

The Role of Plant Water Storage on Water Fluxes within the Coupled Soil-Plant System

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Summary

1. In addition to buffering plants from water stress during severe droughts, plant water storage (PWS) alters many features about the spatio-temporal dynamics of water movement in the soil-plant system. How PWS impacts water dynamics and drought resilience is explored using a multi-layer porous media model.

2. The model numerically resolves soil-plant hydrodynamics by coupling them with leaf-level gas exchange and soil-root inter-facial layers. Novel features of the model are the considerations of a coordinated relation between stomatal aperture variation and whole-system hydraulics and the effects of PWS and nocturnal transpiration ($F_{e,night}$) on hydraulic redistribution (HR) in the soil.

3. The model results suggest that daytime PWS usage and $F_{e,night}$ generate residual water potential gradient ($\Delta\psi_{p,night}$) along the plant vascular system overnight. This $\Delta\psi_{p,night}$ represents a non-negligible competing sink strength that effectively diminish the significance of HR.

4. Considering the co-occurrence of PWS usage and HR during a single extended dry-down, a wide range of plant attributes and environmental/soil conditions selected to enhance or suppress plant drought resilience is discussed. When compared to HR, model predictions suggest that increased root water influx into plant conducting tissues overnight maintain a preferable water status at the leaf thereby delaying the onset of drought stress.

Keyword: drought resilience; hydraulic redistribution; leaf-level gas exchange; nocturnal transpiration; plant water storage; root water uptake

1 Introduction

The ability of xylem tissues to store water is perceived to be part of an evolutionary process that supports physiological function for the whole-plant during severe drought conditions (Tyree and Ewers, 1991; Cruziat et al., 2002; McDowell et al., 2008; Manzoni et al., 2014; Parolari et al., 2014; Sperry and Love, 2015). However, the beneficial effects of plant water storage (PWS) on a wide range of soil-plant hydrodynamic processes has received far less attention. A defining feature of PWS is a time lag between basal sap flux and crown transpiration (Phillips et al., 2004; Chuang et al., 2006). In large tree species and during severe drought conditions, empirical evidence suggests that a significant amount of whole-plant transpiration originates from PWS (Waring and Running, 1978; Waring et al., 1979; Schulze et al., 1985; Goldstein et al., 1998; Maherali and DeLucia, 2001; Phillips et al., 2003). In the presence of PWS, whole-plant transpiration rate exceeds basal sap flux during early morning hours signifying a discharge from PWS. During late afternoon and proceeding into the evening, the basal sap flux can exceed whole-plant transpiration rate suggesting partial refilling of PWS and adjusting xylem pressure to less negative values. These adjustments in xylem pressure may be significant in repairing embolized xylem vessels through bubble dissolution (Waring and Running, 1978; Tyree and Sperry, 1989; Konrad and Roth-Nebelsick, 2003). Such modifications by PWS beg the question as to how root water uptake (RWU) and hydraulic redistribution (HR) in soils as well as leaf-level transpiration rates are impacted by the presence of PWS. At sites where leaf-level gas exchange occurs, the presence of PWS may allow leaves to maintain a water potential state beneficial to carbon uptake over a longer time period (Goldstein et al., 1998; Stratton et al., 2000; Maherali and DeLucia, 2001). However, a daytime dehydration of PWS may reduce beneficial contributions arising from overnight HR due to a competing sink that must be recharged.

One recent review covering the magnitude of HR across a wide range of ecosystems and environmental conditions (Neumann and Cardon, 2012) offers a tantalizing clue that the magnitude of HR predicted by previous models that ignored PWS or nocturnal transpiration ($F_{e,night}$) is consistently higher than those reported by empirical studies. This over-prediction of HR occurs despite model differences in the mechanics of incorporating HR (Siqueira et al., 2008) or in assumed root density profile properties (Schymanski et al., 2008). It has been foreshadowed by Neumann and Cardon (2012) that the exclusion of an above-ground competing sink strength (due to finite PWS or $F_{e,night}$) in such models can be a plausible explanation for the consistent overestimation, which is another motivation for the work here.

