resolved how well normalized TWD can be compared across species, tree ages, and experimental contexts. In this study, we followed the conceptual approach of Peters et al. (2025) but adapted the estimation of the reference stem shrinkage capacity to a species-level pooled metric suitable for short experimental time series. The emergence of a consistent $TWD_{\min, \text{norm}}$ -based C_{net} transition threshold suggests that this approach captured a physiologically meaningful normalization reference. However, defining MDS_{ref} based on the 10 largest MDS values per species influences the absolute scaling of TWD_{norm} and thus the absolute value of the threshold. In addition, data coverage was uneven along the stress gradient, with fewer observations in the highest $TWD_{\min, \text{norm}}$ intervals, which likely contributed to uncertainty in the fitted response curves and threshold estimates.

Future targeted experiments should test the proposed phase framework by combining continuous

whole-tree gas exchange and TWD measurements with direct observations of growth, NSC pools, C allocation, and hydraulic damage. At the same time, normalization procedures need to be further developed, especially for mature trees and field conditions, to evaluate whether $\text{TWD}_{\text{min,norm}}$ can serve as a common hydraulic stress axis across species and measurement contexts.

The increasing availability of high-resolution dendrometer measurements and dendrometer networks, such as TreeNet (Zweifel et al., 2021a) and the Global Dendrometer Network (<https://www.globaldendro.org/>), provides new opportunities to extend this framework beyond controlled experiments. With robust normalization and calibration against independent C balance observations, TWD-derived stress states could help identify periods of likely positive or negative tree-level C balance for dendrometer-equipped trees. In process-based models with TWD-like internal water storage dynamics (Ziegler et al., 2026), the onset of incomplete overnight rehydration ($\text{TWD}_{\text{min,norm}} > 0$) and the C_{net} transition threshold identified here could define transitions between phases of active growth, constrained growth with positive C balance, and no growth with negative C balance. Coupling dendrometer measurements with flux-tower observations (Rao et al., 2026) could further support scaling from tree-level hydraulic stress dynamics to ecosystem-scale C balance responses.

3.4.5 Conclusion

This synthesis of three controlled experimental studies shows that normalized daily minimum tree water deficit ($\text{TWD}_{\text{min,norm}}$) provides a useful hydraulic stress axis for comparing tree-level net C balance (C_{net}) responses across species and experimental drought pathways. Along this axis, daily C_{net} declined consistently and crossed from net C uptake to net C loss within a relatively narrow $\text{TWD}_{\text{min,norm}}$ range, whereas water loss was less consistently described by $\text{TWD}_{\text{min,norm}}$ alone and remained sensitive to atmospheric demand and short-term water availability. Diurnal analyses showed that this transition emerged gradually, rather than through an abrupt cessation of assimilation. Integrating normalized TWD into experimental studies, forest monitoring networks, and ecosystem models may therefore improve the quantification and projection of drought-driven changes in tree-level C balance and help link tree hydraulic stress to ecosystem C dynamics.

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3.5 Supplementary Material for Chapter 3

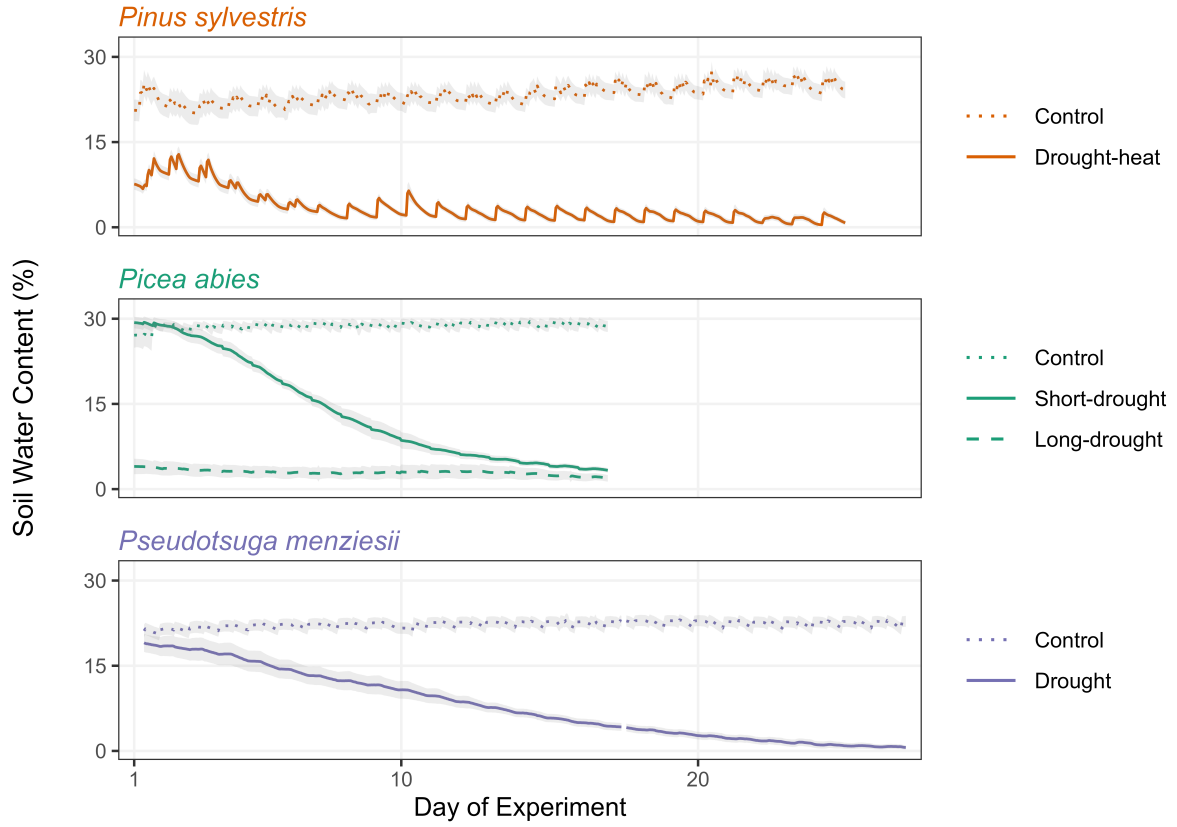


Figure S3.5: Experiment-specific time series of soil water content. Lines show hourly treatment means, and shaded bands indicate standard errors. The x-axis shows day of experiment (DoE), with DoE = 1 denoting the first day included in the present synthesis for each experiment.

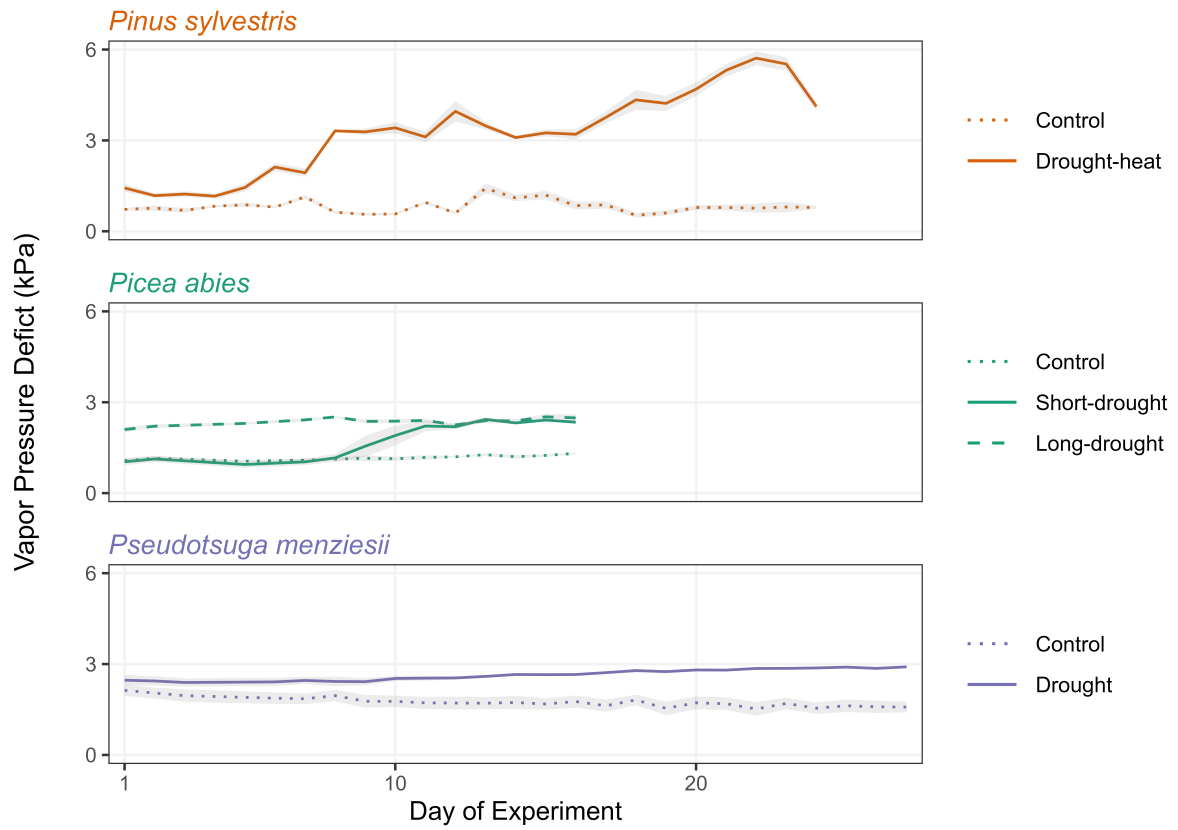


Figure S3.6: Experiment-specific time series of vapor pressure deficit. Lines show daily treatment means, and shaded bands indicate standard errors. The x-axis shows day of experiment (DoE), with DoE = 1 denoting the first day included in the present synthesis for each experiment.

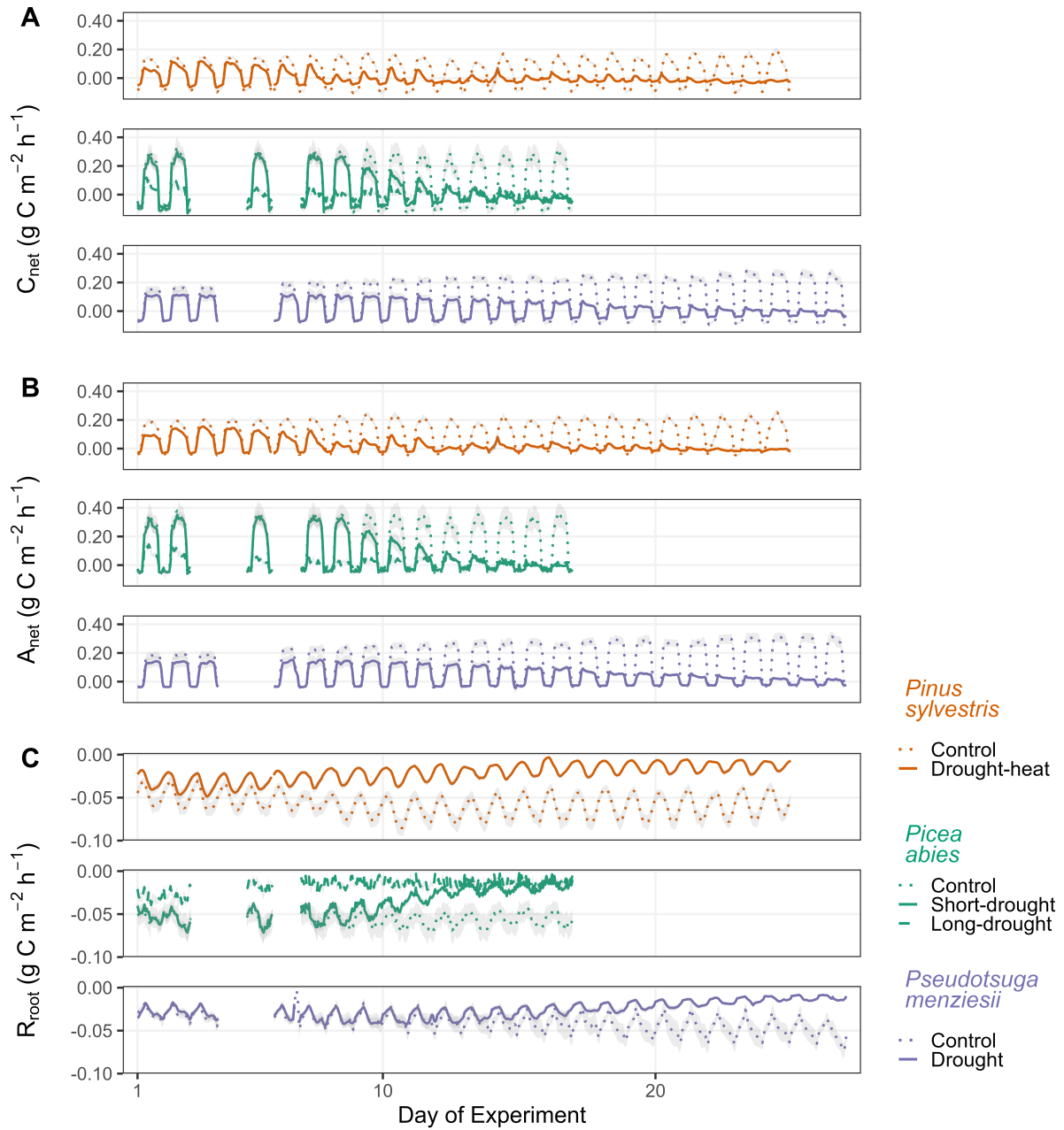


Figure S3.7: Experiment-specific time series of leaf-area-normalized C fluxes. Panels show (A) tree-level net C balance (C_{net}), (B) net shoot assimilation (A_{net}), and (C) root respiratory C loss (R_{root}). C_{net} is defined as the sum of A_{net} and R_{root} . Lines show treatment means, and shaded bands indicate $\pm$ SE. Positive values indicate net C uptake, whereas negative values indicate net C release. The x-axis shows day of experiment (DoE), with DoE = 1 denoting the first day included in the present synthesis for each experiment.

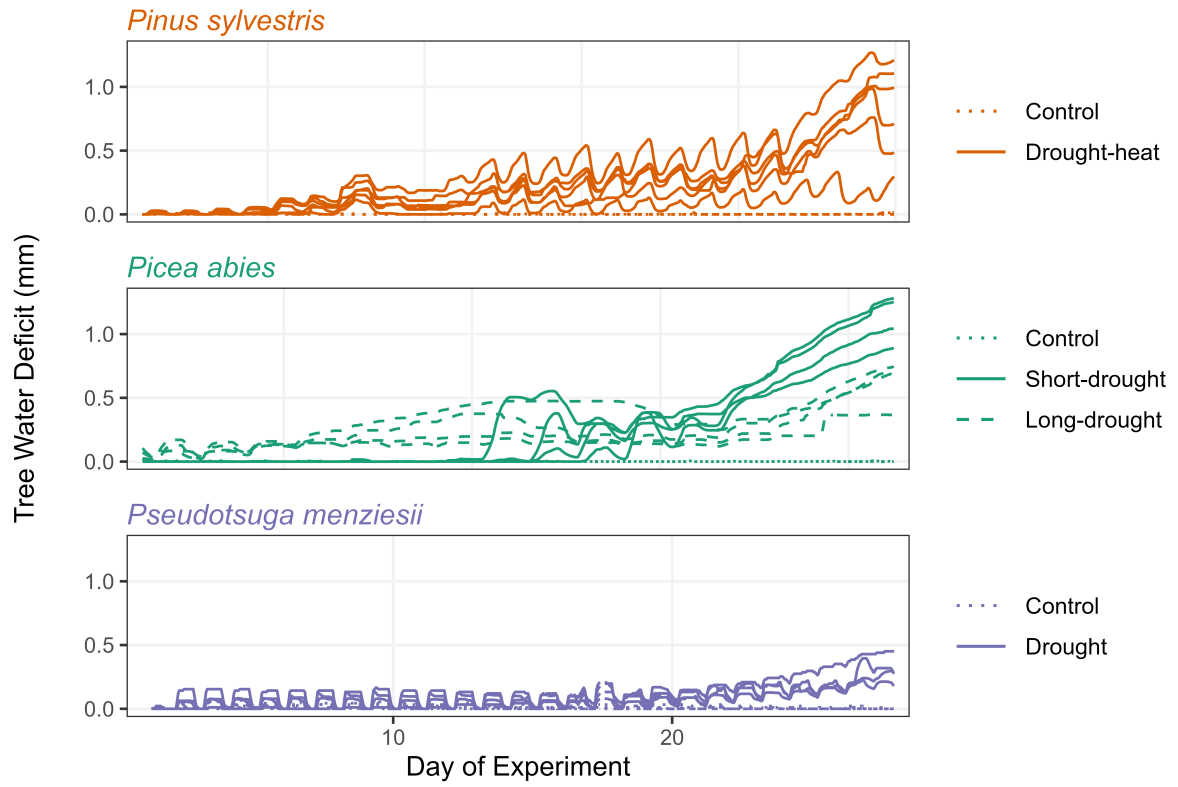


Figure S3.8: Experiment-specific individual-tree trajectories in tree water deficit. The x-axis shows day of experiment (DoE), with DoE = 1 denoting the first day included in the present synthesis for each experiment.

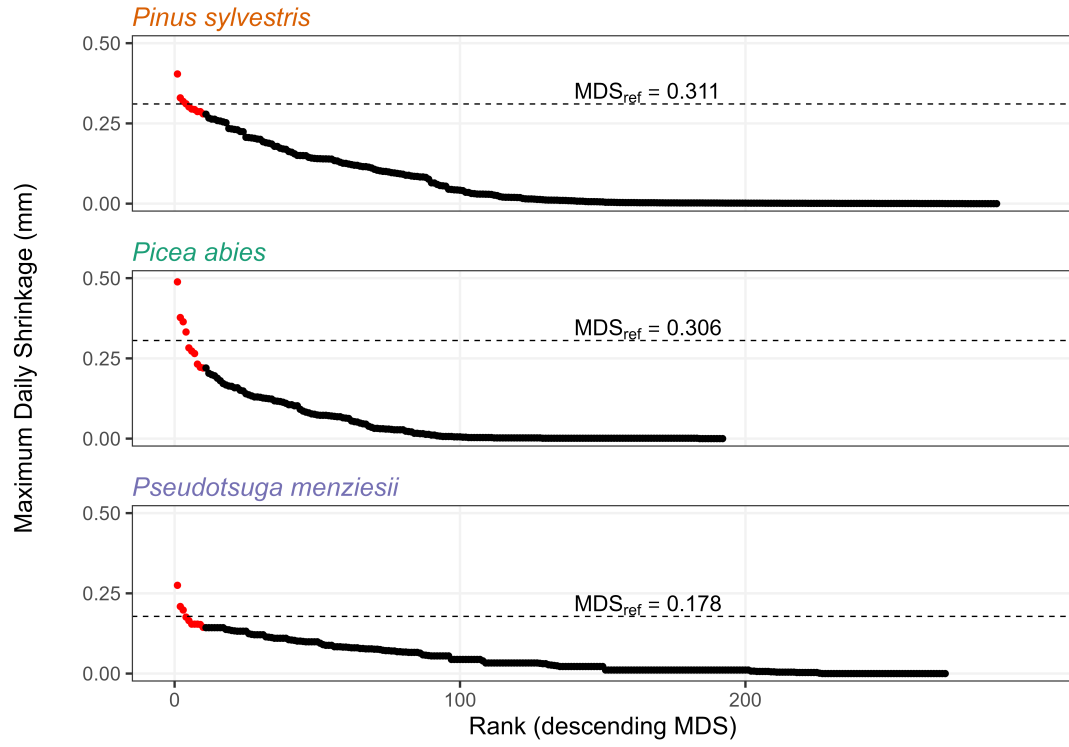


Figure S3.9: Derivation of species-specific reference maximum daily shrinkage (MDS_{ref}). For each species, MDS_{ref} (dashed line) is calculated as the mean of the 10 largest observed maximum daily shrinkage (MDS) values across all trees (red points) and is used to normalize tree water deficit.

