Integration of tree hydraulic processes and functional impairment to capture the drought resilience of a semi-arid pine forest

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15   **Abstract.** Drought stress is imposing multiple feedback responses in plants. These responses span from stomata closure and enzymatic downregulation of photosynthetic activity to structural adjustments in leaf area. Some of these processes are not easily reversible and may persist long after the stress ended. Unfortunately, simulation models widely lack an integrative mechanistic description on how this sequence of tree physiological to structural responses occur.

Here, we suggest an integrative approach to simulate drought stress responses. Firstly, a decreasing plant water potential
20   triggers stomatal closure alongside a downregulation of photosynthetic performance. This is followed by a disconnection of roots and soil and the reliance on internal stem water storage or water uptake from deep soil layers. Consistently, loss in hydraulic functioning is reflected in sapwood loss of functionality and foliage senescence. This new model functionality has been used to investigate responses of tree hydraulics, carbon uptake and transpiration to soil- and atmospheric drought in an extremely dry Aleppo pine (*Pinus halepensis* L.) plantation.

25   Using the hypothesis of a sequential triggering of stress-mitigating responses, the model was able to reflect the carbon uptake and transpiration patterns under varying soil water supply and atmospheric demand - especially during summer - and responded realistically regarding medium-term responses such as leaf and sapwood senescence. In agreement with the high drought resistance observed at the site our model indicated little loss of hydraulic functioning in Aleppo pine, despite the intensive seasonal summer drought.

1 Introduction

Reduced tree growth and increased tree mortality following hot and dry spells have been widely observed (e.g. Thom et al., 2023; Ryan, 2011; Hammond et al., 2021). This trend is expected to extend into the future since rising vapor pressure deficits (VPD) and more irregular precipitation patterns are expected, leading to increases in drought severity (Huber et al., 2021;
35 Tschumi et al., 2022). The extend of tree decline, however, also depends on the ability of tree species to withstand or respond to the stress. This includes responses that are not easily reversible after rewetting, and will therefore impact tree carbon and water balance also beyond stress, introducing so-called legacy effects (Ruehr et al., 2019).

To evaluate tree and forest responses to environmental changes, physiologically-oriented simulation models are essential tools because they are describing various physiological processes in dependence on environmental driving forces, which are then
40 used to derive changes in biomass and dimensional growth (Fontes et al., 2010; Trugman et al., 2019). Nevertheless, the various known internal feedback responses to primary damages (López et al., 2021; Blackman et al., 2023), are still lacking a unified mechanistic formulation. A main reason for this deficit is that several tree processes are involved occurring at various temporal scales. For example, stomatal closure may occur immediately and is easily reversible, but less reversible responses such as loss of xylem, roots or foliage are usually only observed after prolonged and/or severe drought stress (Barbeta and
45 Peñuelas, 2016; Nadal-Sala et al., 2021a; Nardini et al., 2016). Immediate and intermediate responses during drought are stomatal closure, photosynthetic enzyme degradation and a decrease of mesophyll conductance (both regarded as non-stomatal limitations to transpiration) (Dewar et al., 2018). This is followed by xylem embolism, which reduces conductance further, and foliage senescence which is decreasing the evaporating surface (Cardoso et al., 2020). These responses might be consistently considered by hierarchical triggering in dependence on each other, or by a sequential initiation at decreasing levels
50 of plant hydration, for example represented by plant water potential (Walthert et al., 2021). Further long-term responses that may be triggered by resource demand and supply rather than plant water potential include an adjustment of allometric relations such as larger root-to-shoot and root-to-leaf ratios which are favouring water uptake and reducing water losses (Brunner et al., 2015; Lemaire et al., 2021), or competition processes at the stand level that lead to density-dependent tree mortality (Trugman, 2022; Pretzsch and Grote, in press). Despite many of these processes are principally known, the consideration in ecosystem
55 models is still fragmentary or inconsistent.

The full effect of such secondary responses can only be evaluated if not only the mitigating impact on tree water loss but also the trade-off in carbon acquisition and allocation change will be considered (Ruehr et al., 2019; Müller and Bahn, 2022). Already degraded enzymes do need some days for recovery during which the full photosynthetic capacity is not available, and foliage that is lost during a drought event will slow-down desiccation allowing trees to survive longer under hydric stress
60 (Blackman et al., 2023; Blackman et al., 2019) but will not be available for carbon assimilation after stress release, hindering recovery (Galiano et al., 2011). Also, impaired conducting tissue which is inherently related to potentially reduced carbon uptake, does hardly reverse quickly via refilling of embolism (also an energy-consuming process), but mostly depends on re-growth of new xylem tissue (Hammond et al., 2019; Rehschuh et al., 2020; Gauthey et al., 2022). Such secondary effects don't

need a new functionality in ecosystem models but can be considered in existing integrated modelling frameworks, allowing the simulation of stress legacies in ecosystem process-based models. Moreover, the simulation of a mechanistic stress-driven tree mortality might be facilitated, if tissue function has been damaged beyond critical levels (McDowell et al., 2022; Breshears et al., 2018), or if regrowth and repair decrease resources for growing assimilating tissues with detrimental impacts on the acquisition of new carbon and nutrients (Bigler et al., 2007; McDowell et al., 2008; Rukh et al., 2023).

Previous attempts in incorporating explicit definitions on plant hydraulics in process-based models have been proven to capture instantaneous responses of leaf gas exchange to drought stress (e.g. De Kauwe et al., 2015a; Sperry et al., 2017; Tuzet et al., 2017; Cochard, 2021; Sabot et al., 2022). Similarly, plant hydraulics has also been used to investigate tree structural adjustment in response to drought stress, e.g. loss of xylem conductance due to cavitation (Whitehead et al., 1984; Tyree and Sperry, 1989), leaf shedding (Nadal-Sala et al., 2021a) and fine root biomass adjustments (Sperry et al., 1998). Overall, applying hydrological model schemes has been found promising to investigate plant strategies to minimize drought stress that are based on different trait expressions (Mirfenderesgi et al., 2019). However, modelling tree hydraulic processes at stand level is still challenging due to the complex interaction of environmental boundary conditions such as evaporative demand and soil properties, plant morphology (root distribution, individual size), anatomy (xylem conductivity and its vulnerability to embolism), physiology (photosynthetic capacity, stomatal responsiveness) (Trugman et al., 2019; Mencuccini et al., 2019), and the representation of competition when shifting from single-tree to the stand level (Trugman, 2022). Specific problems are for example the consideration of tree capacitance (Blackman et al., 2019; Preisler et al., 2022), water loss after full stomatal closure (Barnard and Bauerle, 2013; Duursma et al., 2019), seasonal acclimation of xylem properties to low water potentials (Feng et al., 2023), or the issue of embolism recovery (Arend et al., 2022).

The importance to consider first level responses for drought stress mitigation as well as their trade-offs have been theoretically highlighted (Li et al., 2022; Trugman et al., 2019) and empirically demonstrated (e.g. Arend et al., 2022) but consistent model implementations are still scarcely found. Current approaches are either concentrating on instantaneous stomatal responses alone (Eller et al., 2020) or directly affecting tree mortality (Yao et al., 2022). The few physiologically-based approaches are computationally demanding and difficult to combine with established stand-level forest models (Ruffault et al., 2022). In order to investigate the implications of sequential hydraulic stress responses, we thus integrated tree hydraulic and stress impairment processes into an existing modelling framework, LandscapeDNDC (Haas et al., 2013). The approach is inspired by recent model innovations (e.g. De Kauwe et al., 2020; De Cáceres et al., 2021; Ruffault et al., 2022) but is not aiming at simulating precise soil and plant water potentials, because these depend on very specific soil and plant properties that are spatially heterogenic and highly dynamic. Instead, we propose a relatively simple but robust model scheme where soil water potentials are derived from generally available soil texture information and one average canopy water potential is assumed to impact responses of all leaves as well as the xylem (see Fig.1). The approach presented here, which is based on two simple but well established hydraulic principles and allometric relationships, is also representing major legacy mechanisms and medium-term feedbacks currently discussed (Trugman, 2022).

To evaluate this new model approach, we looked for a site that already exhibits the whole range of water availability reaching from none to very severe drought and at which long-term measurements exist able to constrain and evaluate the model processes. We have therefore focused on a seasonal-dry forest site dominated by Aleppo pine trees (*Pinus halepensis* Mill.) in Yatir, Israel. The site is characterized by a semi-arid climate with a short wet season in winter, followed by a prolonged dry summer period with no rain and high VPD (Wang et al., 2020). Considering that the forest might be at the verge of survival already while climate projections suggest an additional decrease of precipitation up to a 20%, (IPCC, 2019; D'Andrea et al., 2020) investigations that target the resilience of the trees might be of particular interest.

Our central physiological hypothesis states that a cascade of mechanisms in plants are triggered in response to declining water potential to prevent further dehydration (Novick et al., 2022). The intensity of such responses increases with decreasing water potential (Walthert et al., 2021), and the sensitivity of these responses is inversely related to the carbon costs of their reversal. The suggested model scheme (Fig. 1) represents a consistent implementation of this hypothesis, which will be tested by investigating the transition from wet to extreme dry conditions. In particular, we will target the following questions: i) Can stomatal closure in response to increasing vapor pressure deficit be described in dependence of plant water potential even if soil moisture is not limiting? ii) How does the downregulation of photosynthesis in response to water potential affect stomatal performance during the transition towards dry soil? iii) Is the root-to-soil disconnection buffering the decline of plant water potential and hence reduces damage under very dry soil conditions? iv) Are simulated leaf senescence and sapwood area losses realistically linked to losses of tree hydraulic conductance during prolonged drought periods?

2 Materials and Methods

2.1 Site description

The Yatir forest (Israel, 31.34°N, 35.05°E) is an afforestation of Aleppo pine planted during the 1960's. The site conditions are characterized by an exceptionally dry climate with an annual precipitation of 285 mm, while potential evaporation is > 5-fold higher (Schiller, 2011; Ungar et al., 2013). Typically, the forest experiences a 6-8 month-long rain-free period during summer.

The soil at the site is a Rendzic Leptozol with an extremely clay-enriched layer at ca. 1 m depth, a permanent wilting point of 10.7% volumetric soil water content (SWC), and a high stone content (Klein et al., 2014; Preisler et al., 2019). Van Genuchten parameters have been directly derived from soil water retention curves, measured at four different depths at the investigation site (Klein et al., 2014). During the study period, stand density was determined to be 357 trees ha⁻¹, average diameter at breast height of all trees was about 18.5 cm, and average tree height 9.3 m (based on Rohatyn, 2017 and personal communication). Natural regeneration is negligible (Pozner et al., 2022). Specific initializations for model simulations are given in the supplementary Tables S1.

Carbon and water fluxes and supplementary meteorological data are continuously recorded since the year 2000 with an eddy covariance (EC) tower in the geographical centre of the Yatir forest (Grünzweig et al., 2003). Measurements are carried out according Euroflux standards and data are included in the CarboEuroFlux network (Aubinet et al., 1999). We selected the

130   period between 2012 - 2015 for our study as it provides ample high-quality EC data as well as sap flux measurements and is freely available from the ICOS data portal (Warm Winter 2020 Team, 2022, https://www.icos-cp.eu/data-products/2G60-ZHAK, visited 25.08.2023). We purposefully concentrated on a couple of years in order to omit any potential impact from stand structural changes or increasing atmospheric CO_2 concentration (e.g. Norby et al., 2005).

2.2 Observational data

135   EC measurements of net ecosystem production (NEP) and calculations of gross primary production (GPP) and ecosystem respiration (ER) using site-specific relations to temperature as described in Tatarinov et al. (2016) are provided at the ICOS data portal (Warm Winter 2020 Team, 2022, https://www.icos-cp.eu/data-products/2G60-ZHAK, visited 25.08.2023). Daily values were only calculated with good and very good NEP data quality, according to the Euroflux methodology. All other data was considered as missing values. Days with > 2 half-hourly day-time values missing were excluded from the model evaluation

140   (ca. 35%).

Sap flow measurements are based on up to sixteen trees using lab-manufactured thermal dissipation sensors (Granier and Loustau, 1994) at 30 min intervals. Sap flow was calculated following Granier and Loustau (1994), implementing corrections (Kanety et al., 2014). Sap flow was transformed to tree transpiration using individual tree sapwood basal area. Transpiration at the stand level was obtained by multiplying the average tree sap flux density per unit sapwood area by mean tree sapwood

145   cross-section area and the stand density. All data used for the evaluation are presented in Fig. 2. For further details regarding sap flow measurements see Klein et al. (2014).

Litterfall was collected in 25 litter traps of 0.5 m^2 each, along ten consecutive years (2003 - 2012). Litter was removed from the traps every 1–2 months and sorted into needle, reproductive, woody and residual fractions and oven-dried at 65 ˚C for two days (Maseyk et al., 2008). For the purpose of this analysis, only needle litter was considered. To be able to compare simulated

150   and observed dynamics, total leaf biomass was bootstrapped for the 2003 - 2012 period to derive the annual median (see Fig. S1) and then multiplied by an average needle longevity of 3 years (Maseyk et al., 2008).

SWC was monitored continuously at the site throughout 2013 – 2015. using Trime PICO-64 sensors (IMKO Micromodultechnik GmbH, Ettlingen, Germany) installed at depths of 5, 15, 30, 50, 70 and 100 cm in five soil pits, and averaged over the whole profile. Air temperature and relative humidity were monitored continuously above the canopy at the

155   flux tower (Tatarinov et al., 2016). The measured soil water content together with it's representation by the model is given in the supplements (Fig. S3).

2.3 Model description

2.3.1 LandscapeDNDC and PSIM

LandscapeDNDC (https://ldndc.imk-ifu.kit.edu) is a simulation platform for terrestrial ecosystem models (Grote et al., 2011;
160 Haas et al., 2013) that is originally designed to reproduce atmosphere-biosphere exchange process of carbon, water, and
nitrogen, including trace gas exchanges. For this purpose, detailed soil process modules are provided to be coupled with
ecosystem modules that are parameterized on the species level and cover grasslands, crops and forests. The LandscapeDNDC
model framework uses daily maximum and minimum temperature, radiation, VPD and precipitation as meteorological inputs,
which are downscaled to hourly values. The canopy is divided into multiple layers which height and extension depend on the
165 initialized ecosystem structure, and microclimate is calculated for each layer (using the Empirical Canopy Model, Grote et al.,
2009). Similarly, soil is divided into a user-defined number of layers, each holding chemical and texture information (Holst et
al., 2010). Foliage and fine roots are distributed across the canopy and rooting space, respectively, according to a distribution
function that has been described in Grote and Pretzsch (2002).