The objective is to disentangle the effects of PWS and $F_{e,night}$ on water fluxes from the soil to the leaf from other hydraulic traits on diurnal to daily-time scales. The approach to be followed is based on a vertically resolving numerical model for both the soil and plant systems. This model combines soil-plant hydrodynamics with leaf-level physiological and soil-root constraints. Thus, the leaf-level gas exchange can be impacted by soil water availability through the water potential gradient from the leaf to the soil, and vice versa. The focus here is on forested ecosystems where PWS may be significant during an extended dry-down period. The dry-down time scale is assumed to be sufficiently long to allow PWS to experience multiple discharge-recharge phases under different soil moisture states but sufficiently short so that hydraulic, eco-physiological, leaf area, root distribution, and concomitant allometric properties do not vary appreciably. The model results are then analyzed with particular attention to exogenous environmental factors and endogenous plant attributes promoting the use of PWS versus direct soil water through eight scenarios. While a large number of hydrological and ecological studies have already documented the benefits of HR on carbon-water relations (Domec et al., 2010; Prieto et al., 2012), conditions where plant hydraulic capacitance or $F_{e,night}$ may compete with HR remain unclear. Hence, the overnight competition for water between above-and below-ground reservoirs is discussed

through model calculations. The discussion of the model results finally focuses on the responses of leaf-level gas exchange to progressive drought conditions in the context of the functional role of PWS versus HR.

2 Description

2.1 Modeling framework

There is a plethora of complications when modeling/measuring plant water relations in forested ecosystems including inhomogeneity in leaf arrangements, the plant and soil hydraulic properties, the rooting system, and the temporal variability in environmental variables. Moreover, plant-plant interactions such as competition for light or water and the dynamic nature of plant hydraulic and physiological properties over long time scales (e.g., seasonal) necessitate an intermediate level of modeling approaches as discussed elsewhere (Bohrer et al., 2005). In this approach, the bulk water movement along the primary pathways is modeled with much of the finer scale spatial processes (e.g., cavitation, soil-root contact) being surrogated to non-linearities in hydraulic properties. Hence, within each of the soil-plant compartments, the goal is to retain sufficient representation of key hydrodynamic and physiological processes while allowing for integration to the plant level.

Starting with the above-ground plant compartment, a logical choice is to adopt a 'macroscopic' (i.e., tissue level) approach in analogy to the soil system. The bulk effect of 'microscopic' processes (i.e., cell or pore level) are embedded in the shape of the vulnerability curve and PWS as they relate to xylem water potential. It is to be noted that xylem conduits are more elongated and their diameters are less variable when compared to soil pores. Despite this pore structure difference, the flow and energy losses to friction can still be reasonably approximated by Darcy's law. Hence, a one-dimensional porous media model is employed to describe the transient water flow from the stem base to the leaf parameterized with literature-reported hydraulic attributes of plant tissues. The soil water supply to the plant is represented using a conventional multi-layered scheme that employs Richard's equation adjusted by soil-root interactions reflecting root water influx or efflux (i.e., possible HR). These inter-facial transfer processes depend on soil-to-root conductances along the flow path and the lateral energy gradient between the soil and the root at a given depth.

The porous-media analogy representing water flow through each compartment of the soil-plant system and connections between them is capable of capturing the main features of macroscopic water flow pertinent to PWS dynamics. The complex features of plant hydraulic architecture are not explicitly resolved but the effects of tree size and vertically non-uniform root distribution on plant water relations are captured. The leaf-level water balance employed here provides a representation accounting for the nonlinear relations between stomatal aperture and the time-history of leaf water potential. The latter is limited by soil water availability and the interplay between biological controls through stomata and the aerodynamic modifications due to wind speed. This modeling approach is illustrated in Fig. 1 and detailed information of the formulations and assumptions is given next. The notation and units used throughout are listed in Supporting Information.

