



RESEARCH ARTICLE

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Key Points:

- A new SPAC model is developed to simulate soil/plant water flux and water status at subdaily resolution
- The model uses a dynamic plant resistance system which is described by a plant physiological vulnerability curve
- The model can be easily parameterized under field conditions and particularly useful to assimilate leaf/stem water potential data

Supporting Information:

- Supporting Information S1

Correspondence to:

Z. Deng,
zijuandeng@sydney.edu.au;
deng0066@flinders.edu.au

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A vegetation-focused soil-plant-atmospheric continuum model to study hydrodynamic soil-plant water relations

Zijuan Deng^{1,2,3} , Huade Guan^{1,2}, John Hutson¹, Michael A. Forster^{4,5}, Yunquan Wang⁶, and Craig T. Simmons^{1,2}

¹School of the Environment, Flinders University, Adelaide, South Australia, Australia, ²National Centre for Groundwater Research and Training, Bedford Park, South Australia, Australia, ³Now at Centre for Carbon, Water and Food, Faculty of Agriculture and Environment, University of Sydney, Sydney, New South Wales, Australia, ⁴School of Agriculture and Food Science, University of Queensland, Brisbane, Queensland, Australia, ⁵Edaphic Scientific Pty Ltd., Port Macquarie, New South Wales, Australia, ⁶School of Environmental Studies, China University of Geosciences, Beijing, China

Abstract A novel simple soil-plant-atmospheric continuum model that emphasizes the vegetation's role in controlling water transfer (v-SPAC) has been developed in this study. The v-SPAC model aims to incorporate both plant and soil hydrological measurements into plant water transfer modeling. The model is different from previous SPAC models in which v-SPAC uses (1) a dynamic plant resistance system in the form of a vulnerability curve that can be easily obtained from sap flow and stem xylem water potential time series and (2) a plant capacitance parameter to buffer the effects of transpiration on root water uptake. The unique representation of root resistance and capacitance allows the model to embrace SPAC hydraulic pathway from bulk soil, to soil-root interface, to root xylem, and finally to stem xylem where the xylem water potential is measured. The v-SPAC model was tested on a native tree species in Australia, *Eucalyptus crenulata* saplings, with controlled drought treatment. To further validate the robustness of the v-SPAC model, it was compared against a soil-focused SPAC model, LEACHM. The v-SPAC model simulation results closely matched the observed sap flow and stem water potential time series, as well as the soil moisture variation of the experiment. The v-SPAC model was found to be more accurate in predicting measured data than the LEACHM model, underscoring the importance of incorporating root resistance into SPAC models and the benefit of integrating plant measurements to constrain SPAC modeling.

1. Introduction

Plant-water relations concern how plants extract water from soil, transport water within the plants, and lose water by transpiration from the leaves [Passioura, 2010]. The water transfer path across the soil, plant, and atmosphere is called the soil-plant-atmosphere continuum (SPAC). SPAC models quantify hydraulic states and water fluxes which have long been a focus of agricultural and plant physiological research [Kramer and Boyer, 1995; Slatyer, 1967]. Quantification of the land-atmosphere water flux via SPAC is essential in meteorological and hydrologic modeling as it represents energy and water exchanges between land and the atmosphere. Thus, soil-plant water relations are a key subject in agriculture, hydrology, and atmospheric science.

Understanding SPAC often requires combining plant ecophysiological measurements with hydrological modeling [King and Caylor, 2011]. For example, Draye et al. [2010] showed the advantage of using hydrological models to assist in understanding root-water uptake in the plant physiological field, and emphasized the importance of reflecting the plant's role in hydrological models. However, Sperry et al. [1998], based on a SPAC modeling experiment, showed that maximum tree water use could be limited by hydraulic properties of both soil and plant.

Root water uptake functions in SPAC models are crucial to link soil-plant hydraulic status to water flux. Hopkins and Bristow [2002] classified the root water uptake functions into two types: microscopic and macroscopic. In a microscopic model, roots are explicitly described as assembled pipes that have axial and radial resistances. The root water uptake denotes the summation of the soil water flux extracted by all these roots. However, a macroscopic model represents root water uptake as a sink term in the Richards equation,

calculating water loss from each soil layer in the root zone. LEACHM [Hutson, 2003] and HYDRUS [Šimůnek *et al.*, 1998] are two commonly used macroscopic SPAC models that simulate water flow in the vadose zone. The two models use different types of macroscopic root water uptake functions. HYDRUS employs a stress function (such as Feddes *et al.* [1978]) to impose the constraint of soil moisture deficit on transpiration. The root water uptake is thus determined by the soil moisture condition, the prescribed stress function, and the atmospheric demand. LEACHM applies Darcy's law to describe water flow in the soil-root continuum. The root water uptake rate depends on soil hydraulic conductivity and the soil to root water potential gradient. Both models use an atmospheric boundary condition. Root water uptake is constrained by a prescribed potential transpiration, using constant optimal stomata resistance and neglecting the regulating role of plant storage and resistances in transpiration. Advances in 3-D microscopic root models and recent experimental evidence emphasize the significant role of root resistance in manipulating soil water extraction [Doussan *et al.*, 2006; Dunbabin *et al.*, 2013]. However, microscopic root models require complex parameterization, such as detailed information on root architecture, root length, and root/stem xylem hydraulic conductivity. Therefore, microscopic models are difficult to apply unless extensive, time-consuming, and often costly, field data have been collected.

Alternative SPAC models have coupled soil and root/plant resistance, such as SWIM [Verburg *et al.*, 1996] and SiSPAT [Braud *et al.*, 1995]. However, these models treat root resistance as a fixed empirical value that is invariant with root water potential, and neglect water storage in the plant xylem. They are not appropriate to simulate the transient process of plant water potential, particularly at the subdaily scale. In this regard, more comprehensive ecophysiology models such as TREES model [Mackay *et al.*, 2015] and XFM model [Hentschel *et al.*, 2013] make good contributions. However, both models demand detailed plant hydraulic data such as the root, stem, and leaf vulnerability curves.

Hydrological models such as LEACHM and HYDRUS were commonly parameterized and validated using soil moisture data [Besharat *et al.*, 2010; Vrugt *et al.*, 2001]. Soil moisture is relatively easy to measure but may not be representative of the entire root zone hydraulic status [Jones, 2004, 2008]. In addition, soil moisture varies slowly with time and thus does not reflect diurnal variations of plant hydraulic states in SPAC. In this regard, stem xylem water potential provides valuable information as its diurnal range is influenced by the magnitude of SPAC water transfer, plant storage capacitance, and the soil/plant hydraulic properties. Plant water potential characteristics are key to understanding plant water use strategy [Aroca and Ruiz-Lozano, 2012]. A recent study by Mackay *et al.* [2015] found that plant hydraulic properties, such as the isohydric to anisohydric continuum, are of hydrological significance with differing water use strategy during droughts. However, few studies explored continuous data sets of plant water potential (specifically leaf water potential) within SPAC models [Kumagai, 2001; Mackay *et al.*, 2015; Rings *et al.*, 2013], possibly due to the difficulty of continuous data acquisition with instrumentation such as pressure chambers. Recent advances in plant water potential instrumentation now allow for continuous measurements of stem or leaf water potential and have recently advanced our understanding of how plant water status assists in estimating transpiration [Wang *et al.*, 2014, 2016; Yang *et al.*, 2013].

Given the limitations of previous SPAC models, there is a need to develop a new SPAC model in which the role of vegetation and its response to environmental conditions are represented and can be parameterized with commonly available, or relatively easily attainable, field measurements. Here we propose a new and simple vegetation-focused SPAC model, referred to as v-SPAC that better represents the role of plant physiological functions in SPAC water transfer. Some unique features of the v-SPAC model developed here include (1) the vegetation control on SPAC water transfer is represented by a resistance network composed of root and stem, which is dependent on plant hydraulic states; (2) root and stem resistance are lumped, so can be easily parameterized with stem water potential and sap flow measurements; and (3) a capacitance term is introduced for tree water storage to buffer the effects of daytime transpiration on root water uptake.

The paper is organized as follows: section 2 describes the v-SPAC model structure; section 3 describes the drought experiment with *Eucalyptus crenulata* saplings; section 4 shows the parameterization of the plant resistance in the form of a vulnerability curve and model training with an optimization tool; section 5 presents calibration and prediction results on the experiment and the comparison between v-SPAC and LEACHM modeling; conclusions are summarized in section 6.

2. Model Conceptualization and Formulation

2.1. Model Description

2.1.1. Model Conceptualization

The new model is developed from LEACHM, used to simulate water and solute transport in the unsaturated zone [Hutson, 2003]. Water flow in the soil matrix remains the same as in LEACHM. Water transport in plants is simulated in the v-SPAC model in which the total resistance in the soil to root continuum is composed of a soil-root resistance adopted from the RWU function in LEACHM and a plant resistance which is superimposed into the RWU function. A capacitance term is also added in the v-SPAC model to calculate the storage contribution to the transpiration stream together with soil water extraction by the root. Conceptualization of the v-SPAC model is demonstrated in Figure 1.