Soil carbon and nitrogen related processes are calculated with the MeTr^X soil module (Kraus et al., 2015). The water balance
170 is derived considering all major ecosystem fluxes (evaporation from interception, transpiration, ground surface and soil; runoff;
percolation) and pools (water storage at the leaf surface, at the ground and in each soil layer) and is based on the original model
for denitrification and decomposition (Li et al., 1992). The soil water content and distribution is basically represented with a
bucket approach and soil water potentials are calculated based on soil properties using the equations suggested by Van
Genuchten (1980). Forest carbon gain and losses by growth and maintenance respiration, as well as phenology, allocation and
175 senescence processes are considered within the Physiological Simulation Model (PSIM), which uses the Farquhar model to
estimate hourly carbon assimilation (Farquhar et al., 1980), and is linked to a stomatal conductance module to optimize gas
exchange. For standard simulations the procedure suggested by Leuning (1995) is applied, but alternative approaches are
possible to select or to introduce (see below). Maintenance respiration is calculated based on temperature and nitrogen
concentrations in the different tissues (Cannell and Thornley, 2000). The remaining photosynthates are allocated into different
180 tree compartments (reserves, foliage, fine roots, living wood) according to their respective sink strength, which is based on
allometric relations (defines demand originating from foliage development), tissue loss rates (increases demand), and
environmental limitations (preventing allocation to inactive tissues) (Grote, 1998). In case none of the compartments has any
demands, the carbon is distributed according to allometric ratios between leaves, fine roots and sapwood (in case of
undetermined growth) or between fine roots and sapwood (otherwise). Senescence of tree compartments is generally derived
185 from a specific longevity of each tissue. Currently an enhanced senescence of tissue under stressful environmental conditions
is not considered.

In this configuration, LandscapeDNDC has been used to investigate gas exchange and biomass growth in forested ecosystems
(Rahimi et al., 2021; Cade et al., 2021; Dirnböck et al., 2020). It has also been evaluated at different European forest sites

(Mahnken et al., 2022; Nadal-Sala et al., 2021b) with one result being that the sensitivity of carbon and water fluxes to vapor
190   pressure deficit is generally not sufficiently well represented. Into this framework, we implemented a new hydraulic
conductance scheme as well a mechanism for stress-induced senescence of sapwood and foliage which is described in more
detail below.

2.3.2 Representation of hydraulic conductance

- *Stomatal closure*

195   The newly implemented hydraulic approach into LandscapeDNDC does now allow to calculate canopy water potential based
on soil water potential and fine-root vertical distribution (see also Fig. 1a). Stomatal conductance (gs) is regulated in order to
optimize net photosynthesis at the one hand (A_n, µmol m^{-2}LA s^{-1}), which is calculated here according to Farquhar et al. (1980),
considering a peaked Arrhenius response of photosynthetic parameters with leaf temperature (Medlyn et al., 2002), and
hydraulic safety at the other, calculated from hourly mean canopy water potential following Eller et al. (2020):

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$$gs = g_{MIN} + 0.5\frac{\partial A_{n'}}{\partial C_i}\left[\sqrt{\left(\frac{4\xi}{\partial A_{n'}/\partial C_i}+1\right)}-1\right] \tag{1a}$$

$$\xi = \frac{2}{rp\frac{\delta krc_{rel}}{krc_{rel}\,\delta\Psi_{can\_mean}}1.6\,VPD} \tag{1b}$$

$$rp = \frac{RPMIN}{krc_{rel}} \tag{1c}$$

$$krc_{rel} = e^{\left(-\frac{\Psi_{can\_mean}}{\Psi REF}\right)^{ACOEF}} \tag{1d}$$

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Where $\delta A_n/\delta C_i$ is the increase in net photosynthesis per unit of internal carbon dioxide (C_i) increase – i.e. the gain function
for stomata opening on net assimilation - while ξ is the cost function, which represents the loss in hydraulic conductance with
increasing stomatal opening. The whole plant resistance to water flow (rp, mmol^{-1} m^2 s^1 MPa^1) is calculated from minimum
plant resistance (**RPMIN,** mmol^{-1} m^2 s^1 MPa^1) and root-to-canopy hydraulic conductance (krc_{rel}) (mmol m^{-2} s^{-1} MPa^{-1}) per leaf
210   area (LA), which is calculated in turn from the mean canopy water potential (Ψ_{can_mean}) and species-specific parameters
(**ACOEF, ΨREF**). Ψ_{can_mean} is derived from the average of the predawn canopy water potential (Ψ_{can_PD}) and the hourly
calculated canopy water potential (Ψ_{canopy}, see Eq. (6)) from the previous time step (Eller et al., 2018). Ψ_{can_PD} is the highest
value of Ψ_{canopy} obtained before sunrise. Finally, stomatal conductance cannot decrease below a given minimum conductance
(g_{MIN}). The determination of transpiration considering a minimum conductance larger than zero (i.e. $gs = g_{MIN}$), is bound to
215   produce a stand water deficit (*wdef*) in case that water uptake is not sufficient to compensate for the demand, i.e. if the soil

water storage is fully depleted and evaporative demand is greater than zero. *wdef* accumulates as long as this condition remains but is decreased if sufficient soil water is again available. While immediate transpiration demand is prioritized, refilling is realized concurrently by water uptake from the remaining soil water.

In order to enhance the impact of hydraulic constraints, we additionally consider a non-stomatal down-regulation of photosynthesis – hereafter referred as NSL - that has been suggested by various authors (e.g. De Kauwe et al., 2015a; Drake et al., 2017). We here assume a direct dependency to a declining Ψ_{can_PD}, using an equation suggested by Tuzet et al. (2003) and tested in Nadal-Sala et al. (2021a):

$$A_n' = A_n \left[\frac{1+e^{(\Psi NSL\ ANSL)}}{1+e^{\left((\Psi NSL - \Psi_{can\_PD})ANSL\right)}} \right] \qquad (2)$$

Where **ΨNSL** and **ANSL** are species-specific parameters (see Table 1). The function results in decreases of the photosynthetic potential and thus to further reductions in stomatal conductance. The importance of this mechanism has been tested by running the model with and without the additional impact on photosynthesis.

- *Root-to-soil disconnection and hydraulic conductance*

Ψ_{canopy} is calculated from the gradient between the water potential in the xylem (Ψ_{xylem}, MPa) and from evaporative demand. In order to determine Ψ_{xylem}, however, the root water potential (Ψ_{root}, MPa) has to be defined first. Ψ_{root} is calculated from soil water potential (Ψ_{soil}, MPa) and vertical fine root distribution. Ψ_{soil} is defined for each soil layer based on its water content, specific texture, and water holding capacity according Van Genuchten et al. (1991), with parameters determined according to Klein et al. (2014). Assuming that, when roots are coupled to the soil, Ψ_{root} equilibrates with Ψ_{soil} overnight, it is calculated as the average Ψ_{soil} of all (*n*) layers weighted by the respective fine root biomass fraction (De Kauwe et al., 2015b). The fine root distribution is described according to an empirical function (Grote and Pretzsch, 2002) parametrized with *in situ* data (Preisler et al., 2019). We also consider that under conditions of extremely low water potentials roots decouple from the soil in order to prevent root-to-soil water flow (North and Nobel, 1991; Carminati et al., 2009; Carminati and Javaux, 2020). Under such conditions water uptake is not possible anymore. Ψ_{root} is then defined as:

$$\Psi_{root} = \sum_{i=1}^{n} frf_i \left(\max\left(\Psi_{soil,i}, \Psi_{disconnect} \right) \right) \qquad (3)$$

Where "i" indicates any given soil layer, and frf_i is the relative root fraction per layer, and the species-specific water potential

245   threshold at which the roots are decoupled from the soil is $\Psi_{\text{disconnect}}$ (MPa).

Ψ_{xylem} is based on Ψ_{root}, but we introduced a cumulative dehydration effect that occurs when transpiration demand cannot be supplied by root water uptake:

$$\Psi_{\text{xylem}} = \Psi_{\text{root}} + \Psi_{\text{dehydration}} \tag{4}$$

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Accordingly, $\Psi_{\text{dehydration}}$ (MPa) is derived from the cumulative day-time averaged leaf-to-root pressure gradient. It is described as:

$$\Psi_{\text{dehydration}} = \sum_{1}^{k}\left[\left(\frac{\sum_{1}^{j}\left(\Psi_{\text{can\_mean},j} - \Psi_{\text{root},j} + h\rho g 10^{-6}\right)}{j}\right)\left(\frac{B_F}{(B_S + B_R + B_F)}\right)\right] \tag{5}$$

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Where the numerator of the first term in the square brackets represents the hydraulic gradient between the roots and canopy considering the tree height component. The gradient is averaged throughout all daylight hours "j" of one day, and during the number of days "k" since $\Psi_{\text{soil}} \leq \Psi_{\text{disconnect}}$. The decline of water potential is corrected by average canopy height h (m). The expression ρ is water density at 25 °C (997 kg m^{-3}) and g represents gravitational acceleration (9.8 m s^{-2}). The multiplication

260   by 10^{-6} converts the term to MPa. The second term in the square brackets accounts for the internal water redistribution among the different tree compartments (Tyree and Yang, 1990). Hence, water potential decrease in foliage biomass (B_F) is mitigated by the water storage in the whole living tissue, accounting for the relative importance of capacitance changes (with B_S, B_R representing sapwood and fine root biomass respectively, all in kg m^{-2} ground), under the assumption of homogeneous hydration status within all tree compartments.

265   In order to get Ψ_{canopy}, Ψ_{xylem} is further reduced according to Darcy's law due to actual transpiration rate of the previous timestep (T_{canopy}, mmol m^{-2}LA s^{-1}) and the root-to-canopy hydraulic conductance ($kxyl$, in mmol m^{-2}LA s^{-1} MPa^{-1}), also considering the effect of the average canopy height. The conductance term $kxyl$ is obtained from the previous hour $\Psi_{\text{can\_mean}}$ and the species-specific xylem hydraulic vulnerability curve, assumed to follow a Weibull function (Neufeld et al., 1992).

270    $$\Psi_{\text{canopy}} = \Psi_{\text{xylem}} - \frac{T_{\text{canopy}}}{kxyl} - h\rho g 10^{-6} \tag{6a}$$

$$kxyl = KSPEC \left[e^{-\left(\frac{\Psi_{can\_mean}}{\Psi_{REF}}\right)^{ACOEF}} \right] \tag{6b}$$

KSPEC, **Ψ_{REF}** and **ACOEF** are empirically-determined coefficients (see Table 1) describing the shape of the vulnerability curve as has been obtained from field measurements (Wagner et al., 2022).

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- *Xylem inactivation and leaf senescence*

A new feature of the hydraulic module is the representation of the progressive loss of xylem functionality presented as sapwood area decline as Ψ_{xylem} decreases (see Fig. 1; e.g. Choat et al., 2018; Rehschuh et al., 2020). The loss is calculated based on a hydraulic vulnerability cure represented with a Weibull function as:

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$$\Delta_{xylem,t} = \min \left(e^{-\left(\frac{\Psi_{can\_PD,t}}{\Psi_{REF}}\right)^{ACOEF}} - e^{-\left(\frac{\Psi_{can\_PD,t-1}}{\Psi_{REF}}\right)^{ACOEF}}, 0 \right) BA_{xylem} \tag{7}$$

Where BA_{xylem} is the basal area of xylem per tree (m^{-2} tree^{-1}), $\Delta_{xylem,t}$ is the daily reduction in xylem basal area (m^{-2} tree^{-1}), and $\Psi_{can\_PD,t}$ and $\Psi_{can\_PD,t-1}$ are the canopy pre-dawn Ψ at the present day and the previous day, respectively (both in MPa). **ACOEF**

285 and **Ψ_{REF}** are species-specific parameters (see Table 1). This process is not directly reversible, with xylem functionality being regained only via regrowth of new tissue (see Fig 1b) (Hammond et al., 2019). Finally, leaf area is reduced proportionally to $\Delta_{xylem,t}$ / BA_{xylem}, according to the pipe model (Shinozaki and Yoda, 1964).

2.3.3 Model initialization and parameterization

Parameters for the LandscapeDNDC core processes such as the species-specific temperature sum that determines leaf flushing,
290 the electron transport rate under standard conditions that defines photosynthesis, allometric relations and tissue longevities that drive allocation and senescence were obtained from the literature (Bernacchi et al., 2001; Infante et al., 1999; Kattge and Knorr, 2007; Medlyn et al., 2002; Navas et al., 2003) (see Supplementary Table S2 for *P. halepensis* parameters). Note that some of these parameters are derived directly at the investigation site including the ones describing photosynthesis (Maseyk et al., 2008), foliage (Zinsser, 2017) and fine root distributions (Klein et al., 2014) and thus the absorption properties of canopy
295 and rooting space, which dimensions are defined by the stand and soil inventory information (see 'Site description').

Also, some parameters that were used for the new hydraulic scheme, such as the ones related to xylem vulnerability (Wagner et al., 2022), were available from observations at the Yatir forest (Table 1). Others were only available from general literature.

For example, g_{MIN} was set to 3 mmol m^{-2} LA s^{-1}, the median value reported for pine trees by Duursma et al. (2019), and also consistent with the range given by Machado et al. (2021) for semi-arid plants (1.1 - 6.3 mol m^{-2} s^{-1}). Due to the uncertainty

300 related to the actual value at this site and the importance of the parameter, we carried out an additional sensitivity tests by varying g_{MIN} across the indicated range. Additional hydraulic and photosynthetic parameters were calibrated using an inverse Bayesian calibration (Hartig et al., 2014; Dormann et al., 2018) based on GPP measurements for the 2013 - 2014 period (Table 1). Priors for each parameter were broad enough to allow the model to capture the responses, but constricted enough to bound them to biologically meaningful limits (see Table S3 for the prior distribution for the 6 parameters calibrated). We implemented

305 a Gaussian likelihood function, with a 'Differential Evolution with snooker update' algorithm as a sampler (DEzs, ter Braak and Vrugt, 2008). 50k simulations were run for the calibration, with a burn-in of 30k simulations. The three chains of the calibration had converged at this point, i.e. Gelman-Rubin score for all marginal posteriors < 1.1 (Gelman et al., 2013). The LandscapeDNDC simulations were then run with the median values for each calibrated parameter.