2.2 Plant conducting tissues

Water transport through tracheid aggregates or vessels inter-connected by end-wall pits in the water conducting tissues can be treated as analogous to porous media flow (Edwards et al.,

1986; Tyree, 1988; Fröh and Kurth, 1999; Kumagai, 2001; Aumann and Ford, 2002; Bohrer
 et al., 2005; Chuang et al., 2006; Hentschel et al., 2013; Manzoni et al., 2013c,a, 2014). Thus,
 a mass conservation equation is combined with Darcy's law to describe the water movement at
 the tissue-scale and is given as

$$\frac{\partial V_s(z)\theta_p(z, t)}{\partial t} = -\frac{\partial q_p}{\partial z} dz$$

$$q_p = -A_s(z)K_p(\theta_p)\frac{\partial \psi_p}{\partial z} \quad (1)$$

$$\psi_p = \phi_p + \rho g z$$

where $V_s(z) = \int_z^{z+\Delta z} A_s(z)dz$ is the sapwood volume between height z and $z + \Delta z$ above the
 soil surface, θ_p is the plant (or xylem) water content, and $q_p(z)$ is the sap flow rate driven by
 gradients in total water potential, ψ_p . ρ is the water density, g is the gravitational acceleration,
 K_p is the plant hydraulic specific conductivity, and $A_s(z)$ is the sapwood area profile representing
 the effective cross-sectional area of conducting tissues. ψ_p includes plant pressure potential (i.e.,
 xylem matric potential), ϕ_p , and the gravitational potential $\rho g z$ but ignores the kinetic energy
 head and assumes negligible variations in osmotic potential for long distance water flow in the
 xylem (Fröh and Kurth, 1999). A cone-shaped tree volume is adopted to represent the effective
 tree dimensions using only tree height (H) and $A_s(z)$ that is linked to H by

$$A_s(z) = A_{s,base} \left(1 - \frac{1}{2} \frac{z}{H}\right)^2, \quad (2)$$

where $A_{s,base}$ is the sapwood area at stem base.

In the plant vascular system, the percentage of K_p loss referenced to the maximum specific
 conductivity $K_{p,max}$ at saturation $\theta_{p,sat}$ due to a reduced ϕ_p is commonly described by the
vulnerability curve:

$$K_p(z) = K_{p,max} \exp \left[- \left(\frac{-\phi_p(z)}{c_1} \right)^{c_2} \right], \quad (3)$$

where c_1 and c_2 are constants describing its shape. The monotonic relation between θ_p and ϕ_p
 is approximated by a *plant retention curve* and is given by (Chuang et al., 2006):

$$\frac{\theta_p(z)}{\theta_{p,sat}} = \left(\frac{\phi_0}{\phi_0 - \phi_p(z)} \right)^p, \quad (4)$$

where p and ϕ_0 are constants. This formulation ensures $\phi_p = 0$ at saturation and represents the
 degree of relative change in θ_p with respect to ϕ_p through p . The plant 'retention curve' can
 be further used to infer the specific hydraulic capacitance of a plant tissue $C_p = \partial \theta_p / \partial \phi_p$ by
 which the whole-plant hydraulic capacitance $C_{p,total} = \int_0^H A_s C_p dz$ can be defined to describe
 the ability to store or extract water for a unit change in ϕ_p .