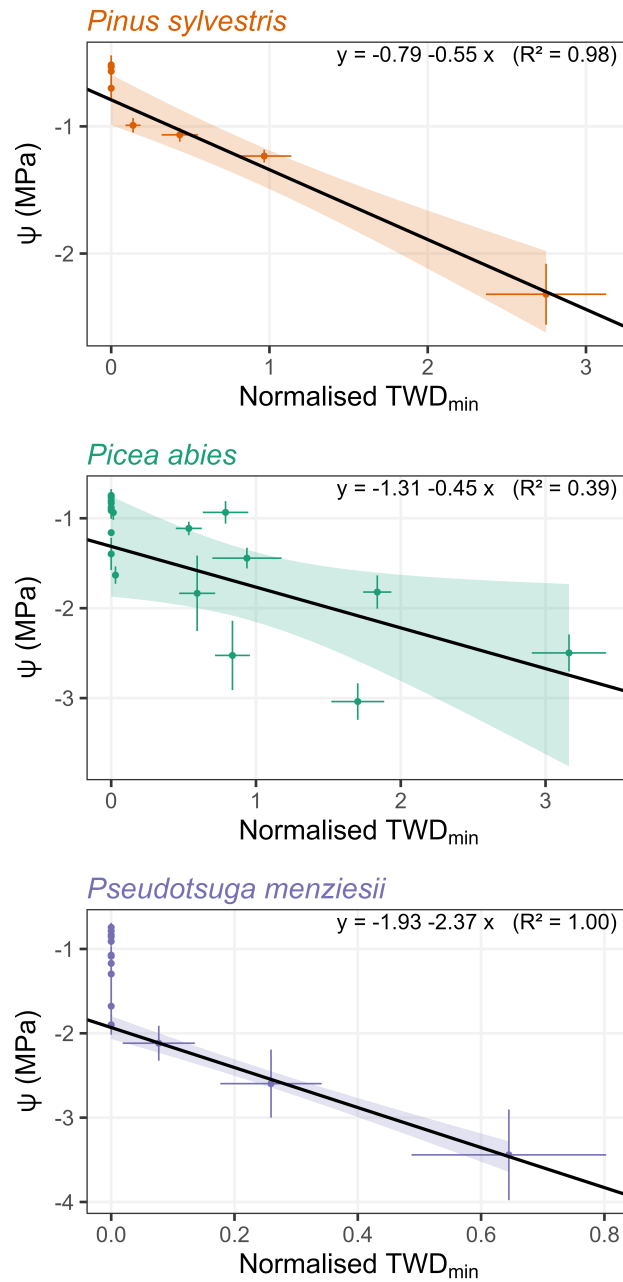


Figure S3.10: Species-specific relationships between midday leaf water potential (ψ) and normalized daily minimum tree water deficit ($TWD_{min,norm}$). Points represent treatment means with error bars indicating $\pm SE$. Solid lines show linear regressions, and shaded bands indicate 95% confidence intervals. The regression fits exclude repeated observations at $TWD_{min,norm} = 0$ except for the lowest ψ value. Regression equations and coefficients of determination (R^2) are given for each species.

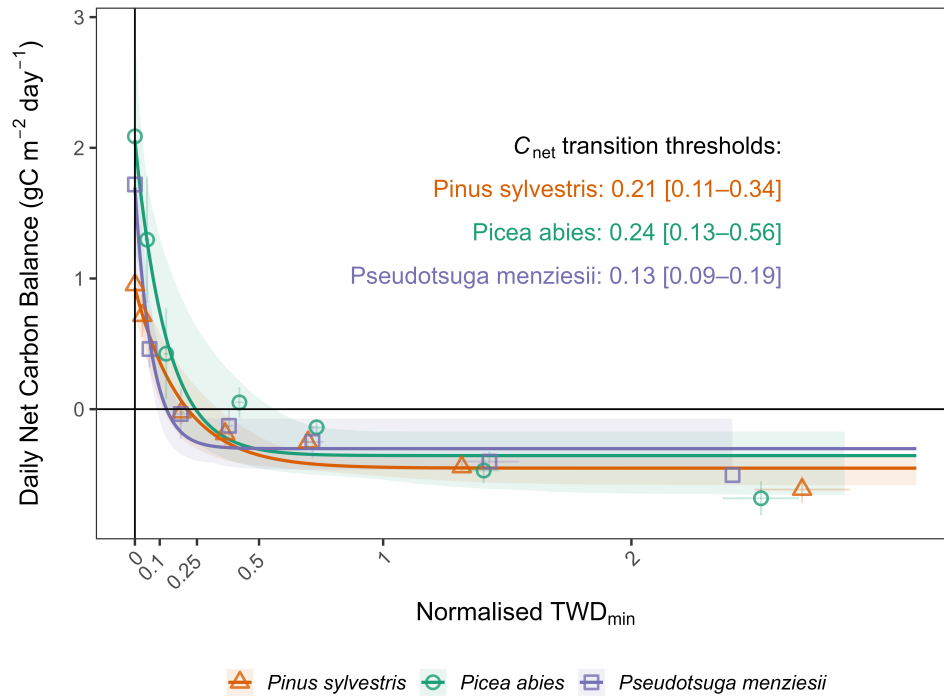


Figure S3.11: Species-specific relationships between daily net carbon balance (C_{net} ; leaf-area normalized) and normalized daily minimum tree water deficit ($\text{TWD}_{\text{min, norm}}$). Positive values indicate net C uptake, whereas negative values indicate net C release. Species-specific tipping points denote the transition from C sink to C source. Points represent species-level means, and error bars indicate $\pm \text{SE}$ per $\text{TWD}_{\text{min, norm}}$ interval (see Table 2). Solid lines show fitted species-specific responses, and shaded bands indicate 95% bootstrap confidence intervals.

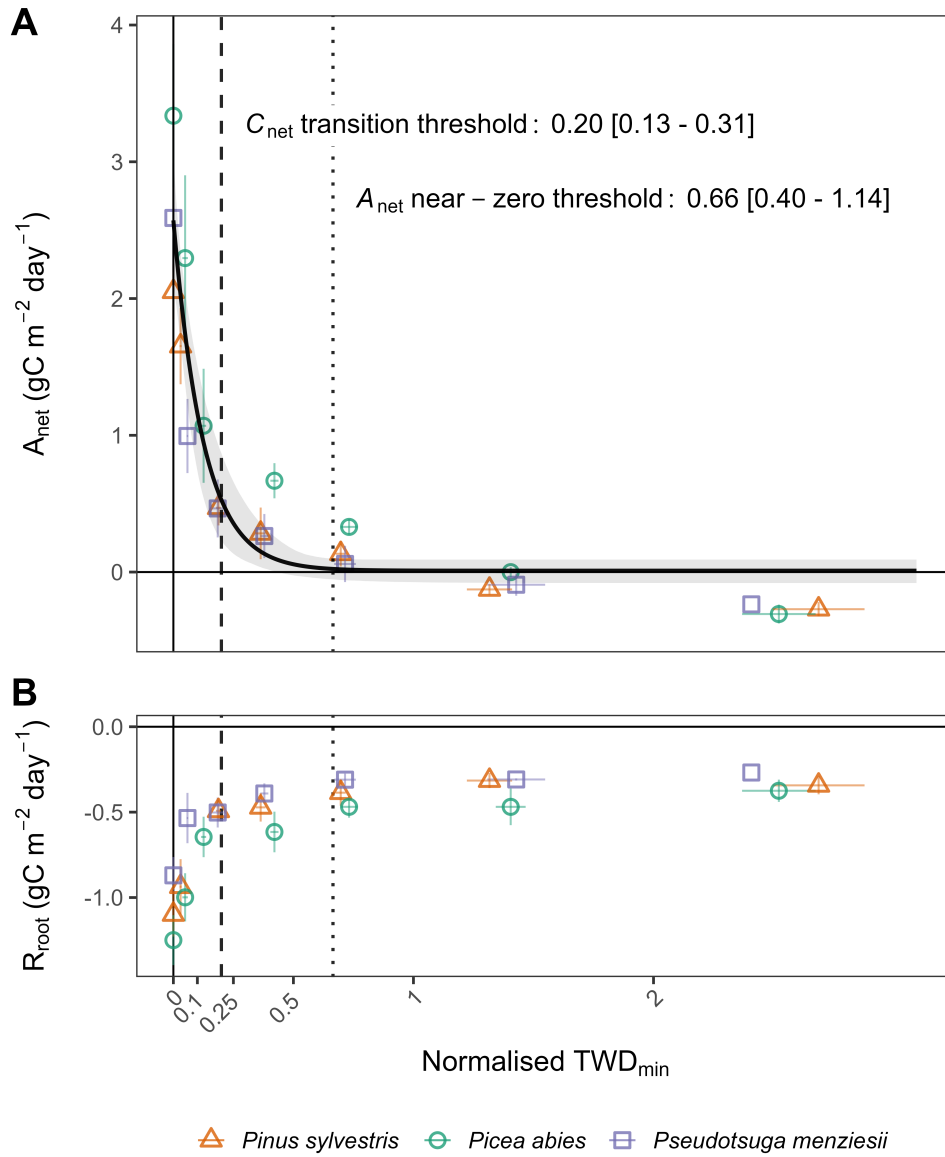


Figure S3.12: Components of tree-level net C balance along the hydraulic stress axis. Panel A shows daily net shoot assimilation (A_{net}), and Panel B shows daily root respiratory C loss (R_{root}), both plotted against normalized daily minimum tree water deficit ($TWD_{min, norm}$). Points represent species-level means, and error bars indicate $\pm SE$ per $TWD_{min, norm}$ interval. The solid curve in Panel A shows the fitted exponential response of A_{net} , with the shaded band indicating the corresponding 95% bootstrap confidence interval. The dashed vertical line indicates the C_{net} transition threshold retrieved in Fig. 2, and the dotted vertical line indicates the A_{net} near-zero threshold.

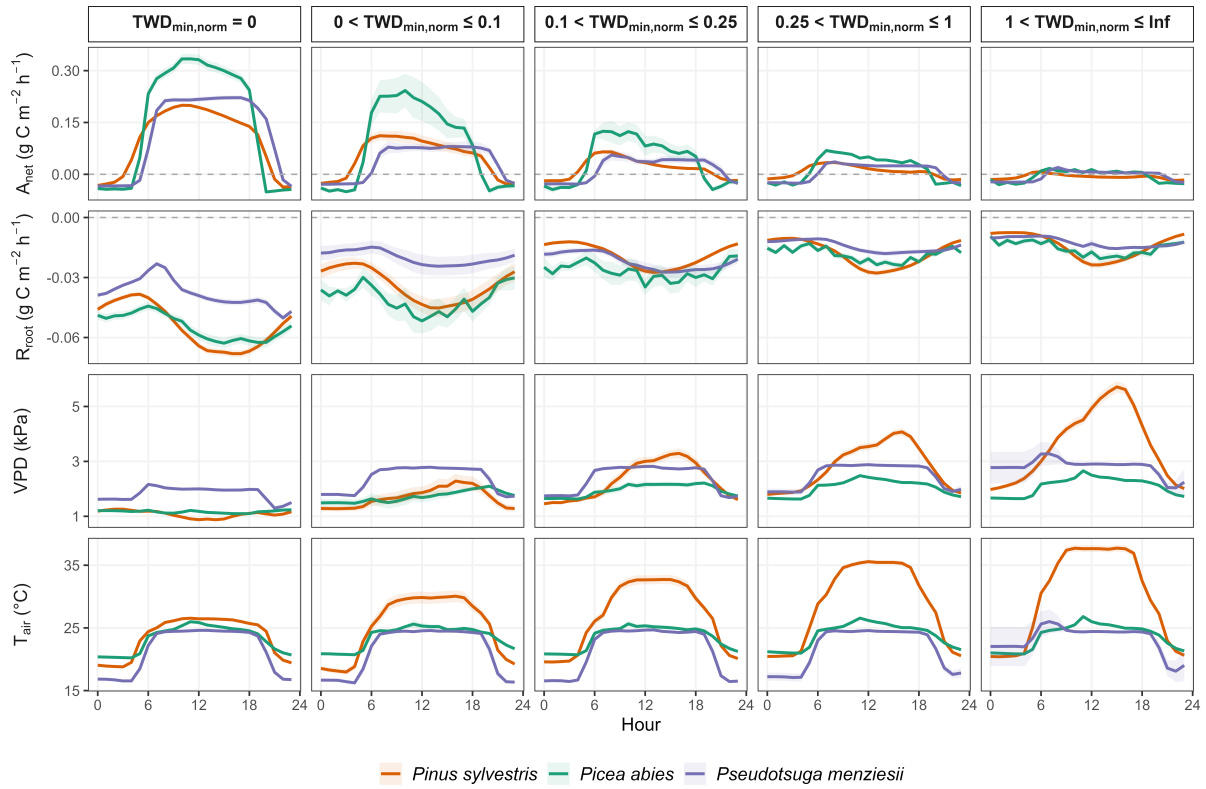


Figure S3.13: Diurnal cycles of leaf-area normalized net shoot assimilation (A_{net}) and root respiration (R_{root}), vapor pressure deficit (VPD) and temperature (T_{air}) across intervals of normalized daily minimum tree water deficit ($\text{TWD}_{\text{min,norm}}$), representing increasing hydraulic drought stress from left to right. Intervals correspond to the stress classes used throughout the analysis, with intervals 4–5 and 6–7 combined for visualization (see Table 2). Lines show species-specific hourly means, and shaded bands indicate $\pm \text{SE}$. Interval statistics are given in Table S1.

Table S3.4: Sample sizes and atmospheric conditions per species and $\text{TWD}_{\min, \text{norm}}$ interval. Reported are the number of trees contributing to each interval (n_{trees}), the number of days represented (n_{days}), and the total number of observations (n_{total}), along with mean midday vapor pressure deficit ($\text{VPD}_{\text{midday}}$) and temperature (T_{midday}). Midday values are defined as means across all observations between 10:00 and 16:00.

Species	$\text{TWD}_{\min, \text{norm}}$ interval	n_{trees}	n_{days}	n_{total}	$\text{VPD}_{\text{midday}}$ (kPa)	T_{midday} ($^{\circ}\text{C}$)
<i>Pinus sylvestris</i>	$\text{TWD}_{\min, \text{norm}} = 0$	12	24	167	0.92	26.4
	$0 < \text{TWD}_{\min, \text{norm}} \leq 0.1$	8	14	21	1.98	29.8
	$0.1 < \text{TWD}_{\min, \text{norm}} \leq 0.25$	5	12	21	3.05	32.6
	$0.25 < \text{TWD}_{\min, \text{norm}} \leq 0.5$	6	17	22	3.47	34.7
	$0.5 < \text{TWD}_{\min, \text{norm}} \leq 1$	5	14	32	3.86	35.9
	$1 < \text{TWD}_{\min, \text{norm}} \leq 2$	5	8	16	5.13	38.2
	$2 < \text{TWD}_{\min, \text{norm}} \leq \infty$	4	3	9	5.15	36.6
<i>Picea abies</i>	$\text{TWD}_{\min, \text{norm}} = 0$	9	16	99	1.14	25.4
	$0 < \text{TWD}_{\min, \text{norm}} \leq 0.1$	5	5	6	1.77	25.2
	$0.1 < \text{TWD}_{\min, \text{norm}} \leq 0.25$	5	4	7	2.16	25.2
	$0.25 < \text{TWD}_{\min, \text{norm}} \leq 0.5$	6	11	21	2.34	25.7
	$0.5 < \text{TWD}_{\min, \text{norm}} \leq 1$	8	11	27	2.35	25.8
	$1 < \text{TWD}_{\min, \text{norm}} \leq 2$	8	11	21	2.44	25.7
	$2 < \text{TWD}_{\min, \text{norm}} \leq \infty$	5	3	11	2.40	25.4
<i>Pseudotsuga menziesii</i>	$\text{TWD}_{\min, \text{norm}} = 0$	10	27	229	1.98	24.5
	$0 < \text{TWD}_{\min, \text{norm}} \leq 0.1$	3	5	6	2.76	24.5
	$0.1 < \text{TWD}_{\min, \text{norm}} \leq 0.25$	4	5	8	2.77	24.5
	$0.25 < \text{TWD}_{\min, \text{norm}} \leq 0.5$	4	7	12	2.84	24.5
	$0.5 < \text{TWD}_{\min, \text{norm}} \leq 1$	4	6	9	2.90	24.5
	$1 < \text{TWD}_{\min, \text{norm}} \leq 2$	3	4	5	2.89	24.4
	$2 < \text{TWD}_{\min, \text{norm}} \leq \infty$	1	1	1	2.93	24.4

4 TWIST: A DIAGNOSTIC FRAMEWORK FOR REPRESENTING TREE WATER DEFICIT DYNAMICS IN PROCESS-BASED FOREST MODELS

This chapter has been submitted as:

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Abstract

Dendrometer-derived tree water deficit (TWD) contains physiologically rich information and is increasingly used to monitor tree drought stress, yet process-based forest models rarely include a directly comparable representation of TWD dynamics. Existing hydraulic models can represent internal water storage in detail, but their parameter demands limit broader application. Here, we introduce the Tree Water Imbalance and Storage Tracker (TWIST), a parsimonious and physiologically interpretable framework that derives volume-based TWD dynamics. The module is driven by transpiration and relative soil water content and uses three empirical parameters to control transpiration-driven internal water depletion, deficit refilling, and additional soil-water uptake limitation. It also derives relative tree water content (RWC_{tree}) from the simulated deficit and an estimate of the available internal water pool. We tested TWIST by coupling it to the process-based ecosystem model LandscapeDNDC. Parameters were optimized for 2018 and evaluated independently for 2019–2024 against normalized dendrometer-derived TWD at a Czech beech site. Simulated TWD trajectories broadly agreed with observed daily and seasonal

dynamics, while RWC_{tree} translated them into a physiologically interpretable proxy for internal dehydration. TWIST demonstrated capability to reproduce key TWD drought-response patterns, including diurnal depletion–replenishment cycles, reduced nocturnal rehydration with declining soil moisture, and progressive deficit accumulation. By representing TWD and RWC_{tree} as diagnostic model outputs, TWIST makes dendrometer-derived drought-stress information more directly usable in forest models. It thereby provides a practical basis for linking tree-level drought-stress signals with stand-level simulations and, potentially, remotely sensed indicators of canopy water status.

4.1 Introduction

Internal tree water storage plays a crucial role in buffering imbalances between transpirational water loss and soil water uptake (Salomón et al., 2017; Preisler et al., 2022). While storage contributes substantially to daily transpiration (Čermák et al., 2007; Verbeeck et al., 2007; Betsch et al., 2011; Köcher et al., 2013; Preisler et al., 2022), it becomes particularly critical under drought, when soil water supply is limited (Klein et al., 2014; Klein et al., 2016; Preisler et al., 2019). Water released from tree tissues can prolong the duration of dehydration and delay the onset of hydraulic damage (Gleason et al., 2014). Even with fully closed stomata, residual water losses persist (Blackman et al., 2019; Duursma et al., 2019), and progressive dehydration can ultimately lead to hydraulic failure and cellular damage (Mantova et al., 2021; Mantova et al., 2022; McDowell et al., 2022). Consequently, internal water storage dynamics are fundamental for understanding the progression of drought stress and the persistence of long-term drought legacy effects (Müller and Bahn, 2022).

The relevance of such observations is amplified under ongoing climate change, which is increasing the frequency, duration, and intensity of drought events (Gazol et al., 2025; Chen et al., 2025). Such droughts already cause widespread growth limitations (Bose et al., 2025) and forest mortality across Europe (Senf et al., 2020) and worldwide (International Tree Mortality Network, 2025).

Continuous observations of tree water status are therefore increasingly important for detecting drought stress in forests (Novick et al., 2022; Restrepo-Acevedo et al., 2026). High-resolution dendrometers provide such observations by recording reversible stem shrinkage, from which tree water deficit (TWD) can be derived as an indicator of tree hydration status (Zweifel et al., 2001; Zweifel and Häsler, 2001). TWD carries physiologically rich information (De Swaef et al., 2015; Sevanto, 2025) due to its close relation to ψ (Dietrich et al., 2018; Ziegler et al., 2024) and its direct link to cell turgor pressure and growth processes (Zweifel et al., 2021b; Peters et al., 2023). Daily TWD fluctuations integrate atmospheric demand, soil water supply (Zweifel et al., 2005; Oberhuber et al., 2023), and species-specific water-use strategies (Sánchez-Costa et al.,

2015; Peters et al., 2025), whereas unrecovered TWD over consecutive days indicates sustained drought stress and may reveal thresholds related to stomatal closure, turgor loss, and hydraulic impairment (Andriantelomanana et al., 2024; Ziegler et al., 2024; Peters et al., 2025). With the growing availability of long-term data from coordinated dendrometer networks, including the Swiss TreeNet (Zweifel et al., 2021b), the Czech DendroNetwork (<https://dendronet.cz/>), and the Global Dendrometer Network (<https://globaldendro.org/>), TWD is increasingly used to monitor tree drought stress. However, this growing observational capacity is not yet matched by a comparable representation of TWD dynamics in process-based forest models.

Process-based models are essential tools for estimating the effects of drought on forests. They allow scaling physiological processes from individual trees to stands, integrate multiple stressors over time, and can explore drought conditions beyond the observed range – providing insights that are difficult to obtain from measurements or statistical modeling alone. However, while current process-based schemes often capture drought effects on stomatal conductance, they rarely include variables directly comparable to dendrometer-derived TWD. This limits the use of dendrometer observations to evaluate modeled drought-stress dynamics and restricts the transfer of the physiological information contained in TWD into model frameworks. In addition, the effects of drought on tissue integrity, growth, and mortality remain only partially represented, as the underlying physiological mechanisms are insufficiently captured (Hartmann et al., 2018).