2.3.4 Statistical analysis

310 All analyses were performed using the software R, version 4.1.2 (R Core Team, 2021). The parameter calibration of LandscapeDNDC was done using the "Bayesiantools" package (Hartig et al., 2019). When a Type I linear relationship has been applied, simulated vs. observed evaluation was given as Spearman's R^2 and Root Mean Square Error (RMSE). To assess the relationship between measured sap flow – as a proxy for transpiration – and modelled daily plant Ψ gradient ($\Delta\Psi_{plant}$, in MPa), calculated as Ψ_{can_PD} - min($\Psi_{can,mean}$) a Type II linear regression was implemented using the "segmented" package

315 (Muggeo and Muggeo, 2017). To derive the threshold at which the modelled daily Ψ_{canopy} became uncoupled from VPD but driven by SWC we performed a truncated linear analysis with the "Bayesiantools" package.
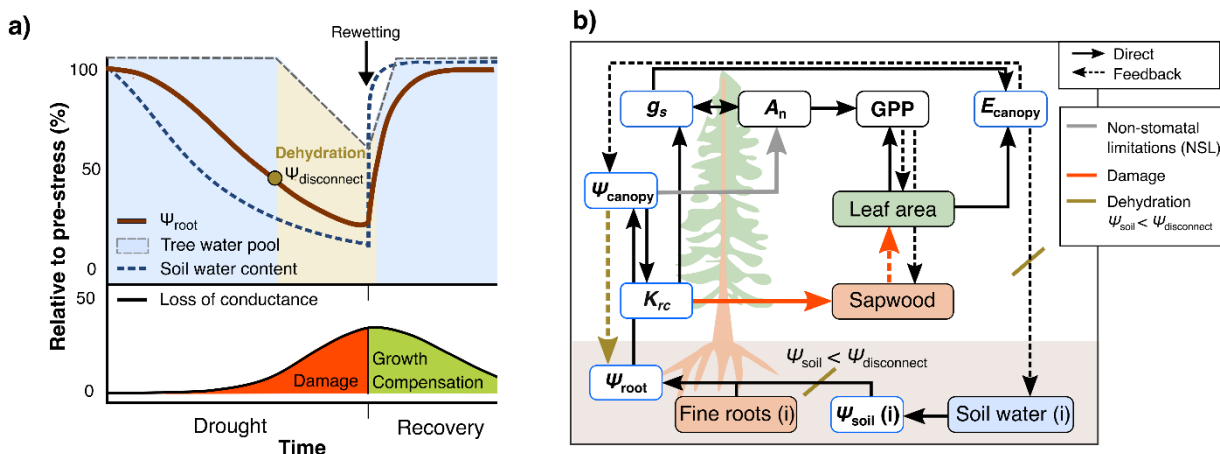
Figure 1: Conceptual scheme of the hydraulic approach and functional damages implemented into the model framework. (a) Theoretical progression of drought and recovery alongside SWC dynamics and its relative impacts on root water potential and the tree water pool. Once the root water potential (Ψ_{root}) falls below a threshold, the roots disconnect from the soil ($\Psi_{disconnect}$) and trees begin to dehydrate, emptying an internal tree water pool. During this stage, the functional damage to the trees increases following losses of hydraulic conductance. Following re-wetting, functional impairment is slowly reversed, for instance via regrowth of leaf and sapwood area. (b) Schematic overview of hydraulic processes, including the degradation of photosynthetic enzymes (non-stomatal limitation, NSL) decreasing photosynthesis rates (A_n) and gross primary productivity (GPP), further affecting stomatal conductance (g_s) and transpiration (E_{canopy}). The root-soil disconnect ($\Psi_{soil} < \Psi_{disconnect}$) is highlighted, triggering tree dehydration and biomass loss induced by declining root-to-canopy hydraulic conductance ($kxyl$).

Table 1: Key parameters for the new hydraulic module in LandscapeDNDC for Aleppo pine applied to the Yatir forest. Parameters have been derived from Bayesian calibration and the literature. For the Bayesian approach, median and the 95% credible intervals (CI) per parameter are given.

Equation	Parameter	Unit	Median [CI]	Description	Source
1	$RPMIN$	mmol^{-1} m^{2}LA s MPa	3.8 [2.8, 4.4]	minimum whole-plant resistance	Bayesian
1	g_{MIN}	mmol H$_2$O m^{2}LA s	3.0	minimum leaf conductance	Duursma et al. (2019)
2	$ANSL$	Unitless	3.5 [3.2, 3.8]	curve parameter for effect on A_n	Bayesian
2	ΨNSL	MPa	-1.01 [-1.06, -1]	reference Ψ_{canopy} for effect on A_n	Bayesian
3	$\Psi_{disconnect}$	MPa	-1.75 [-1.56, -1.95]	Ψ_{soil} threshold of soil-root disconnect	Bayesian
6	$KSPEC$	mmol m^{-2} LA s^{-1} MPa^{-1}	1.9 [1.7, 2.5]	Specific xylem conductance	Bayesian
1, 6, 7	$ACOEF$	Unitless	7.5	curve parameter for Ψ_{canopy} impact on conductance	Wagner *et al.* (2022)
1, 6, 7	ΨREF	MPa	-3.8	reference Ψ_{canopy} for conductance vulnerability curve	Wagner *et al.* (2022)

3 Results

3.1 Model evaluation

335   The simulated GPP dynamics after model calibration captured the observed GPP pattern with a Pearson's correlation coefficient of more than 0.8 (Fig. 2). The impact of the summer drought on tree water relations was reflected in the GPP dynamics with lowest uptake rates during the driest period (April-October). This clearly represents a huge improvement over previous versions of the LandscapeDNDC model (see Fig. S2) and indicates the suitability of the newly implemented hydraulic processes to capture GPP dynamics particularly during extreme drought. The agreement was only slightly higher during the

340   period used for the Bayesian parameter calibration than when strictly comparing to the evaluation period, indicating a low bias in the calibrated parameters.
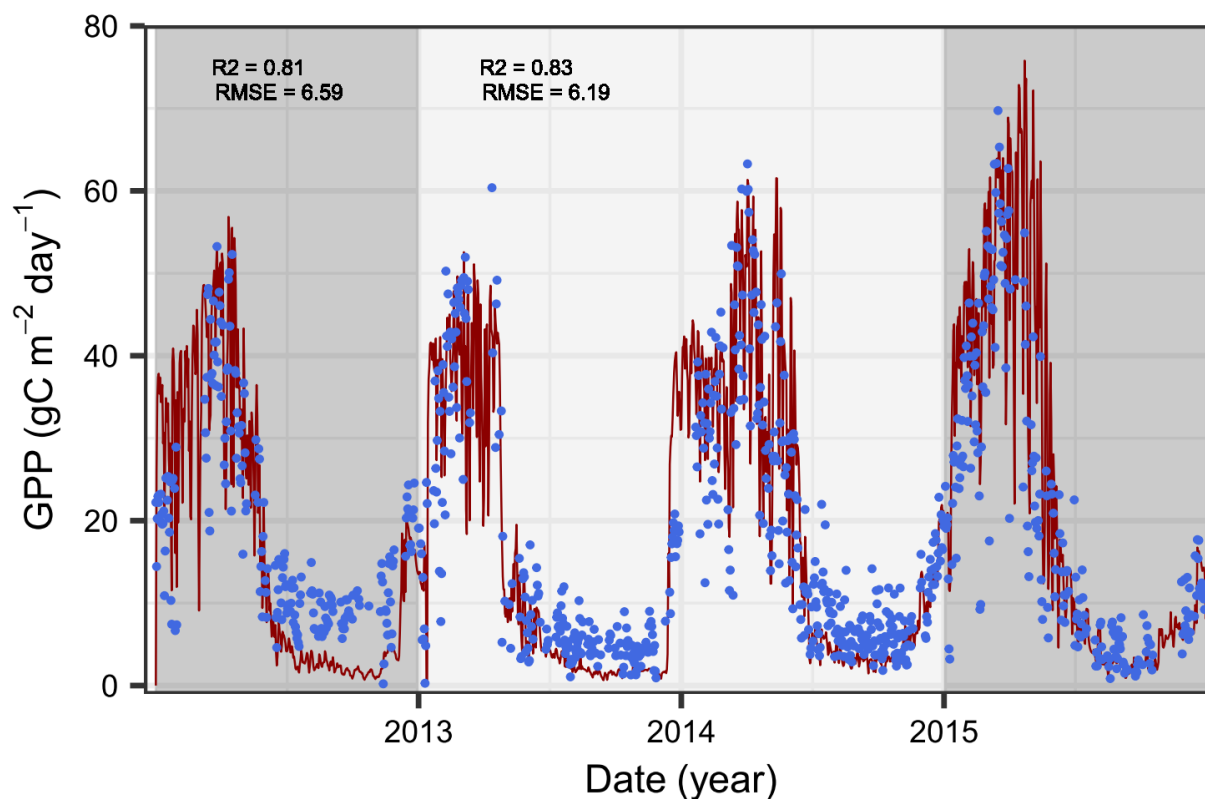
Figure 2: Comparison of simulated (red lines) and observed (blue dots) gross primary production (GPP) in Yatir forest. The periods

345   used for the Bayesian calibration (2013-2014, light grey) and model evaluation (2012 and 2015, dark grey) are highlighted and the goodness of fit between model and observations are indicated as the Pearson's correlation (R2) and the root mean square error (RMSE).

3.2 Sensitivity of tree water relations to seasonal drought and VPD

The model simulations captured the strong seasonality of water availability at the Yatir forest with mild and relatively wet
350   winter conditions and dry summer periods. This was reflected in the modelled root water potential (Ψ_{root_PD}) ranging between
-0.7 MPa during the wet winter season and -2.3 MPa during the dry summer period, which also agrees well with observations
(Fig. 3a). The modelled daily gradient in water potential over the three simulation years was consistent with Darcy's law, as
apparent in the high agreement with the observed transpiration rates (Fig. 3b). Further we found good agreement of simulated
and observed transpiration rates (Fig. 3c), while properly reproducing soil water content (SWC) dynamics (see Fig. S3).

355   Our simulations further showed that internal tree hydraulic dynamics were not only strongly driven by soil water content (Fig.
4a) but were also highly sensitive to changes in VPD. This is particularly expressed during non-drought conditions. VPD was
a major driver of gs as long as soil water content was above 15.8% (95% CI [15.4, 16.5]), a threshold value at which the
maximum daily water potential gradient ($\Delta\Psi_{plant} = \Psi_{plant\_PD} - \min(\Psi_{plant\_mean})$) abruptly changed (Fig 4a). Below this threshold,
the VPD effect on stomatal behaviour is vastly reduced, while the sensitivity to SWC is clearly apparent (Fig. 4b). Hence,
360   during the wet season, stomatal conductance depends mostly on evapotranspiration demand, while during summer stomatal
conductance is mostly limited by soil water availability. The turning point of this bimodal behaviour is characterized by the
threshold soil water potential $\Psi_{disconnect}$ (here -1.75 MPa). Thus, tree dehydration rate depends strongly on g_{MIN} and VPD
during the dry season, and relies entirely on additional water supply such as tree water storage (Fig. S4).

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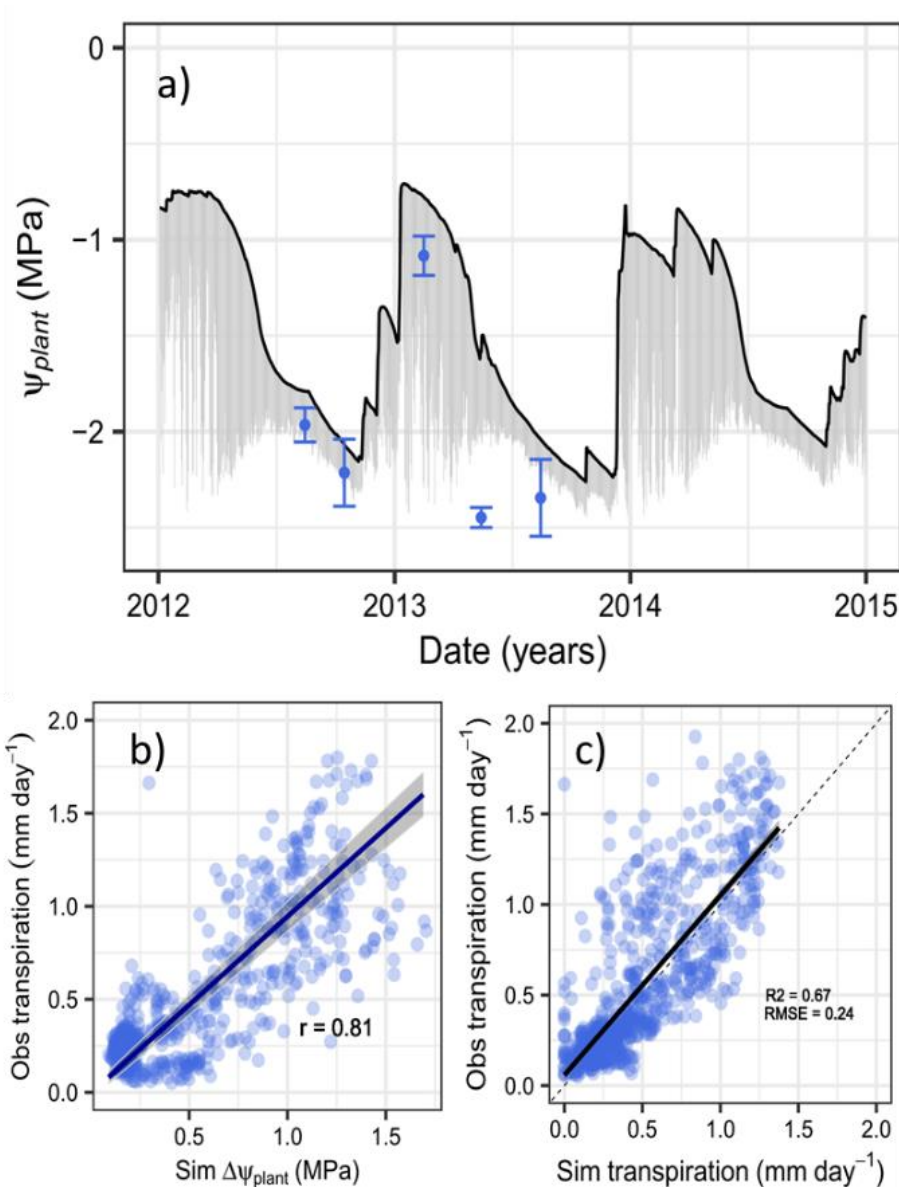


Figure 3: Simulated and observed water potential and transpiration responses to seasonal drought at the Yatir forest. Dynamics of simulated plant pre-dawn water potential ($\Delta \Psi_{plant}$) compared with observations at Yatir forest from 2012 to 2014. a) Seasonal dynamics in pre-dawn plant water potential (black line) and the daily water potential gradient (grey area). For comparison, observations of midday leaf water potentials ($\pm$ SD) are included (blue circles) as reported by Preisler et al. (2019) for healthy trees at the Yatir site. b) Relationship

370 between simulated $\Delta \Psi_{plant}$ and observed transpiration rates are given with Pearson's correlation coefficient for a Type II regression. c) Comparison of observed against simulated daily transpiration.