Unlike soils, there are a number of potential mechanisms responsible for changes in PWS.
 These include elasticity, capillarity and cavitation release. They were proposed by Zimmermann
 (1983) and experimentally shown by Tyree and Yang (1990) to be present in woody cells (i.e.,
 xylem conduits). Unlike living cells (e.g., phloem), woody cells have rigid walls with high elastic
 modulus so that the elastic storage in xylem conduits due to alternating shrinkage and swelling
 may be minor (Brough et al., 1986). The capillary storage, which occurs in cavitared conduits,
 can release water by bringing the menisci towards the narrow ends of tracheids or vessels when

water potential decreases but store water in the opposite way. This implies that cavitated conduits can still partially maintain a water continuum (Tyree and Zimmermann, 2002). Since capillary storage can rapidly release or store water, Brough et al. (1986) demonstrated that the diurnal pattern of the xylem water content can be attributed mainly to such capillarity mechanism. Under sufficiently low water potential condition, the water release through cavitation events occurs when the water-filled volume is replaced by air bubbles (Tyree and Sperry, 1989; Tyree et al., 1994). Moreover, the delay in repair of cavitated conduits can induce hysteresis in both vulnerability and plant retention curves (Sperry and Tyree, 1990; Brodribb and Cochard, 2009), which is not considered here but can be accommodated in the present framework.

The consideration of PWS adjusts $\psi_p(z)$ along the plant vascular system and thus impacts stomatal behaviors. Stomatal closure occurs before $\psi_p(z)$ is substantially reduced and reaches a threshold that causes 'runaway cavitation' (Bond and Kavanagh, 1999; Sparks and Black, 1999). When this threshold is reached, the more dysfunctional cells due to cavitation lead to more negative water potential and further cavitation events occur in an irreversible manner. As shown in Fig. 2a, the incipient runaway cavitation is commonly defined at ϕ_p where 12 % of K_p losses occur (i.e., air-entry point; P_{12}). The slope of the vulnerability curve reaches maximum around this threshold (Domec and Gartner, 2001). However, the onset of water stress sensed by plants (i.e., stomatal closure) is dictated by a critical xylem water potential (i.e., P_c) that may be larger than P_{12} . It is to be noted that P_c and the corresponding loss of K_p are not *a priori* specified here (see Section 2.4).

2.3 Soil-root interaction

Water transport in unsaturated soils is described by one-dimensional Richards' equation modified to include water uptake/release by the rooting system within each soil layer. Hence, at each soil layer, an 'effective' source/sink term Q_r is added (Volpe et al., 2013; Manoli et al., 2014; Bonetti et al., 2015) to yield :

$$\begin{aligned} \frac{\partial \theta_s(z_s, t)}{\partial t} &= -\frac{\partial q_s}{\partial z_s} - Q_r(z_s, t) \\ q_s &= -K_s(\theta_s) \frac{\partial \psi_s}{\partial z_s} \end{aligned} \quad (5)$$

$$\psi_s = \phi_s - z_s$$

where θ_s is the soil water content at depth z_s below the soil surface, q_s is the Darcian flux driven by the vertical gradient of total soil water potential ψ_s , ϕ_s is the soil matric potential, K_s is the soil hydraulic conductivity, and Q_r is the water uptake (denoted with superscript '+') or release (denoted with superscript '-') rate from absorbing roots. In Equation 5, the Clapp and Hornberger formulations (Clapp and Hornberger, 1978) are used to represent the soil water retention curve and soil hydraulic conductivity function, and are given by:

$$\phi_s = \phi_{s,sat} \left(\frac{\theta_s}{\theta_{s,sat}} \right)^{-b}, \quad (6)$$

$$K_s = K_{s,max} \left(\frac{\theta_s}{\theta_{s,sat}} \right)^{2b+3}, \quad (7)$$

where $\theta_{s,sat}$, $\phi_{s,sat}$ and $K_{s,max}$ are the near saturated water content, air entry water potential and saturated hydraulic conductivity, respectively, and b is an empirical constant that varies with soil texture.