2.1.2. Soil Water Transport and Root Water Uptake Function

Water flow in soil is governed by the Richards equation and root water uptake (RWU) is described with the scheme of Nimah and Hanks [1973],

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[K(\theta) \frac{\partial \psi_s}{\partial z} + 1 \right] - RWU(z, t), \tag{1}$$

where θ ($\text{m}^3 \text{m}^{-3}$) is volumetric water content, ψ_s (mm) is soil water pressure head, K (mm/d) is soil hydraulic conductivity, t (day) is time, z (mm) is depth, positive downward, and RWU is a sink term representing water loss per unit time by root water uptake (day). The original RWU (based on Nimah and Hanks [1973]) function in LEACHM is shown in equation (2) as follows:

$$RWU(z, t) = -K(\theta) \cdot \frac{[\psi_s(z, t) - \psi_x(t) - z \cdot (R_c + 1)] \cdot RDF(z)}{\Delta x \Delta z}, \tag{2}$$

where $K(\theta)$ (mm/d) is soil hydraulic conductivity, ψ_x (mm) is water potential at root or stem xylem (water potential at root collar in original LEACHM), R_c (mm) accounts for friction loss in the root, “+ 1” accounts the hydraulic head loss due to gravity, RDF is the fraction of the total active root density in the soil depth

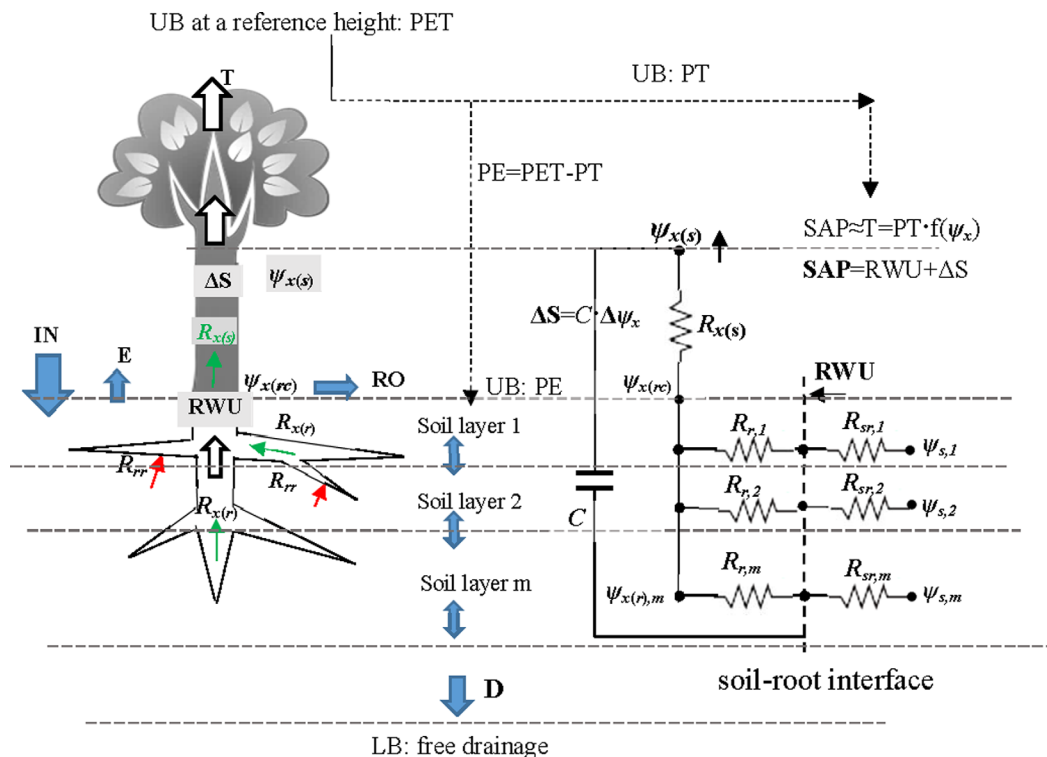


Figure 1. Illustration of water transfer in the v-SPAC model (see the list of symbols and abbreviations in the notation section). The blue arrows in the left section of the figure show the hydrological processes modeled in LEACHM. Other arrows show the processes and parameters modified or added in the v-SPAC model compared to LEACHM.

increment Δz (mm), and Δx is the conceptual distance from a point in the soil where ψ_s is measured to the plant root. Soil hydraulic conductivity K is calculated following *Mualem* [1976]:

$$K(\theta) = K_s \Theta^{0.5} [1 - (1 - \Theta^{1/m})^m]^2, \tag{3}$$

where K_s is saturated hydraulic conductivity and Θ is soil moisture saturation, which is calculated with the van Genuchten water retention function [van Genuchten, 1980],

$$\Theta = \frac{\theta - \theta_r}{\theta_s - \theta_r} = \frac{1}{[1 + (\alpha h)^n]^m}, \tag{4}$$

where θ_s is volumetric soil water content at saturation, θ_r is residual moisture content, h is the soil water pressure head (in kPa). α , n , and m are parameters in the van Genuchten water retention function where α has unit of 1/kPa, n and m are dimensionless, and $m = 1 - 1/n$.

2.1.3. The Resistance Terms

Root diameter changes diurnally and root resistance itself changes with root water potential which also varies with time [Nobel and Cui, 1992]. In v-SPAC, it is assumed that the overall root resistance is dependent on root xylem water potential (ψ_x) and that root shrinkage is accompanied with a drop of root water content. Therefore, water potential links the resistance and the storage component. The resistance for water flow from soil to plant xylem is described in two parts: the bulk soil to the soil-root interface resistance transformed from the original RWU function in LEACHM (see equation (2)) and the resistance of water transfer from the soil-root interface to root (and to stem) xylem. The latter is lumped into an integrated vulnerability curve (described in section 4).

2.1.3.1. The Resistance From the Bulk Soil to the Soil-Root Interface

The resistance of water transfer from the bulk soil to the soil-root interface (R_{sr}) is transformed into equation (5) from the original RWU function in LEACHM (see equation (2)),

$$R_{sr}(z, t) = \frac{\Delta x}{RDF(z) \cdot K(\theta)}, \tag{5}$$

where R_{sr} is described by soil hydraulic conductivity ($K(\theta)$) and an equivalent path length (Δx) for water transfer from soil to root ($\Delta x = 10$ mm is the usual default in LEACHM). The SWIM model sets Δx dependent on RDF at each soil layer, that is, Δx becomes shorter and R_{sr} is smaller if there is a larger root density. In *Janott et al.* [2011], Δx is 2 mm inferred from an independent microscopic experiment, while K is weighted between soil hydraulic conductivity of the bulk soil and that at the root surface water potential. In v-SPAC, Δx is a calibrated parameter rather than a prescribed constant.

R_c in the original RWU function in LEACHM (see equation (2)) is also difficult to determine. From its definition, it should be primarily dependent on the axial root resistance and the overall ratio of radial to axial root resistances at the corresponding soil depth. Since the root resistance is simulated in v-SPAC, R_c is not used in the model, i.e., R_c is zero.

The root distribution function, RDF, is described by an exponential function similar to *Hentschel et al.* [2013], so that the root density decreases with increasing depth,

$$RDF(z) = \lambda \beta^{(z/L)}, \tag{6}$$

where β is the shape parameter within a range of 0 to 1 (when β equals to 1, RDF corresponds to a uniform root density, when β is close to 0, RDF shows a steep exponential decrease of root length density from soil surface to the bottom root zone). L is the root zone depth, and λ is a weighting parameter to make

$$\sum_{z=0}^L RDF(z) = 1, \text{ which means } \lambda = 1 / \sum_{z=0}^L \beta^{(z/L)}.$$

2.1.3.2. Resistance in the Plant: The Integrated Vulnerability Curve

A vulnerability curve describes hydraulic conductivity loss (HCL) with reduction of xylem water potential of a stem or root segment [Sperry et al., 1998]. Here we propose an “integrated vulnerability curve (IVC)” to represent the function of whole plant resistance (R_p) in response to plant water status (ψ_x). IVC defines the overall change of R_p , consisting of resistance components at the soil-root interface, in root cortex, root xylem, root collar, and finally in the stem xylem.

The curve is described by a Weibull function [e.g., Sperry et al., 1998],

$$R_p = R_{\min} \cdot \exp [(-\psi_x/d)^b], \quad (7)$$

where R_{\min} is the minimum plant resistance (equivalent to the maximum hydraulic conductance at full hydration). The parameters d and b can be obtained by the dehydration method, air injection method, and centrifuge method for single root/stem segment or the vacuum chamber method for entire shoot or root system [Cochard et al., 2013]. Each root may have different d and b values and are dependent on root length and root age, which are only practical for lab experiment and 3-D modeling such as in Doussan et al. [2006]. The vacuum chamber is a destructive method and limited by the size of the chamber. These traditional methods thus cannot be used to determine a vulnerability curve for mature trees in field conditions. In our experiments, the parameters are obtained from in situ measurements on trees, thus representing the hydrodynamics of the whole plant in the field. By analyzing concurrent measurements of nighttime sap flow and stem xylem water potential, the total plant resistance can be derived (see details in section 4 on deriving IVC parameters).

The plant resistance (R_p) in the model is described as the sum of the total root resistance ($R_{r,t}$) and the stem xylem resistance $R_{x(s)}$,

$$R_p = R_{r,t} + R_{x(s)}. \quad (8)$$

Both $R_{r,t}$ and $R_{x(s)}$ should be described by vulnerability curves, each has three parameters (see equation (7)). To reduce the dimension of the model, stem resistance $R_{x(s)}$ is neglected, and $R_{r,t}$ is approximated as R_p for our experiment. The approximation is reasonable as $R_{r,t}$ usually dominates over $R_{x(s)}$ [Hunt et al., 1991; Jackson et al., 2000; De Micco and Aronne, 2012; Tyree and Zimmermann, 2002].