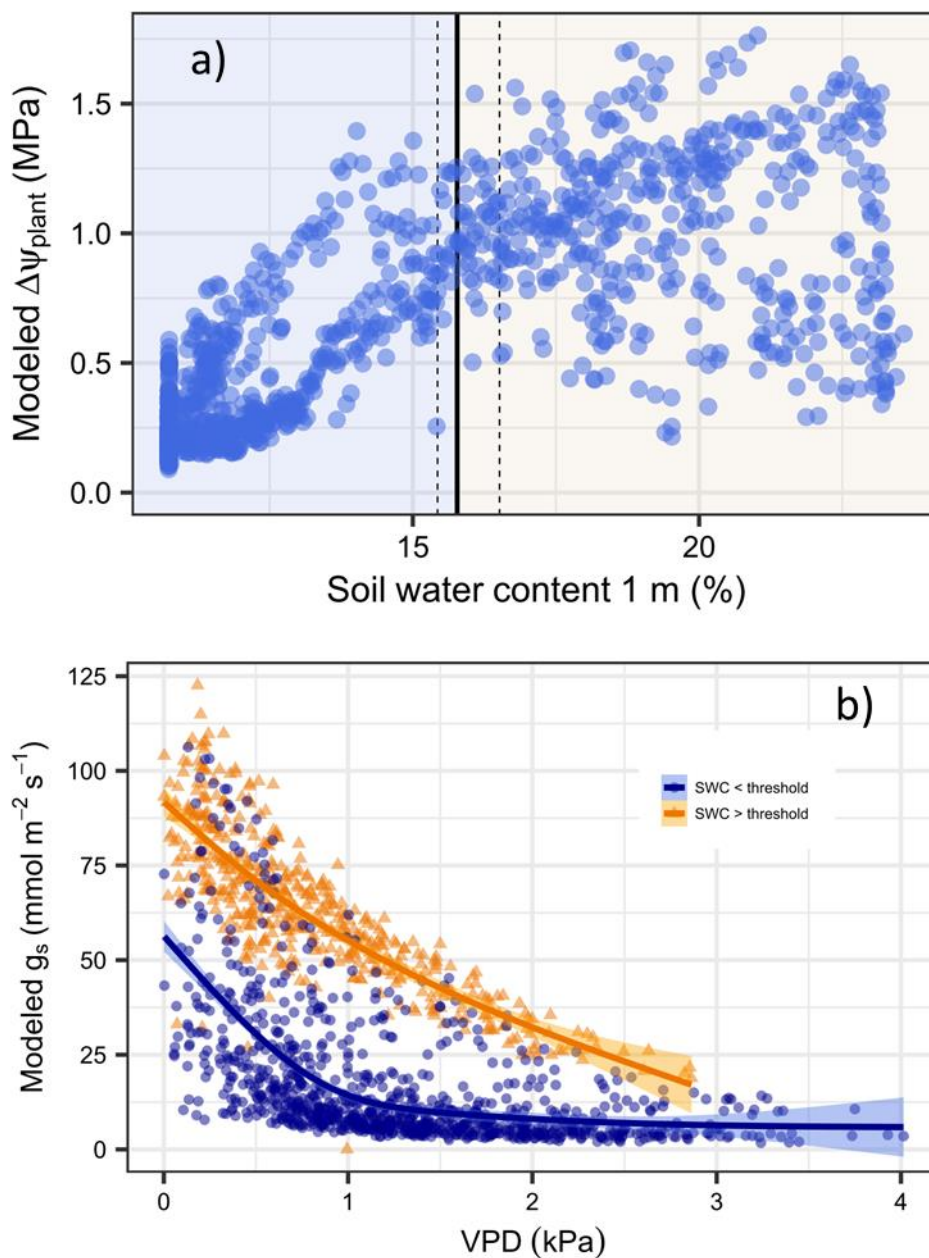



Figure 4: Identification of dominant drivers for plant pre-dawn water potential ($\Delta \Psi_{plant}$) in Aleppo pines at the Yatir forests. a)
$\Delta \Psi_{plant}$ in relation to soil water content (SWC, in %). Vertical lines indicate the SWC at which a shift in the driver dominance occurs (solid
line = median, dashed lines = 95% confidence intervals). b) Relationships between daytime daily averaged stomatal conductance and daytime
daily averaged VPD for SWC above (orange triangles) and below (blue dots) the SWC threshold.

3.3 Sensitivity of tree water relations to non-stomatal limitations

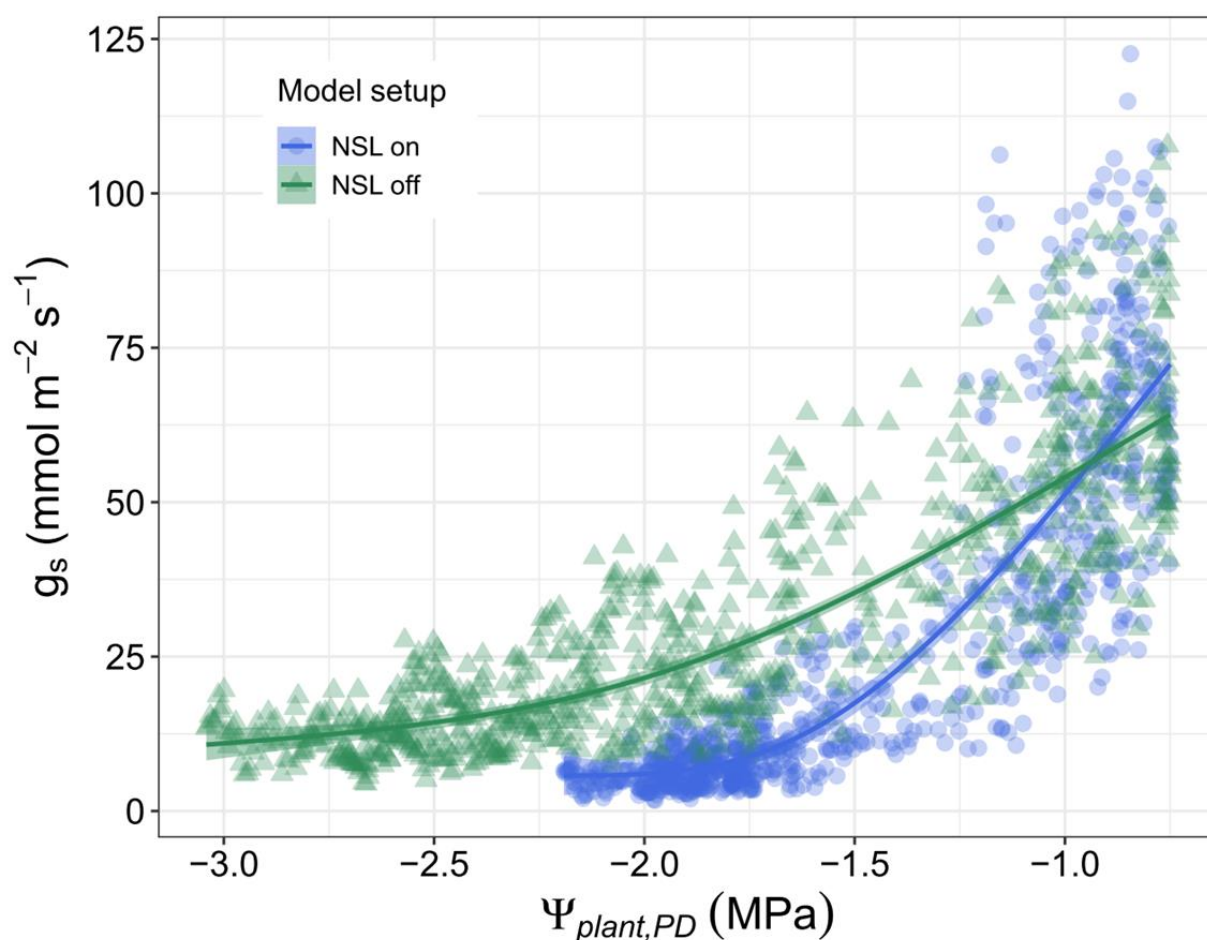
The effect of the non-stomatal limitations routine on tree water relations became clearly visible when comparing the model
380   with and without the NSL setup (Fig. 5). We found a much weaker gs response to Ψ_{root_PD}, and stomatal closure was
consequently reached at an unrealistic low water potential for Aleppo pine. The boosting of stomatal closure via NSL which
affects photosynthesis directly and gs indirectly, also results in an earlier reduction of transpiration and therefore in a delay of
tree dehydration during summer drought.

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Figure 5: The impact on non-stomatal limitations (NSL) on gs. Stomatal conductance derived from model runs with and without the
NSL routine versus pre-dawn plant water potentials ($\Delta \Psi_{plant}$) during the dry-down from March to August for all years (2012 – 2015).

3.4 Hydraulic impairment and leaf shedding

390 Based on the evaluated plant water potentials, the additional stress-induced loss of xylem area according to Eq. (7) is accumulating to 3.4–6.3% per year of total sapwood area. The net loss of sapwood, which is composed on tissue loss by age as well as by low plant water potentials - occurs solely during the dry season when allocation to sapwood is zero or close to zero (Fig. 6, brown areas). It starts at Ψ_{root_PD} values of -1.25 MPa, far away from both P12 (-2.9 MPa) and P50 (-3.6 MPa) - i.e. the plant water potential at which a 12% and a 50% of xylem conductance has been lost, respectively. The additional stress-

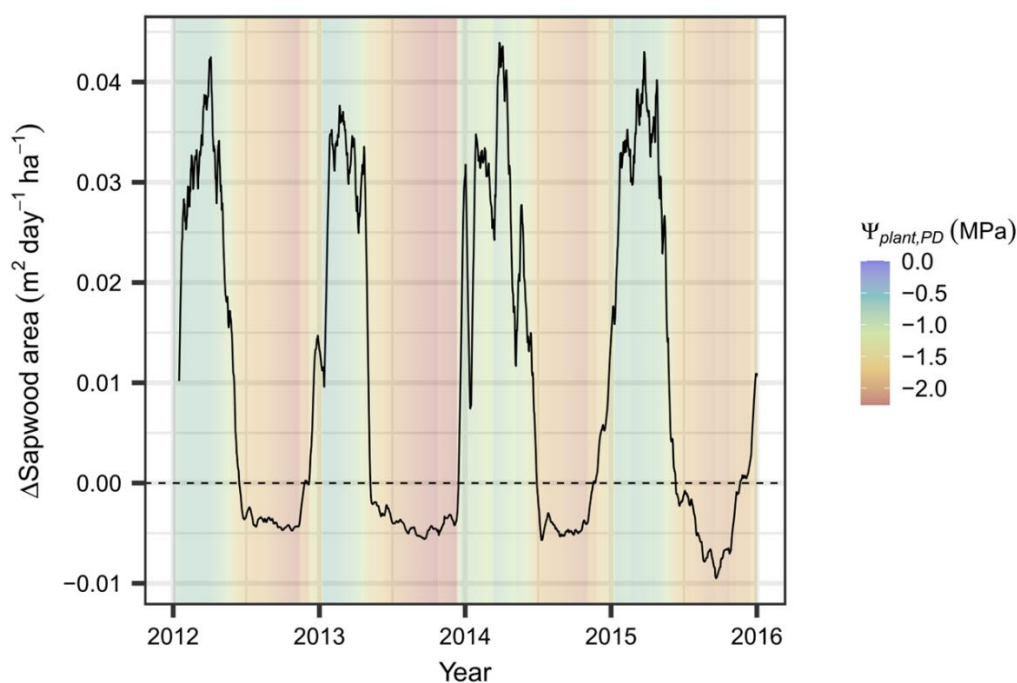
395 induced loss of conductance, albeit relatively small, is responsible for the differences in functional sapwood area during the dry seasons of the different years, i.e. being most expressed in the exceptional dry year 2015. During the wet season, sapwood growth generally copes with - or even exceeds- - the demands for foliage supply (determined by the sapwood area / foliage area ratio, Supplement Table 1) and is thus positive (Fig. 6, green areas).

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Figure 6: Simulated sapwood area dynamics at Yatir forest. Simulated net gains and losses of active sapwood area (ΔSapwood area) are presented as 7-day moving average during 2012 - 2015. The corresponding daily predawn plant water potential is given as coloured background area.

405   The overall pattern of foliage litterfall reproduced the observed seasonal dynamics reasonably well (Fig. 7). In our model, flushing and phenological leaf senescence are determined to start by the onset of the wet period in January and end by mid-September, closely after the onset of the dry period. According to our model concept, functional xylem losses translate into additional foliage losses during the dry season, resulting in an stress-induced litterfall between September and December. However, similar to the relatively small amount of drought-induced loss in sapwood area it was only small.

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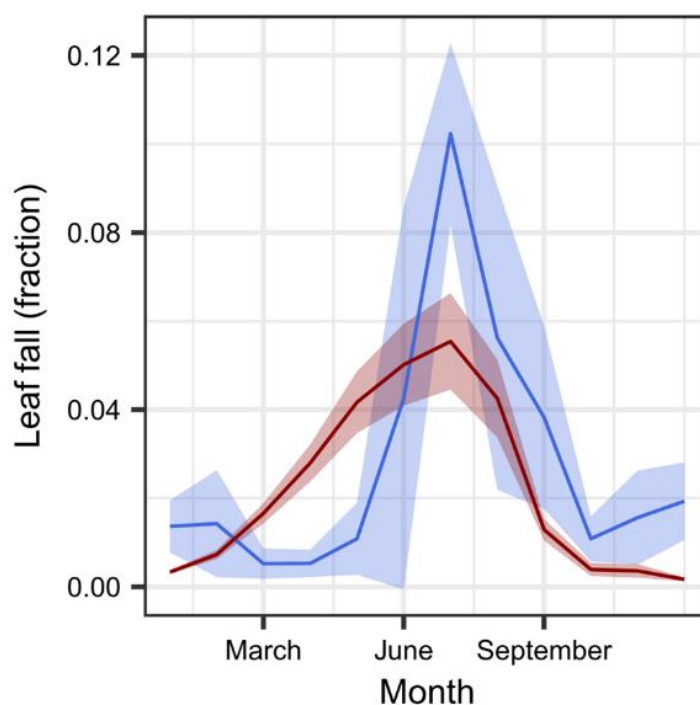
Figure 7: Seasonality of leaf litterfall from observations in the Yatir forest and respective simulation results. Simulated (red) and observed (blue) monthly median litterfall is shown as a fraction of average leaf biomass. Note that simulations are from 2012 - 2015, while observations were integrated from 2003 - 2012. The shaded areas represent the 95% CI.