Mechanistic representations of drought stress often rely on tree water potential (ψ) or hydraulic impairment metrics. However, accurate ψ simulations remain challenging due to its non-linear, species-specific behavior and its sensitivity to soil texture – a highly variable site property. Drought-induced mortality is usually associated with percentage loss of conductivity (PLC) thresholds, as implemented in models such as ParFlow-TREES (Tai et al., 2018) or LPJ-GUESS (Meyer et al., 2025), but such approaches are difficult to constrain empirically due to species-specific vulnerability curves and methodological uncertainties (Cochard et al., 2013; Li et al., 2016; Feng et al., 2023).

Given these limitations, a stronger focus on tree water pools, which can be represented at a more integrative scale, may improve our ability to understand and anticipate drought impacts, as highlighted by Martinez-Vilalta et al. (2019). Despite increasing efforts to incorporate plant hydraulics into ecosystem frameworks, such explicit formulations of internal water storage and deficit dynamics remain rare. A meaningful representation of tree water status requires indicators that capture internal storage dynamics, respond consistently to dehydration, and can be directly compared with observations. TWD and relative tree water content (RWC_{tree}) could meet these criteria.

While TWD provides an observation-linked measure of internal water deficit dynamics, RWC_{tree} complements it by expressing modeled deficits relative to available internal water storage. As the ratio of current to fully saturated water content, it reflects the physical consequences of cellular

dehydration (Martinez-Vilalta et al., 2019) and has been linked to multiple drought-induced processes, including declines in stomatal and hydraulic conductance. Previous studies have also associated RWC with key physiological transitions such as turgor loss, metabolic impairment, and cellular damage (Bartlett et al., 2012; Lawlor and Cornic, 2002; Trueba et al., 2019; Sapes and Sala, 2021; Trifilò et al., 2023). Compared with ψ , RWC-based thresholds appear to show less inter-specific and organ-specific variability (Trueba et al., 2019; Trifilò et al., 2023), although uncertainty remains regarding their measurement and their relationship to hydraulic failure (Martinez-Vilalta et al., 2019). Nevertheless, RWC_{tree} can provide a physiologically interpretable proxy of relative internal hydration, with potential relevance for ecosystem-scale assessments of vegetation water content (Binks et al., 2024).

Representing TWD and RWC_{tree} in process-based forest models could create a direct interface between tree-level drought monitoring and model-based drought assessment. Several existing approaches can reproduce stem diameter variation, ranging from detailed mechanistic models (Peramaki et al., 2001; Peramaki et al., 2005; Steppe et al., 2006) to formulations designed primarily for interpreting dendrometer signals (Sevanto, 2001; Zweifel et al., 2005). In parallel, detailed hydraulic models such as SurEau and FETCH4 (Cochard et al., 2021; Ruffault et al., 2022; Missik et al., 2025), as well as hydraulically enhanced ecosystem models such as ED2-Hydro, ORCHIDEE-CAN-HYD, and FATES-HYDRO (Xu et al., 2016; Yao et al., 2022; Xu et al., 2023) already simulate tissue water storage and related hydraulic processes. These approaches provide important physiological detail, but they were generally not designed to yield a simple, diagnostically useful TWD state variable that can be constrained using dendrometer observations. A complementary need therefore remains for physiologically interpretable formulations that require few empirical parameters and make dendrometer-observable TWD dynamics usable in model simulations.

Therefore, in this study, we develop and test a tree water module, termed TWIST, that derives TWD dynamics from transpiration and relative soil water content and additionally estimates RWC_{tree} from modeled deficits and available internal water storage. TWIST is designed as a diagnostic add-on module that provides a parsimonious, physiologically interpretable representation of internal water deficit dynamics and allows model outputs to be compared with dendrometer-derived TWD. Specifically, we (i) present the module and illustrate its behavior under contrasting soil moisture conditions, (ii) integrate it within the process-based model LandscapeDNDC (Haas et al., 2013; Nadal-Sala et al., 2024) and evaluate it using multi-year dendrometer observations from a temperate beech forest site, and (iii) explore its response under an idealized rainfall-suppression stress test to examine boundary-case model behavior.

4.2 Materials and Methods

In this section, we first introduce the Tree Water Imbalance and Storage Tracker (TWIST) module, a lightweight water storage framework that simulates volume-based TWD and RWC_{tree} (Section 4.2.1), and then describe how it is coupled to the process-based ecosystem model LandscapeDNDC (Section 4.2.2). We next summarize the study site, observational data, normalization procedure, parameter calibration, and uncertainty analysis used for model evaluation against multi-year dendrometer observations (Sections 4.2.3–4.2.5). Finally, we introduce the “rainfall-suppression stress test”, designed to assess model behavior under imposed soil-water depletion (Section 4.2.6).

4.2.1 The TWIST Module

Simulating tree water deficit dynamics

TWIST is a simple diagnostic mass-balance module that represents internal tree water storage and deficit as the cumulative imbalance between transpirational demand (E) and soil water uptake (U), modulated by soil moisture limitation and species-specific rehydration capacity (Fig. 4.1). It was developed as a lightweight, mechanistically inspired, and physiologically interpretable set of equations that can be coupled to process-based ecosystem models, without resolving explicit ψ gradients or tissue-specific hydraulic properties. An R implementation is provided for reproducibility (see Data and code availability).

The module requires E and relative soil water content (θ_{rel}) – ranging from 1 at field capacity to 0 at the wilting point – as inputs. Here, E denotes water loss through the plant pathway rather than total evapotranspiration. The formulation is flexible regarding temporal resolution, spatial scale, and units: E can be provided at any time step (typically sub-daily) and for individual trees or entire stands. The resulting simulated TWD represents the accumulated internal water deficit and is expressed as a volume- or mass-based water amount per tree or ground area (e.g., $\text{L H}_2\text{O m}_{\text{ground}}^{-2}$ or $\text{kg H}_2\text{O tree}^{-1}$). This differs from dendrometer-derived TWD, which is expressed as stem shrinkage (μm) and represents a proxy for internal water deficit rather than a direct volume-based deficit.

TWD is updated at each time step (t) according to the previously accumulated deficit TWD_{t-1} (initialized at 0) and the current E and uptake rates:

$$\text{TWD}_t = \text{TWD}_{t-1} + E - U \quad (4.2.1)$$

Thus, when transpiration exceeds uptake ($E > U$), TWD increases, whereas it decreases when water uptake exceeds transpiration.

The calculation of U forms the core of the module. It is influenced by species- and site-specific hydraulic limitations represented by three empirical parameters – F_E , F_{TWD} and F_θ – and by

the drought limitation function $f_{\text{drought}}(\theta_{\text{rel}})$:

$$U = (F_E \cdot E + F_{\text{TWD}} \cdot \text{TWD}_{t-1}) \cdot f_{\text{drought}} \quad (4.2.2)$$

$$f_{\text{drought}} = \min\left(\frac{\theta_{\text{rel}}}{F_\theta}, 1\right) \quad (4.2.3)$$

The three parameters are dimensionless and constrained between 0 and 1. F_E controls the fraction of current transpiration demand that can be compensated by water uptake within the same time step. Higher F_E values therefore reduce the immediate accumulation of TWD, whereas lower values increase the lag between water loss and replenishment. The parameter F_{TWD} controls the fraction of the previously accumulated deficit that can be replenished within a time step, thereby regulating the pace of TWD recovery. The parameter F_θ defines the θ_{rel} below which U becomes additionally limited. For $\theta_{\text{rel}} < F_\theta$, f_{drought} declines linearly with decreasing θ_{rel} , resulting in direct limitation of U . At wilting point ($\theta_{\text{rel}} = 0$), f_{drought} becomes zero and U ceases entirely. A schematic representation of all fluxes is shown in Fig. 4.1.

Conceptually, TWIST represents water uptake as a response to two demand components, namely E and TWD_{t-1} , rather than resolving explicit ψ gradients or tissue-specific capacitances. F_E and F_{TWD} scale how efficiently these demands can be met under non-limiting soil moisture conditions, thereby controlling the lag between water loss, uptake, and storage replenishment. They can therefore be interpreted as effective empirical controls related to resistances along the soil-root-xylem pathway and the xylem-storage pathway, but should not be mistaken for direct estimates of specific hydraulic traits. Additional limitation due to soil drying is represented through $f_{\text{drought}}(\theta_{\text{rel}})$. Thus, the parameters are empirical in the present implementation, but their roles remain linked to interpretable hydraulic processes rather than acting as purely abstract fitting coefficients.

Suitable parameters for a specific site and species can be estimated with the automated calibration method described in Section 4.2.5. All variables, units, and parameter values used in this study are summarized in Table 4.1a. To examine how individual parameters influence TWD simulation behavior, a sensitivity analysis (one parameter is varied while the others are held constant) is presented in Fig. 4.6.

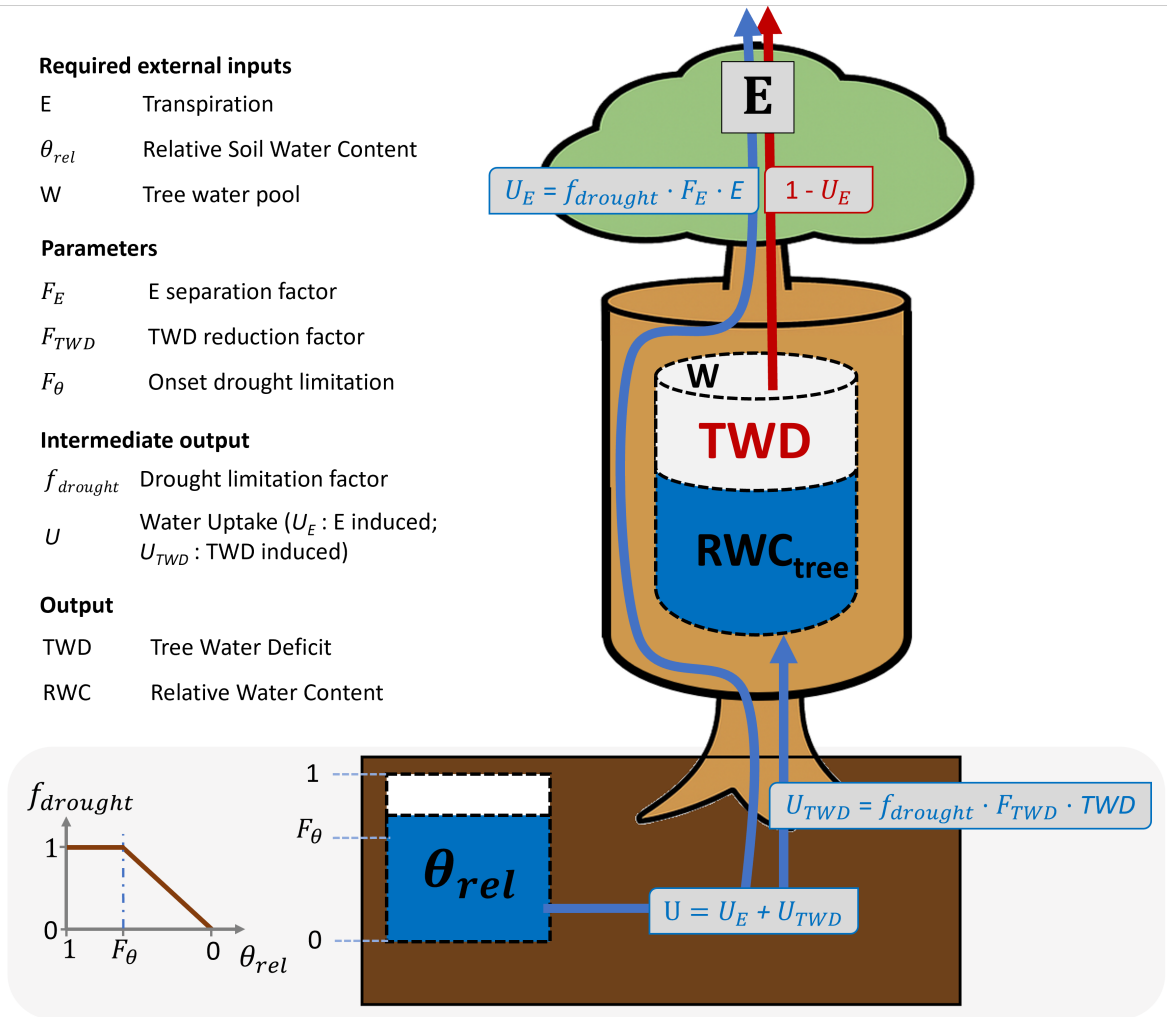


Figure 4.1: Illustration of the TWIST module concept for simulating tree water deficit (TWD) and relative tree water content (RWC_{tree}). TWIST derives diagnostic proxies of internal water status from externally supplied inputs – transpiration (E), relative soil water content (θ_{rel}), and the available tree water pool (W ; e.g. based on Eq. 4.2.5). At each time step t , soil water uptake (U) compensates the fraction F_E of E (U_E) and the fraction F_{TWD} of the existing TWD (U_{TWD}). When θ_{rel} drops below the threshold F_θ , U is further reduced through the drought limitation function $f_{drought}$. TWD decreases when $U > E$ (rehydration) and increases when $U < E$ (depletion), resulting in changes of RWC_{tree}. Blue arrows indicate water uptake from the soil, and the red arrow represents the depletion of internal water storage. Further details on variable definitions, units, and parameter values are provided in Table 4.1.

Table 4.1: Variables and parameters used in the TWIST module to simulate (a) tree water deficit (TWD) and (b) relative tree water content (RWC_{tree}) at the Štítná *Fagus sylvatica* site. Symbols, units, and brief descriptions are provided.

Symbol	Description	Unit	Values / Comments
(a) TWD simulations			
<i>Inputs</i>			
E	Transpiration	flexible [†]	
θ_{rel}	Relative soil water content	–	1 = field capacity, 0 = wilting point
<i>Parameters</i>			
F_E	E separation factor	–	0.83 (0.62–0.91) *
F_{TWD}	TWD reduction factor	–	0.19 (0.16–0.21) *
F_{θ}	θ_{rel} at which drought limitation starts	–	0.84 (0.69–0.96) *
<i>Intermediate output</i>			
U	Soil water uptake	same as E [†]	Eq. 4.2.2
f_{drought}	Drought limitation factor	–	Eq. 4.2.3
<i>Output</i>			
TWD	Tree water deficit	water amount per scale [†]	Eq. 4.2.1
(b) RWC_{tree} simulations			
<i>Inputs</i>			
m_{sapwood}	Dry-weight sapwood mass	kg per scale [†]	
<i>Parameters</i>			
ρ_{sat}	Fully saturated wood density	kg dm ^{−3}	1.07 (Wagenführ, 2007)
ρ_{dry}	Oven-dried wood density (m_{sapwood} relative to fresh volume)	kg dm ^{−3}	0.58 (Dietz, 1975)
<i>Intermediate output</i>			
W	Estimated maximum available internal water storage	water amount per scale [†]	Eq. 4.2.5
<i>Outputs</i>			
RWC_{tree}	Relative tree water content	–	0–1; Eq. 4.2.4

[†] E and U represent water amounts per time step, defined either per tree or per unit ground area. Their cumulative imbalance results in TWD, expressed as an accumulated water amount at the same spatial scale, but without a time step dimension. The formulas can operate at flexible temporal resolutions and spatial scales: inputs (E , θ_{rel} , m_{sapwood}) should be defined consistently at the tree-level or per unit ground area (stand-level). In this study, the module was coupled to LandscapeDNDC using hourly stand-level E and U fluxes (L H₂O m_{ground}^{−2} h^{−1}), while TWD and W were expressed as accumulated stand-level water amounts (L H₂O m_{ground}^{−2}).

* Best-fit parameter values are shown together with the full range (min–max) of acceptable solutions, defined as parameter sets yielding calibration performance within 5% of the optimal solution (see Methods for details on sampling and selection criteria). The parameter values were estimated for this specific case study and are expected to be species- and site-specific.

Simulating relative tree water content

To obtain a model-derived proxy of tissue hydration, TWIST derives relative water content within the tree or stand from TWD:

$$\text{RWC}_{\text{tree}} = \frac{W - \text{TWD}}{W} \quad (4.2.4)$$

Here, W denotes the maximum amount of water stored in the tree or stand at full saturation. In this study, we estimate it from dry-weight sapwood mass (m_{sapwood}) – a commonly modeled variable – and the standard density parameters ρ_{sat} and ρ_{dry} , which relate water-saturated and oven-dry sapwood mass, respectively, to fresh sapwood volume:

$$W = \left(\frac{\rho_{\text{sat}}}{\rho_{\text{dry}}} - 1 \right) \cdot m_{\text{sapwood}} \quad (4.2.5)$$

This formulation approximates the available internal water storage as the difference between saturated and dry sapwood mass ($m_{\text{sat-sapwood}} - m_{\text{sapwood}}$), assuming that leaf, root, and core wood compartments contribute negligibly to total storage. W must share the same unit as TWD ($1 \text{ kg H}_2\text{O} \approx 1 \text{ L H}_2\text{O}$) to ensure that RWC_{tree} remains dimensionless. All values and units used for RWC_{tree} simulations are summarized in Table 4.1b.

Thus, RWC_{tree} equals 1 when tissues are fully saturated and declines as TWD increases. To ensure mass balance, TWD cannot exceed the total available water storage W , which constrains $\text{RWC}_{\text{tree}} \geq 0$. A value of 0 would correspond to complete depletion of the modeled available water storage (oven-dried conditions). RWC_{tree} therefore provides a comparable diagnostic proxy of relative tree water status over time.

Required inputs and coupling concept

TWIST is designed as a diagnostic add-on module that can be coupled to process-based models providing E , θ_{rel} , and an estimate of W at consistent temporal and spatial scales, thereby generating TWD dynamics that can be compared with dendrometer-derived TWD. In this sense, drought-induced reductions in E are not calculated by TWIST itself; rather, they must be realistically represented by the coupled model. TWIST then diagnostically derives TWD and RWC_{tree} from these inputs. To ensure mass balance, water loss from the tree water pool should be limited to W in coupled implementations, thereby preventing physically impossible states such as $\text{RWC}_{\text{tree}} < 0$. This upper bound is a technical mass-balance constraint rather than a biologically meaningful endpoint; in living trees, severe dysfunction or mortality would be expected before RWC_{tree} approaches zero. Apart from this constraint, no direct feedbacks of TWD or RWC_{tree} on stomatal conductance, E , growth, or mortality are currently implemented, although such extensions are conceptually possible. In coupled applications, indirect effects on

subsequent processes may nevertheless arise because TWIST modifies the effective soil water uptake and, in turn, the simulated soil water balance.

Idealized module behavior experiment

To illustrate the diagnostic response of TWIST under declining soil moisture and reduced E , an idealized simulation is presented in Fig. 4.2. Here, prescribed daily E cycles and fixed θ_{rel} values served as module input, while parameter values were set according to the best fit for the Štítná site. Each column represents responses under different soil water conditions, ranging from field capacity to wilting point, with gradually decreasing E amplitudes that resemble stomatal closure. For each time series, TWD was initialized as zero, and the module calculated f_{drought} , U , and the resulting TWD for each time step according to Eqs. 4.2.1–4.2.3. This idealized module response experiment was designed to illustrate simulated TWD responses rather than to reproduce specific measurements.

4.2.2 Coupling with the LandscapeDNDC ecosystem model

For this work, TWIST was integrated into LandscapeDNDC to enable multi-year stand-level simulations of TWD and RWC_{tree} for specific forest sites.

General LandscapeDNDC properties

LandscapeDNDC is a process-based ecosystem model designed to simulate coupled carbon, water, and nitrogen fluxes between vegetation, soil, and the atmosphere at the site scale (Grote et al., 2011a; Haas et al., 2013). The model comprises a flexible, modular system and has been applied across various ecosystems, including forests, croplands, and grasslands (Grote et al., 2011b; Molina-Herrera et al., 2016; Dirnböck et al., 2020; Cade et al., 2021; Kraus et al., 2022; Sifounakis et al., 2024). It represents vegetation and soil as dynamically interacting compartments, integrating canopy microclimate, plant physiology, plant dimensional growth, and soil biogeochemistry. Simulations are initialized with actual soil- and vegetation properties (i.e., without significant spin-up periods) and are driven by meteorological forcing (temperature, vapor pressure deficit (VPD), precipitation, radiation, pressure), CO_2 concentration, nitrogen deposition, and ecosystem management at daily to sub-daily resolution. The model calculates above- and below-ground processes within distinct canopy- and soil layers.

For each soil layer, soil water content (SWC) is simulated and normalized between the layer-specific field capacity and wilting point. A mean relative SWC (θ_{rel}) is then derived as the weighted average across all soil layers, where weighting follows the vertical distribution of fine roots. For forest applications, Nadal-Sala et al. (2024) recently integrated tree hydraulic processes into LandscapeDNDC, enabling the simulation of soil and plant ψ and the calculation

of transpirational water loss E via stomatal regulation following Eller et al. (2020). Thus, E is simulated dynamically in response to meteorological forcing and plant water status. In the original configuration (without the TWIST module), the resulting transpired water is removed directly from the soil layers until a species-specific soil water potential threshold is reached, at which point fine-root water uptake ceases completely (soil-to-root decoupling).