The effective root resistances in each soil layer ($R_{r,i}$) are assumed to be in parallel and inversely proportional to RDF (as in LEACHM and SiSPAT),

$$R_{r,i} = \frac{R_{r,t}}{\text{RDF}_i} \approx \frac{R_p}{\text{RDF}_i}. \quad (9)$$

Note that $R_{r,i}$ is not simply the sum of the axial root resistance $R_{x(r),i}$ and the radial root resistance $R_{rr,i}$ in soil layer i . $R_{r,i}$ is an effective root resistance, so that the root water uptake is described by Darcy's law with corresponding average soil water potential (ψ_s).

Finally, the root water uptake in each soil layer (RWU_{*i*}) is calculated as follows:

$$\text{RWU}_i = \frac{\psi_{s,i} - \psi_{r,i}}{R_{r,i} + R_{sr,i}}. \quad (10)$$

Note that RWU_{*i*} has a unit of "mm/d" which is converted to equivalent soil water content loss in the Richards equation (see equation (2)) by dividing by the soil depth increment (Δz) (unit of RWU in equation (2) is day). R_p , R_{\min} , $R_{r,i}$ are all normalized by land surface domain area. All calibrated and reported R_p , R_{\min} , R_r are normalized values with units of day.

2.1.4. Storage Dynamics of Trees

Root water uptake (RWU) is assumed to be equal to transpiration (T) in hydrological models. In fact, there is a mismatch in timing between RWU and T due to tree storage buffering [Cermak et al., 2007]. During the morning, sap flow rises earlier in the upper crown of a tree than in its stem base in response to solar radiation; in the afternoon, sap flow at its stem base persists when transpiration has reduced significantly [Cermak et al., 2007]. Instantaneous transpiration is hence different from root water uptake due to the transient process of loss or gain of the storage in a tree. To represent this process, a capacitance term is included in v-SPAC to simulate the dynamic plant water storage and its effect.

Water is stored in xylem fiber, bark, and primary tissues of a tree. Timescales for water release from tree storage component can be in seconds to hours [Pirson and Zimmermann, 1982]. The storage change is accompanied with a change in xylem water potential (ψ_x) [Sperry et al., 1998],

$$\Delta S = C \cdot \Delta \psi_x, \quad (11)$$

where C is a lumped capacitance of the plant storage compartment. The capacitance varies with species, age, and water status (or relative water content) [Pirson and Zimmermann, 1982]. C is reported between $1 \times$

$10^{-6} \text{ m}^3 \text{ MPa}^{-1}$ to $350 \times 10^{-6} \text{ m}^3 \text{ MPa}^{-1}$ in grass, softwood, and hardwood species [Hunt et al., 1991]. As there is a scarcity of capacitance data [Scholz et al., 2011], a constant capacitance is used for simplicity as in Sperry et al. [1998]. It is worth noting that in porous media (PM) models, C is assumed to reduce with a drop of xylem water potential ($C = \frac{c}{-\psi_x}$, in which c is a constant) [Chuang et al., 2006; Janott et al., 2011; Kumagai, 2001]. In v-SPAC, both forms are enabled to calculate the storage change. Here, for model testing, a constant capacitance is used.

Unlike LEACHM, where actual transpiration (T) equals root water uptake (RWU), in v-SPAC both RWU and plant storage change (ΔS) will contribute to T (in which a positive ΔS represents storage refilling in the trees),

$$T = \text{RWU} - \Delta S. \tag{12}$$

2.1.5. Transpiration Reduction Function (Significance of ψ_x)

In addition to resistance in soil, roots, or stem xylem, water transfer in SPAC is also controlled by leaves. A reduction function is used to represent the stomatal control on transpiration. A similar approach can be found in Hentschel et al. [2013]. The reduction function is used to represent the stress of environmental conditions on transpiration. In this study, the reduction function is associated with plant water potential, similar to the stress function in HYDRUS which is based on soil water potential. Instead of using an exponential function as in Hentschel et al. [2013], we apply a simple piecewise linear function. The reduction function $f(\psi_x)$ is derived from correlation between the maximum sap flow rate in a day and its concurrent xylem water potential (ψ_x),

$$f(\psi_x) = \begin{cases} 1 & (\psi_x \geq p_1) \\ \frac{\psi_x - p_2}{p_1 - p_2} & (p_2 \leq \psi_x < p_1) \\ 0 & (\psi_x < p_2) \end{cases}, \tag{13}$$

where $f(\psi_x)$ is the transpiration reduction function, describing reduced transpiration rates with decreasing plant water potential, p_1 denotes stem water potential (ψ_x) above which transpiration retains a constant optimal transpiration rate, p_2 denotes ψ_x below which, transpiration drops to zero with increased water stress. Parameters p_1 and p_2 are obtained from observation of the maximum transpiration rate of a day and its corresponding stem water potential.

2.2. Model Flowchart

The model is built upon the LEACHM soil water transport component. The model starts with initial soil moisture profile, a prescribed upper flux boundary and a lower boundary in the soil profile (see Figure 2). A given xylem water potential (ψ_x) will be iterated till both the water flux and water potential converge. The soil and plant resistance/conductivity and capacitance will be updated in each iteration step. Figure 2 illustrates the flowchart of simulating transpiration and plant water status in v-SPAC.

There are two options for prescribing the upper transpiration flux boundary (F). In option 1, the observed sap flow rate (SAP) is used as flux boundary ($F = \text{SAP}$) to parameterize the SPAC hydraulic system which will be used for model calibration. The parameterized plant hydraulic system embraces all the resistances occurred in water transfer from the root surface to the point where the water potential is measured. In option 2, a reduced potential transpiration ($F = \text{PT} * f(\psi_x)$) is applied as a flux boundary to predict the actual transpiration. Therefore, option 2 is used for model testing and application. The potential evapotranspiration (PET) is first calculated with the FAO method [Allen et al., 1998] and then partitioned to potential transpiration (PT) and potential evaporation (PE) based on leaf area index (discussed in section 4). PE is prescribed as the upper boundary condition of the soil surface (also in option 1). The upper boundary of the tree canopy is prescribed as reduced PT by the transpiration reduction function $f(\psi_x)$, and is updated with each iteration of ψ_x . For both options, the model starts with a given ψ_x which will be adjusted until the sum of flux (RWU- ΔS) is equal to or less than PT. To be strict, the predicted flux is actually the sap flow rate (SAP) where the sap flow sensor is installed on the tree trunk rather than the transpiration (T) from the canopy. However, SAP will be a good approximation of actual T if the sap flow sensor is installed at the bottom of the crown (highest position in stem before branching), as ΔS from the crown is usually neglected due to limited storage buffering of leaf

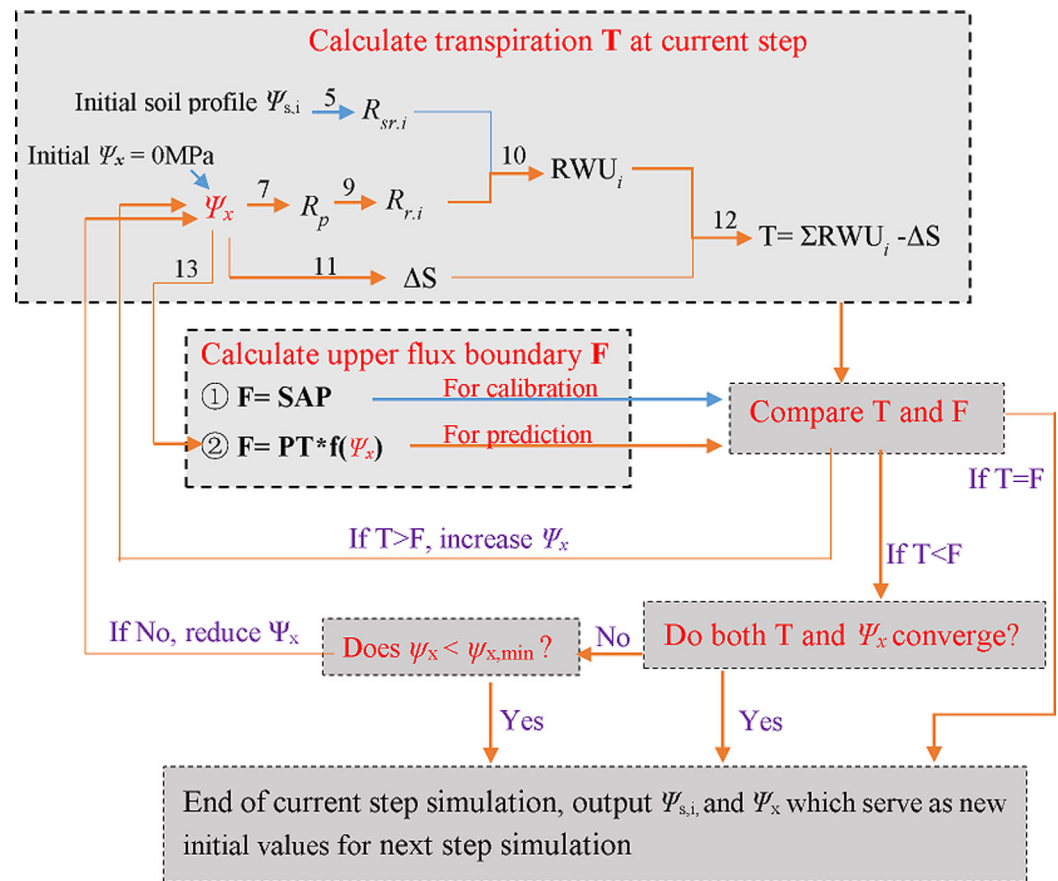


Figure 2. A flowchart for simulating plant water flux/water status in v-SPAC. F is the upper flux boundary. SAP is observed sap flux. PT is calculated potential transpiration. Refer to the equations for other symbols. Note: the orange arrows identify the terms needed to be updated in iterations within each simulation step. The blue arrows are determined values in each simulation step. The numbers above the arrows are the equation number in the text.

water content [De Micco and Aronne, 2012]. Therefore, interpretation of the observed or predicted sap flow rate depends on where the sap flow sensor is installed. The higher the installation point, the closer SAP approximates to T; the lower the installation point, the closer SAP approaches RWU.