415

3.5 Sensitivities of drought-induced tissue senescence to g_{MIN} and root-soil disconnection

Hydraulic damage in the model is mostly restricted to the period after the roots become disconnected from the soil, and dehydration during this period depends largely on residual evaporation (g_{MIN}). Therefore, we have tested the sensitivity of the model to variations in the two parameters g_{MIN}, and $\Psi_{\text{disconnect}}$. The selected range was determined based on published values

420   for conductance under dry conditions (Klein et al., 2011; Llusia et al., 2016) and observed ranges of predawn water potentials

in in *P. halepensis* at different sites (Atzmon et al., 2004), in order to highlight its pivotal role in the new model formulation. Over the observed range, an increase of both, g_{MIN} as well as $\Psi_{disconnect}$ results in a linearly increased sapwood area damage and percent loss of conductivity (Fig. 8). The selected parameter combination does fall in the lower range of conductivity loss that has been observed at the site (Fig. 8, grey area), at the same time, the analysis shows that the tissue damage is sensitive in

425 particular to $\Psi_{disconnect}$ and can easily be under- or overestimated.
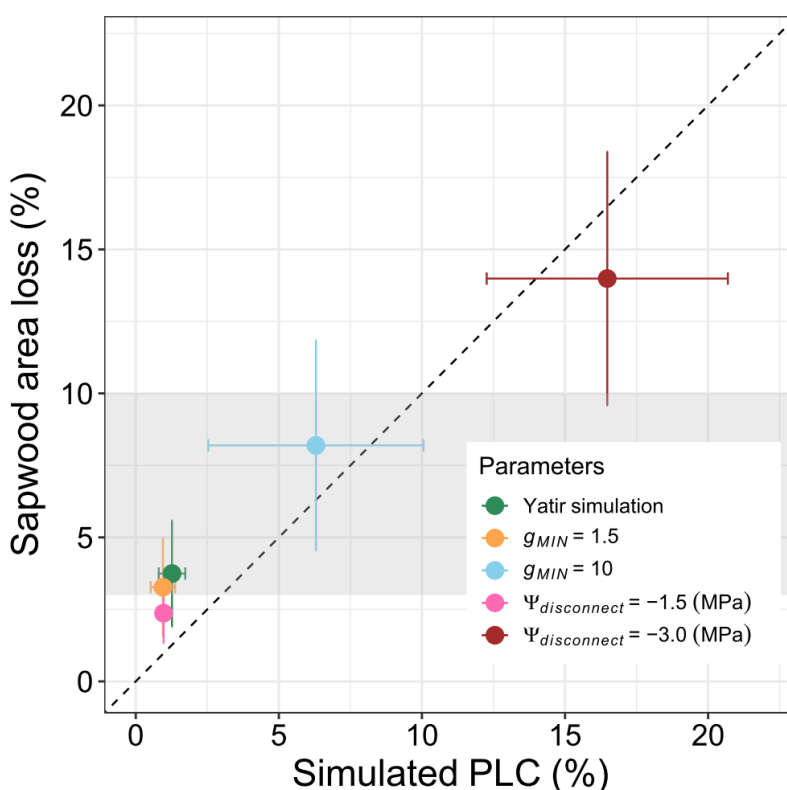
Figure 8: Impacts of changes in hydraulic key parameters g_{MIN} and $\Psi_{disconnect}$ on sapwood area loss. Simulated sapwood area loss is shown as annual averages obtained during the 2012 - 2015 period in relation to simulated maximum percent loss of conductance during
430 summer (PLC, in %). For comparison, sapwood area losses of about 3-10 % as reported in Wagner et al. (2022) and Feng et al. (2023) for the 2020 - 2021 period, are indicated as grey shaded area.

4 Discussion

Our simulations indicate a tight coordination of drought-induced physiological responses in a seasonal summer dry forest
435   ranging from decreasing water potential to stomatal closure, soil root-disconnection and tissue senescence. In the selected case
study, *P. halepensis* shows an expressed isohydric behaviour which is in close agreement with previous observations (Fotelli
et al., 2019; Klein et al., 2011). Accordingly, a seasonal differentiation in the importance of environmental drivers on stomatal
conductance was clearly apparent: during the period with sufficient soil water supply, the main influence on gs was VPD,
whereas during the rest of the year SWC was the limiting factor to stomatal opening and GPP. Later, when drought developed
440   further, we were able to reflect the importance of g_{MIN} for the dehydration processes and hence tissue damage under prolonged
drought stress. Simulations corroborated by measurements indicate that the stress-induced damage of Aleppo pines in Yatir
was relatively small, thus highlighting the adaptation of this species to seasonal drought at this site.

4.1 Drought stress mitigation due to enhanced stomatal sensitivity

Within the hydraulic scheme, the stomatal conductance mechanism needs to account not only for various drivers but has to
445   consider each of them appropriately during any specific phase of stress. For example, stomata regulation under humid to
moderately dry condition is most sensitive to VPD (Novick et al., 2016; Tatarinov et al., 2016). This sensitivity is captured
well with the introduced hydraulic approach which decreases gs under increasing VPD to avoid excessively low water
potentials (question i). The enhanced sensitivity of stomata is particularly triggered by the consideration of photosynthesis
decline under drought stress. This is a mechanism well suitable to represent isohydric behaviour, which is supported by the
450   finding that NSL effects are indeed particularly observed in isohydric species such as birches, poplar and pines (Uddling et al.,
2005; Salmon et al., 2020).

The observed shift in Aleppo pines' water management from demand (VPD)-driven to supply (SWC)-limited driving factors
is best represented by accounting for a very sensitive direct impact of drought stress on assimilation. Such a consideration has
been demonstrated to be particular suitable under conditions of a steep decline in water availability (question ii). The
455   integration of the NSL effect considerably enhances stomatal sensitivity to drought via a feedback mechanism from limited
photosynthetic carbon uptake (Flexas and Medrano, 2002; Tissue et al., 2005; Gallé et al., 2007; Zhou et al., 2013). Hence it
enables a very steep response and avoids the necessity of a rather unrealistically low water potential under drought stress
(Sabot et al 2022). Hoshika et al. (2022) found an important role of photosynthesis downregulation form deciduous as well as
evergreen oaks, and Wilson et al. (2000) estimated that this mechanism is responsible for approximately 75 % of the stomatal
460   regulation in several deciduous trees. Nevertheless, the sensitivity of this mechanism is certainly species-specific (Lobo-do-
Vale et al., 2023) and may strongly vary with foliage age (see e.g.Wilson et al., 2000). Consequently, accounting for this NSL
effect has been considered recently in various models (Dewar et al., 2022; Nadal-Sala et al., 2021a; Salmon et al., 2020) and
might be essential to represent fast stomatal, particularly isohydric responses to high evaporation demand (e.g. Yang et al.,
2019; Gourlez de la Motte et al., 2020).

465   The vulnerability curves previously established for *P. halepensis* all indicate a medium sensitivity for a declining plant water potential with 50% of the conductance lost at about -3.5 to -5 MPa (Gattmann et al., 2023; Oliveras et al., 2003; Wagner et al., 2022). However, soil water potentials in Yatir can easily drop below -10 MPa in the upper layers (Klein et al., 2014). To avoid plant dehydration but still using the measured vulnerability curves, we therefore defined that the roots disconnect from the soil (calibrated at about -1.75 MPa), which lead to a slow-down of the water potential decrease and conductance loss, and also a

470   slow-down of soil water depletion. The optimized threshold is very close to the approximately -2 MPa reported by Klein et al. (2014), strengthening our notion that this mechanism is very important to constrain the hydraulic damage of a drought stressed plant (question iii). The consideration of root detachment from the soil when calculating the resistance increase with decreasing soil water is increasingly recognized and implemented into hydraulic models (e.g. Lei et al., 2023). This is based on the experimental evidence that roots loose contact from the soil under dry conditions (Carminati et al., 2009; Rodriguez-

475   Dominguez and Brodribb, 2020), which has been suggested as a determining factor for soil water depletion, slowing down soil drying (Carminati and Javaux, 2020). In fact, considering soil-to-root decoupling using a Ψ_{soil} threshold can be seen as a simplification of more complex models, which simulate a steep root-to-soil conductance decline explicitly (Cochard et al., 2021; Sperry et al., 2017; De Cáceres et al., 2023). Such complex plant hydraulic models provide a high degree of realism and a higher tissue-level resolution, but can be subject to more uncertainties related to parameterization, soil layer composition,

480   fine root distribution, fine root size and density (e.g. Cochard et al., 2021; Haverd et al., 2016).

   The sustained transpiration during summer without a further depletion of soil water reserves, which agrees well with *in situ* observations (Preisler et al., 2019), clearly demonstrates the importance of **residual water loss** via leaf leakiness and bark transpiration in tree dehydration processes (Márquez et al., 2021; Machado et al., 2021). This is in agreement with previous work highlighting the importance of stem internal water reserves for the survivorship of Aleppo pine in the Yatir forest during

485   the summer dry season (Preisler et al., 2022).

4.2 Consideration of structural hydraulic constraints

   Although we were not able to refer simulated loss of sapwood area directly to measurements, independent observations at the same site indicate that the projected sapwood area reduction of up to 6% is close to *in situ* branch embolism observed at Aleppo pine trees during summer, which were indicated as 8–10% (Wagner et al., 2022). Other reported values for *P. halepensis*

490   embolism that have been measured near Tel Aviv, Israel, indicate less than 5% of functional loss at the end of summer (Feng et al., 2023). Albeit Aleppo pines showed to be well-adapted to the extreme drought conditions, an increase in critical stress damage can still be expected under future hotter and drier conditions that increase the residual water loss and may amplify hydraulic damage, particularly under high VPD conditions (e.g. Wagner et al., 2022). Similarly, leaf area loss was within observed limits of litterfall, although could not be evaluated directly with the available data. This is partly due to the small

495   difference between litterfall due to needle longevity and stress-induced senescence, and partly originates from the time difference between the death of needles and actual litterfall.

Based on the result at the quite extreme site in Israel, we think that the model opens the possibility to address prime legacy impacts of drought stress through linking tree hydraulics to stress-induced leaf senescence and sapwood inactivation (question iv). Stress-induced structural adjustments have been identified as a stress response signal, resulting in a reduction of drought

500   vulnerability, for instance by decreasing leaf area available for evaporation (Hochberg et al., 2017; Wolfe et al., 2016). On the other hand, tissue losses are costly and if not replaced by reserves as soon as conditions are favourable again, will lead to a lower 'income' of carbon. Thus, the introduction of a mechanistic representation of sapwood and foliage mortality provides the possibility to integrate hydraulic failure and carbon starvation into a unified model framework. That is, on the one hand, the loss of hydraulic conductivity provide means to trigger tree death directly based on a threshold of xylem damage beyond

505   which regrowth is impossible (Hammond et al., 2019; Trugman et al., 2018). On the other hand, an increasing demand of carbon to regenerate conductive woody tissue will lead to a shortfall of supply for building new leaves (and roots), reducing tree C uptake and potentially inducing a long-term decline process under recurrent drought stress. If a tree will be able to survive and recover or if the additional carbon demand will result in its delayed death, depends on the balance between resource supply and demand, which are both strongly influenced by stand structure, competition and climatic boundary conditions

510   (Camarero, 2021).

4.3 Further model developments

In order to better capture forest responses to increases in extreme events, process-based models such as LandscapeDNDC that are integrating micro-environmental, physiological and tree growth processes are important tools - not only to project carbon and water fluxes but also to implement mitigation efforts of forest management. Here we consider two main avenues of further

515   model developments, which include a better description of tree capacitance as well as understanding of senescence responses to drought. Both are not only limited by modelling capabilities but also by limitations of our current understanding.

Our modified model allows for residual transpiration after full stomatal closure that originates from undefined water sources (as described above), such as **tree capacitance or deep soil-water access**. While the importance of such water reserves is generally undisputed (e.g. Gleason et al., 2014; Ripullone et al., 2020) and has recently been found as a major determinant for

520   survival or decline (Schmied et al., 2023), the supply of water from the plant tissue is nevertheless limited and thus needs to be constrained. The limitation on water storage depends on structural variables, namely stem dimension (Zweifel et al., 2020) and wood traits (Christoffersen et al., 2016), but its availability may also be described dynamically, e.g. in dependence on xylem activity [water is released only after cavitation occurred, Hölttä et al. (2009)]. In turn, the dehydration rate is determined by leaf leakiness, incomplete stomatal closure and bark transpiration, among others (Duursma et al., 2019). Hence, the residual

525   conductance g_{MIN} and the stem water capacitance are key for tree survivorship as drought progresses (Blackman et al. 2019). Since g_{MIN} is not directly affected by the increase in water potential, a logical next step is to link the depletion of stem water content to the process of hydraulic failure (Scholz et al., 2011). Alternatively, residual conductance may be implemented

dynamically, for example in dependence on air temperature (Schuster et al., 2016). To our knowledge, none of these processes are considered in ecosystem- or forest models yet.

530 **Drought-induced defoliation** has been addressed with the suggested model approach but it is questionable if foliage dynamics should respond to sapwood dynamics following the pipe model theory (Yoda et al., 1963) since this does not allow for preventive leaf shedding. An alternative has been proposed with the "hydraulic fuse" hypothesis Hochberg et al. (2017), which postulates a direct dependence of leaf shedding to plant water potential in order to capture protective acclimation processes to drought (Wolfe et al., 2016; Li et al., 2020). However, the benefit of losing leaves depends on the costs of rebuilding new ones,

535 and also on the xylem hydraulic failure risk at faster declining water potentials. Thus the tendency to shed leaves protectively may be less expressed in trees with higher leaf longevity (Mediavilla et al., 2022), or in the exceptional case of trees being able to refill the embolized vessels (Choat et al., 2018). Also, we still lack empirical evidence to link leaf senescence to xylem water potential thresholds. Deriving such relationships in a range of tree species would provide exciting possibilities for further model development. Aleppo pines -albeit considered as relative drought-resistant species – have been shown to die by

540 hydraulic failure once a specific threshold of xylem disfunction has been reached (Morcillo et al., 2022).

The implementation of a hydraulic strategy into a process-based model allows for feedback responses and enables to represent individual responses of different species, or evaluate the suitability of different strategies under future environmental conditions. Such an approach could be used to investigate for example the benefit of a high resistance strategy with costly tissues (e.g. evergreen species, high wood density), compared to a highly vulnerable species with tissues less costly to

545 reproduce (Saunders and Drew, 2022).

4 Conclusions

In order to capture drought impacts on forest functioning, models need to address both, the quickly reversible physiological responses as well as the slowly reversible impacts from functional impairment and structural damage. This is highly challenging since they need to be addressed in good agreement with the observations while adhering to the maximum

550 parsimony principia. Based on these considerations, the presented approach is able to reflect instantaneous responses as well as potential long-term structural losses from seasonal drought in a semi-arid pine forest. We consider it thus as a prerequisite for a mechanistical representation of a progressive decline of tree functioning and consequent mortality following recurrent and intense droughts. The mechanistic link between stress-induced damages from hydraulic impairment and carbon allocation processes may be suitable to shed new light on the hydraulic failure and carbon starvation continuum resulting in tree mortality.

555

Supplement link < to be provided >

Software and model code

The LandscapeDNDC model source code for released versions of the model is permanently available online at the Radar4KIT database (https://doi.org/10.35097/438; Butterbach-Bahl et al., 2021). The published model version has been used as the basis for integration of the new hydraulic scheme is "win64 ldndc-1.30.4" which can also be freely downloaded upon request from the following KIT institutional website: https://ldndc.imk-ifu.kit.edu/download/download-model.php (last access: 25. August 2023). The new model options described in this paper are also documented in the online-model description (https://ldndc.imk-ifu.kit.edu/doc/ldndc-doxy.php, assessed 25.08.2023). All input data to run the model are either freely available from the internet (see site description) or are provided in the supplement (soil properties, initial stand properties, species-specific parameters).

Author contribution

DN-S, RG and NKR designed the conceptual approach, determined the modelling setup and led the manuscript writing. RG, DN-S and DK coded the hydraulic module into LandscapeDNDC. DN-S performed the data analysis. DY, FT, UH, YW and TK contributed to the field measurements at Yatir forest and provided the observational data. All co-authors contributed to writing and revising the manuscript.

Competing interests

The authors declare that they have no conflict of interest

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References

Arend, M., Link, R. M., Zahnd, C., Hoch, G., Schuldt, B., and Kahmen, A.: Lack of hydraulic recovery as cause of post-drought foliage reduction and canopy decline in European beech, New Phytol., 234, 1195-1205, 10.1111/nph.18065, 2022.