LandscapeDNDC also simulates a range of other ecosystem processes, including total evapotranspiration, stomatal-conductance-dependent carbon assimilation, allocation of carbon and nitrogen into distinct compartments (foliage, fine roots, sapwood, and structural reserves), respiration and senescence, which decreases the living biomass of all compartments, including sapwood.

The most sensitive LandscapeDNDC parameters for photosynthesis and water balance (Table S4.3) were set within physiologically plausible ranges to resemble site-measured seasonal dynamics of total evapotranspiration (Fig. S4.8), gross primary productivity (Fig. S4.9), and SWC (Fig. S4.10).

Integration of TWIST in LandscapeDNDC

In contrast to the original setup of Nadal-Sala et al. (2024), TWIST introduces an explicit tree water pool W in LandscapeDNDC (Eq. 4.2.5). Soil water uptake is estimated by Eq. 4.2.2, allowing imbalances between uptake and transpirational water loss to drive gradual depletion and refilling of this pool. The LandscapeDNDC variables θ_{rel} (-), E ($\text{L m}_{\text{ground}}^{-2} \text{h}^{-1}$), and m_{sapwood} ($\text{kg m}_{\text{ground}}^{-2}$) were used as inputs for the newly developed equations. Because E in LandscapeDNDC already responds dynamically to plant water status via stomatal regulation, TWIST is driven by a drought-responsive rather than unconstrained E signal. To prevent physically impossible states, depletion of the tree water pool was limited to the available storage W , such that TWD cannot exceed W and RWC_{tree} cannot fall below zero.

4.2.3 Evaluation site

TWIST was evaluated during seven consecutive years (2018–2024) at the Štítná forest site, located in the Czech Republic ($49^{\circ}02'09.510'' \text{ N}$, $17^{\circ}58'11.640'' \text{ E}$; 550 m above sea level). The stand consists of European beech trees (*Fagus sylvatica* L.; 286 trees ha^{-1} ; DBH = $37 \pm 13 \text{ cm}$; height = $31 \pm 7 \text{ m}$ (mean $\pm$ std; measured 2018)). At the site, meteorological measurements, eddy covariance ecosystem flux measurements, SWC measurements, and stem diameter measurements were conducted. All meteorological and ecosystem exchange measurements were conducted above the forest canopy at 44 m height. The eddy covariance system consists of a Gill ultrasonic anemometer (HS-50, Gill Instruments, UK) and a LI-COR infrared gas analyzer (LI-7200, LI-COR, NE, USA). Processing of raw 20 Hz data was performed by EddyPro Software (LI-COR, NE, USA) with settings described in McGloin et al. (2019). Quality-controlled half-hourly

products were post-processed using the standardized ONEFlux processing pipeline (Pastorello et al., 2020) by the FLUXNET network.

Half-hourly SWC measurements were performed at 5, 10, and 30 cm soil depths using ThetaProbe sensors (ML2x 355, Delta-T, UK).

Automatic, high-resolution band dendrometers (DRS26; EMS Brno, Czech Republic; $1\ \mu\text{m}$ resolution) were used to monitor changes in stem circumference of five individuals ($\text{DBH} = 46 \pm 10\ \text{cm}$; height = $33 \pm 3\ \text{m}$ (mean $\pm$ std)). The sensors were installed approximately 1.3 m above ground level. Stem dynamics were recorded continuously at half-hourly intervals on trees in the co-dominant and dominant canopy layers within the eddy-covariance tower footprint. Circumference measurements were converted to changes in stem radius. To isolate water-related, reversible stem variations, we applied the zero-growth concept (Zweifel et al., 2016), which assumes that irreversible radial growth occurs only when new stem-radius maxima are reached, while short-term deviations below these maxima reflect reversible water-related shrinkage. This approach enabled direct calculation of observed TWD (stem shrinkage; μm).

To avoid frost-related artifacts in the observed TWD data (Zweifel and Häsler, 2000), an individual growing-season period was defined for each year. The start of the season was set to the first day after 1 April on which TWD returned to 0 (indicating full recovery from winter effects), and the end of the season to the last day before the daily mean air temperature dropped below 5°C .

4.2.4 Normalization of TWD

To compare the temporal dynamics of observed and simulated TWD (TWD_{obs} and TWD_{sim} , respectively), all values were normalized following the procedure of Peters et al. (2025). For the dendrometer measurements, maximum daily shrinkage (MDS) was calculated for each tree and each day as the difference between the daytime maximum TWD_{obs} (10 am–11 pm) and the pre-dawn minimum TWD_{obs} (4–8 am), and the 99th percentile of all daily MDS (MDS_{q99}) was determined. Next, the TWD_{obs} time series of each tree was divided by its MDS_{q99} , yielding a normalized TWD (TWD_{norm}) per individual. Across the seven measurement years and across all five trees, the average MDS_{q99} was $33.2 \pm 2.3\ \mu\text{m}$ (mean $\pm$ sd). The mean and standard deviation of all individual TWD_{norm} trajectories were used for further analysis.

For TWD_{sim} , an equivalent normalization was applied using the 99th percentile of the maximum daily water loss (MDWL_{q99} ; volume-based analogue of MDS) across the study period, resulting in $\text{MDWL}_{q99} = 1.01\ \text{L m}^{-2}$ (equivalent to $35.0\ \text{L tree}^{-1}$).

According to Peters et al. (2025), this normalization enables the identification of relative drought stress thresholds and facilitates comparison of tree water status across individuals and species, independent of absolute stem size or shrinkage magnitude. Applied to TWD_{sim} , it also bridges differences in units (water-volume deficit vs. stem shrinkage) and spatial scales

(stand-level vs. tree-level), thereby enabling comparison of tree-level dendrometer signals with stand-level model dynamics.

4.2.5 Parameter calibration and model evaluation

The three TWIST parameters were calibrated against the temporal dynamics of Štítná dendrometer-derived TWD observations in 2018, while 2019–2024 were used for independent evaluation. 2018 was selected as a calibration year because its second half was exceptionally warm and dry at the Štítná site (Nezval et al., 2025), while its first half also included extended periods without strong SWC limitation (Fig. S4.10), overall providing a wide range of conditions. Parameter estimation was restricted to bounded intervals of 0–1 for F_E and F_{TWD} , and 0.01–1 for F_θ . For each tested parameter set, TWIST was run over the full simulation period (2018–2024). Only time steps with available observations were used for scoring. Simulated and observed TWD were each normalized over the full available time series, as described above. The calibration objective combined the root mean square error (RMSE) between simulated and observed TWD_{norm} at hourly resolution with the RMSE of daily mean TWD_{norm} , thereby constraining both sub-daily dynamics and day-to-day variation. To give both components comparable influence, hourly and daily RMSE were scaled by the corresponding errors of a fixed reference parameter set ($F_E = 0.6$, $F_{TWD} = 0.3$, $F_\theta = 0.7$), used solely as an internal scaling baseline, and weighted equally. The optimization was performed with a bounded L-BFGS-B algorithm, a method that efficiently handles box-constrained parameter spaces (Byrd et al., 1995), using a multi-start approach with 10 initial parameter sets, including the reference parameter set and 9 randomly sampled starts within the parameter bounds. The best-fit solution was defined as the parameter set yielding the minimum combined objective value during the calibration period.

Model evaluation was performed independently for the 2019–2024 growing seasons using the calibrated best-fit parameter set without further adjustment. Performance was quantified at both hourly and daily resolution using RMSE, bias, and R^2 between simulated and observed TWD_{norm} . To further characterize parameter robustness and equifinality, the bounded parameter space was additionally explored by uniform random sampling of 8000 parameter combinations. Each sampled set was evaluated with the same objective function as used for calibration. Acceptable solutions were defined as all parameter sets with an objective value within 5% of the optimized best fit. The corresponding parameter distributions are reported in Table S4.4, and all acceptable parameter sets are listed in Table S4.5. For reproducibility and new applications, the calibration R code is provided (see Data and code availability).

4.2.6 Rainfall-suppression stress test

To explore TWIST behavior under imposed soil water depletion, an idealized stress test was simulated by suppressing rainfall after the 2018 TWD peak in mid-August at the Štítná site. All

other meteorological drivers (temperature, radiation, and VPD) were prescribed as a repetition of the observed weather conditions during the peak drought period (14–23 August; Fig. 4.7).

This setup produced continuous soil moisture depletion, allowing us to examine how TWD and RWC_{tree} evolve when residual water loss persists in the absence of soil water recharge. The experiment was therefore used as a technical boundary-case test of model behavior, not as a realistic drought scenario.

All data processing, statistical analyses, and visualizations were conducted in R (R Core Team, 2022).

4.3 Results

4.3.1 Theoretical TWIST module behavior

The theoretical example presented in Fig. 4.2 illustrates how TWIST represents the transition from complete to incomplete nocturnal TWD recovery across the soil moisture gradient. Under well-watered conditions (Fig. 4.2a), the simulated uptake did not fully cover E during the day, resulting in an increase in TWD, but the deficit could be fully replenished during the night. As θ_{rel} declined and drought limitation began to constrain uptake ($f_{\text{drought}} < 1$, Fig. 4.2b–d), an increasing fraction of E could no longer be balanced by U , causing higher daytime TWD peaks and slower replenishment.

At moderate soil dryness (Fig. 4.2b), TWD still returned towards zero at night, but recovery took several hours longer compared with wet conditions. When θ_{rel} dropped further (Fig. 4.2c), storage refilling was incomplete and a residual TWD persisted into the following day. This carry-over deficit marks the onset of TWD accumulation, where daily minimum TWD progressively increases despite reduced E . Under extreme drought (Fig. 4.2d), soil water uptake ceased entirely ($U = 0$), and the minor residual E occurring despite stomatal closure directly translated into continuous TWD increase.

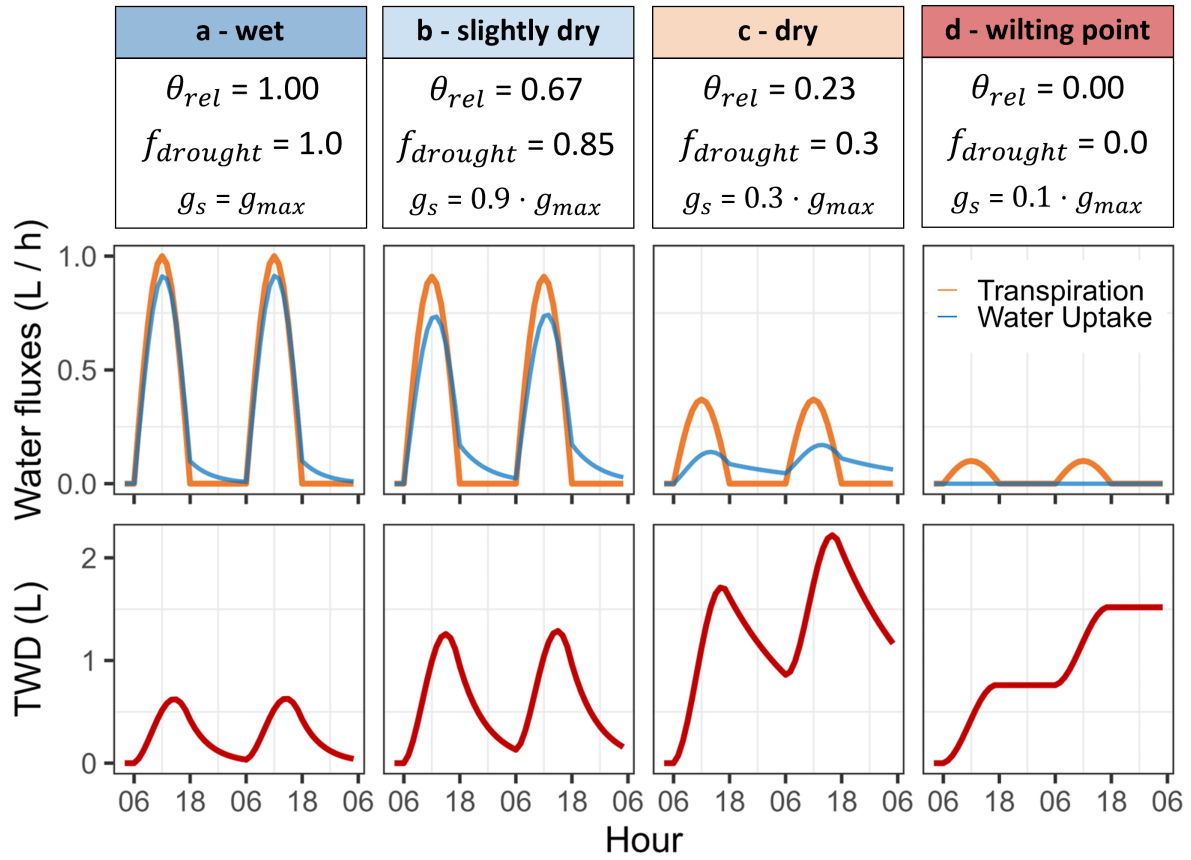


Figure 4.2: Conceptual representation of the TWIST module behavior exemplified under four increasing drought intensities (a-d). A fixed relative soil water content (θ_{rel}), ranging from field capacity in (a) to wilting point in (d), determines the drought limitation factor ($f_{drought}$; Eq. 4.2.3) in each column. In parallel, the amplitude of daily transpiration is reduced to resemble drought-induced reductions of stomatal conductance (g_s) until its minimum $g_{min} = 0.1 \cdot g_{max}$ is reached. Vapor pressure deficit is assumed to be constant. Top panels show two diurnal courses of transpiration (orange) and the resulting soil water uptake (blue; Eq. 4.2.2). Imbalances between soil water uptake and transpiration result in dynamic changes in tree water deficit (TWD; red; Eq. 4.2.1) as shown in the bottom panels.

4.3.2 TWIST module evaluation

To assess model performance, TWIST was coupled to the ecosystem model LandscapeDNDC and applied to the Štítná beech forest site (Fig. 4.3a). Parameters were optimized based on the 2018 growing season and evaluated across the remaining years. For the calibration year, the best-fit parameter set was derived by minimizing the mismatch between simulated and observed TWD (Section 4.2.5). The resulting simulation shows close agreement in both temporal dynamics and relative amplitude (Fig. 4.3b). The timing of drought onset, peak, and recovery was well captured, resulting in high agreement (hourly $R^2 = 0.92$) and low error (hourly RMSE = 0.24).

Minor deviations in normalized peak amplitudes and the magnitude of diurnal cycles occurred, but the low overall hourly bias of -0.06 indicates no strong systematic over- or underestimation during the calibration period.

Table 4.2: Model performance metrics for calibration (2018) and independent evaluation (2019–2024) periods, based on hourly and daily aggregated data. RMSE denotes the root mean square error, calculated from either hourly values or daily means of normalized tree water deficit, Bias denotes the mean error, and R^2 the coefficient of determination.

Metric	Calibration (2018)	Evaluation (2019–2024)
Hourly RMSE (–)	0.24	0.40
Daily RMSE (–)	0.20	0.39
Hourly Bias (–)	-0.06	-0.05
Daily Bias (–)	-0.06	-0.05
Hourly R^2 (–)	0.92	0.42
Daily R^2 (–)	0.94	0.42

This calibrated parameter set was subsequently applied without further adjustment to the independent evaluation period 2019–2024 (Fig. 4.3c). During this evaluation period, the model captured the general normalized TWD dynamics across contrasting conditions, although performance varied between years. Good agreement was observed for years such as 2019, 2022, and 2024, whereas lower agreement was observed in 2021 and 2023. This variability is reflected in reduced overall performance metrics compared to the calibration period (e.g., hourly $R^2 = 0.42$, RMSE = 0.40, bias = -0.05 ; Table 4.2).

At the sub-daily scale, the model reproduced the characteristic diurnal dynamics of water depletion during daytime and rehydration during nighttime (Fig. 4.3d). The amplitude of these fluctuations was not always reproduced exactly, but deviations did not show a consistent directional bias across years. Instead, both over- and underestimation occurred depending on period and year. Nevertheless, the overall temporal structure was captured consistently across both wet and dry periods. In particular, the transition from complete nocturnal recovery under moist conditions to persistent deficits under drought was well represented. Together with the comparison of hourly and daily performance metrics (Table 4.2), this indicates that the model captures both short-term fluctuations and the broader day-to-day development of TWD reasonably well.

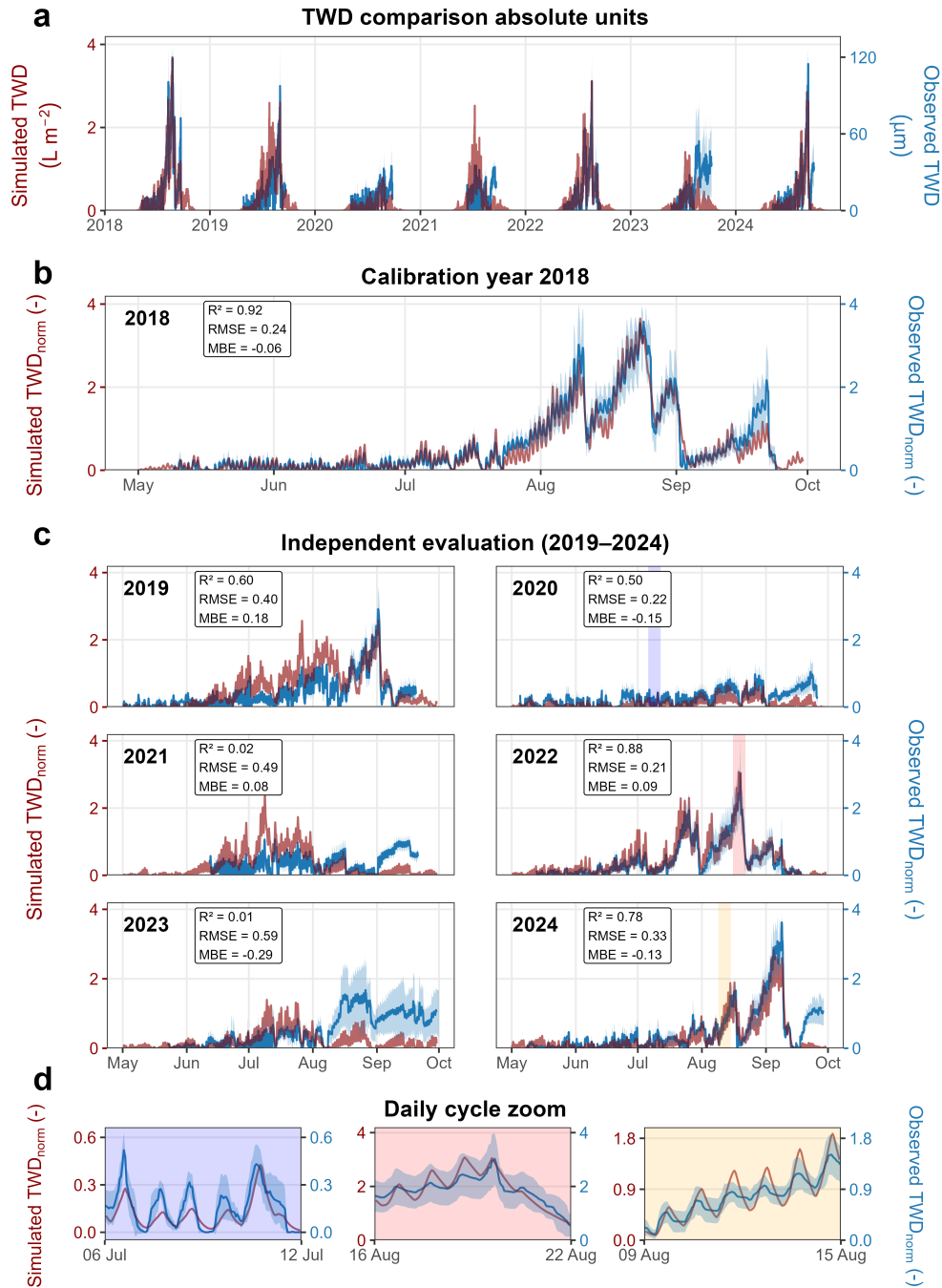


Figure 4.3: Evaluation of simulated tree water deficit (TWD; red) against dendrometer-based TWD observations (blue; $n = 5$, mean $\pm$ sd) at the Štítná forest site for the years 2018–2024. (a) shows absolute values for context, where simulated TWD represents the derived water volume deficit at the stand-level (L m^{-2} ground area), while observed TWD denotes stem diameter shrinkage at the tree-level (μm). (b) shows the calibration year 2018, for which the three TWIST parameters were optimized by minimizing the RMSE of hourly values and daily means between simulated and observed normalized TWD (hourly shown; daily values see Table 4.2). (c) presents independent evaluation for the years 2019–2024 using the calibrated best-fit parameter set. (d) zooms into the color-coded periods highlighted in (c), illustrating short-term TWD dynamics.

Overall, the results indicate that the parameter set calibrated for 2018 captured the main TWD patterns across subsequent years, albeit with lower performance than in the calibration year.