Contributions to soil water storage (i.e., $\partial\theta_s/\partial t$) by the flux-gradient term are often referred to as the *Darcian redistribution* (i.e., $-\partial q_s/\partial z_s$). The depletion or replenishment rate of soil water storage through Q_r is determined by the water potential gradient across the root membrane and the average path length traveled radially by water molecules from the soil to the soil-root interface in series and is given as:

$$Q_r = -k [(\psi_{sb} - \psi_s) - \psi_s] a_R$$

$$k = \frac{k_r k_s}{k_r + k_s}$$
(8)

where k is the total soil-to-root conductance, ψ_{sb} is the water potential at the stem base, $a_R = 2\pi r B$ is the root surface density, r is the effective root radius, B is the root length density, k_r and $k_s = K_s/l$ are respectively the root membrane permeability and the conductance associated with the radial flow within the soil to the nearest rootlet, and $l = 0.53/\sqrt{\pi B}$ is the length scale characterizing the mean radial distance for the movement of water molecules from the bulk soil to the root surface within the rhizosphere (Vogel et al., 2013). Formulated in this manner, the root water potential ψ_r is hydrostatically distributed (i.e., $\psi_r = \psi_{sb} - z_s$) assuming that the water storage and energy losses are negligible within the transporting roots (Lafolie et al., 1991; Siqueira et al., 2008). When compared to above-ground compartments, significantly larger hydraulic conductivity (Kavanagh et al., 1999) but smaller water storage capacity (Waring et al., 1979) in the rooting system suggests that this assumption may not be too restrictive for tree species. Independent model runs also confirm the negligible effects of root water storage and resistance on both above- and below-ground water dynamics so that they are not considered hereafter. The coupling between the below- and above-ground plant system is accomplished by imposing a continuous water potential from soil (ψ_s) to stem base (ψ_{sb}) and its resulting ‘net’ root water uptake (RWU_{net}) supplied to the stem base can be expressed by the water balance for the bulk rooting system:

$$q_{p, sb} = RWU_{net} = \left[\int_0^{L_R} (Q_r^+ + Q_r^-) dz_s \right] \rho A_{soil}$$
(9)

where $q_{p, sb}$ is the sap flow rate at the stem base, A_{soil} is the soil surface area covering the roots, and L_R is the rooting depth.

During daytime, inevitable water loss from leaves creates a significant water potential gradient from roots to leaves and induces water extraction throughout the rooting system (i.e., $Q_{r, day}^- = 0$ for all z_s) if the upper layers of the soil are not too dry and do not serve as competing sinks. However, the root water uptake at night from wet soil layers may be released back to dry soil layers or refills the xylem volume where the xylem water has been depleted by previous daytime transpiration. While the former mechanism is commonly coined as ‘hydraulic redistribution’ and the amount of redistributed soil water through the rooting system can be quantified by $\left| \int_0^{L_R} Q_r^- dz_s \right| \rho A_{soil}$, the ‘nocturnal refilling’ to PWS is used to emphasize the later mechanism.

2.4 Leaf-level water balance

The water balance in the foliage described elsewhere (Kumagai, 2001) is modified to include a leaf-lamina resistance and is used as the upper boundary condition for water transport within

the plant system. The leaf-level water balance can be given as:

$$A_l(\Delta z_l) \left[C_l \frac{\partial \psi_l}{\partial t} \right] = -[q_{p,top} - F_e]$$

$$q_{p,top} = A_l \frac{(\psi_{p,top} - \psi_l)}{r_l} \quad (10)$$

$$F_e = A_l f_e m_v$$

where A_l is the leaf area, Δz_l is the effective leaf thickness, ψ_l is the leaf water potential, C_l is the hydraulic capacitance of the leaf, r_l is the leaf-lamina resistance, $q_{p,top}$ is the sap flux entering the leaf, F_e is the total crown transpiration flux, $\psi_{p,top}$ is the water potential at the distal conductive segment attached to the leaf, and f_e is the leaf-level transpiration rate that can be converted to mass-based units using the molecular weight of water m_v and up-scaled to F_e using leaf area A_l . For simplicity, C_l is assumed to be independent of ψ_l though this dependency can be readily incorporated if known.