In summary, the v-SPAC model retains the soil water transport routine in LEACHM. Soil water extraction by the root remains as a sink term in the equation in both models but the RWU function itself is modified (see equations (10) and (12) for v-SPAC model versus equation (2) for LEACHM model). The dynamics of plant resistance (equations (3)–(9)) and storage (equation (11)) are added in v-SPAC. In LEACHM, PET is calculated based on the FAO method or Penman-Monteith equations in which a constant maximum stomata conductance/minimum stomata resistance is used. However, v-SPAC prescribes a transpiration boundary condition that is dependent on plant water status in addition to the atmospheric demand. Specifically, PT is further reduced with a scaling function depending on plant water stress (see equation (13)). The convergence criterion of simulation thus diverges between the two models. In LEACHM, the root water potential will iterate until RWU is equal to the prescribed boundary (PT) or less than PT when the root water potential reaches a minimum value ($\psi_{r,min}$); while in v-SPAC, the sum flux ($RWU - \Delta S$) will be compared to the prescribed boundary. The minimum root water potential ($\psi_{r,min}$) is prescribed in both LEACHM and v-SPAC and is often assigned the minimum value of observed or reported ψ_x time series. Here $\psi_{r,min}$ is assigned as -3.5 MPa for the species in the experiment.

3. Field Experiments and Data

A water-controlled experiment was conducted on a drought sensitive species *E. crenulata* to test the models with data sets for soil moisture content, stem xylem, water potential and sap flow rate. The site was located



Figure 3. Experiment settings of *E. crenulata* saplings in Armidale, New South Wales.

in Armidale, New South Wales (151.776°E, 30.706°S) (see Figure 3), where six potted *E. crenulata* saplings were grown from August 2013 and monitored from 23 September to 27 October 2013.

The saplings (1.5–2 m tall) were randomly divided into two groups: the “wet treatment” group included saplings 1, 3, and 5; the “drought treatment” had four replicates (saplings 2, 4, 6, and 7) (see Figure 4). All saplings were irrigated with 1.5 L of water every other day, except that the drought treatment saplings had water withheld twice, for 5 and 14 days. PSY1 psychrometers and SFM1 sap flowmeters (ICT international, Armidale, Australia) were installed on 22 September 2013 to monitor stem xylem water potential and sap flow rate. Soil water content was measured with EC-5 capacitance based sensors (Decagon Devices) and soil water potential by a WP4C Dewpoint Water Potential Meter and a 2100F Tensiometer with a dial gauge. The saturated hydraulic conductivities of the soil in each pot vary in the range of 3–10 m/d (measured at –5 cm/s suction rate with Decagon Mini-Disk Infiltrometer) although the soils were well mixed and

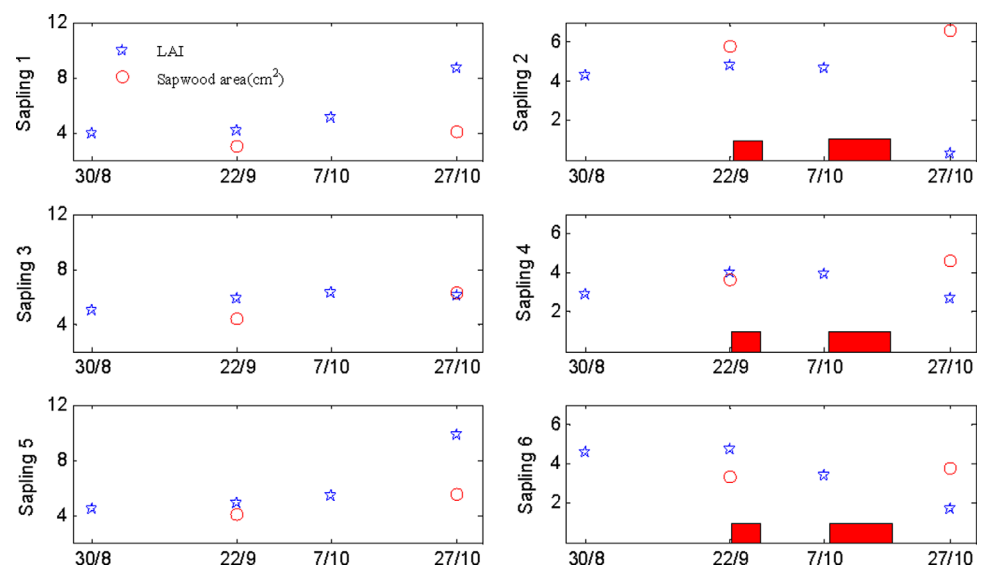


Figure 4. The leaf area index (LAI, normalized by pot opening area) and sapwood area (cm²) of six *E. crenulata* saplings over the growing season in year 2013 (x axis in date format dd/mm). The red boxes denote the periods when the saplings had water withheld.

assumed uniform over all pots. Leaf area was measured with CI-202 Leaf Area Meter (CID Biosciences, US). The bark thickness and the sapwood area were measured at the end of the experiment by cutting the stems at the point where the SFM1 needles were installed. See details on the experiment in supporting information Text S1 and further information can be found in Forster [2012] and Doronila and Forster [2015].

4. Integrated Vulnerability Curve (IVC) and Model Parameterization

A vulnerability curve (VC) describes the dependence of plant hydraulic conductivity loss (HCL) on reduced xylem water potential (ψ_x). Here we propose to parameterize the curve with a plot of sap flow rate (SAP) versus stem ψ_x (SS plot). The obtained VC represents the total resistance from the soil-root interface to the point where stem ψ_x is measured, thus is not the traditional VC derived for one xylem segment. We refer to it here as integrated VC (IVC). IVC is obtained from the SS plot as shown in Figure 5 (top). It is assumed that soil water potential (ψ_s) is constant within a certain short period so that ψ_x at zero nighttime SAP from sub-daily (for sandy soil) or weekly (for clay soil) observations could be a good approximation of the corresponding ψ_s . We can see from the SS plot that the ψ_x points of each period (7 P.M. to 7 A.M. the next day) appear in a line of the same color (ψ_x is shown in circles). ψ_s for this period is then inferred as the interception of the line at zero SAP. This inferred ψ_s is comparable to that calculated from the water retention curve with observed soil water content at 5 cm ($\psi_{s,5}$ in solid squares) and at 15 cm ($\psi_{s,15}$ in solid diamonds). Supporting evidence for the observation can be also found in Bucci *et al.* [2004]. The plant resistance (R_p) at each ψ_x is then calculated as the slope of the SS plot (i.e., $R_p(\psi_x) = (\psi_s - \psi_x)/SAP$). The resulted (ψ_x, R_p) points will then be used to obtain the parameters R_{min}, d, b by fitting the IVC (see equation (7)). The points (ψ_x, R_p) are converted to percentage value ($\psi_x, 1 - R_{min}/R_p * 100\%$), which then form the HCL curve. The resulting IVC of *E. crenulata* is shown in the form of HCL in Figure 5 and in the form of resistance in Figure 6 (the resistance is normalized by sapwood area/pot opening area). It shows that the IVC of *E. crenulata* is within the range of root and stem VC of the *Acer negundo* reported in Sperry *et al.* [1998] (see Figure 5, bottom).