4.3.3 TWD and RWC_{tree} dynamics at the site

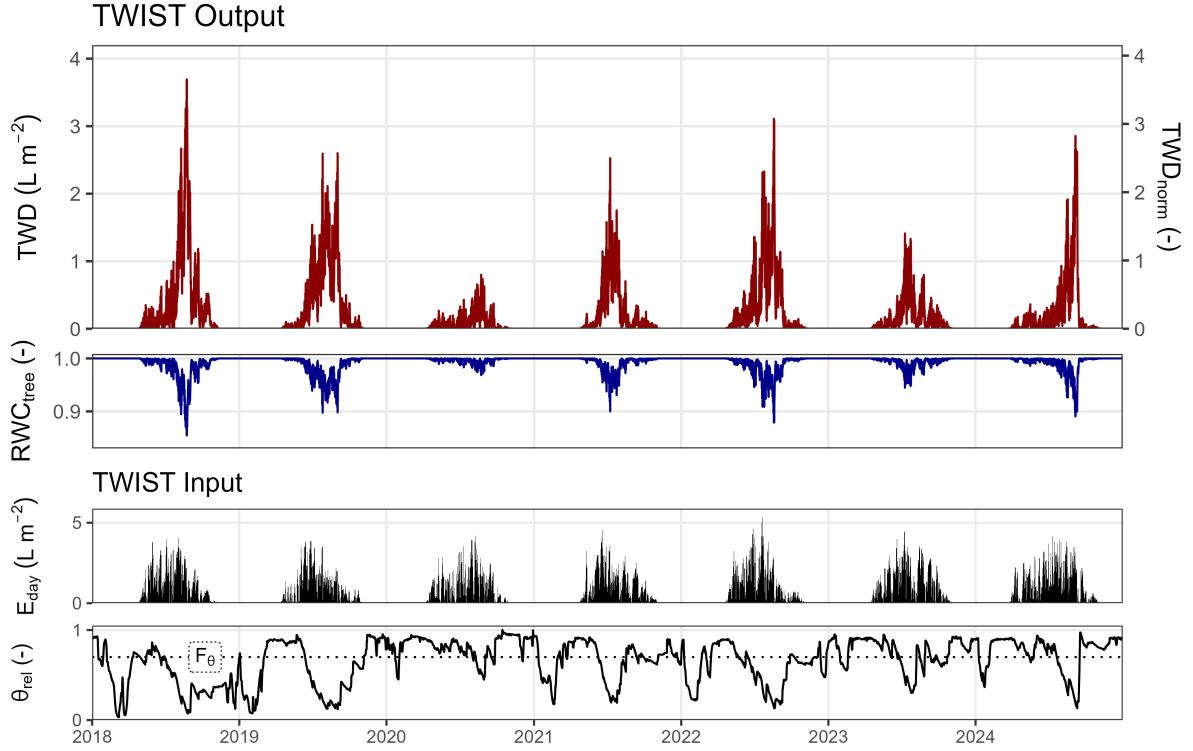


Figure 4.4: Seasonal dynamics of simulated tree water deficit (TWD) and relative tree water content (RWC_{tree}) at the Štítná forest site 2018–2024. Hourly TWD is shown both as absolute values (left axis; liters per m^2 ground) and as normalized deficit (right axis; for normalization procedure see Section 4.2.4). Hourly transpiration (aggregated to daily values, E_{day}) and relative soil water content (θ_{rel} ; 1 = field capacity, 0 = wilting point) were simulated by the LandscapeDNDC model and used as inputs for the TWIST module. In the θ_{rel} panel, the F_{θ} threshold indicating the onset of additional soil water uptake limitation is shown as a dotted line.

The calibrated parameter set was used to analyze the temporal dynamics of TWD and RWC_{tree} at the site (Fig. 4.4). Periods of high E combined with declining θ_{rel} led to a progressive accumulation of TWD, while rainfall events and increasing θ_{rel} triggered recovery of internal water reserves. This resulted in a pronounced seasonal cycle, with TWD peaks during dry summer periods indicating increased internal water depletion. The highest peak occurred in 2018 ($\sim 3.6 \text{ L m}^{-2}$). Similarly high peaks were simulated in 2019, 2021, 2022, and 2024 ($\sim 2.6\text{--}3.1 \text{ L m}^{-2}$), whereas

substantially lower values were observed in 2020 ($\sim 0.8 \text{ L m}^{-2}$) and 2023 ($\sim 1.4 \text{ L m}^{-2}$).

The complementary RWC_{tree} signal closely mirrored TWD, expressing the relative depletion of internal water storage (on average $\sim 25.3 \text{ L m}^{-2}$; equivalent to $\sim 884 \text{ L tree}^{-1}$). RWC_{tree} remained close to 1 under moist conditions (e.g., 2020), and declined to approximately 0.86 during the drought year 2018, reflecting partial tissue dehydration. Together, TWD and RWC_{tree} provided a consistent representation of tree water dynamics and its seasonal variability at the site.

4.3.4 Parameter space and equifinality

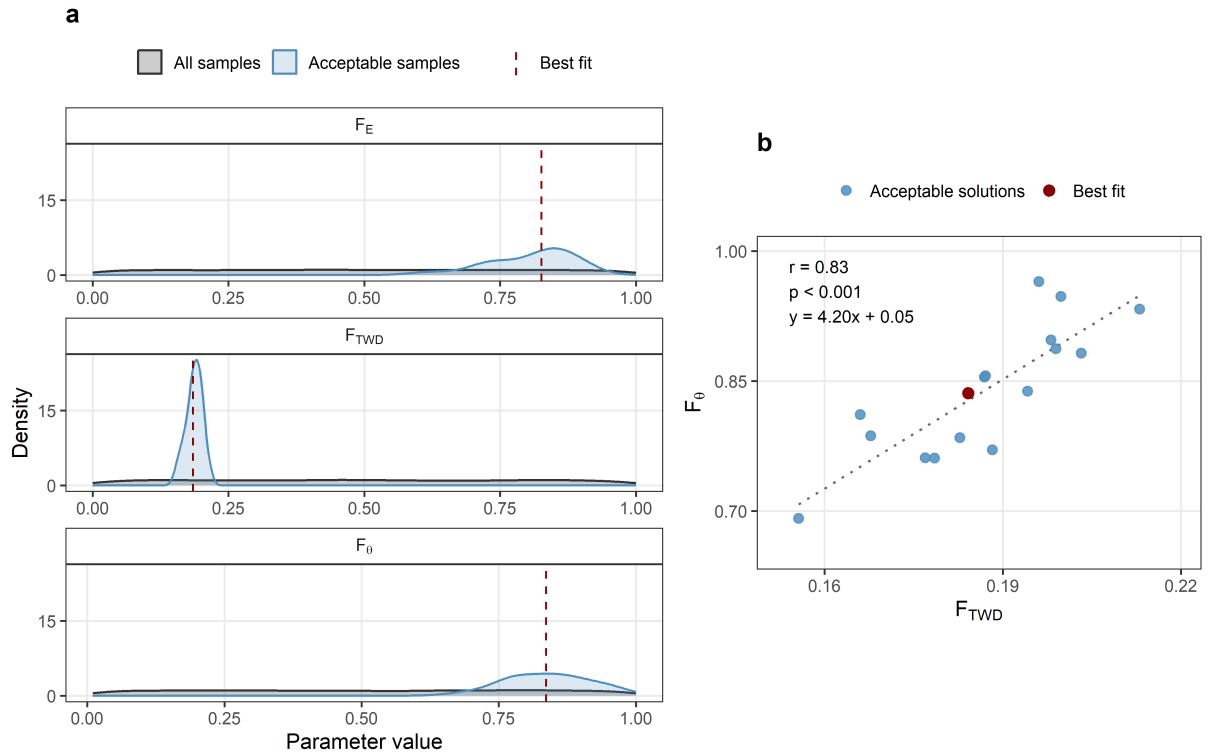


Figure 4.5: Parameter calibration and uncertainty analysis of the three TWIST model parameters based on the 2018 calibration period. (a) Distributions of all sampled parameter combinations (uniform sampling within the parameter bounds; $n = 8000$; grey) and the subset of acceptable solutions ($n = 17$; blue), defined as parameter sets with an objective value within 5% of the best-fit objective value. Dashed vertical lines indicate the best-fit parameter values. (b) Relationship between F_{TWD} and F_θ . Blue points represent acceptable parameter combinations, and the red point indicates the best-fit solution. The dashed line shows a linear regression fitted to the acceptable solutions. The annotated value denotes the Pearson correlation coefficient (r) between F_{TWD} and F_θ across all acceptable solutions, indicating the strength and direction of their linear relationship. Similar relationships including the F_E parameter are shown in Fig. S4.11.

Building on the calibrated parameter set used in the model evaluation, the parameter space was further explored to assess parameter uncertainty and equifinality. This exploration showed that only a small subset of parameter combinations yielded performance comparable to the best-fit solution (Fig. 4.5a). Acceptable performance occurred only within a narrow region of the sampled parameter space, indicating that good model performance was restricted to specific parameter combinations rather than broadly distributed across the parameter domain. The parameters F_E and F_θ exhibited comparable ranges, with acceptable values of $F_E = 0.83$ (0.62 – 0.91) and $F_\theta = 0.84$ (0.69 – 0.96), respectively (best-fit value and full min–max range of acceptable solutions; see also Table S4.4). In contrast, F_{TWD} was more tightly constrained, with acceptable values of 0.19 (0.16 – 0.21).

Within this constrained parameter space, a clear relationship emerged between F_{TWD} and F_θ (Fig. 4.5b). Acceptable solutions, i.e. parameter sets yielding model performance within 5% of the best-fit solution, followed a distinct positive linear trend ($r = 0.83$, $p < 0.001$), indicating that combinations of higher F_{TWD} were associated with higher F_θ values. A weaker but significant positive relationship was also found between F_E and F_{TWD} (Fig. S4.11; $r = 0.50$, $p = 0.039$), suggesting partial parameter compensation within the set of acceptable solutions. In contrast, no significant relationship was detected between F_E and F_θ (Fig. S4.11).

These patterns illustrate that acceptable model performance is confined to a limited and structured region of the parameter space.

4.3.5 Parameter sensitivity

The sensitivity analysis highlighted distinct roles of the three TWIST parameters in controlling TWD_{sim} dynamics under contrasting moisture conditions (Fig. 4.6).

The parameter F_E primarily controlled the amplitude of daily TWD cycles. Lower values led to stronger daytime depletion and higher diurnal peaks, while higher values reduced the magnitude of these fluctuations. In contrast, F_θ governed the response under prolonged dry conditions by regulating the onset and strength of soil moisture limitation. Lower F_θ values delayed the reduction of water uptake and thus maintained lower TWD levels, whereas higher values enhanced drought limitation and promoted stronger deficit accumulation. The parameter F_{TWD} influenced both short- and long-term dynamics. Lower values reduced the efficiency of TWD compensation, resulting in slower recovery, higher daily peak amplitudes, and greater deficit accumulation under drought. Higher values accelerated rehydration and dampened both diurnal variability and longer-term TWD build-up.

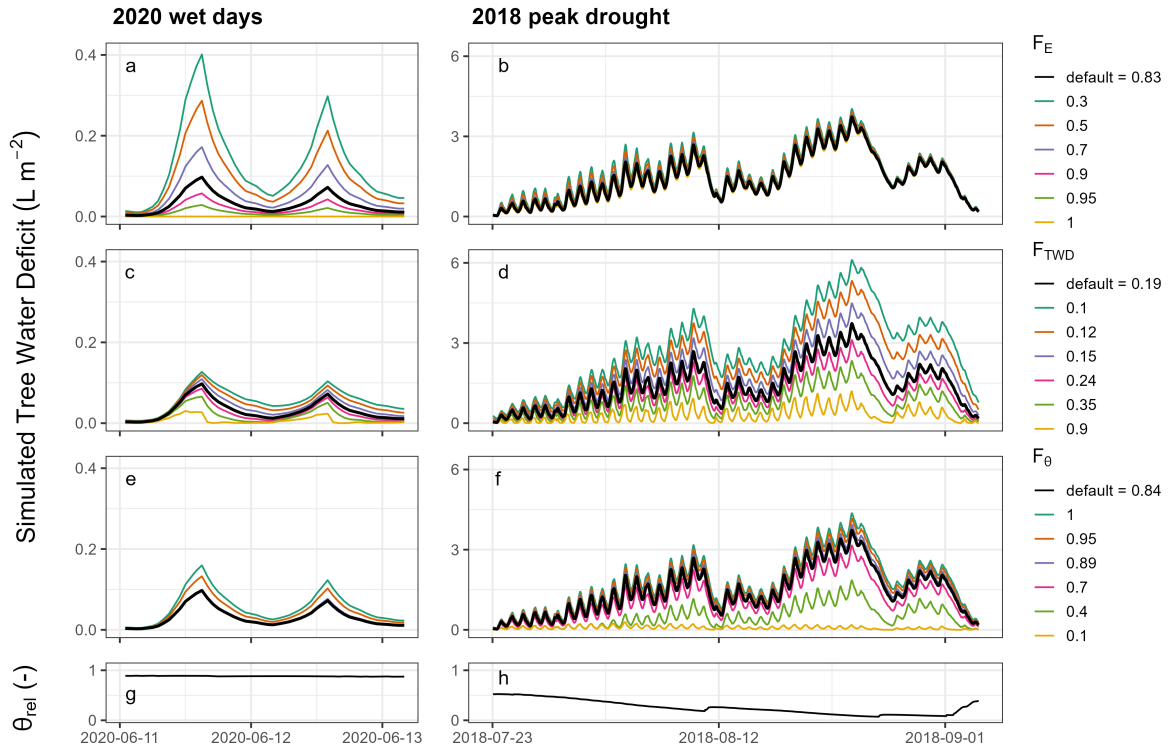


Figure 4.6: Sensitivity analysis of the three TWIST parameters F_E (a,b), F_{TWD} (c,d), and F_θ (e,f) for two exemplary wet days in 2020 (a,c,e,g) and the 2018 peak drought period (b,d,f,h) at the Štítná beech forest site. Each parameter was varied individually while the remaining parameters were kept at their site-specific best-fit values ($F_E = 0.83$, $F_{TWD} = 0.19$, $F_\theta = 0.84$). The model inputs consist of transpiration and relative soil water content (θ_{rel} ; g,h) simulated by LandscapeDNDC.

4.3.6 Rainfall-suppression stress test

To examine TWIST behavior under imposed water depletion, a rainfall-suppression stress test was simulated (Fig. 4.7). This experiment was not intended to represent a fully realistic drought trajectory, especially after RWC_{tree} fell below 0.6, where mortality risk would be expected to increase (Sapes and Sala, 2021; Trifilò et al., 2023). Instead, it was used to test how TWIST outputs evolve under boundary-case conditions. In contrast to the observed 2018 conditions, where rainfall in late August partially restored θ_{rel} , soil moisture in the test simulation declined continuously and asymptotically approached the wilting point ($\theta_{rel} = 0$). During the first days of the scenario period, minor nocturnal TWD replenishment still occurred due to water uptake from the soil, further reducing θ_{rel} . With increasing dryness, soil water uptake became progressively restricted, resulting in a steady increase in TWD driven by residual E . This behavior corresponds to phase (d) of the theoretical response illustrated in Fig. 4.2.

RWC_{tree} mirrored the TWD trajectory, showing a continuous decline throughout the simulation. By September 9, RWC_{tree} approached 0.6, and by 7 October, it approached 0, representing the lower technical bound for internal water storage. Once this lower bound was reached, further depletion was no longer allowed, and TWD_{sim} therefore reached a plateau.

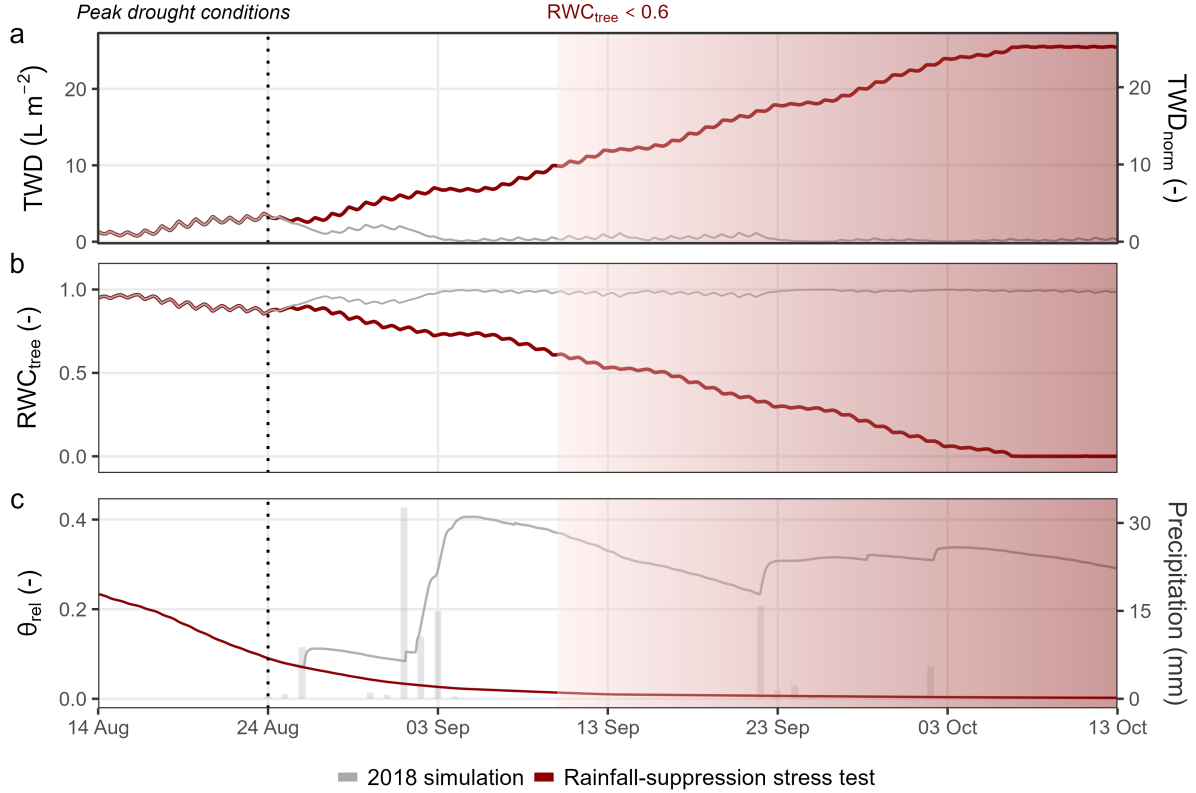


Figure 4.7: Simulated tree and soil water dynamics at the Štítná site during an idealized rainfall-suppression stress test. The baseline simulation (grey) is driven by the observed 2018 meteorological forcing, while the test simulation (dark red) artificially extends the dry-period forcing by looping the last observed dry-period weather conditions (14–23 August; peak drought conditions). The vertical dashed line marks the start of the imposed test forcing, defined by the timing of the highest TWD peak observed in 2018 (24 August). Panels show (top to bottom): (a) tree water deficit (TWD; absolute values on the left axis, normalized values on the right axis), (b) relative tree water content (RWC_{tree}), and (c) relative soil water content (θ_{rel} ; left axis) with daily precipitation (bars; right axis). The shaded red area indicates the period during which RWC_{tree} falls below 0.6, shown as an indicative reference threshold associated with severe plant water stress in previous studies; dynamics beyond this range are shown to illustrate numerical model behavior rather than realistic dynamics of living trees.

4.4 Discussion

This study shows that dendrometer-observable TWD dynamics can be represented in process-based models using a simple water-balance framework. TWIST does not replace detailed hydraulic models, but provides a model-compatible diagnostic state variable that can be compared with dendrometer-derived TWD dynamics.

4.4.1 Process-based simulation of TWD and its physiological meaning

TWD reflects the transient imbalance between E and water uptake, thereby encoding key information on internal tree water status and drought progression. Dendrometer-derived and simulated TWD are closely linked but differ in their physical representation: dendrometer signals quantify stem shrinkage as an observation-based proxy for water depletion in elastic tissues (Steppe et al., 2006), whereas TWD_{sim} is a model state variable representing actual volumetric water deficit across tree tissues or at the stand-scale. Although these quantities are not directly equivalent, they are expected to track the same underlying depletion–rehydration dynamics and are therefore comparable in their temporal patterns.

A more mechanistic representation of plant hydraulics could, in principle, simulate TWD and RWC_{tree} in greater detail and resolve transport pathways and storage processes across compartments, as done, for instance, in models such as SurEau and FETCH4 (Cochard et al., 2021; Ruffault et al., 2022; Missik et al., 2025). Likewise, hydraulically enhanced ecosystem models such as ED2-Hydro, ORCHIDEE-CAN-HYD and FATES-HYDRO explicitly represent tissue water storage and hydraulic traits within broader vegetation dynamics (Xu et al., 2016; Yao et al., 2022; Xu et al., 2023). These approaches offer important physiological detail, but also require substantially more parameters and a more detailed representation of hydraulic compartments and traits, making them increasingly difficult to constrain and transfer across sites and species. TWIST therefore occupies an intermediate position: it is less mechanistic than full hydraulic models, but easier to constrain and directly comparable with widely available dendrometer observations.