585 Atzmon, N., Moshe, Y., and Schiller, G.: Ecophysiological response to severe drought in *Pinus halepensis* Mill. trees of two provenances, Plant Ecol., 171, 15-22, 10.1023/b:vege.0000029371.44518.38, 2004.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T.: Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology, Advances in Ecological
590 Research, 30, 113-175, 10.1016/S0065-2504(08)60018-5, 1999.

Barbeta, A., and Peñuelas, J.: Sequence of plant responses to droughts of different timescales: lessons from holm oak (*Quercus ilex*) forests, Plant Ecology & Diversity, 9, 321-338, 10.1080/17550874.2016.1212288, 2016.

Barnard, D. M., and Bauerle, W. L.: The implications of minimum stomatal conductance on modeling water flux in forest canopies, J. Geophys. Res. - Biogeosci., 118, 1322-1333, 10.1002/jgrg.20112, 2013.

595 Bernacchi, C. J., Singsaas, E. L., Pimentel, C., Portis, A. R., and Long, S. P.: Improved temperature response functions for models of Rubisco-limited photosynthesis, Plant Cell Environ., 24, 253-259, 10.1111/j.1365-3040.2001.00668.x, 2001.

Bigler, C., Gavin, D. G., Gunning, C., and Veblen, T. T.: Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains, Oikos, 116, 1983-1994, 10.1111/j.2007.0030-1299.16034.x, 2007.

Blackman, C. J., Li, X., Choat, B., Rymer, P. D., De Kauwe, M. G., Duursma, R. A., Tissue, D. T., and Medlyn, B. E.:
600 Desiccation time during drought is highly predictable across species of *Eucalyptus* from contrasting climates, New Phytol., 224, 632-643, 10.1111/nph.16042, 2019.

Blackman, C. J., Billon, L.-M., Cartailler, J., Torres-Ruiz, J. M., and Cochard, H.: Key hydraulic traits control the dynamics of plant dehydration in four contrasting tree species during drought, Tree Physiol., doi: 10.1093/treephys/tpad075, 10.1093/treephys/tpad075, 2023.

605 Breshears, D. D., Carroll, C. J. W., Redmond, M. D., Wion, A. P., Allen, C. D., Cobb, N. S., Meneses, N., Field, J. P., Wilson, L. A., Law, D. J., McCabe, L. M., and Newell-Bauer, O.: A Dirty Dozen Ways to Die: Metrics and Modifiers of Mortality Driven by Drought and Warming for a Tree Species, Frontiers in Forests and Global Change, 1, 10.3389/ffgc.2018.00004, 2018.

Brunner, I., Herzog, C., Dawes, M., Arend, M., and Sperisen, C.: How tree roots respond to drought, Front. Plant Sci., 6,
610 10.3389/fpls.2015.00547, 2015.

Butterbach-Bahl, K., Grote, R., Haas, E., Kiese, R., Klatt, S., and Kraus, D.: LandscapeDNDC (v1.30.4). Karlsruhe Institute of Technology (KIT), 2021.

Cade, S. M., Clemitshaw, K. C., Molina-Herrera, S., Grote, R., Haas, E., Wilkinson, M., Morison, J. I. L., and Yamulki, S.: Evaluation of LandscapeDNDC Model Predictions of CO_2 and N_2O Fluxes from an Oak Forest in SE England, Forests, 12,
615 1517, 10.3390/f12111517, 2021.

Camarero, J. J.: The drought–dieback–death conundrum in trees and forests, Plant Ecology & Diversity, 14, 1-12, 10.1080/17550874.2021.1961172, 2021.

Cannell, M. G. R., and Thornley, J. H. M.: Modelling the components of plant respiration: Some guiding principles, Ann. Bot., 85, 45-54, 10.1006/anbo.1999.0996, 2000.

620 Cardoso, A. A., Batz, T. A., and McAdam, S. A. M.: Xylem Embolism Resistance Determines Leaf Mortality during Drought in *Persea americana*, Plant Physiol., 182, 547-554, 10.1104/pp.19.00585, 2020.

Carminati, A., Vetterlein, D., Weller, U., Vogel, H.-J., and Oswald, S. E.: When Roots Lose Contact, Vadose Zone J., 8, 805-809, 10.2136/vzj2008.0147, 2009.

Carminati, A., and Javaux, M.: Soil Rather Than Xylem Vulnerability Controls Stomatal Response to Drought, Trends Plant Sci., 25, 868-880, 10.1016/j.tplants.2020.04.003, 2020.

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., and Medlyn, B. E.: Triggers of tree mortality under drought, Nature, 558, 531-539, 10.1038/s41586-018-0240-x, 2018.

Christoffersen, B. O., Gloor, M., Fauset, S., Fyllas, N. M., Galbraith, D. R., Baker, T. R., Rowland, L., Fisher, R. A., Binks, O. J., Sevanto, S. A., Xu, C., Jansen, S., Choat, B., Mencuccini, M., McDowell, N. G., and Meir, P.: Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro), Geosci. Model Dev., 9, 4227-4255, 10.5194/gmd-9-4227-2016, 2016.

Cochard, H.: A new mechanism for tree mortality due to drought and heatwaves, Peer Community Journal, 1, article no. e36, 10.24072/pcjournal.45, 2021.

Cochard, H., Pimont, F., Ruffault, J., and Martin-StPaul, N.: SurEau: a mechanistic model of plant water relations under extreme drought, Ann. For. Sci., 78, 55, 10.1007/s13595-021-01067-y, 2021.

D'Andrea, E., Rezaie, N., Prislan, P., Gričar, J., Collalti, A., Muhr, J., and Matteucci, G.: Frost and drought: Effects of extreme weather events on stem carbon dynamics in a Mediterranean beech forest, Plant Cell Environ., 43, 2365-2379, 10.1111/pce.13858, 2020.

De Cáceres, M., Mencuccini, M., Martin-StPaul, N., Limousin, J.-M., Coll, L., Poyatos, R., Cabon, A., Granda, V., Forner, A., Valladares, F., and Martínez-Vilalta, J.: Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: A modelling approach, Agric. Forest Meteorol., 296, 108233, 10.1016/j.agrformet.2020.108233, 2021.

De Cáceres, M., Molowny-Horas, R., Cabon, A., Martínez-Vilalta, J., Mencuccini, M., García-Valdés, R., Nadal-Sala, D., Sabaté, S., Martin-StPaul, N., Morin, X., D'Adamo, F., Batllori, E., and Améztegui, A.: MEDFATE 2.9.3: a trait-enabled model to simulate Mediterranean forest function and dynamics at regional scales, Geosci. Model Dev., 16, 3165-3201, 10.5194/gmd-16-3165-2023, 2023.

De Kauwe, M. G., Kala, J., Lin, Y. S., Pitman, A. J., Medlyn, B. E., Duursma, R. A., Abramowitz, G., Wang, Y. P., and Miralles, D. G.: A test of an optimal stomatal conductance scheme within the CABLE land surface model, Geosci. Model Dev., 8, 431-452, 10.5194/gmd-8-431-2015, 2015a.

De Kauwe, M. G., Zhou, S. X., Medlyn, B. E., Pitman, A. J., Wang, Y. P., Duursma, R. A., and Prentice, I. C.: Do land surface models need to include differential plant species responses to drought? Examining model predictions across a latitudinal gradient in Europe, Biogeosciences, 12, 7503-7518, 10.5194/bg-12-7503-2015, 2015b.

De Kauwe, M. G., Medlyn, B. E., Ukkola, A. M., Mu, M., Sabot, M. E. B., Pitman, A. J., Meir, P., Cernusak, L., Rifai, S. W., Choat, B., Tissue, D. T., Blackman, C. J., Li, X., Roderick, M., and Briggs, P. R.: Identifying areas at risk of drought-induced tree mortality across South-Eastern Australia, Glob. Change Biol., 26, 5716-5733, 10.1111/gcb.15215, 2020.

Dewar, R., Mauranen, A., Mäkelä, A., Hölttä, T., Medlyn, B., and Vesala, T.: New insights into the covariation of stomatal, mesophyll and hydraulic conductances from optimization models incorporating nonstomatal limitations to photosynthesis, New Phytol., 217, 571-585, 10.1111/nph.14848, 2018.

Dewar, R., Hölttä, T., and Salmon, Y.: Exploring optimal stomatal control under alternative hypotheses for the regulation of plant sources and sinks, New Phytol., 233, 639-654, 10.1111/nph.17795, 2022.

Dirnböck, T., Kraus, D., Grote, R., Klatt, S., Kobler, J., Schindlbacher, A., Seidl, R., Thom, D., and Kiese, R.: Substantial understory contribution to the C sink of a European temperate mountain forest landscape, Landscape Ecol., 35, 483–499, 10.1007/s10980-019-00960-2 2020.

Dormann, C. F., Calabrese, J. M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K., Beale, C. M., Ciuti, S., Elith, J., Gerstner, K., Guelat, J., Keil, P., Lahoz-Monfort, J. J., Pollock, L. J., Reineking, B., Roberts, D. R., Schröder, B., Thuiller, W.,

665   Warton, D. I., Wintle, B. A., Wood, S. N., Wüest, R. O., and Hartig, F.: Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference, Ecological Monographs, 88, 485-504, 10.1002/ecm.1309, 2018.

Drake, J. E., Power, S. A., Duursma, R. A., Medlyn, B. E., Aspinwall, M. J., Choat, B., Creek, D., Eamus, D., Maier, C., Pfautsch, S., Smith, R. A., Tjoelker, M. G., and Tissue, D. T.: Stomatal and non-stomatal limitations of photosynthesis for four
670   tree species under drought: A comparison of model formulations, Agric. Forest Meteorol., 247, 454-466, 10.1016/j.agrformet.2017.08.026, 2017.

Duursma, R. A., Blackman, C. J., Lopéz, R., Martin-StPaul, N. K., Cochard, H., and Medlyn, B. E.: On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls, New Phytol., 221, 693-705, 10.1111/nph.15395, 2019.

675   Eller, C. B., Rowland, L., Oliveira, R. S., Bittencourt, P. R. L., Barros, F. V., da Costa, A. C. L., Meir, P., Friend, A. D., Mencuccini, M., Sitch, S., and Cox, P.: Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics, Philosophical Transactions of the Royal Society B: Biological Sciences, 373, 20170315, 10.1098/rstb.2017.0315, 2018.

Eller, C. B., Rowland, L., Mencuccini, M., Rosas, T., Williams, K., Harper, A., Medlyn, B. E., Wagner, Y., Klein, T., Teodoro,
680   G. S., Oliveira, R. S., Matos, I. S., Rosado, B. H. P., Fuchs, K., Wohlfahrt, G., Montagnani, L., Meir, P., Sitch, S., and Cox, P. M.: Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate, New Phytol., 226, 1622-1637, 10.1111/nph.16419, 2020.

Farquhar, G. D., Von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, Planta, 149, 78-90, 10.1007/BF00386231, 1980.

685   Feng, F., Wagner, Y., Klein, T., and Hochberg, U.: Xylem resistance to cavitation increases during summer in *Pinus halepensis*, Plant Cell Environ., 46, 1849-1859, 10.1111/pce.14573, 2023.

Flexas, J., and Medrano, H.: Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited, Ann. Bot., 89, 183-189, 10.1093/aob/mcf027, 2002.

Fontes, L., Bontemps, J.-D., Bugmann, H., Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., and Skovsgaard,
690   J. P.: Models for supporting forest management in a changing environment, For. Syst., 19, 8-29, 10.5424/fs/201019S-9315, 2010.

Fotelli, N. M., Korakaki, E., Paparrizos, A. S., Radoglou, K., Awada, T., and Matzarakis, A.: Environmental Controls on the Seasonal Variation in Gas Exchange and Water Balance in a Near-Coastal Mediterranean *Pinus halepensis* Forest, Forests, 10, 10.3390/f10040313, 2019.

695   Galiano, L., Martínez-Vilalta, J., and Lloret, F.: Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode, New Phytol., 190, 750-759, 10.1111/j.1469-8137.2010.03628.x, 2011.

Gallé, A., Haldimann, P., and Feller, U.: Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery, New Phytol., 174, 799-810, 10.1111/j.1469-8137.2007.02047.x, 2007.

Gattmann, M., McAdam, S. A. M., Birami, B., Link, R., Nadal-Sala, D., Schuldt, B., Yakir, D., and Ruehr, N. K.: Anatomical
700   adjustments of the tree hydraulic pathway decrease canopy conductance under long-term elevated CO_2, Plant Physiol., 191, 252-264, 10.1093/plphys/kiac482, 2023.

Gauthey, A., Peters, J. M. R., Lòpez, R., Carins-Murphy, M. R., Rodriguez-Dominguez, C. M., Tissue, D. T., Medlyn, B. E., Brodribb, T. J., and Choat, B.: Mechanisms of xylem hydraulic recovery after drought in *Eucalyptus saligna*, Plant Cell Environ., 45, 1216-1228, 10.1111/pce.14265, 2022.

705   Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., and Rubin, D. B.: Bayesian Data Analysis, 3rd ed., Chapman and Hall/CRC, New York, 675 pp., 2013.

Gleason, S. M., Blackman, C. J., Cook, A. M., Laws, C. A., and Westoby, M.: Whole-plant capacitance, embolism resistance and slow transpiration rates all contribute to longer desiccation times in woody angiosperms from arid and wet habitats, Tree Physiol., 34, 275-284, 10.1093/treephys/tpu001, 2014.

710   Gourlez de la Motte, L., Beauclaire, Q., Heinesch, B., Cuntz, M., Foltýnová, L., Sigut, L., Manca, G., Ballarin, I., Vincke, C., Roland, M., Ibrom, A., Lousteau, D., and Bernard, L.: Non-stomatal processes reduce gross primary productivity in temperate forest ecosystems during severe edaphic drought, Philosophical Transactions of the Royal Society B: Biological Sciences, 375, 20190527, 10.1098/RSTB-2019-0527, 2020.

Granier, A., and Loustau, D.: Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data, Agric.
715   Forest Meteorol., 71, 61-81, 10.1016/0168-1923(94)90100-7, 1994.

Grote, R.: Integrating dynamic morphological properties into forest growth modeling. II. Allocation and mortality, Forest Ecol. Manage., 111, 193-210, 10.1016/S0378-1127(98)00328-4, 1998.

Grote, R., and Pretzsch, H.: A model for individual tree development based on physiological processes, Plant Biol., 4, 167-180, 10.1055/s-2002-25743, 2002.

720   Grote, R., Lavoir, A. V., Rambal, S., Staudt, M., Zimmer, I., and Schnitzler, J.-P.: Modelling the drought impact on monoterpene fluxes from an evergreen Mediterranean forest canopy, Oecologia, 160, 213-223, 10.1007/s00442-009-1298-9, 2009.

Grote, R., Korhonen, J., and Mammarella, I.: Challenges for evaluating process-based models of gas exchange at forest sites with fetches of various species, For. Syst., 20, 389-406, 10.5424/fs/20112003-11084, 2011.