Soil water retention curves were derived from direct $\psi_s-\theta$ measurements (see supporting information Text S1). Other unknown parameters were inversely optimized using the Markov chain Monte Carlo (MCMC)

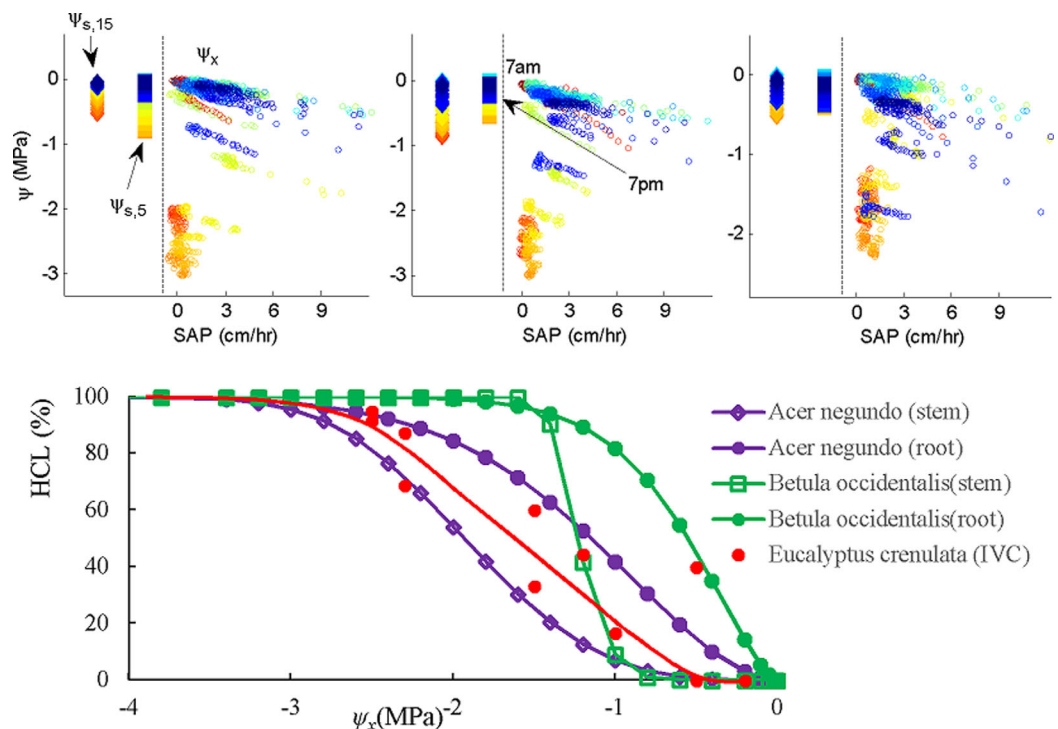


Figure 5. The concurrent nighttime sap flow rate (SAP) versus stem xylem water potential (ψ_x in circles, ψ_s in diamond and squares) of *E. crenulata* saplings 2, 4, 6, from 7 P.M. to 7 A.M. the next day (at 15 min interval) (SS plot, top) and the hydraulic conductivity loss of the *E. crenulata* with ψ_x compared to other species (HCL plot, bottom).

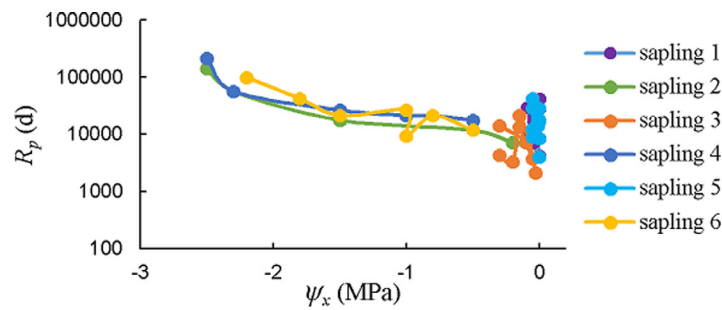


Figure 6. The integrated vulnerability curves (IVC) of saplings *E. crenulata*.

sampling scheme with the Differential Evolution Adaptive Metropolis (DREAM) algorithm [Vrugt et al., 2009] (coded in Matlab). The algorithm posts the inverse problem in a Bayesian inference, so that a posterior distribution is produced for the sampling parameters, given a known prior distribution of the parameters. The posterior probability distribution function (pdf)

describes the likelihood of the parameter within the calibration range in light of the observation data, which helps us to understand the uncertainties of the optimized results. In this study, a uniform distribution is assigned to all unknown parameters within the calibration range since we have no prior knowledge of the distribution but only the range of parameters from literature. The MCMC chain number is set as 10 and the iteration steps is set to 5000 times per chain to ensure the convergence of the parameterization. The convergence is diagnosed with the Gelman and Rubin statistics (R_{stat}) [Gelman and Rubin, 1992]. Here we set the cutoff value of R_{stat} as 1.2, below which the MCMC chains are deemed well mixed and the parameterization is converged (a small number of R_{stat} , for example 1.3, also works, we use 1.2 following Minasny et al. [2011]). The v-SPAC model (in FORTRAN) was called at each iteration by DREAM. Usually, an analytical form of the posterior pdf of the parameters cannot be obtained with complex models such as HYDRUS and LEACHM; therefore, we approximate the posterior pdf from the last 10,000 generated samples with the DREAM algorithm. Similar practices for hydrological applications and geo-statistics using DREAM can be found in Scharnagl et al. [2011] and Minasny et al. [2011].

For model parameterization, the measured sap flow rate was used as known upper flux boundary (see option F = SAP in Figure 2). The model was trained over stem water potential (ψ_x) of sapling 4 (before the severe drought) and tested with all other saplings regardless of their different water treatments. The efficiency of model calibration using stem water potential (ψ_x) was tested with parameter identifiability. Here we refer to a parameter as identifiable if the uncertainty is reasonably small as defined in Scharnagl et al. [2011].

Table 1. The v-SPAC Parameter Settings and Calibration Range for the Experiment

	Numerical Settings
Training period	23 Sep to 16 Oct 2013 (sapling 4, before the end of second drought treatment)
Validation period	16 Oct to 27 Oct 2013 of sapling 4 and 23 Sep to 16 Oct 2013 for all other saplings
Optimization target	Stem xylem water potential
Soil profile (mm)	250
Soil segment (mm)	10
Domain land surface area (cm ²)	471.2 (the pot opening area)
Sapwood area (cm ²)	3.66 (sapling 4)
d (MPa) (in VC)	1.0
b (in VC)	0.74
α (kPa ⁻¹) (in WRC)	0.145
n (in WRC)	1.323
θ_s (in WRC)	0.33
θ_r (in WRC)	0.004
p_1 (MPa) (in $f(\psi_x)$)	-1.5
p_2 (MPa) (in $f(\psi_x)$)	-3.5
K_s (mm/d)	[500 10000]
Δx (mm)	[0.0001 10]
R_{min} (d)	[100 10000]
C (mm·MPa ⁻¹)	[0 5]
β (in RDF)	1
L (mm) (in RDF)	250

Table 1 shows the details of modeling settings and calibration. Root depth (L) of the potted saplings was fixed at the pot depth of 250 mm and RDF of the potted saplings was set as a uniform distribution owing to the confined space.

Initial conditions: the initial soil water profile was estimated by spinning the model with climatic forcing data several months before the starting date of simulation. The lower boundary is set as free drainage. The upper boundary condition varied for different simulation purposes. For model parameterization, the sap flow observation was used (F = SAP, see Figure 2), while to test the predictive capacity of the model, potential transpiration was used (F = PT*f(ψ_x)) as the flux boundary. The PT/PET ratio was assumed as 1 at LAI = 6. The ratio was linearly scaled between 0 and 1 corresponding to LAI = 0 to 6. For example, PT/PET = 4/6 at LAI of 4. The maximum PT was constrained at 1.2*PET.

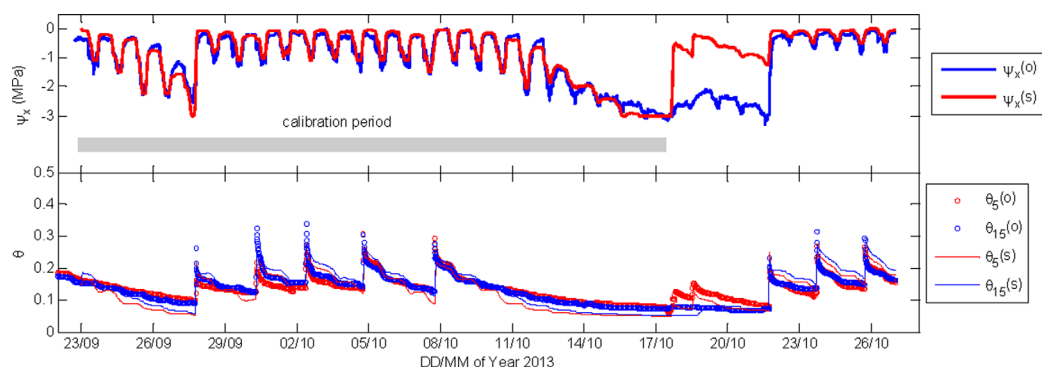


Figure 7. The calibration results of *E. crenulata* (sapling 4).

5. Results and Discussion

5.1. The v-SPAC Model Calibration and Validation

The data of *E. crenulata* sapling 4 (prior to 17 October 2013) was used for model calibration. The model was validated over the period from the end of the second controlled drought (since 17 October 2013) and the whole period for all other five saplings. The results show that the v-SPAC model predicted ψ_x as well as θ (although θ was not used for calibration) (see Figure 7). The coefficients of determination (R^2) are 0.65 and 0.90 for ψ_x and θ , respectively, for the prediction period for sapling 4 (16 October to 27 October 2013). It indicates that soil moisture sensors captured the root zone water status in the confined pot space. Table 2 gives the optimized parameter sets. It shows that K_s is within the measured range 3–10 m/d. Using ψ_x and SAP seems sufficient for inverse modeling to obtain the soil hydraulic conductivity (K_s). The optimized capacitance (C) is at 0.03 mm MPa^{-1} approximating 3% of the total plant volume (assuming sapwood area is the same all through the main stem). The calibrated R_{\min} is 2300 day, comparing well with those inferred from the SS plot (1500–3000 day). The parameter Δx approaches zero ($< 2 \mu\text{m}$), implying the marginal contribution of soil to root resistance (R_{sr}) to the total hydraulic resistance in the soil-plant continuum. However, it is more likely that the integrated vulnerability curve (IVC) derived from the SS plot already integrates the R_{sr} , as the plant resistance is inferred over the water potential gradient from the bulk soil to the stem which may have included the water path from bulk soil to root surface (the site where R_{sr} occurs). Since Δx is at a micrometer scale, the parameter (R_{sr}) in the v-SPAC model could be eliminated.