We show that TWIST can represent different stages of drought severity (Fig. 4.2). The module reproduces the characteristic diurnal pattern of daytime TWD increase followed by nocturnal recovery (De Schepper et al., 2012). As soil moisture declines, daily TWD amplitudes increase (Fig. 4.2b), indicating emerging soil water limitation (Peters et al., 2025). Progressive drying prolongs the replenishment of nocturnal storage, reducing the time available for stem growth (Zweifel et al., 2021b). With further drying, incomplete night-time recovery (Fig. 4.2c) marks the transition to full growth cessation. Residual pre-dawn TWD is then closely linked to sharp declines in midday stomatal conductance (Ziegler et al., 2024; Peters et al., 2025), underscoring its value as a robust drought indicator. As stomatal closure intensifies, E decreases, and daily

TWD amplitudes decline (Peters et al., 2025). Under severe drought (Fig. 4.2d), soil water uptake approaches zero, effectively disconnecting roots from the surrounding soil matrix (Nadal-Sala et al., 2024), while continued dehydration from residual water loss (Duursma et al., 2019) further increases TWD. By reproducing these characteristic TWD patterns, TWIST provides a diagnostic representation of physiologically meaningful water-deficit dynamics that are typically absent from ecosystem models (Martinez-Vilalta et al., 2019).

4.4.2 Evaluation of TWD and RWC_{tree} simulations and associated uncertainties

Applied to field conditions, TWIST captured the main temporal patterns of TWD across the calibration and evaluation periods (Figs. 4.3, 4.4). Agreement was highest in 2018, as expected, because this year was used for calibration. During 2019–2024, performance declined but the main dynamics were still reproduced without further parameter adjustment. Notably, years with pronounced TWD peaks were reproduced more consistently than wetter years with only weak depletion signals, suggesting that stronger drought responses are more clearly constrained by the coupled setup.

A major source of uncertainty arises from the driving inputs. Errors in estimating E or θ_{rel} directly affect the simulated timing and magnitude of TWD, including both seasonal peak values and sub-daily dynamics. In the present setup, both TWIST input variables were simulated by LandscapeDNDC. The underlying LandscapeDNDC water balance was evaluated against observations of seasonal total evapotranspiration (Fig. S4.8) and SWC (Fig. S4.10). The model matched these observations reasonably well, although deviations remained. Uncertainty in θ_{rel} is likely particularly important, because this variable must condense vertically heterogeneous soil water availability into a single quantity that reflects the effective accessibility of soil water to the stand. Errors in E , in turn, propagate directly into the amplitude of diurnal TWD cycles, and a combination of low θ_{rel} and high E can contribute to exaggerated TWD accumulation. Since TWD_{sim} integrates these drivers, uncertainties in input forcing and TWIST parameterization cannot be fully disentangled here and should instead be regarded as part of the performance of the LandscapeDNDC-TWIST system as a whole. In principle, TWIST could also be driven more directly by measurements. In practice, however, deriving the required inputs consistently is not straightforward, because E must be separated from ecosystem evapotranspiration and SWC must be converted into θ_{rel} referenced to field capacity and wilting point. Process-based ecosystem models are therefore useful because they provide these quantities in a temporally and structurally consistent form. Additional measurements, particularly sap-flux-based E estimates and more detailed soil moisture observations, could further constrain these uncertainties.

The calibrated parameter space was constrained but not unique, indicating that the three TWIST parameters are identifiable within a limited range while still allowing partial equifinality (Fig. 4.5). The sensitivity analysis further revealed distinct functional roles of the parameters

(Fig. 4.6). F_θ and F_{TWD} mainly governed the seasonal evolution of drought stress, as reflected in their relatively high rank correlations with model performance ($\rho = -0.61$ and 0.29 , respectively; Table S4.4). The strong coupling between these two parameters indicates that they are not independently constrained, but jointly determine model behavior. In contrast, F_E primarily controlled the amplitude of daily TWD cycles and showed only a weak relationship with overall model performance ($\rho = -0.05$). This is consistent with the observed model behavior, where sub-daily TWD amplitudes were sometimes over- or underestimated (Fig. 4.3d), making F_E comparatively challenging to constrain. The significant relationship between F_E and F_{TWD} (Fig. S4.11) indicates partial interdependence, as F_{TWD} also influences diurnal amplitudes. Overall, these results show that suitable combinations of F_θ and F_{TWD} reproduce the seasonality of TWD well, while F_E primarily influences sub-daily TWD dynamics.

Although the parameters used in TWIST are empirical and not directly measurable, they can be related to physiological and anatomical properties of the soil–plant water transport system. In conceptual terms, F_E controls the lag between current transpirational water loss and compensating soil water uptake, and may therefore be linked to vertical resistance along the xylem pathway. F_{TWD} controls the efficiency with which previously accumulated deficits are replenished, and may relate to radial and axial resistances between conductive xylem and storage compartments. F_θ determines the onset of additional soil moisture limitation and is likely influenced by rooting depth, soil properties, and the effective accessibility of soil water. These interpretations should not be understood as direct estimates of specific hydraulic traits; however, they indicate that the calibrated parameters are linked to physiologically interpretable roles.

Two structural assumptions are particularly important and associated with further uncertainty: the shape of the drought limitation function f_{drought} and the estimate of the available internal water pool W . First, the choice of f_{drought} (Eq. 4.2.3) remains simplified, and alternative formulations may be worth testing. Second, RWC_{tree} depends on the estimate of W , which is based on sapwood biomass in this study. If water exchange between sapwood and heartwood occurs (Treydte et al., 2021), the effective W may be larger than assumed here. Direct observations of tissue water content would therefore be particularly valuable for constraining physiologically realistic RWC_{tree} ranges (e.g. Matheny et al., 2015; Martius et al., 2024).

Despite these uncertainties, the simulated outputs TWD_{norm} and RWC_{tree} provide physiologically interpretable diagnostic indicators of plant water status. According to Peters et al. (2025), $\text{TWD}_{\text{norm}} = 1$ marks the onset of drought stress and stomatal closure, while values around 1.6 indicate turgor loss in *Fagus sylvatica*. These thresholds were repeatedly exceeded at the Štítná site during dry years, indicating pronounced drought stress. Likewise, simulated RWC_{tree} declined to values around 0.86 in 2018, corresponding to a temporary depletion of roughly 14 % of the internal water pool. This degree of depletion is consistent with 2018 having been exceptionally warm and dry at the Štítná site (Nezval et al., 2025). In previous studies,

comparable levels of depletion have been associated with hydraulic impairment in *Fagus sylvatica* seedlings (Rosner et al., 2019). Although mature trees are expected to tolerate somewhat greater depletion (Rosner et al., 2019), these values are consistent with pronounced physiological stress.

4.4.3 Boundary-case behavior under suppressed soil water recharge

The rainfall-suppression stress test represents a numerical boundary case in which the soil water pool was progressively depleted without replenishment (Fig. 4.7). In this setup, RWC_{tree} approached zero, corresponding to complete exhaustion of the modeled internal tree water storage. However, experimental studies have associated severe damage and mortality risk with RWC_{tree} values around 0.6 (Birami et al., 2018; Trueba et al., 2019; Sapes and Sala, 2021; Trifilò et al., 2023), and $RWC_{\text{tree}} = 0$ is unlikely to be reached under natural conditions. In LandscapeDNDC, no drought-induced tree mortality is currently implemented, and the depletion of RWC_{tree} towards zero is a direct consequence of residual E losses despite stomatal closure under sustained drought forcing. However, this progression likely overestimates water loss in natural systems, where severe tissue damage, mortality, and associated changes in residual water loss would alter the trajectory before complete depletion is reached. We therefore interpret the trajectory before $RWC_{\text{tree}} \approx 0.6$ as the physiologically relevant part of the test, whereas the subsequent dynamics primarily reflect the numerical behavior of TWIST after conditions associated with severe damage or mortality have likely been exceeded. The stress test should therefore be interpreted as a numerical boundary case rather than a biologically realistic mortality trajectory.

These dynamics have direct implications for the interpretation of TWD_{norm} . Because water depletion is limited to the available storage W , TWD plateaued once $RWC_{\text{tree}} = 0$ was reached. The maximum simulated TWD_{norm} values reached 26, but these primarily reflect continued water loss beyond physiologically meaningful conditions. A more physiologically interpretable reference point is therefore obtained at $RWC_{\text{tree}} \approx 0.6$, where TWD_{norm} was approximately 10. This is higher than the reported value of ~ 3 for drought-stressed mature *Fagus sylvatica* (Peters et al., 2025), but closer to the values reported for *Larix decidua* and *Pinus sylvestris* saplings at drought-induced tree death (8.4 and 12.0, respectively; TWD_{norm} time series shown in Fig. S4.12; Ziegler et al., 2024). However, such comparisons remain tentative, because published TWD_{norm} values near lethal dehydration are still scarce, the Peters et al. (2025) values refer to severe drought stress rather than mortality, and the values reported by Ziegler et al. (2024) were obtained for conifer saplings rather than mature beech trees.

4.4.4 Ways forward

A key way forward lies in applying TWIST to link expanding dendrometer observations with forest modeling frameworks. Because the module requires only E , θ_{rel} , and an estimate of available internal water storage, it can be integrated into models that already simulate transpiration

and soil moisture dynamics. The presented calibration workflow should further facilitate the derivation of site- and species-specific parameter sets where suitable evaluation data are available. With appropriate parameterization, the framework could in principle be applied across species, stand structures, and environmental conditions. This would allow TWIST to provide a diagnostic representation of internal tree water dynamics largely absent from current ecosystem models, enabling a direct link between such models and tree-level dendrometer drought-stress monitoring.

A second priority for future work is to move beyond the diagnostic role of TWIST by implementing feedbacks on drought-sensitive processes in coupled models. For example, stomatal regulation (Peters et al., 2025) or minimum leaf conductance (Bartlett et al., 2012; Trueba et al., 2026) could be related to TWD_{norm} or RWC_{tree} , allowing E to respond to progressive tree water depletion. Likewise, the close link of RWC_{tree} to cell turgor may provide a physiologically meaningful basis for representing drought-induced growth limitation and changes in carbon allocation (Potkay et al., 2022; Potkay and Feng, 2023). A further step could be to use RWC_{tree} thresholds or cumulative exposure to low-hydrated conditions to explore representations of progressive hydraulic impairment and mortality risk (Mantova et al., 2021; Mantova et al., 2022). However, such direct feedback is not yet implemented, and the corresponding threshold values require further evaluation before they can be applied more generally.

A further opportunity lies in testing whether RWC_{tree} can be related to remotely sensed indicators of canopy water status (Konings et al., 2019), thereby contributing to broader efforts to connect vegetation water content with ecosystem function (Binks et al., 2024). Because TWIST can be applied at stand scale while being constrained by tree-level dendrometer observations, it may provide a route for transferring physiological information from dendrometer measurements to broader ecosystem-scale assessments.

Combined datasets that link dendrometer records with coordinated ecosystem flux measurements, remote sensing products, soil moisture observations, sap flow, biomass estimates, or direct measurements of tissue water content would be particularly valuable for constraining TWIST parameters, testing transferability across sites and species, and developing feedback formulations that move TWIST beyond its current diagnostic role.

4.4.5 Conclusion

We presented TWIST, a diagnostic framework for translating imbalances between transpiration and water uptake into volume-based tree water deficit (TWD) dynamics. Despite its parsimonious structure, the module reproduced characteristic TWD patterns, including diurnal depletion–refilling cycles, incomplete nocturnal recovery, and progressive seasonal deficit accumulation. By generating a model state variable that can be compared with dendrometer-derived TWD, TWIST provides a practical interface between tree-level drought monitoring and process-based stand-level simulations. The derived relative tree water content (RWC_{tree}) further expresses

water deficits relative to an estimated internal water pool, which may also facilitate links to remotely sensed observations of canopy water status indicators. Together, TWD and RWC_{tree} provide complementary diagnostic indicators of internal tree hydration status, a component still often missing from current ecosystem models (Martinez-Vilalta et al., 2019). TWIST requires only a small number of inputs commonly available in process-based models, and the provided parameter calibration routine may support broader application. By making TWD available as a model-compatible diagnostic variable, TWIST creates a direct route for using expanding dendrometer datasets to evaluate and improve simulations of forest drought stress.

Acknowledgments

This study benefited from ongoing efforts to improve measurement standards and harmonize eddy covariance data processing within the FLUXNET and ICOS networks. In the preparation of this manuscript, the authors used ChatGPT (GPT-5.5, OpenAI) to support language refinement and code development for data analysis, plotting, and parameter calibration/evaluation. All AI-assisted output was reviewed, edited, and validated by the authors, who take full responsibility for the final content.

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4.5 Supplementary Material for Chapter 4

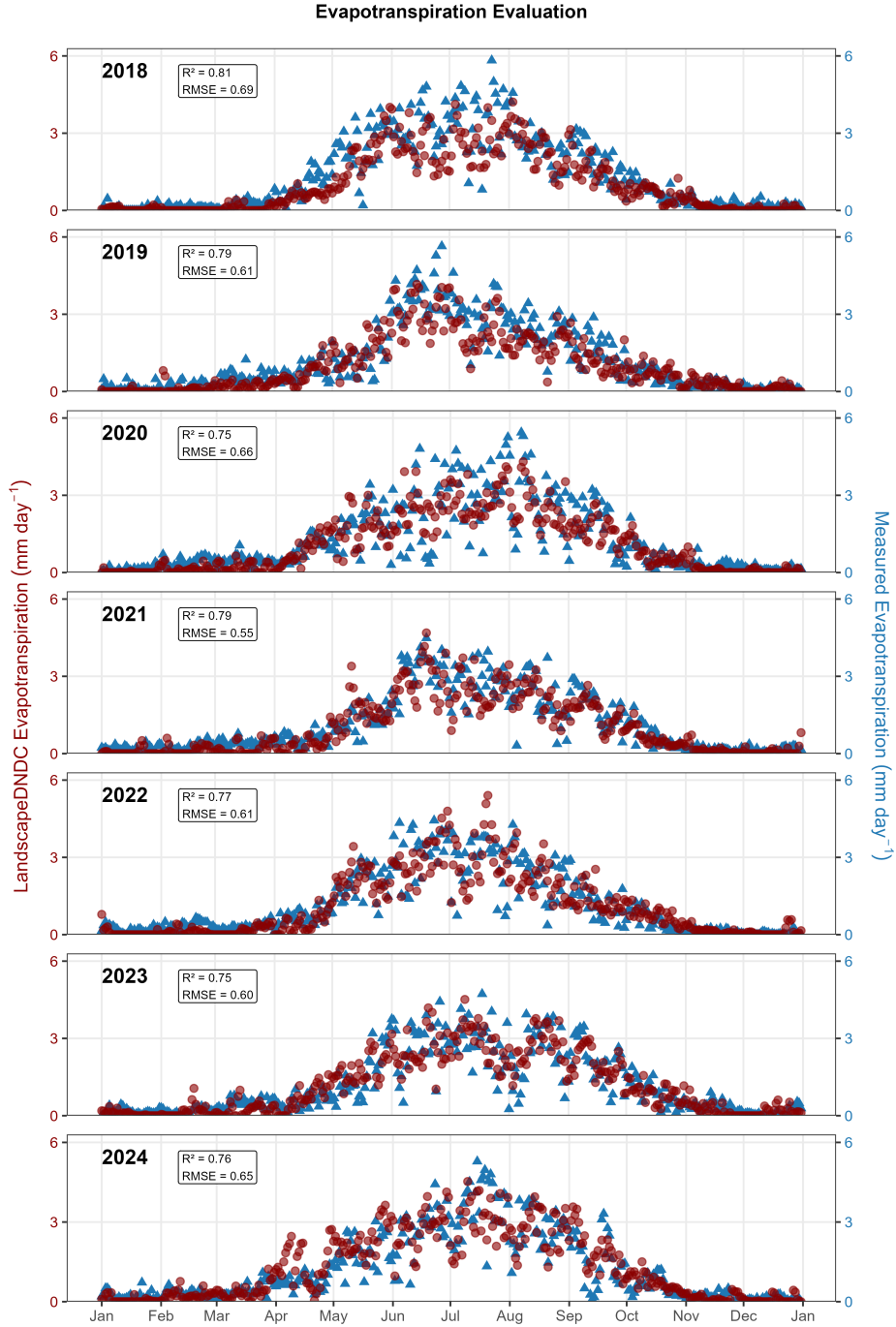


Figure S4.8: Evaluation of LandscapeDNDC-modeled Evapotranspiration (red) against observations (blue) at the Štítná forest site for the years 2018–2024, with statistical metrics (R^2 , RMSE) quantifying model–data agreement.

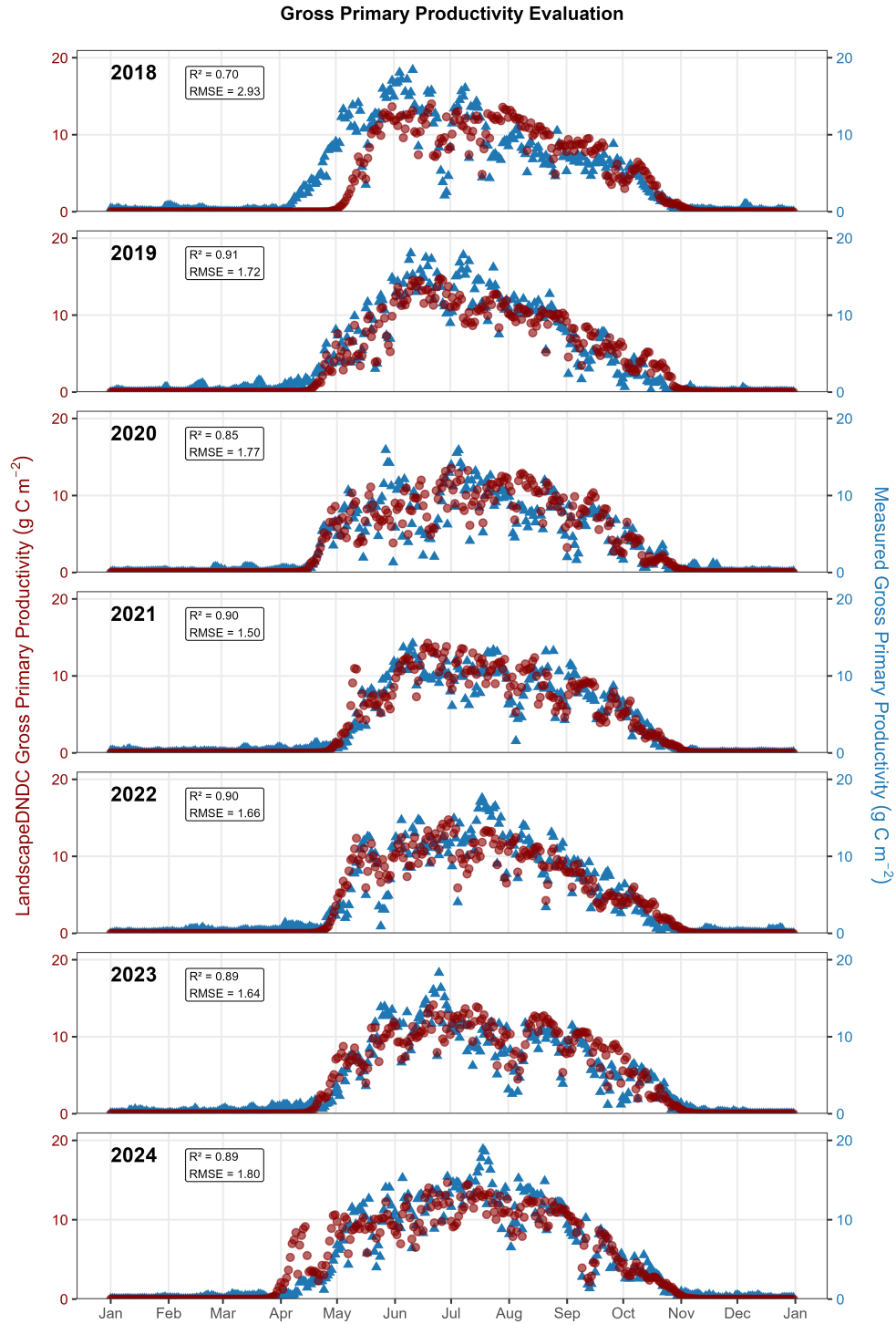


Figure S4.9: Evaluation of LandscapeDNDC-modeled Gross Primary Productivity (red) against observations (blue) at the Štítná forest site for the years 2018–2024, with statistical metrics (R^2 , RMSE) quantifying model–data agreement.