725   Grünzweig, J. M., Lin, T., Rotenberg, E., Schwartz, A., and Yakir, D.: Carbon sequestration in arid-land forest, Glob. Change Biol., 9, 791-799, 10.1046/j.1365-2486.2003.00612.x, 2003.

Haas, E., Klatt, S., Fröhlich, A., Werner, C., Kiese, R., Grote, R., and Butterbach-Bahl, K.: LandscapeDNDC: A process model for simulation of biosphere-atmosphere-hydrosphere exchange processes at site and regional scale, Landscape Ecol., 28, 615-636, 10.1007/s10980-012-9772-x, 2013.

730   Hammond, W. M., Yu, K. L., Wilson, L. A., Will, R. E., Anderegg, W. R. L., and Adams, H. D.: Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality, New Phytol., 223, 1834-1843, 10.1111/nph.15922, 2019.

Hammond, W. M., Johnson, D. M., and Meinzer, F. C.: A thin line between life and death: radial sap flux failure signals trajectory to tree mortality, Plant Cell Environ., 44, 1311-1314, 10.1111/pce.14033, 2021.

735   Hartig, F., Dislich, C., Wiegand, T., and Huth, A.: Technical Note: Approximate Bayesian parameterization of a process-based tropical forest model, Biogeosciences, 11, 1261-1272, 10.5194/bg-11-1261-2014, 2014.

Hartig, F., Minunno, F., Paul, S., Cameron, D., and Ott, T.: BayesianTools: General-purpose MCMC and SMC samplers and tools for Bayesian statistics. R package version 0.1, 6. 2019.

Haverd, V., Cuntz, M., Nieradzik, L. P., and Harman, I. N.: Improved representations of coupled soil–canopy processes in the
740   CABLE land surface model (Subversion revision 3432), Geosci. Model Dev., 9, 3111-3122, 10.5194/gmd-9-3111-2016, 2016.

Hochberg, U., Windt, C. W., Ponomarenko, A., Zhang, Y.-J., Gersony, J., Rockwell, F. E., and Holbrook, N. M.: Stomatal Closure, Basal Leaf Embolism, and Shedding Protect the Hydraulic Integrity of Grape Stems, Plant Physiol., 174, 764-775, 10.1104/pp.16.01816, 2017.

Holst, J., Grote, R., Offermann, C., Ferrio, J. P., Gessler, A., Mayer, H., and Rennenberg, H.: Water fluxes within beech stands
745   in complex terrain, Int. J. Biometeorol., 54, 23-36, 10.1007/s00484-009-0248-x, 2010.

Hölttä, T., Cochard, H., Nikinmaa, E., and Mencuccini, M.: Capacitive effect of cavitation in xylem conduits: results from a dynamic model, Plant Cell Environ., 32, 10-21, 10.1111/j.1365-3040.2008.01894.x, 2009.

Hoshika, Y., Paoletti, E., Centritto, M., Gomes, M. T. G., Puértolas, J., and Haworth, M.: Species-specific variation of photosynthesis and mesophyll conductance to ozone and drought in three Mediterranean oaks, Physiologia Plantarum, 174, e13639, 10.1111/ppl.13639, 2022.

Huber, N., Bugmann, H., Cailleret, M., Bircher, N., and Lafond, V.: Stand-scale climate change impacts on forests over large areas: transient responses and projection uncertainties, Ecological Applications, 31, e02313, 10.1002/eap.2313, 2021.

Infante, J. M., Damesin, C., Rambal, S., and Fernandez-Ales, R.: Modelling leaf gas exchange in holm-oak trees in southern Spain, Agric. Forest Meteorol., 95, 203-223, 10.1016/S0168-1923(99)00033-7, 1999.

IPCC: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems, Report, 2019.

Kanety, T., Naor, A., Gips, A., Dicken, U., Lemcoff, J. H., and Cohen, S.: Irrigation influences on growth, yield, and water use of persimmon trees, Irrigation Science, 32, 1-13, 10.1007/s00271-013-0408-y, 2014.

Kattge, J., and Knorr, W.: Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species, Plant Cell Environ., 30, 1176-1190, 10.1111/j.1365-3040.2007.01690.x, 2007.

Klein, T., Cohen, S., and Yakir, D.: Hydraulic adjustments underlying drought resistance of *Pinus halepensis*, Tree Physiol., 31, 637-648, 10.1093/treephys/tpr047, 2011.

Klein, T., Rotenberg, E., Cohen-Hilaleh, E., Raz-Yaseef, N., Tatarinov, F., Preisler, Y., Ogée, J., Cohen, S., and Yakir, D.: Quantifying transpirable soil water and its relations to tree water use dynamics in a water-limited pine forest, Ecohydrology, 7, 409-419, 10.1002/eco.1360, 2014.

Kraus, D., Weller, S., Klatt, S., Haas, E., Wassmann, R., Kiese, R., and Butterbach-Bahl, K.: A new LandscapeDNDC biogeochemical module to predict CH_4 and N_2O emissions from lowland rice and upland cropping systems, Plant Soil, 386, 125-149, 10.1007/s11104-014-2255-x, 2015.

Lei, G., Zeng, W., Huu Nguyen, T., Zeng, J., Chen, H., Kumar Srivastava, A., Gaiser, T., Wu, J., and Huang, J.: Relating soil-root hydraulic resistance variation to stomatal regulation in soil-plant water transport modeling, J. Hydrol., 617, 128879, 10.1016/j.jhydrol.2022.128879, 2023.

Lemaire, C., Blackman, C. J., Cochard, H., Menezes-Silva, P. E., Torres-Ruiz, J. M., and Herbette, S.: Acclimation of hydraulic and morphological traits to water deficit delays hydraulic failure during simulated drought in poplar, Tree Physiol., 41, 2008–2021, 10.1093/treephys/tpab086, 2021.

Leuning, R.: A critical appraisal of a combined stomatal-photosynthesis model for C3 plants, Plant Cell Environ., 18, 339-355, 10.1111/j.1365-3040.1995.tb00370.x, 1995.

Li, C., Frolking, S., and Frolking, T. A.: A model of nitrous oxide evolution from soil driven by rainfall events: 1. Model structure and Sensitivity, J. Geophys. Res., 97, 9759-9776, 10.1029/92JD00509, 1992.

Li, X., Smith, R., Choat, B., and Tissue, D. T.: Drought resistance of cotton (*Gossypium hirsutum*) is promoted by early stomatal closure and leaf shedding, Functional Plant Biology, 47, 91-98, 10.1071/FP19093, 2020.

Li, X., Xi, B., Wu, X., Choat, B., Feng, J., Jiang, M., and Tissue, D.: Unlocking Drought-Induced Tree Mortality: Physiological Mechanisms to Modeling, Front. Plant Sci., 13, 10.3389/fpls.2022.835921, 2022.

Llusia, J., Roahtyn, S., Yakir, D., Rotenberg, E., Seco, R., Guenther, A., and Peñuelas, J.: Photosynthesis, stomatal conductance and terpene emission response to water availability in dry and mesic Mediterranean forests, Trees-Struct. Funct., 30, 749-759, 10.1007/s00468-015-1317-x, 2016.

Lobo-do-Vale, R., Rafael, T., Haberstroh, S., Werner, C., and Caldeira, M. C.: Shrub Invasion Overrides the Effect of Imposed Drought on the Photosynthetic Capacity and Physiological Responses of Mediterranean Cork Oak Trees, Plants, 12, 1636, 10.3390/plants12081636, 2023.

López, R., Cano, F. J., Martin-StPaul, N. K., Cochard, H., and Choat, B.: Coordination of stem and leaf traits define different
790 strategies to regulate water loss and tolerance ranges to aridity, New Phytol., 230, 497-509, 10.1111/nph.17185, 2021.

Machado, R., Loram-Lourenço, L., Farnese, F. S., Alves, R. D. F. B., de Sousa, L. F., Silva, F. G., Filho, S. C. V., Torres-Ruiz, J. M., Cochard, H., and Menezes-Silva, P. E.: Where do leaf water leaks come from? Trade-offs underlying the variability in minimum conductance across tropical savanna species with contrasting growth strategies, New Phytol., 229, 1415-1430, 10.1111/nph.16941, 2021.

795 Mahnken, M., Cailleret, M., Collalti, A., Trotta, C., Biondo, C., D'Andrea, E., Dalmonech, D., Gina, M., Makela, A., Minunno, F., Peltoniemi, M., Trotsiuk, V., Nadal-Sala, D., Sabate, S., Vallet, P., Aussenac, R., Cameron, D., Bohn, F., Grote, R., and Augustynczik, A.: Accuracy, realism and general applicability of European forest models, Glob. Change Biol., 28, 6921-6943, 10.1111/gcb.16384, 2022.

Márquez, D. A., Stuart-Williams, H., and Farquhar, G. D.: An improved theory for calculating leaf gas exchange more 800 precisely accounting for small fluxes, Nature Plants, 7, 317-326, 10.1038/s41477-021-00861-w, 2021.

Maseyk, K. S., Lin, T., Rotenberg, E., Grünzweig, J. M., Schwartz, A., and Yakir, D.: Physiology-phenology interactions in a productive semi-arid pine forest, New Phytol., 178, 603-616, 10.1111/j.1469-8137.2008.02391.x, 2008.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., and Yepez, E. A.: Mechanisms of plant survival and mortality during drought: Why do some plants survive while others 805 succumb to drought?, New Phytol., 178, 719-739, 10.1111/j.1469-8137.2008.02436.x, 2008.

McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., Arend, M., Breshears, D. D., Brodribb, T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., Mackay, D. S., Mantova, M., Martínez-Vilalta, J., Medlyn, B. E., Mencuccini, M., Nardini, A., Oliveira, R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J. M., Trowbridge, A. M., Trugman, A. T., Wiley, E., and Xu, C.: 810 Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit, Nature Reviews Earth & Environment, 3, 294-308, 10.1038/s43017-022-00272-1, 2022.

Mediavilla, S., Martínez-Ortega, M., Andrés, S., Bobo, J., and Escudero, A.: Premature losses of leaf area in response to drought and insect herbivory through a leaf lifespan gradient, J. Forestry Res., 33, 39-50, 10.1007/s11676-021-01351-7, 2022.

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X., Montpied, P., 815 Strassmeyer, J., Walcroft, A., Wang, K., and Loustau, D.: Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data, Plant Cell Environ., 25, 1167-1179, 10.1046/j.1365-3040.2002.00891.x, 2002.

Mencuccini, M., Manzoni, S., and Christoffersen, B.: Modelling water fluxes in plants: from tissues to biosphere, New Phytol., 222, 1207-1222, 10.1111/nph.15681, 2019.

820 Mirfenderesgi, G., Matheny, A. M., and Bohrer, G.: Hydrodynamic trait coordination and cost–benefit trade-offs throughout the isohydric–anisohydric continuum in trees, Ecohydrology, 12, e2041, 10.1002/eco.2041, 2019.

Morcillo, L., Muñoz-Rengifo, J. C., Torres-Ruiz, J. M., Delzon, S., Moutahir, H., and Vilagrosa, A.: Post-drought conditions and hydraulic dysfunction determine tree resilience and mortality across Mediterranean Aleppo pine (*Pinus halepensis*) populations after an extreme drought event, Tree Physiol., 42, 1364–1376, 10.1093/treephys/tpac001, 2022.

825 Muggeo, V. M., and Muggeo, M. V. M.: Package 'segmented'. In: Biometrika, 516, 2017.

Müller, L. M., and Bahn, M.: Drought legacies and ecosystem responses to subsequent drought, Glob. Change Biol., 28, 5086-5103, 10.1111/gcb.16270, 2022.

Nadal-Sala, D., Grote, R., Birami, B., Knüver, T., Schwarz, S., and Ruehr, N.: Leaf shedding and non-stomatal limitations of photosynthesis improve hydraulic resistance of Scots pine saplings during severe drought stress, Front. Plant Sci., 12, 715127, 830 10.3389/fpls.2021.715127 2021a.

Nadal-Sala, D., Grote, R., Birami, B., Lintunen, A., Mammarella, I., Preisler, Y., Rotenberg, E., Salmon, Y., Tatrinov, F., Yakir, D., and Ruehr, N.: Assessing model performance via the most limiting environmental driver (MLED) in two differently stressed pine stands, Ecological Applications, 31, e02312, 10.1002/eap.2312, 2021b.

Nardini, A., Casolo, V., Dal Borgo, A., Savi, T., Stenni, B., Bertoncin, P., Zini, L., and McDowell, N. G.: Rooting depth, water relations and non-structural carbohydrate dynamics in three woody angiosperms differentially affected by an extreme summer drought, Plant Cell Environ., 39, 618-627, 10.1111/pce.12646, 2016.

Navas, M.-L., Ducout, B., Roumet, C., Richarte, J., Garnier, J., and Garnier, E.: Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status, New Phytol., 159, 213-228, 10.1046/j.1469-8137.2003.00790.x, 2003.

Neufeld, H. S., Grantz, D. A., Meinzer, F. C., Goldstein, G., Crisosto, G. M., and Crisosto, C.: Genotypic Variability in Vulnerability of Leaf Xylem to Cavitation in Water-Stressed and Well-Irrigated Sugarcane, Plant Physiol., 100, 1020-1028, 10.1104/pp.100.2.1020, 1992.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R.: Forest response to elevated CO_2 is conserved across a broad range of productivity, PNAS, 102, 18052-18056, 10.1073/pnas.050947810, 2005.

North, G. B., and Nobel, P. S.: Changes in Hydraulic Conductivity and Anatomy Caused by Drying and Rewetting Roots of *Agave deserti* (*Agavaceae*), American Journal of Botany, 78, 906-915, 10.2307/2445169, 1991.

Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., Papuga, S. A., Blanken, P. D., Noormets, A., Sulman, B. N., Scott, R. L., Wang, L., and Phillips, R. P.: The increasing importance of atmospheric demand for ecosystem water and carbon fluxes, Nature Clim. Change, 6, 1023-1027, 10.1038/nclimate3114, 2016.

Novick, K. A., Ficklin, D. L., Baldocchi, D., Davis, K. J., Ghezzehei, T. A., Konings, A. G., MacBean, N., Raoult, N., Scott, R. L., Shi, Y., Sulman, B. N., and Wood, J. D.: Confronting the water potential information gap, Nature Geosci., 15, 158-164, 10.1038/s41561-022-00909-2, 2022.

Oliveras, I., Martínez-Vilalta, J., Jimenez-Ortiz, T., José Lledó, M., Escarré, A., and Piñol, J.: Hydraulic properties of *Pinus halepensis*, *Pinus pinea* and *Tetraclinis articulata* in a dune ecosystem of Eastern Spain, Plant Ecol., 169, 131-141, 10.1023/A:1026223516580, 2003.

Pozner, E., Bar-On, P., Livne-Luzon, S., Moran, U., Tsamir-Rimon, M., Dener, E., Schwartz, E., Rotenberg, E., Tatarinov, F., Preisler, Y., Zecharia, N., Osem, Y., Yakir, D., and Klein, T.: A hidden mechanism of forest loss under climate change: The role of drought in eliminating forest regeneration at the edge of its distribution, Forest Ecol. Manage., 506, 119966, 10.1016/j.foreco.2021.119966, 2022.