Prediction of sap flow rate and stem water potential of sapling 1 from the well-watered group and sapling 2 from the drought treatment group are shown in Figure 8 (results of other saplings are shown in supporting information Figures S1–S3). The modeling results demonstrate the robustness of v-SPAC in simulating plant water potential, sap flow rate, and soil water content for all irrigation schedules (R^2 are 0.58, 0.73, 0.74 for ψ_x , θ , and SAP, respectively, for sapling 1 and 0.84, 0.90, 0.85 for sapling 2).

However, the model overestimates ψ_x of the saplings in the drought treatment group during the first 4 days since rewatering on 18 October 2013. One possible reason is that the plant resistance increased significantly after the severe drought so that R_{\min} or the VC parameters do not fit any more. Plants can adapt to drought by growth of root Casparian bands which will increase root resistance permanently [Aroca and Ruiz-Lozano, 2012]. Plants may also go through reversible anatomic change such as embolism of xylem that can be repaired gradually after rehydration [Tyree and Zimmermann, 2002]. The rehydration may take from hours to weeks depending on the severity of the dehydration. The gap between soil and root can also

enlarge due to shoot/soil shrinkage which can be gradually refilled after rewatering [Carminati et al., 2009]. To test these possibilities, we conduct a new simulation starting from the second drought where the soil and plant hydraulic state calculated from the previous simulation are used now as the initial conditions (see Figure 9). We see that the simulated ψ_x rematches the observed data after 4 days of rewatering as long as the plant resistance

Parameters	Optimized Values	Estimated ^a
K_s (mm/d)	5,200	3000–10,000
Δx (mm)	0.0	
R_{\min} (d)	2,300	1,500–3,000
C (mm·MPa ⁻¹)	0.03	

^a K_s was estimated from infiltration measurements; R_{\min} was inferred from the VC.

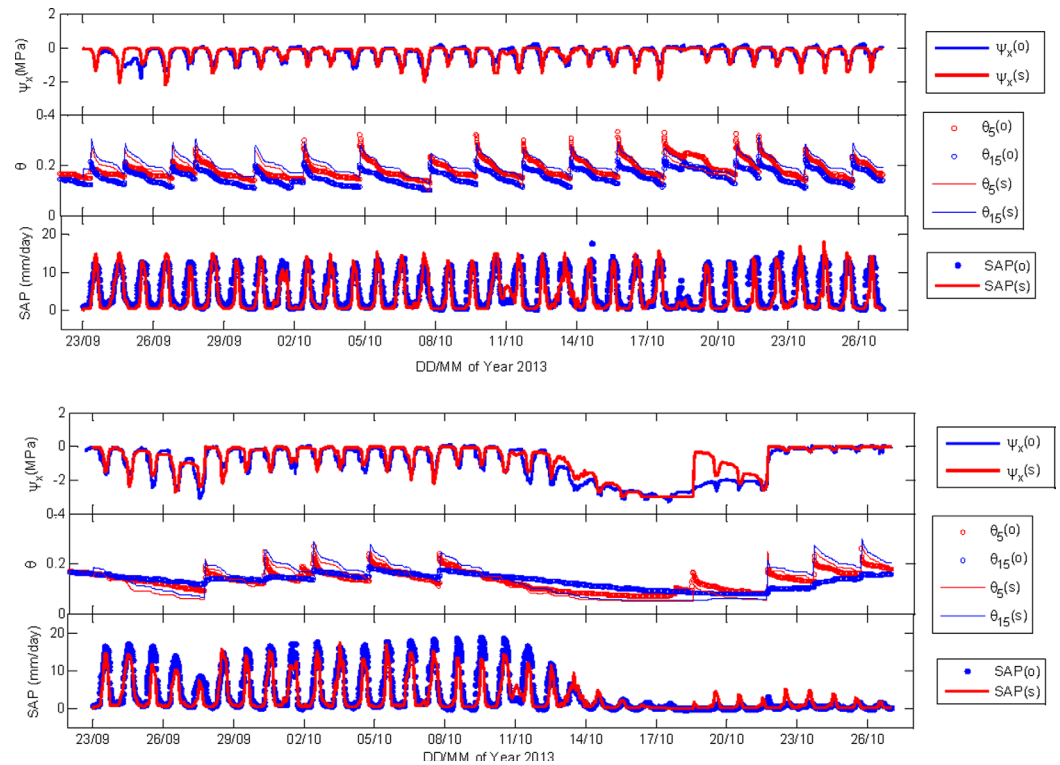


Figure 8. The prediction of ψ_x , θ , and SAP of *E. crenulata* sapling 1 (top) and sapling 2 (bottom) with optimized parameters from the sapling 4 calibration.

parameter (R_{min}) remains the same, suggesting that the anatomical change of the plant is reversible. Increasing the soil to root interfacial resistance (enlarge Δx), indeed explained partially the reduction of ψ_x , which indicates that the soil-root gap may have gone through the cycle of enlarging during the drought and narrowing down after a few days of rewatering. The drought could also have made the shallow root hydraulically ineffective [Mackay et al., 2015]. Here we test it by assigning dead roots in the top 5 cm (see legend of RDF5 = 0 in Figure 9). It gives similar results as increasing the soil-root resistance (enlarging Δx). However, disabling the top root functioning alone could not reduce ψ_x (results not shown) in the first few days of watering, implying the significant impact of the soil-root resistance on plant water stress during the drought. Still, there is a period (19 October to 22 October) that could neither be explained by the plant resistance nor the soil-root resistance nor combined.

The failure of the model to simulate the immediate rewatering period might be due to the simplification of the plant hydraulic system. The v-SPAC model simplifies the plant part from a partial differential equation to an ordinary differential equation problem in which the time variable is eliminated. As v-SPAC only has

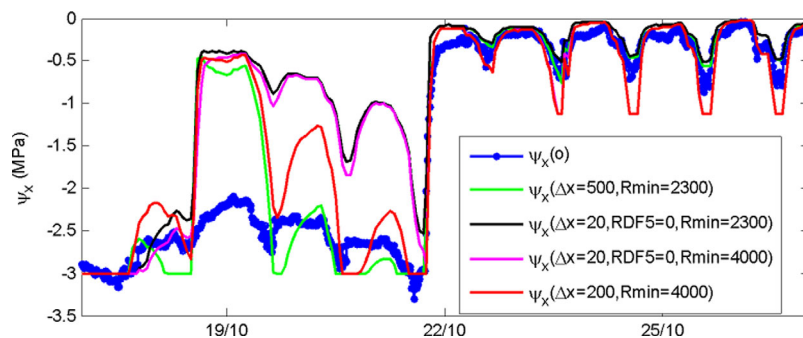


Figure 9. Simulation of ψ_x after the second drought with varied soil-root resistance (Δx), plant resistance (R_{min}), and RDF (RDF5 = 0 indicates dead roots in the top 5 cm of soil).

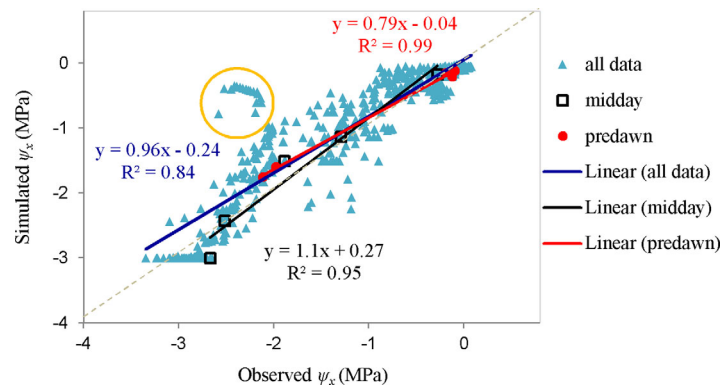


Figure 10. Modeled versus measured ψ_x for *E. crenulata* sapling 2. The filled circles and open squares are weekly predawn and mIDDay ψ_x values. The points in yellow circle are from the recovery period (18–21 Oct 2013).

space variables for the plant part, the recovery process (storage gain and loss from root to stem) is then deemed as an immediate process. The PM model instead includes both time and space variables and is expected to capture the time delay of the stem water potential recovery. For example, the TREES model [Mackay et al., 2015] could predict the chronic impairment of tree hydraulic dysfunction on water potential. However, to predict the exact timing of recovery of stem with

the PM model is not trivial. It is demonstrated in Janott et al. [2011] that there was an apparent transition in the plant water retention curve (WRC) of European beech (*Fagus sylvatica*) below -3.0 MPa. The capacitance (C) of the xylems may also undergo apparent transition through varied water status [Tyree and Yang, 1990]. This indicates that without the prior knowledge of the plant hydraulic properties under severe stress conditions, the PM model is unable to predict the transition of the water potential and water flux under severe drought and rewatering conditions. Importantly, Hunt and Nobel [1987] reported that it took 100 times longer for a stem (*Ferocactus acanthodes*) to rehydrate from 85 to 95% in relative water content than the root (within 1000 versus 10 min), indicating that the parameters of VC, WRC, and C must be treated differently along the plant hydraulic path to correctly simulate the time response. It appears that a simple model such as v-SPAC that does not require detailed hydraulic properties of the plant is especially advantageous in simulating plant water status and flux under modest stress conditions, which is the case for the first drought treatment of the *E. crenulata* saplings. By comparing with plant water potential measurement, the v-SPAC simulation provides diagnostic information about whether a plant hydraulic system has been undermined during a dry period, and for how long the plant hydraulically recovers from such damage. In the future, v-SPAC can be improved by adding other parameters, which, however, will inevitably increase the model dimension (such as three more parameters for plant WRC and additional three for each VC).