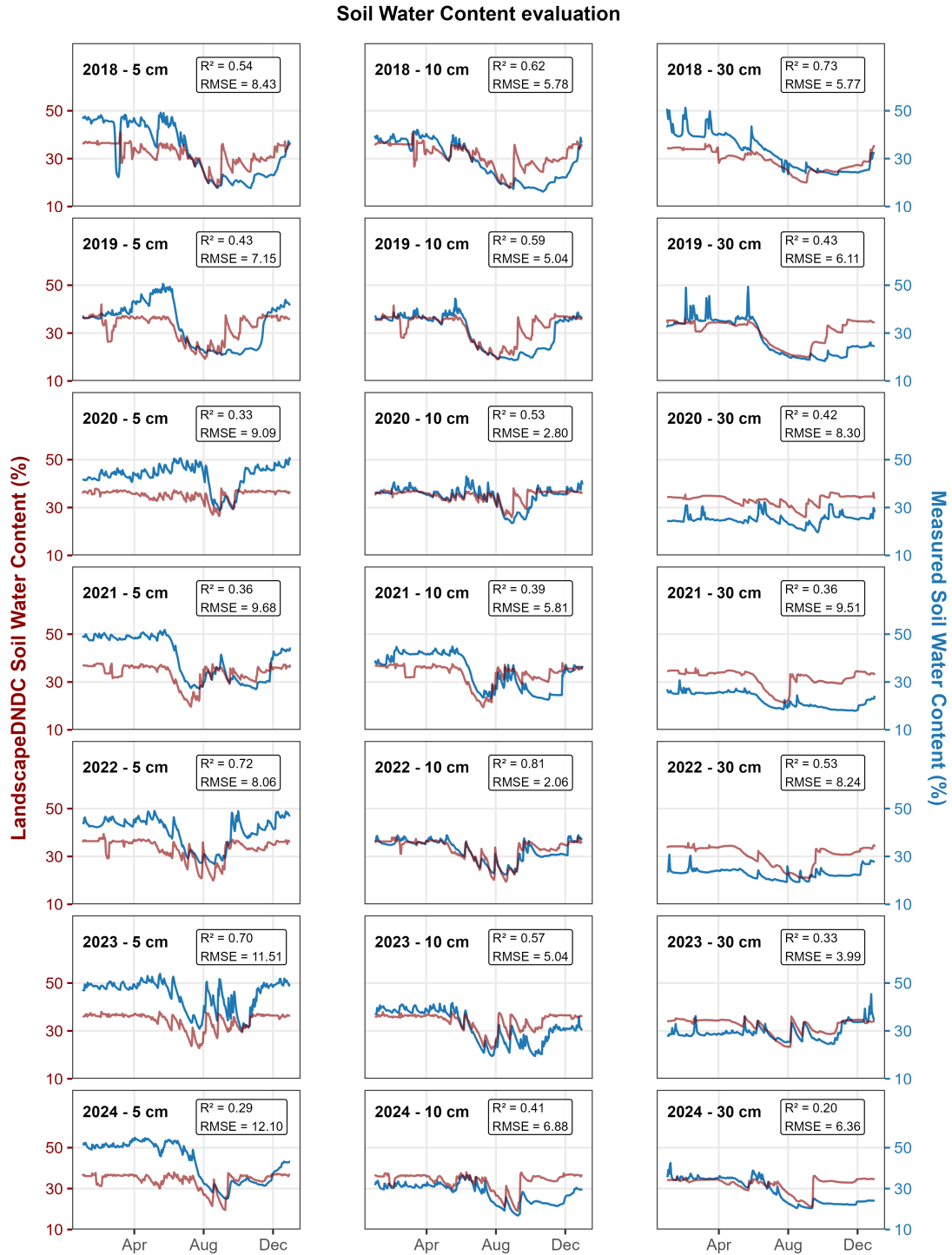


Figure S4.10: Evaluation of LandscapeDNDC-modeled soil water content (red) against measured (blue) at the Štítná forest site for the years 2018–2024 in three different depths, with statistical metrics (R^2 , RMSE) quantifying model–data agreement.

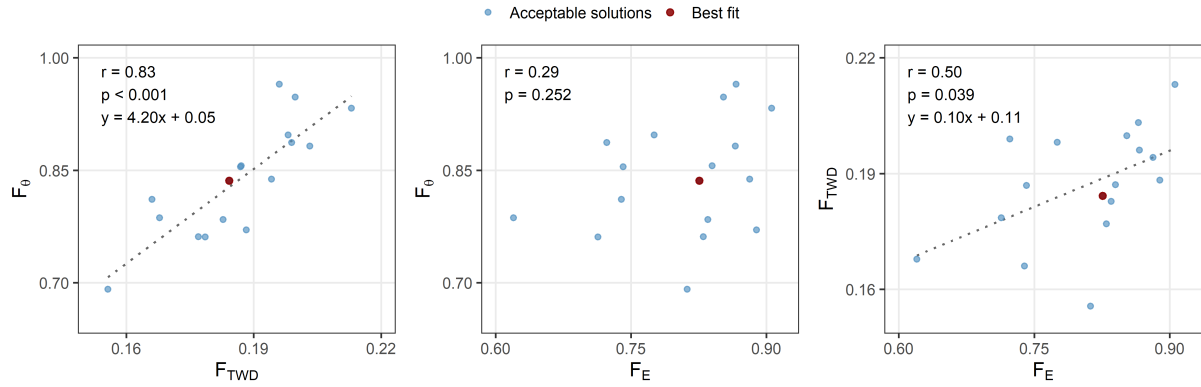


Figure S4.11: Relationships between TWIST model parameters based on the subset of acceptable solutions (defined as parameter sets with an objective value within 5% of the best-fit objective value; $n=17$). Scatterplots show pairwise relationships between the parameters F_E , F_{TWD} and F_θ . Blue points represent acceptable parameter combinations, and the red point indicates the best-fit solution. The annotated values denote the Pearson correlation coefficient (r) between parameter pairs across all acceptable solutions, indicating the strength and direction of their linear dependency. A linear regression fit (dashed line) is only shown if a significant relationship was evident ($p<0.05$).

For comparison: Ziegler et al. (2024) TWD, updated with MDS normalization

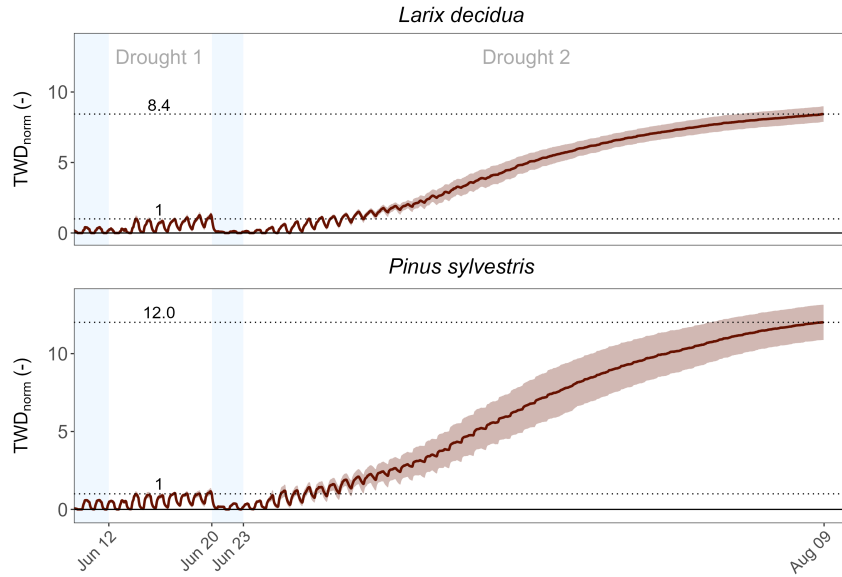


Figure S4.12: Dendrometer-derived TWD development under lethal dehydration in a greenhouse experiment covering two species, adapted from Ziegler et al. (2024). In contrast to the original paper, the normalization procedure was changed to MDS normalization (Peters et al., 2025) applied to the treatment mean timeseries to allow comparison with the current study.

Table S4.3: Selected LandscapeDNDC parameters required for transpiration demand and stomatal conductance calculations at the Štítná *Fagus sylvatica* site.

Parameter	Unit	Value	Description
RPMIN	mmol m ⁻¹ m ² LA s MPa	1.4	Minimum whole-plant resistance
GSMIN	mmol H ₂ O m ⁻² s ⁻¹	4.3	Minimum leaf conductance
GSMAX	mmol H ₂ O m ⁻² s ⁻¹	81.5	Maximum leaf conductance
A_EXP	–	6.2	Curve parameter for non-stomatal-limitation effect on photosynthesis
A_REF	MPa	-4.8	Reference ψ for non-stomatal-limitation effect on photosynthesis
CWP_REF	mmol MPa ⁻¹ m ⁻² s ⁻¹	10	Specific xylem conductance
PSI_EXP	–	6.5	Curve parameter for ψ impact on conductance
PSI_REF	MPa	-3.6	Reference ψ for conductance vulnerability curve
MFOLOPT	kgDW m ⁻² ground	0.25	Foliage biomass for mature stands

Table S4.4: TWIST best-fit parameter values and distribution of acceptable solutions. Acceptable solutions ($n = 17$) are defined based on the 2018 calibration period as parameter sets yielding calibration performance within 5% of the best-fit solution (see Methods). Reported are the best-fit value, median (q50), interquartile range (q25–q75), and full acceptable range (min–max) for each parameter. Spearman rank correlation coefficients (ρ), calculated across the full 2018–2024 time series, indicate the sensitivity of model performance to parameter variation.

Parameter	Best fit	min	q25	median	q75	max	Spearman ρ
F_E	0.83	0.62	0.74	0.83	0.87	0.91	-0.05
F_{TWD}	0.19	0.16	0.18	0.19	0.20	0.21	0.29
F_θ	0.84	0.69	0.78	0.84	0.89	0.96	-0.61

Table S4.5: TWIST individual parameter sets and associated performance metrics for all acceptable solutions ($n = 17$), defined as parameter sets yielding calibration performance within 5% of the best-fit solution (see Methods). Reported are model parameters, objective function values (obj), normalization factor (q99), and performance metrics for calibration (c) and evaluation (e) periods at hourly (h) and daily (d) resolution.

ID	F_E	F_{TWD}	F_θ	obj	q99	cRMSE _h	cRMSE _d	cBias _h	cBias _d	cR _h ²	cR _d ²	eRMSE _h	eRMSE _d	eBias _h	eBias _d	eR _h ²	eR _d ²
1	0.83	0.18	0.84	0.88	0.99	0.23	0.19	-0.02	-0.02	0.92	0.94	0.41	0.40	-0.03	-0.03	0.42	0.42
2	0.84	0.19	0.86	0.88	0.99	0.23	0.19	-0.01	-0.01	0.92	0.94	0.41	0.40	-0.02	-0.02	0.42	0.42
3	0.88	0.19	0.84	0.88	0.94	0.23	0.19	-0.04	-0.04	0.92	0.94	0.41	0.40	-0.05	-0.05	0.42	0.42
4	0.84	0.18	0.78	0.88	0.93	0.23	0.19	-0.04	-0.04	0.92	0.94	0.41	0.40	-0.05	-0.05	0.42	0.42
5	0.83	0.18	0.76	0.89	0.92	0.23	0.19	-0.04	-0.04	0.92	0.94	0.41	0.40	-0.05	-0.05	0.42	0.42
6	0.85	0.20	0.95	0.89	1.03	0.23	0.19	0.01	0.01	0.92	0.94	0.42	0.40	0.00	0.00	0.42	0.42
7	0.91	0.21	0.93	0.89	0.99	0.23	0.19	-0.04	-0.04	0.92	0.94	0.41	0.39	-0.04	-0.04	0.42	0.42
8	0.74	0.19	0.85	0.89	1.03	0.23	0.19	0.00	0.00	0.92	0.94	0.41	0.39	0.00	0.00	0.42	0.42
9	0.78	0.20	0.90	0.89	1.03	0.23	0.19	-0.01	-0.01	0.92	0.94	0.41	0.39	-0.01	-0.01	0.42	0.42
10	0.87	0.20	0.88	0.89	0.98	0.23	0.19	-0.04	-0.04	0.92	0.94	0.41	0.39	-0.04	-0.04	0.42	0.42
11	0.72	0.20	0.89	0.90	1.04	0.23	0.20	-0.01	-0.01	0.92	0.94	0.40	0.39	0.00	0.00	0.42	0.42
12	0.74	0.17	0.81	0.91	1.03	0.23	0.20	0.03	0.03	0.92	0.94	0.42	0.41	0.01	0.01	0.42	0.42
13	0.62	0.17	0.79	0.91	1.06	0.24	0.20	0.02	0.02	0.91	0.94	0.41	0.40	0.02	0.02	0.42	0.42
14	0.81	0.16	0.69	0.91	0.89	0.23	0.20	-0.02	-0.02	0.92	0.94	0.42	0.41	-0.04	-0.04	0.42	0.42
15	0.71	0.18	0.76	0.91	1.00	0.23	0.20	-0.04	-0.04	0.92	0.94	0.40	0.38	-0.03	-0.03	0.42	0.42
16	0.87	0.20	0.96	0.91	1.04	0.24	0.20	0.03	0.03	0.92	0.94	0.42	0.41	0.02	0.02	0.42	0.42
17	0.89	0.19	0.77	0.92	0.89	0.23	0.20	-0.07	-0.07	0.92	0.94	0.41	0.40	-0.08	-0.08	0.42	0.42

5 SYNTHESIS

Dendrometer-derived tree water deficit (TWD) is increasingly used as a proxy for tree water status, but its physiological interpretation, transferability, and model compatibility remain only partly resolved. The three studies presented in this thesis address these issues from complementary perspectives. Chapter 2 improves the physiological interpretation of TWD by linking it to water potential, stomatal conductance, severe drought, and recovery dynamics. Chapter 3 shows that normalized TWD can provide a common axis for drought-stress responses across experimental systems. Chapter 4 develops a module that enables the representation of TWD-like dynamics in process-based modeling frameworks. Together, these studies support the interpretation of TWD as a continuous and integrative indicator linking environmental controls, tree water-use strategies, and drought responses, as summarized in the synthesis framework in Fig. 5.1. Building on this framework, this synthesis argues that the main value of TWD lies not in providing specific, universal drought thresholds but in linking temporal drought-stress patterns, physiological transition zones, and model-compatible representations of internal tree water dynamics.

5.1 Beyond stem shrinkage: physiological information gained from TWD

At the most reduced level, TWD can be understood as the observable outcome of an imbalance between tree water loss and uptake, resulting in changes of internal water storage (Zweifel et al., 2005). This interpretation is made explicit in the TWIST module concept presented in Chapter 4, where TWD is represented as the deficit within a single tree water pool, which is depleted by transpiration and replenished by soil water uptake. Real trees are, of course, more complex than this simplified representation: water is stored and redistributed across multiple tissues and compartments, with water flows between them being shaped by water potential gradients and hydraulic resistance (Cochard et al., 2021). While TWIST estimates TWD directly as a volume-based deficit, dendrometer-derived TWD captures the shrinkage of elastic tissues rather than water loss itself, and therefore also depends on tissue anatomy and elasticity (Steppe et al., 2006; Restrepo-Acevedo et al., 2026). Nevertheless, the simplified balance framework captures the central physiological meaning of TWD as a proxy for changing tree water content. This

simplification is useful here because it provides a common language for interpreting the empirical relationships observed in Chapters 2 and 3 and the model representation developed in Chapter 4.

The balance framework also illustrates why TWD provides different information than external drought indicators. Soil water availability, atmospheric demand, and temperature describe environmental forcing, but they do not directly indicate how trees experience and buffer such conditions (Novick et al., 2022). TWD, in contrast, reflects the interaction of external forcing with tree-specific traits and water-use strategies (Zweifel et al., 2005; Sánchez-Costa et al., 2015; Martinetti et al., 2025, Fig. 5.1A). In this sense, TWD is not simply a measure of general drought severity but rather an integrated tree-level drought-stress response. This integrative character is central to its physiological value because it links environmental conditions to the internal hydration state of living tissues, which in turn affects tree function.

An important part of physiological information lies in the temporal pattern of TWD (Fig. 5.1B). A diurnal increase in TWD that fully recovers overnight indicates reversible daily use of internal water stores, with daytime depletion compensated by nocturnal replenishment. Increasing diurnal TWD amplitudes indicate that more internal tree water is mobilized, for example, under higher atmospheric demand or reduced water uptake (King et al., 2013; Peters et al., 2025). When nocturnal water uptake is insufficient to fully replenish internal water stores, pre-dawn TWD exceeds 0, indicating a shift from fully reversible daily dynamics toward sustained internal water depletion. Under more severe dehydration, TWD may increase almost monotonically, suggesting that residual water losses continue while uptake is strongly constrained or may cease. Recovery after stress release then provides information on whether drought-induced changes remained reversible or if hydraulic or cellular legacy effects persist. These temporal patterns are discussed in more detail as physiological transition zones in Section 5.3.

In addition to these temporal patterns, TWD magnitudes and normalized TWD values also provide essential information. In Chapter 2, TWD closely tracked declines in water potential and stomatal conductance as dehydration progressed to lethal conditions. Chapter 3 extended this link from discrete physiological measurements to whole-tree gas exchange dynamics, showing that stomatal conductance, transpiration, and daily net carbon balance decline along a normalized TWD axis. However, TWD did not fully constrain stomatal conductance and transpiration, which are also influenced by vapor pressure deficit, heat, and short-term water availability. In contrast, normalized TWD constrained the daily tree-level net carbon balance more consistently, suggesting that it may provide a stronger axis for functional carbon limitation than for instantaneous water loss.

Tree water deficit (TWD) as an integrative drought-stress signal

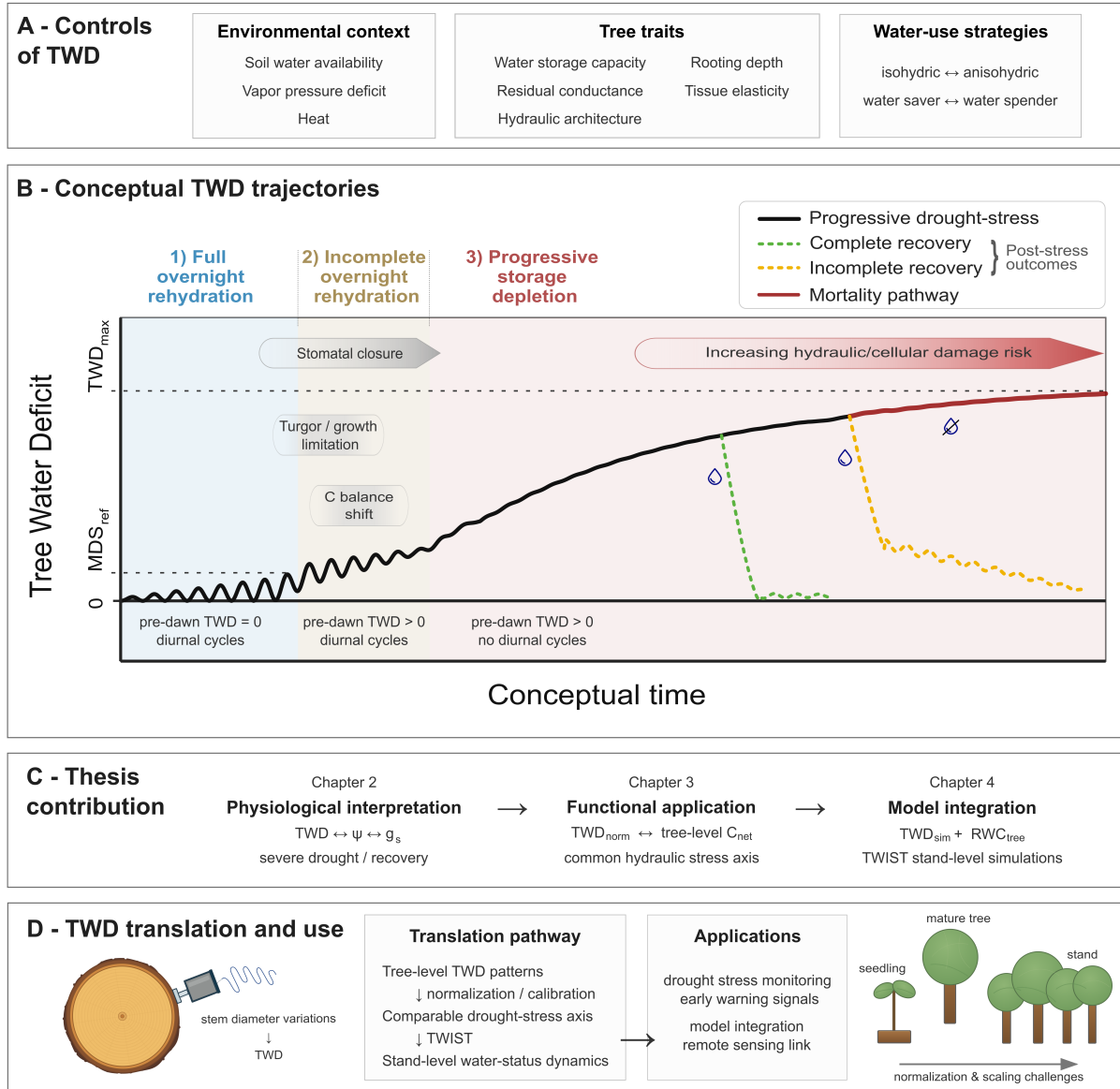


Figure 5.1: Thesis synthesis figure introducing tree water deficit (TWD) as an integrative drought-stress signal. Panel (A) presents factors that control TWD development. Panel (B) shows conceptual TWD trajectories during progressive dehydration across three phases: 1) full overnight rehydration of daytime TWD, 2) incomplete overnight rehydration, and 3) progressive storage depletion resulting in monotonically increasing TWD. Blue drops mark stress release, after which trajectories may show complete (green) or incomplete (yellow) recovery, while continued dehydration results in mortality (red). Dashed horizontal lines indicate normalization references, with MDS_{ref} representing the highest daily shrinkage amplitude and TWD_{max} the maximum absolute TWD in the time series. Panel (C) summarizes the thesis contribution as a progression from physiological interpretation to functional application and model integration. Panel (D) introduces how TWD can be translated from tree-level patterns into comparable drought-stress metrics and stand-level water-status dynamics.