Preisler, Y., Tatarinov, F., Grünzweig, J. M., Bert, D., Ogée, J., Wingate, L., Rotenberg, E., Rohatyn, S., Her, N., Moshe, I., Klein, T., and Yakir, D.: Mortality versus survival in drought-affected Aleppo pine forest depends on the extent of rock cover and soil stoniness, Funct. Ecol., 33, 901-912, 10.1111/1365-2435.13302, 2019.

Preisler, Y., Hölttä, T., Grünzweig, J. M., Oz, I., Tatarinov, F., Ruehr, N. K., Rotenberg, E., and Yakir, D.: The importance of tree internal water storage under drought conditions, Tree Physiol., 42, 771–783, 10.1093/treephys/tpab144, 2022.

Pretzsch, H., and Grote, R.: Tree mortality. Revisited under changed climatic and silvicultural conditions, Progress in Botany, doi: 10.1007/124_2023_69, 1-43, 10.1007/124_2023_69, in press.

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria, 2021.

Rahimi, J., Ago, E. E., Ayantunde, A., Berger, S., Bogaert, J., Butterbach-Bahl, K., Cappelaere, B., Cohard, J. M., Demarty, J., Diouf, A. A., Falk, U., Haas, E., Hiernaux, P., Kraus, D., Roupsard, O., Scheer, C., Srivastava, A. K., Tagesson, T., and

Grote, R.: Modelling Gas Exchange and Biomass Production in West African Sahelian and Sudanian Ecological Zones, Geosci. Model Dev., 14, 3789-3812, 10.5194/gmd-14-3789-2021, 2021.

875 Rehschuh, R., Cecilia, A., Zuber, M., Faragó, T., Baumbach, T., Hartmann, H., Jansen, S., Mayr, S., and Ruehr, N. K.: Drought-induced xylem embolism limits the recovery of leaf gas exchange in Scots pine, Plant Physiol., 184, 852-864, 10.1104/pp.20.00407, 2020.

Ripullone, F., Camarero, J. J., Colangelo, M., and Voltas, J.: Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of Mediterranean oaks, Tree Physiol., 40, 591-604, 10.1093/treephys/tpaa026, 880 2020.

Rodriguez-Dominguez, C. M., and Brodribb, T. J.: Declining root water transport drives stomatal closure in olive under moderate water stress, New Phytol., 225, 126-134, 10.1111/nph.16177, 2020.

Rohatyn, S.: Alterations in ecosystem water cycle associated with land-use changes under different precipitation regimes, M.Sc., Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot, 70 pp., 2017.

885 Ruehr, N., Grote, R., Mayr, S., and Arneth, A.: Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress, Tree Physiol., 39, 1285–1299, 10.1093/treephys/tpz032, 2019.

Ruffault, J., Pimont, F., Cochard, H., Dupuy, J. L., and Martin-StPaul, N.: SurEau-Ecos v2.0: a trait-based plant hydraulics model for simulations of plant water status and drought-induced mortality at the ecosystem level, Geosci. Model Dev., 15, 5593-5626, 10.5194/gmd-15-5593-2022, 2022.

890 Rukh, S., Sanders, T. G. M., Krüger, I., Schad, T., and Bolte, A.: Distinct Responses of European Beech (*Fagus sylvatica* L.) to Drought Intensity and Length - A Review of the Impacts of the 2003 and 2018-2019 Drought Events in Central Europe, Forests, 14, 248, 10.3390/f14020248, 2023.

Ryan, M. G.: Tree responses to drought, Tree Physiol., 31, 237-239, 10.1093/treephys/tpr022, 2011.

Sabot, M. E. B., De Kauwe, M. G., Pitman, A. J., Medlyn, B. E., Ellsworth, D. S., Martin-StPaul, N. K., Wu, J., Choat, B., 895 Limousin, J.-M., Mitchell, P. J., Rogers, A., and Serbin, S. P.: One Stomatal Model to Rule Them All? Toward Improved Representation of Carbon and Water Exchange in Global Models, J. Adv. Model. Earth Syst., 14, e2021MS002761, 10.1029/2021MS002761, 2022.

Salmon, Y., Lintunen, A., Dayet, A., Chan, T., Dewar, R., Vesala, T., and Hölttä, T.: Leaf carbon and water status control stomatal and nonstomatal limitations of photosynthesis in trees, New Phytol., 226, 690-703, 10.1111/nph.16436, 2020.

900 Saunders, A., and Drew, D. M.: Measurements done on excised stems indicate that hydraulic recovery can be an important strategy used by *Eucalyptus* hybrids in response to drought, Trees-Struct. Funct., 36, 139-151, 10.1007/s00468-021-02188-7, 2022.

Schiller, G.: The case of Yatir Forest, in: Forest Management and the Water Cycle, edited by: Bredemeier, M., Cohen, S., Godbold, D. L., Lode, E., Pichler, V., and Schleppi, P., Ecological Studies, Springer Netherlands, 163-186, 2011.

905 Schmied, G., Pretzsch, H., Ambs, D., Uhl, E., Schmucker, J., Fäth, J., Biber, P., Hoffmann, Y.-D., Šeho, M., Mellert, K. H., and Hilmers, T.: Rapid beech decline under recurrent drought stress: Individual neighborhood structure and soil properties matter, Forest Ecol. Manage., 545, 121305, 10.1016/j.foreco.2023.121305, 2023.

Scholz, F. G., Phillips, N. G., Bucci, S. J., Meinzer, F. C., and Goldstein, G.: Hydraulic Capacitance: Biophysics and Functional Significance of Internal Water Sources in Relation to Tree Size, in: Size- and Age-Related Changes in Tree Structure and 910 Function, edited by: Meinzer, F. C., Lachenbruch, B., and Dawson, T. E., Springer Netherlands, Dordrecht, 341-361, 2011.

Schuster, A.-C., Burghardt, M., Alfarhan, A., Bueno, A., Hedrich, R., Leide, J., Thomas, J., and Riederer, M.: Effectiveness of cuticular transpiration barriers in a desert plant at controlling water loss at high temperatures, AoB PLANTS, 8, 10.1093/aobpla/plw027, 2016.

Shinozaki, K., and Yoda, K.: A quantitative analysis of plant form - the pipe model theory. I. Basic analyses, Japanese Journal of Ecology, 14, 97-105, 10.18960/SEITAI.14.3_97, 1964.

Sperry, J. S., Adler, F. R., Campbell, G. S., and Comstock, J. P.: Limitation of plant water use by rhizosphere and xylem conductance: results from a model, Plant Cell Environ., 21, 347-359, 10.1046/j.1365-3040.1998.00287.x, 1998.

Sperry, J. S., Venturas, M. D., Anderegg, W. R. L., Mencuccini, M., Mackay, D. S., Wang, Y., and Love, D. M.: Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost, Plant Cell Environ., 40, 816–830, 10.1111/pce.12852, 2017.

Tatarinov, F., Rotenberg, E., Maseyk, K., Ogée, J., Klein, T., and Yakir, D.: Resilience to seasonal heat wave episodes in a Mediterranean pine forest, New Phytol., 210, 485–496, 10.1111/nph.13791, 2016.

ter Braak, C. J. F., and Vrugt, J. A.: Differential Evolution Markov Chain with snooker updater and fewer chains, Statistics and Computing, 18, 435-446, 10.1007/s11222-008-9104-9, 2008.

Thom, D., Buras, A., Heym, M., Klemmt, H.-J., and Wauer, A.: Varying growth response of Central European tree species to the extraordinary drought period of 2018 – 2020, Agric. Forest Meteorol., 338, 109506, 10.1016/j.agrformet.2023.109506, 2023.

Tissue, D. T., Griffin, K. L., Turnbull, M. H., and Whitehead, D.: Stomatal and non-stomatal limitations to photosynthesis in four tree species in a temperate rainforest dominated by *Dacrydium cupressinum* in New Zealand, Tree Physiol., 25, 447-456, 10.1093/treephys/25.4.447, 2005.

Trugman, A. T., Detto, M., Bartlett, M. K., Medvigy, D., Anderegg, W. R. L., Schwalm, C., Schaffer, B., and Pacala, S. W.: Tree carbon allocation explains forest drought-kill and recovery patterns, Ecol. Lett., 21, 1552-1560, 10.1111/ele.13136, 2018.

Trugman, A. T., Anderegg, L. D. L., Sperry, J. S., Wang, Y., Venturas, M., and Anderegg, W. R. L.: Leveraging plant hydraulics to yield predictive and dynamic plant leaf allocation in vegetation models with climate change, Glob. Change Biol., 25, 4008-4021, 10.1111/gcb.14814, 2019.

Trugman, A. T.: Integrating plant physiology and community ecology across scales through trait-based models to predict drought mortality, New Phytol., 234, 21-27, 10.1111/nph.17821, 2022.

Tschumi, E., Lienert, S., van der Wiel, K., Joos, F., and Zscheischler, J.: The effects of varying drought-heat signatures on terrestrial carbon dynamics and vegetation composition, Biogeosciences, 19, 1979-1993, 10.5194/bg-19-1979-2022, 2022.

Tuzet, A., Perrier, A., and Leuning, R.: A coupled model of stomatal conductance, photosynthesis and transpiration, Plant Cell Environ., 26, 1097-1116, 10.1046/j.1365-3040.2003.01035.x, 2003.

Tuzet, A., Granier, A., Betsch, P., Peiffer, M., and Perrier, A.: Modelling hydraulic functioning of an adult beech stand under non-limiting soil water and severe drought condition, Ecol. Modelling, 348, 56-77, 10.1016/j.ecolmodel.2017.01.007, 2017.

Tyree, M. T., and Sperry, J. S.: Vulnerability of Xylem to Cavitation and Embolism, Annu. Rev. Plant Physiol., 40, 19-36, 10.1146/annurev.pp.40.060189.000315, 1989.

Tyree, M. T., and Yang, S.: Water-storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms, Planta, 182, 420-426, 10.1007/BF02411394, 1990.

Uddling, J., Hall, M., Wallin, G., and Karlsson, P. E.: Measuring and modelling stomatal conductance and photosynthesis in mature birch in Sweden, Agric. Forest Meteorol., 132, 115-131, 10.1016/j.agrformet.2005.07.004, 2005.

Ungar, E. D., Rotenberg, E., Raz-Yaseef, N., Cohen, S., Yakir, D., and Schiller, G.: Transpiration and annual water balance of Aleppo pine in a semiarid region: Implications for forest management, Forest Ecol. Manage., 298, 39-51, 10.1016/j.foreco.2013.03.003, 2013.

Van Genuchten, M. T.: A closed-form equation for predicting the hydraulic conductivity of unsaturated soils, Soil Sci. Soc. Am. J., 44, 892-898, 10.2136/sssaj1980.03615995004400050002x, 1980.

955 Van Genuchten, M. T., Leij, F. J., and Yates, S. R.: The RETC Code for Quantifying the Hydraulic Functions of Unsaturated Soils, U.S. Salinity Laboratory, U.S. Department of Agriculture, Riverside, California, Research Report, 93, 1991.

Wagner, Y., Feng, F., Yakir, D., Klein, T., and Hochberg, U.: In situ, direct observation of seasonal embolism dynamics in Aleppo pine trees growing on the dry edge of their distribution, New Phytol., 235, 1344-1350, 10.1111/nph.18208, 2022.

Walthert, L., Ganthaler, A., Mayr, S., Saurer, M., Waldner, P., Walser, M., Zweifel, R., and von Arx, G.: From the comfort 960 zone to crown dieback: Sequence of physiological stress thresholds in mature European beech trees across progressive drought, Sci. Total Environ., 753, 141792, 10.1016/j.scitotenv.2020.141792, 2021.

Wang, H., Gitelson, A., Sprintsin, M., Rotenberg, E., and Yakir, D.: Ecophysiological adjustments of a pine forest to enhance early spring activity in hot and dry climate, Environ. Res. Lett., 15, 114054, 10.1088/1748-9326/abc2f9, 2020.

Warm Winter 2020 Team, I. E. T. C.: Warm Winter 2020 ecosystem eddy covariance flux product for 73 stations in 965 FLUXNET-Archive format—release 2022-1 (Version 1.0). ICOS Carbon Portal, 2022.

Whitehead, D., Edwards, W. R. N., and Jarvis, P. G.: Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*, Can. J. For. Res., 14, 940-947, 10.1139/x84-166, 1984.

Wilson, K. B., Baldocchi, D. D., and Hanson, P. J.: Quantifying stomatal and non-stomatal limitations to carbon assimilation resulting from leaf aging and drought in mature deciduous tree species, Tree Physiol., 20, 787-797, 970 10.1093/treephys/20.12.787, 2000.

Wolfe, B. T., Sperry, J. S., and Kursar, T. A.: Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis, New Phytol., 212, 1007-1018, 10.1111/nph.14087, 2016.

Yang, J., Duursma, R. A., De Kauwe, M. G., Kumarathunge, D., Jiang, M., Mahmud, K., Gimeno, T. E., Crous, K. Y., Ellsworth, D. S., Peters, J., Choat, B., Eamus, D., and Medlyn, B. E.: Incorporating non-stomatal limitation improves the 975 performance of leaf and canopy models at high vapour pressure deficit, Tree Physiol., 39, 1961–1974, 10.1093/treephys/tpz103, 2019.

Yao, Y., Joetzjer, E., Ciais, P., Viovy, N., Cresto Aleina, F., Chave, J., Sack, L., Bartlett, M., Meir, P., Fisher, R., and Luyssaert, S.: Forest fluxes and mortality response to drought: model description (ORCHIDEE-CAN-NHA, r7236) and evaluation at the Caxiuanã drought experiment, Geosci. Model Dev., 15, 7809–7833, 10.5194/gmd-15-7809-2022, 2022.

980 Yoda, K., Kira, T., Ogawa, H., and Hozumi, K.: Self-thinning in overcrowded pure stands under cultivated and natural conditions, J. Mol. Biol., 14, 107-129, 1963.

Zhou, S., Duursma, R. A., Medlyn, B. E., Kelly, J. W. G., and Prentice, I. C.: How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress, Agric. Forest Meteorol., 182–183, 204-214, 10.1016/j.agrformet.2013.05.009, 2013.

985 Zinsser, J.: Vertical distribution of plant area density and canopy surface temperature of a semi-arid forest, Yatir Israel, Master, Institute of Meteorology and Climate Research - Atmospheric Environmental Research Karlsruhe Institute for Technology, Karlsruhe, 94 pp., 2017.

Zweifel, R., Etzold, S., Haeni, M., Feichtinger, L., Meusburger, K., Knuesel, S., von Arx, G., Hug, C., De Girardi, N., and Giuggiola, A.: Dendrometer, sap flow, meteorology and soil volumetric water content measurements during a long-term 990 irrigation experiment in a Scots pine forest at Pfynwald, Swiss Rhone valley (2011-2017). PANGAEA, 2020.