The simulation of the six *E. crenulata* saplings raises the issue of accurately upscaling data from tree measurements to plot, forest or catchment. It shows that SAP and ψ_x of saplings 1, 2, and 5 can be reproduced with the same parameter sets of sapling 4. But saplings 3 and 6 predictions can be greatly improved if the capacitance and the resistance are scaled with sapwood area or leaf area index (see supporting information Figures S1 and S3). Upscaling with sapwood area or leaf area index is a common method to calculate stand sap flux rate from individual trees [Asbjornsen et al., 2011]. Other information on individual difference may be valuable for the upscaling consideration. For example, the growth of sapling 3 seems to be suppressed although it was well watered while sapling 2 already showed negative growth after the first controlled

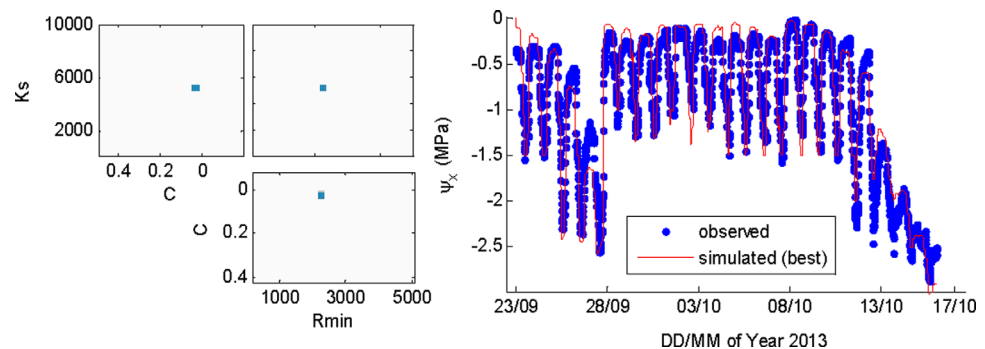


Figure 11. The calibration of *E. crenulata* sapling 4, ignoring soil to root resistance (R_{sr}) ($\Delta x = 0, R_{sr} = 0$). RMSE = 0.18 MPa.

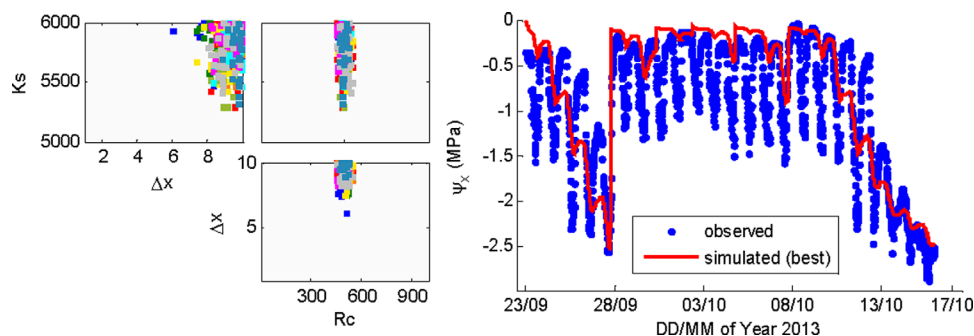


Figure 12. The calibration results of *E. crenulata* sapling 4 with LEACHM against soil moisture content. RMSE = 0.46 MPa.

modest drought from the LAI time series (see Figure 4). It is worth mentioning that saplings 2 and 3 had the largest leaf-specific hydraulic conductivities (normalized by leaf area) at the beginning of the water treatments (from 23 September 2013).

The correlation between the observed and simulated water potential for the eucalypt saplings is much improved by deleting the recovery period after the second severe drought (see the points in yellow circle in Figure 10; $R^2 = 0.92$ without the points while $R^2 = 0.84$ for all data). The result shown in Figure 10 also indicates the significance of subdaily sampling during this critical period. In practice, leaf water potential is collected much less frequently for long-term studies (e.g., collected at predawn or midday weekly). R^2 increased from the subdaily resolution (15 min in this study, $R^2 = 0.84$) to weekly resolution ($R^2 = 0.99$ for predawn and $R^2 = 0.95$ for midday), which however could miss capturing the recovery period. High-resolution sampling is thus vital for model testing in these critical periods. The stem water potential data at subdaily resolution is valuable to be integrated to models for constraining the plant hydraulic properties at tree scales.

5.2. Model Comparison Between v-SPAC and LEACHM

The v-SPAC model showed advantages in easy parameterization with concurrent stem water potential and sap flow measurements. It can capture a more realistic picture in soil/plant water balance and water status compared to other hydrological models that ignore root resistance dynamics. We showcased the significance of the transient root resistance in the v-SPAC model by comparing it to LEACHM model.

From previous modeling experience, we see that Δx can be neglected in the v-SPAC modeling for the *E. crenulata* saplings. Calibration of sapling 4 is performed with Δx being set to zero (see Figure 11). It shows that the parameters can be identified (no correlation between the parameters, see the left figure), indicating the sufficiency of stem water potential as the optimization target and the robustness of the model structure.

The LEACHM model is optimized with soil moisture as commonly done in soil hydrological modeling. The calibration results show that LEACHM captures the overall trend of the plant water status but fails to depict the diurnal pattern (see Figure 12). It gives a far too narrow diurnal range of root water potential during wet

Table 3. Posterior Moments of Parameters for *E. crenulata* Sapling 4 Between the v-SPAC and LEACHM Simulations With DREAM

v-SPAC	K_s (mm/d)	C (mm/MPa)	R_{min} (d)	Observed ψ_x (MPa)	Simulated ψ_x (MPa)
Best fitting	5200	-0.08	2300	-0.92	-0.92
Standard deviation	260	0.03	130	0.75	0.83
0.25 percentile	4700	-0.10	2000	-2.55	-2.94
Median	4700	-0.08	2000	-0.68	-0.69
97.5 percentile	5240	-0.03	2300	-0.10	-0.06
LEACHM	K_s (mm/d)	Δx (mm)	R_c	Observed ψ_x (MPa)	Simulated ψ_x (MPa)
Best fitting	5800	9.03	510	-0.92	-0.76
Standard deviation	210	1.40	70	0.75	0.80
0.25 percentile	5200	4.17	450	-2.55	-2.37
Median	5800	9.53	500	-0.68	-0.30
97.5 percentile	6000	10.00	730	-0.10	-0.07

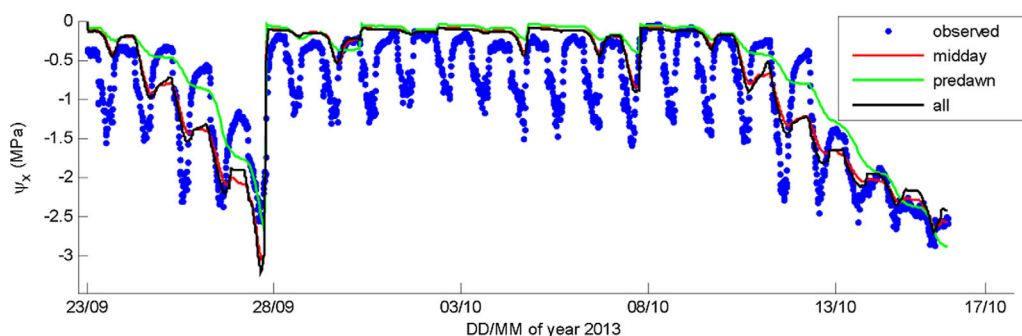


Figure 13. The calibration results of *E. crenulata* sapling 4 with LEACHM against stem water potential.

condition. The root-mean-square error (RMSE) of ψ_x is much larger than that of the v-SPAC model (0.46 versus 0.18 MPa). R^2 for the calibrated ψ_x by v-SPAC is 0.93, and 0.67 predicted by LEACHM. It implies that diurnal patterns of plant water potential cannot be predicted if the root resistance dynamics are not characterized in models. R^2 for the calibrated θ by LEACHM is 0.84, while R^2 is 0.89 for θ predicted by v-SPAC for the same period. It suggests that v-SPAC can even capture the soil water status slightly better than LEACHM by calibrating against plant water potential data set only. A careful examination of the parameterization results reveals that K_s and Δx are not identifiable in LEACHM (see Figure 11 (left) versus Figure 12 (left)), as is also indicated in corresponding Table 3 on posterior probability of parameters between the two simulations. Previous studies also suggest that parameterization (such as that for the water retention curve) with only soil moisture may be insufficient [Scharnagl et al., 2011]. For example, for a simple soil evaporation experiment (even without root water uptake), Zhang et al. [2003] showed that a soil moisture data set would not be sufficient for soil hydraulic parameterization unless soil water potential was added. This suggests that stem water potential provides a good constraint in SPAC modeling, as shown here in the v-SPAC model calibration, especially for cases when soil water potential is not available (see Figure 11).