The physiological basis for these relationships is conceptually clear. Increasing TWD implies that elastic tissues have lost water and volume, which is associated with reduced turgor, declining relative water content, and shifts in tissue water potential (Steppe et al., 2006; De Schepper et al., 2012; De Swaef et al., 2015). These changes directly affect several drought-sensitive processes. Reduced turgor constrains cell expansion and growth (Peters et al., 2021; Zweifel et al., 2021b). Meanwhile, declining water potential increases hydraulic risk and triggers stomatal closure, thereby reducing transpiration and carbon assimilation while respiratory carbon losses continue. (Flexas, 2002; Choat et al., 2012; Buckley, 2019). Thus, the observed links between TWD, water potential, stomatal regulation, carbon balance, and hydraulic damage risk are physiologically plausible consequences of tissue dehydration. The key question is therefore not whether TWD contains physiological information, but how consistently this information can be interpreted across species, stress trajectories, and observational scales.

Together, these findings show that the added value of TWD lies in its ability to integrate multiple dimensions of drought response into a single signal. However, this strength is also its main interpretive challenge: because TWD reflects the combined effects of soil water availability, atmospheric demand, water-use regulation, and tissue hydration, it cannot be attributed to a single underlying process without additional context. Physiological interpretation requires information on environmental conditions and functional tree responses, and direct comparison across trees, species, sites, or model outputs requires appropriate normalization, which is addressed in the following section.

5.2 From local TWD signals to transferable stress metrics

When the objective shifts from interpreting a single time series to comparing drought stress across contexts, normalization becomes essential. Absolute TWD amplitudes are installation-specific because stem shrinkage depends not only on drought intensity, but also on tree size and age, tissue anatomy, elasticity, bark properties, sensor position, rooting depth, soil properties, microclimate, and previous stress history (De Swaef et al., 2015; Andriantelomanana et al., 2024; Restrepo-Acevedo et al., 2026). Thus, the same absolute TWD value does not necessarily indicate the same physiological stress level in different trees. Normalization is therefore the step that can turn TWD from a local dendrometer signal into a transferable stress metric (Fig. 5.1D). It is also a prerequisite for defining comparable TWD–function relationships and thresholds across species, study systems, or model representations.

In Chapter 2, normalizing TWD relative to the deficit reached during lethal dehydration provided an experimentally meaningful stress scale covering the full gradient from well-watered conditions to mortality. However, such a reference is rarely available in field monitoring. Mortality-based normalization is therefore useful for controlled experiments including lethal conditions,

but cannot provide a broadly applicable reference for monitoring.

A more operational approach was introduced by Peters et al. (2025), who normalized TWD to a common reference value based on diurnal stem-radius dynamics, namely the highest possible maximum daily shrinkage (MDS_{ref}) within a time series (Fig. 5.1B). In practice, MDS_{ref} is estimated as the 99% percentile of observed maximum daily shrinkage values, with stable estimates requiring approximately two to three years of data, including periods of sufficient drought stress. Because MDS_{ref} represents the observed shrinkage capacity of elastic tissues, this approach reduces differences in absolute shrinkage amplitudes while retaining a physiological interpretation.

Chapters 3 and 4 modified this MDS_{ref} -based normalization concept. In Chapter 3, the approach was adapted to shorter experimental time series, allowing different species and experimental setups to be compared along a common normalized TWD axis. In Chapter 4, the same logic was applied to simulated TWD dynamics, enabling comparison of dendrometer-derived and modeled TWD dynamics despite differences in units and scale. In this sense, normalization served as a translation between dendrometer observations and model outputs.

Despite this progress, it remains unresolved whether MDS_{ref} -based normalization is sufficient to enable broad transferability. The method is attractive because the reference can be derived from dendrometer time series themselves, but MDS_{ref} may still depend on data availability, measurement context, and stress history, and could change over time. Thus, MDS_{ref} -based normalization is promising, but still requires further testing.

One motivation for TWD normalization is the potential to derive continuous estimates of water potential from dendrometer measurements (Dietrich et al., 2018). However, if establishing universal relationships between water potential and TWD remains difficult, installation-specific calibration offers a complementary route. Such an approach already exists for optical dendrometers that measure tissue shrinkage in petioles or needles, a response that also correlates with water potential (Bourbia et al., 2025). Similarly, absolute TWD measured with classical dendrometers can be calibrated locally against repeated water potential measurements. Chapter 2 suggests that this relationship can be tight and approximately linear during progressive dehydration, but that hydraulic damage or recovery hysteresis may temporarily alter it. Such calibrations would not provide a universal stress axis, but could make individual dendrometer installations more physiologically informative. At the same time, the temporal stability of such calibrations remains uncertain because new xylem formation, bark development, changes in tissue elasticity, or sensor repositioning may alter the TWD–water potential relationship and necessitate recalibration.

Taken together, the interpretation of TWD depends on the level of application: temporal patterns can be investigated within individual time series, installation-specific calibration can support local estimates of tree water status, and normalization is required when TWD is used as a transferable stress metric, particularly if TWD-based thresholds are applied.

5.3 Physiological transition zones and early-warning signals along the TWD axis

As demonstrated in Chapter 3, appropriately normalized TWD has the potential to serve as a comparable drought-stress axis across experimental contexts. Along this axis, the relevant information is not limited to single critical values. Instead, accumulating TWD can indicate a sequence of physiological transitions, ranging from reversible drought responses to functional limitations, impaired recovery, and increasing mortality risk (Fig. 5.1B). Independent of normalization, this stress progression can be conceptually separated into three phases: 1) full overnight rehydration of daytime TWD, 2) incomplete overnight rehydration, and 3) progressive storage depletion with strongly reduced diurnal cycles. These phases provide a pattern-based way to distinguish low stress, functional limitations, and severe or potentially damaging stress.

The transition from phase 1 to phase 2 is marked by the loss of full overnight rehydration, expressed as pre-dawn TWD remaining above zero. This indicates that the previous day's water deficit was not fully replenished overnight and, according to the zero-growth concept (Zweifel, 2016), that radial growth is likely constrained by turgor limitation. In Chapter 2, this state was also associated with strong stomatal restriction at the following midday. It is also the TWD range in which the highest diurnal TWD amplitudes are expected, indicating that stomata still allow for substantial daytime water loss, while water uptake is already insufficient to fully buffer transpirational demand (Peters et al., 2025). With increasing drought severity, stomatal closure can reduce daytime water loss, thereby decreasing diurnal TWD amplitudes even as pre-dawn TWD continues to increase. Thus, phase 1 represents low stress conditions, whereas the transition to phase 2 marks the onset of turgor limitation on growth and the downregulation of gas exchange. As seen in Chapter 3, phase 2 is associated with rapid stomatal closure, reduced transpiration, and the transition from positive to negative daily carbon balance.

The transition from phase 2 to phase 3 occurs when diurnal TWD cycles are substantially reduced, and TWD increases more monotonically, indicating that residual water losses continue while water uptake is strongly limited. The slope of this increase may therefore provide information on residual water losses, shaped by atmospheric water demand and contributions from minimum stomatal conductance, cuticular conductance, and bark water loss (Blackman et al., 2019; Duursma et al., 2019). A progressive flattening of the TWD trajectory may further indicate that the remaining extractable water in elastic tissues becomes increasingly depleted or more tightly bound. Chapter 2 links such TWD levels to increasing hydraulic and tissue damage risks, altered TWD–water potential relationships, and ultimately mortality. While these interpretations remain partly conceptual, they illustrate how TWD trajectories can provide information beyond absolute deficit magnitude.

If stress is relieved by newly available soil water, the recovery pattern of TWD provides

additional diagnostic information on whether drought-stress impacts remained reversible. The shape of this recovery trajectory may also provide information on effective capacitance, although this interpretation requires further testing. Apparent complete recovery, expressed as TWD returning to zero, suggests effective rehydration of all elastic tissues, whereas incomplete recovery of TWD may indicate tissue damage due to cell necrosis or impaired hydraulic function (Mantova et al., 2021). The ratio of unrecovered to recovered TWD could therefore serve as a proxy for overall damage and recovery potential. The absence of any TWD reduction despite stress release likely indicates a complete loss of hydraulic or cellular functionality and, therefore, mortality (Andriantelomanana et al., 2024).

When TWD normalization achieves sufficient transferability, these pattern-based interpretations can be complemented by functional thresholds. Chapter 3 provides one example: daily tree-level net carbon balance shifted from net carbon uptake to net carbon loss at approximately $TWD_{\min, \text{norm}} = 0.20$. Other potential thresholds, such as the onset of hydraulic damage derived in Chapter 2, turgor loss (Peters et al., 2025), or mortality risk (Andriantelomanana et al., 2024), may also become useful. However, as discussed in the previous section, normalization needs further exploration, and functional thresholds require more rigorous evaluation before they can be applied broadly.

Importantly, even before normalization is fully resolved, the pattern-based interpretations developed here provide a useful framework. For monitoring, they can help translate continuous dendrometer records into interpretable stress states, ranging from reversible daily dehydration to functional limitation, severe stress, and recovery failure.

5.4 TWD as a bridge between tree-level observations and ecosystem models

The preceding sections focused on the physiological interpretation of TWD at the tree level. This is the scale at which dendrometers provide their strongest information, because they record diameter dynamics of individual stems. However, many questions motivating drought monitoring and model projections concern stands and ecosystems. A central step is therefore to translate the physiological information contained in tree-level TWD into model-compatible variables that can be linked to stand-level fluxes and broader monitoring approaches (Fig. 5.1D).

This model-compatible representation is particularly relevant because process-based ecosystem models remain limited in their representation of drought legacy effects and drought-induced forest decline (Anderegg et al., 2015; Hartmann et al., 2018), partly because internal tree water storage and its depletion are rarely represented (Martinez-Vilalta et al., 2019; Bugmann et al., 2019). While water-potential-based approaches provide a physiologically powerful link to hydraulic stress, they are also complex due to their dependence on nonlinear soil–plant water relations.

Storage-based metrics offer a complementary approach by integrating cumulative imbalances of water fluxes, which is more straightforward to represent yet remains physiologically relevant. Models that explicitly resolve internal water dynamics exist and can provide detailed mechanistic insight, but are often complex and thus limited in broad application (e.g. Cochard et al., 2021).

Chapter 4 addresses these gaps with the TWIST module, which translates the TWD concept into a model-compatible representation of internal tree water dynamics, thereby making the physiological information contained in TWD patterns available in process-based models. TWIST uses transpiration and relative soil water availability to simulate depletion and rehydration of an internal tree water pool, from which both TWD, expressed as a volumetric water deficit, and relative tree water content are derived as diagnostic variables of internal water status. When driven by stand-level transpiration, TWIST provides a model-based framework for linking tree-level dendrometer data to stand-level assessments.

In this framework, scaling does not require a direct translation of dendrometer-measured stem shrinkage into stand-level water loss. Instead, the relevant link is whether observed and simulated TWD dynamics describe comparable patterns, including the timing, relative intensity, duration, and recovery of drought stress. Simulated TWD and relative tree water content can therefore be evaluated against dendrometer observations and related to ecosystem-scale fluxes and remotely sensed proxies of canopy water status. This creates a two-way link between observations and models: dendrometer measurements can be interpreted beyond individual trees, while ecosystem models gain diagnostic variables of internal water status.

Beyond its diagnostic role, TWIST provides a conceptual basis for functional feedback loops within ecosystem models. If simulated TWD and/or relative tree water content can be linked to stomatal regulation, photosynthesis, growth, allocation, recovery, or damage risk, internal water deficit dynamics could become active components of simulated drought responses rather than merely diagnostic outputs. Thus, Chapter 4 extends the thesis from interpreting dendrometer-derived tree-level TWD toward representing TWD as a model-compatible component of ecosystem-scale assessments.

5.5 Limitations and future directions

5.5.1 Physiological interpretation and transferability

The physiological basis for interpreting TWD in Chapters 2 and 3 is derived from controlled experiments with potted seedlings. This experimental setting was essential for imposing severe drought and combining dendrometer signals with water potential and gas exchange measurements at high temporal resolution. At the same time, it limits direct transfer to mature forest trees, which differ from young trees in crown exposure, rooting environment, growth dynamics, and the use of stored water (Oberhuber, 2017). In addition, potted experiments restrict rooting volume and

simplify soil heterogeneity, competition, and microclimate variation. The relationships identified here therefore provide a mechanistic basis for interpreting TWD, but their transferability requires further evaluation under field conditions.

A central next step is to test whether the TWD–water potential relationships observed in Chapter 2 also hold in mature trees exposed to severe or lethal drought. Such data are still scarce because severe dehydration in mature field trees is rarely captured, and repeated physiological measurements are often constrained. Key open questions are whether the relationship remains approximately linear during progressive dehydration, shifts near hydraulic damage, and shows hysteresis or incomplete recovery after stress release. Addressing these questions would require combining dendrometers with repeated or continuous water potential measurements, hydraulic vulnerability information, and observations of recovery following natural drought or within throughfall-exclusion setups in mature forest stands.

Transferability also remains a central challenge. As discussed above, MDS_{ref} -based normalization is a promising route toward comparing TWD across different contexts, but its robustness has not yet been tested broadly enough. Future work should therefore evaluate whether this normalization preserves physiologically meaningful relationships across age classes, tree sizes, species, sites, and drought trajectories. In parallel, alternative normalization approaches should be developed and compared, including installation-specific TWD–water potential calibrations where universal normalized relationships are not achievable.

5.5.2 Functional consequences, growth, and recovery

Chapter 3 indicates that normalized TWD can constrain daily carbon balance across species, but the underlying experiments were not specifically designed to test this relationship. The synthesized setups differed in experimental duration, watering regimes, and atmospheric conditions, and lacked a common framework of coordinated water potential and non-structural carbohydrate measurements. Targeted experiments combining dendrometer measurements with whole-tree gas exchange, measurements of carbon pools and allocation, and direct growth observations are therefore needed to test TWD–carbon balance relationships more rigorously. Such experiments could also evaluate the zero-growth concept at the cellular level, because cambial activity, cell division, cell enlargement, and wall thickening may become partly uncoupled under declining turgor and carbon availability.

Chapter 3 also showed that TWD relates to gas exchange, but stomatal conductance and transpiration were also influenced by vapor pressure deficit and heat. Future studies should therefore explicitly account for atmospheric demand, particularly under compound drought and heat stress (Werner et al., 2025), and test when TWD alone is sufficient to indicate functional limitation and when combined TWD–atmospheric-demand metrics are needed.

Beyond immediate functional limitation, TWD recovery dynamics and their relation to drought-

induced tissue damage should be further tested. Chapter 2 provided insight into TWD recovery after severe drought, but rewatering occurred only at one advanced stress stage, and hydraulic impairment or cellular damage were not directly measured. Future experiments could rewater drought-stressed trees at different TWD levels and then follow TWD, water potential, and gas exchange during recovery, while also quantifying hydraulic impairment and cellular damage, for example, through electrolyte leakage (Andriantelomanana et al., 2024). Such designs would help identify when dehydration remains reversible, when recovery becomes incomplete, and when TWD dynamics indicate lasting damage or increased mortality risk.

5.5.3 Modeling and upscaling

The main limitation of the modeling approach developed in Chapter 4 is also its main strength: TWIST represents internal tree water dynamics in a deliberately simple way. It uses a single, coarsely estimated internal water pool and does not distinguish between tissue-specific storage compartments. Simulated TWD represents a volumetric water deficit rather than stem shrinkage, which strengthens its physiological interpretation but currently limits evaluation against dendrometer-derived TWD to normalized temporal dynamics. This reduced complexity supports broad application, but robustness and transferability remain to be tested beyond the single species and site evaluated in Chapter 4.

Parameter uncertainty represents a related limitation. The three TWIST parameters are empirical controls rather than direct measurements of hydraulic traits, but they likely depend on measurable tree properties, including tissue characteristics, hydraulic conductivity, and root distribution. Future applications could test whether TWIST parameters can be constrained by measurable morphological or physiological traits, or whether empirical species-, tree size-, and site-dependent parameterizations are required.

Future TWIST evaluations should further combine dendrometer-derived TWD with independent observations of internal water storage, such as tissue water content measurements, to assess whether simulated absolute water deficits are physiologically plausible. In addition, TWIST inputs may also be constrained with supplemental observations, such as sap-flow-based transpiration estimates (Poyatos et al., 2021) and detailed soil moisture measurements. Because TWIST is driven by transpiration and relative soil water availability, uncertainty in these inputs propagates directly into simulated outputs. Overall, such evaluations would help determine whether the simplified model structure is sufficient or whether more detailed hydraulic representations are needed (e.g. Cochard et al., 2021).

A further step is to implement and test functional links from simulated TWD or relative tree water content to stomatal conductance, photosynthesis, growth, allocation, recovery, and damage risk. Such coupling would move TWIST beyond its current diagnostic role and could help improve model representations of drought impacts, legacy effects, and potential forest decline

(Hartmann et al., 2018; Kannenberg et al., 2020).

For upscaling applications, a key unresolved question is how individual-tree TWD signals vary within a stand, especially in structurally complex forests. Evaluation in Chapter 4 was based on five dendrometer-equipped trees, which is typical but unlikely to capture the full range of variability. Dense dendrometer installations at selected sites could help determine how many trees are needed to characterize stand-level drought dynamics and whether TWIST can adequately represent aggregated stand-level signals rather than mirroring individual-tree responses. If robust, such stand-level water deficit signals may provide a key link to eddy-covariance fluxes (Baldocchi, 2003) and to remotely sensed proxies of canopy water status (Konings et al., 2019), which integrate responses over flux-tower footprints or satellite pixels rather than individual trees. In coupled model applications, this would make it possible to test whether forest water-deficit dynamics help constrain drought-related reductions in carbon and water fluxes, post-drought legacy effects, and, eventually, damage or mortality patterns observed at broader ecosystem scales.

5.6 Conclusion

This thesis aimed to advance tree water deficit (TWD) as a physiological indicator of drought stress by strengthening its interpretation, extending its functional use, and translating it into a model-compatible representation of internal tree water dynamics.

The three studies presented here provide several key insights. Dendrometer-derived TWD remains closely linked to water potential during severe dehydration, whereas incomplete recovery of TWD introduces hysteresis and may indicate hydraulic or cellular damage. Temporal TWD patterns themselves contain physiologically meaningful information, reflected in the diurnal TWD amplitudes and overall TWD accumulation. In particular, pre-dawn $TWD > 0$ provides a directly applicable stress signal, indicating incomplete overnight replenishment of internal water stores and restrictions in gas exchange. When normalized, TWD can serve as a comparable functional drought-stress axis that captures a sequence of physiological responses, including declining water potential, stomatal closure, increasing hydraulic risk, and declining carbon gain. Most notably, daily tree-level net carbon balance shifted from net carbon uptake to net carbon loss at approximately $TWD_{min, norm} = 0.20$, with species-specific thresholds occurring within a comparatively narrow range. With the newly developed TWIST module, internal water deficit dynamics and relative tree water content can be simulated as diagnostic outputs in process-based models, thereby linking tree-level dendrometer observations to simulated stand-level forest dynamics. Together, these contributions show how TWD can connect dendrometer-based monitoring, functional drought responses, and ecosystem-scale process-based modeling.

The increasing availability of dendrometer data – including through coordinated networks such

as TreeNet (Zweifel et al., 2021b) and the Global Dendrometer Network (<https://globaldendro.org/>) – provides a major opportunity. The results of this thesis show that such data can already yield physiologically meaningful information for monitoring and modeling, with TWD serving as a continuous, pattern-based indicator of internal tree water status. Realizing the full potential of TWD, however, will require (i) targeted research into robust normalization and signal transferability across species, tree sizes, sites, and drought contexts, (ii) an improved understanding of recovery and hysteresis effects, and (iii) stronger model links between simulated water deficits, functional responses, and mortality risk. Future coordinated efforts should therefore link dendrometer measurements to environmental monitoring, other tree-level physiological measurements such as water potential and sap flow, ecosystem-scale flux observations, remote-sensing proxies of water status, and model simulations. Such integration could further strengthen the use of TWD for drought-stress monitoring and improve model-based assessments of forest responses to increasing drought under climate change.

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