The LEACHM model was also calibrated against the stem water potential (ψ_x) and its sub-data set of predawn or midday ψ_x which are two commonly measured traits in plant water studies (see Figure 13). None of the three simulations show any advantages over that against soil water content (see Figure 13 that R^2 are 0.73 and 0.65 for ψ_x and θ versus Figure 12 that R^2 are 0.65 and 0.84 for ψ_x and θ). The lack of capacitance term in LEACHM and the constant root resistance (R_c) will only tune the calibration toward either an overestimation or underestimation of ψ_x . It suggests that the plant water potential becomes a useful calibration constraint only in models with root dynamics represented (see Figure 11 versus Figure 13).

Water balance calculation is compared between the two models (Table 4). LEACHM and v-SPAC show marginal differences in soil water balance. Possibly, the confined root space and the fast drainage of the sandy soil make soil moisture the dominant factor limiting transpiration, which reduced the significance of plant resistance, hence, the difference between the two simulation results.

The minimum requirement of forcing data for the two models is summarized in Table 5. In v-SPAC, the stem water potential is the key data set. If stem water potential data are not available then alternate measurements, particularly, leaf water potential, can be used in the v-SPAC. However, the midday or the predawn and minimum leaf water potentials are required to quantify the plant hydraulic properties. Sap flow rate

Table 4. The Plant and Soil Water Balance of *E. crenulata* Sapling 4 Calculated With v-SPAC and LEACHM (Numbers in Brackets) (Unit: mm)

		Drought 1 23–27 Sep	Postdrought 27 Sep to 10 Oct	Drought 2 10 Oct to 17 Oct	Postdrought 17 Oct to 27 Oct
Plant water balance (mm)	RWU	22.38 (21.02)	62.89 (61.14)	17.91 (16.91)	11.99 (11.70)
	T	–22.41	–61.93	–18.05	–11.92
	ΔS	–0.03	0.96	–0.13	0.07
Soil water balance (mm)	IN	0.00 (0.00)	159.15 (159.15)	0.00 (0.00)	104.29 (104.29)
	D	–1.02 (–0.98)	–45.88 (–47.85)	–0.10 (–0.10)	–28.56 (–29.62)
	E+RWU	–29.89 (–28.86)	–90.98 (–90.04)	–23.85 (–22.84)	–27.93 (–27.79)
	ΔS	–30.87 (–29.84)	22.42 (21.27)	–23.90 (–22.88)	47.75 (46.86)

Table 5. Minimum Required Forcing Data for Parameterization of v-SPAC and LEACHM

Data Requirement	v-SPAC	LEACHM
Plant measurement	Stem water potential Sap flow rate (with sapwood area) Leaf area index	Plant water flux ^a Root distribution function (RDF) ^a Leaf area index
Soil measurement	WRC (e.g., soil texture) ^a	Soil water content WRC (e.g., soil texture) ^a
Meteorological measurement	Rainfall (radiation, relative humidity, wind speed, air temperature) ^a	Rainfall (radiation, relative humidity, wind speed, air temperature) ^a

^aA data set that may not be required for model calibration.

can be replaced if not available with potential transpiration. Field soil moisture measurement is not required in the v-SPAC model; soil parameters can be calibrated, but, soil texture measurement will be of great value in v-SPAC to constrain the WRC, thus reducing the dimension of the model. LEACHM is particularly useful for agricultural applications, such as irrigation or fertilization scheduling and nitrate leaching [Hutson *et al.*, 1997; Jabro *et al.*, 1995]. It requires minimal plant (crop) data, and that required is more easily available than for trees (such as root depth). The model can be calibrated with soil water content or the water flux in plant. In both models, meteorological measurement is required for potential evapotranspiration calculation. Leaf area index or vegetation coverage over land is used for potential transpiration and potential evaporation partitioning.

In summary, the data requirement of v-SPAC model is primarily stem/leaf water potential and sap flow measurements. The v-SPAC model will show great advantages in forestry ecohydrology, with easy parameterization in field conditions, although may be similar in agricultural applications to the LEACHM model due to the added plant water transport module.

6. Conclusions and Future Work

In this study, we present a new coupled soil-plant-atmosphere continuum model (v-SPAC) in which the plant’s control of water transfer in the continuum is emphasized. The v-SPAC model incorporates a dynamic plant resistance and capacitance system to represent plant’s hydraulic regulation on water flux and water status. A so-called integrated vulnerability curve is proposed to characterize the whole plant resistance system from in situ measurement which facilitates the model parameterization. The testing results with a water controlled experiment demonstrate the capacity of the v-SPAC model in predicting the diurnal pattern of both sap flow and stem xylem water potential.

This study underscores the importance of integrating plant hydraulic properties into hydrological models. Comparison between LEACHM and v-SPAC shows that LEACHM can capture the overall evolution of soil and plant water status based on known soil hydraulic properties, while v-SPAC, by integrating plant hydraulic properties can simulate plant water status and water flux at subdaily resolution. The comparison highlights the issue of data sufficiency in model calibration. It is insufficient to use soil moisture for constraining the LEACHM model, while the v-SPAC model identifies the plant water status as the key data set to constrain hydraulic properties of the soil-plant continuum.

Models are only capable of performing well if necessary mechanisms are incorporated and they are well parameterized. The improvement of the current model’s capacity to simulate the plant’s response in severe drought and its hydraulic recovery relies on a profound understanding of the underlying mechanisms. The model capacity is traded-off with model efficiency, depending on how detailed microscopic mechanisms can be practically represented in models.

Notation

Flux Terms

PET (mm/d)	potential evapotranspiration
PT (mm/d)	potential transpiration
T (mm/d)	actual transpiration
PE (mm/d)	potential evaporation

E (mm/d)	actual evaporation
ET (mm/d)	actual evapotranspiration
RWU (mm/d)	root water uptake from soil moisture
SAP (mm/d)	sap flux normalized by land surface
SAP (cm/h)	sap velocity in tree stem xylem
IN (mm/d)	rainfall or irrigation infiltration to soil surface
RO (mm/d)	surface runoff
D (mm/d)	drainage below root zone
ΔS (mm/d)	storage change (soil or plant)
SAPmax (cm/h)	maximum sap velocity at day time

Water State Terms

θ_s	water content at soil saturation
θ_r	residual soil moisture content
Θ	soil moisture saturation
ψ_s (MPa)	soil water potential
ψ_x (MPa)	xylem water potential
$\psi_{x(rc)}$ (MPa)	xylem water potential at root collar
$\psi_{r,m}$ (MPa)	xylem water potential at node m
$\psi_{x(s)}$ (MPa)	xylem water potential at stem
$\psi_{x,pd}$ (MPa)	predawn (stem) xylem water potential
ψ_L (MPa)	leaf water potential
$\psi_{L,min}$ (MPa)	minimum leaf water potential
$\psi_{r,min}$ (MPa)	minimum root water potential

Resistance or Conductance Terms (d is day)

K (mm/d)	soil hydraulic conductivity
K_s (mm/d)	saturated soil hydraulic conductivity
K_{sr} (mm/d)	soil to root hydraulic conductivity
R_{sr} (d)	the resistance of water transfer from bulk soil to soil-root interface
$R_{sr,i}$ (d)	the resistance of water transfer from bulk soil to soil-root interface in soil layer i
R_p (d)	plant resistance of water transport from soil-root interface to stem xylem
R_{min} (d)	minimum plant resistance/inverse of saturated hydraulic conductance of the plant
$R_{r,t}$ (d)	total resistance of root system
$R_{r,i}$ (d)	effective root resistance in soil layer i normalized by land surface area
R_{rr} (d)	radial root resistance; resistance of water transfer from root surface to root xylem
$R_{x(r/s)}$ (d)	xylem resistance in longitudinal direction; resistance of water transfer within root, stem or leaf conduit (such as vessel, tracheids)
R_c	friction loss in the root in LEACHM (not used in v-SPAC model)

Other Terms

HC	hydraulic conductivity
HCL	hydraulic conductivity loss
VC	vulnerability curve, to describe the plant resistance change with plant water status
IVC	integrated vulnerability curve
d (MPa)	parameter in the vulnerability curve
b	parameter in the vulnerability curve
C (mm/MPa)	capacitance of tree storage (lumped)
Δx (mm)	the effective distance from measured bulk soil to root surface
RDF	root length density distribution function
L (mm)	maximum root depth
β (in RDF)	shape parameter in RDF
λ (in RDF)	normalization factor to constrain sum of RDF all soil layers to unit one
$f(\psi_x)$	transpiration reduction function

p_1 (MPa) (in $f(\psi_x)$)	the point of ψ_x above which the sap flow rate equals that under fully available water
p_2 (MPa) (in $f(\psi_x)$)	the point of ψ_x below which the sap flow rate equals zero
WRC	water retention curve: relation between water content and water potential
α (1/kPa) (in soil WRC)	parameter in Van Genuchten WRC function
n (in soil WRC)	parameter in Van Genuchten WRC function
m (in soil WRC)	parameter in Van Genuchten WRC function
VPD (kPa)	vapor pressure deficit
UB	upper boundary
LB	lower boundary
LAI ($\text{m}^2 \text{m}^{-2}$)	leaf area index

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