The consideration of the resistance to water flow through the leaf lamina is necessary because r_l may significantly contribute to whole-plant resistance that determines the leaf-level water status (Cruiziat et al., 2002; Taneda and Tatenno, 2011) and in turn limits the response of the leaf-level gas exchange to drought stress. The effects of boundary layer conductance on leaf-level gas exchange is also included (Huang et al., 2015) so as to eliminate the use of vapor pressure deficit as surrogate for actual evaporative demand (i.e., well-coupled leaf-to-atmosphere condition). It is to be noted that the well-coupled condition, which is widely used to interpret responses of stomata to their environment, may not be valid in natural settings (e.g., low wind speed or prevalence of broadleaf species). Since $F_{e,night}$ typically accounts for 10-30% of daily transpiration (Dawson et al., 2007; Caird et al., 2007; Novick et al., 2009), this water leakage from both guard cells and cuticle is also accounted for through a residual conductance (g_{res}) when nighttime evaporative demand is finite. The leaf-gas exchange model utilizes a Fickian mass transfer formulation across the laminar boundary layer attached to the leaf surface, which is then combined with the biochemical demand for CO_2 described by the Farquhar photosynthesis model for C_3 species (Farquhar et al., 1980). A leaf-level energy balance (Campbell and Norman, 1998) model and an optimal water use strategy (i.e., maximizing the 'net' carbon gain at a given f_e) are used to determine variations in stomatal conductance (g_{s,CO_2}) and leaf-level assimilation rate (f_c) and f_e . The model description can be found elsewhere (Huang et al., 2015) and is not repeated.

Adopting an optimality hypothesis in the leaf-gas exchange model is equivalent to maximizing the objective function (or Hamiltonian)

$$h_a(g_{s,CO_2}) = f_c - \lambda f_e, \quad (11)$$

where the species-specific cost of water parameter λ is known as the marginal water use efficiency (WUE) and measures the cost of water loss in carbon units. Mathematically, λ is the Lagrange multiplier for the unconstrained optimization problem and is approximately constant on time scales comparable to stomatal aperture fluctuations (Cowan and Farquhar, 1977). However, λ can gradually increase on a daily time scale due to reduction in soil water availability during a dry-down (Manzoni et al., 2013b) and ultimately results in complete stomatal closure. The linkage between λ and ψ_l derived from a meta-analysis of approximately 50 species (Manzoni et al., 2011) is adopted for the description of the increasing λ as drought progresses and is given by:

$$\lambda(\bar{\psi}_l) = \lambda^* \frac{c_a}{c_a^*} \exp[-\beta \bar{\psi}_l] \quad (12)$$

where λ^* is the marginal WUE under well-watered soil conditions at a reference atmospheric CO_2 concentration $c_a^* = 400$ ppm, $\bar{\psi}_l$ is computed as an averaged ψ_l over the previous 24 hours period and represents a hydraulic signal that constrains the variation of stomatal aperture, and β is a species-specific sensitivity parameter. Again, it should be emphasized that the hydraulic signal at the leaf-level, $\bar{\psi}_l$ is not an instantaneous ψ_l because the unconstrained optimization problem requires λ to vary on much longer time scales than fluctuations in stomatal aperture as earlier noted. Because of this time integration of ψ_l , a dynamic PWS also impacts g_{s,CO_2} , suggesting that a reduced soil water availability does not guarantee an immediate drop in $\bar{\psi}_l$. In lieu of Ball-Berry (Ball et al., 1987) or Leuning (Leuning, 1995) semi-empirical models, the use of such optimality hypothesis to maximize h_a reflects how the regulation of water loss through stomatal guard cells respond to water status at the leaf without invoking *ad hoc* correction functions (e.g., Tuzet et al. (2003)) to 'externally' reduce maximum g_{s,CO_2} or f_e as deviations from well-watered soil conditions during dry-down. It also allows a direct coupling between the carbon and water economy of the leaf through h_a that must be positive to ensure optimality. To illustrate, the value of λ increases with decreasing $\bar{\psi}_l$ leading to a gradual stomatal closure during a dry-down until a critical point (i.e., $\bar{\psi}_{l,c}$) is reached as shown in Fig. 2b. Upon assuming that stomata *per se* operate only with a finite optimal 'net' carbon gain (i.e., $h_a > 0$ when $\lambda < \lambda_c$), the critical point can now be defined as λ_c where the carbon gain is completely canceled out by the water cost in carbon units (Fig. 2c). This assumption may be plausible and ensures no more water loss (i.e., complete stomatal closure) when finite net carbon gain (i.e., $h_a > 0$) cannot be attained by g_{s,CO_2} (inset in Fig. 2c). The duration (T_c) before complete stomatal closure is reached can then be tracked. Also, the total carbon uptake (C_{uptake}) that occurs while maintaining finite assimilation is given as:

$$C_{\text{uptake}} = \int_0^{T_c} f_c(g_{s,\text{CO}_2}(t)) dt. \quad (13)$$

Thus, the species-specific λ - $\bar{\psi}_l$ relation can accommodate a wide range of plant water use strategy such as isohydric/anisohydric and is hereafter referred to as a 'leaf-level hydraulic signal curve'. Furthermore, the xylem water potential with respect to $\bar{\psi}_{l,c}$ (i.e., P_c) is shown to be larger than P_{12} indicating that complete stomatal closure actually occurs before runaway cavitation as discussed earlier (Fig. 2a). Hence, a coordination between stomatal closure and P_c arises naturally from the Hamiltonian to be maximized, which is one of the main novelties linking leaf-to-xylem.

2.5 Model setup

Eight scenarios (S1~S8) were constructed to explore the variations in environmental factors and plant traits (Table 1). To contrast the effects of plant attributes on the use of PWS, HR and C_{uptake} within T_c , the parameters C_p , g_{res} , LAI and H are reduced in scenarios S2, S3, S7 and S8, relative to S1 while all other model parameters and environmental conditions are maintained the same. Using identical total root density and L_R , the effects of root distribution are explored by a comparison between constant and power-law rooting profiles in S4 and S6, respectively. How site factors impact soil-plant water dynamics, different soil types (i.e., sandy clay loam; S4) and lower boundary conditions (i.e., constant water table; S5) are specified and compared with the S1 (sandy soil with free drainage at the bottom of the soil column). The modeling approach is designed for a single tree but can be used for whole stand/canopy when horizontal homogeneity is assumed for all soil-plant attributes across each compartment. While tree age can be accommodated by prescribed physiological, hydraulic and allometric attributes, the plant water use strategy (i.e., isohydric or anisohydric) is not assumed and is embedded in

the leaf-level hydraulic signal curve. Since the physiological, hydraulic and allometric attributes for each compartment are rarely available from a single experiment, a literature survey was conducted with a focus on coniferous species in general and pine plantation trees in specific to obtain consistent parameters (Supporting Information). For all runs, the initial conditions are specified as near saturation in the plant vascular system and the soil column across all layers. The whole system is then allowed to drain for 12 hours (i.e., one night duration) only by gravitational forces without activating leaf-level gas exchange and $F_{e,night}$. With this initialization, the amount of water in the system is approximately identical for all scenarios except for the cases of constant groundwater level (i.e., S5). Subsequently, the model calculations repeat with prescribed atmospheric variables on a periodic 24-hour basis (Supporting Information) and that cause leaf-level gas exchange to operate. An additional data set described in Supporting Information is specifically used to evaluate the model performance for the water usage in the plant and the soil.

3 Results

3.1 General features of the modeled PWS usage

Using S1 as an example, Fig. 3a shows the typical diurnal pattern of F_e and $q_{p, sb}$ along with modeled time delay between their peaks due to PWS. The computed delay is approximately 1.5 hours and is well within the range of 0.1 to 2.5 hours reported elsewhere (Goldstein et al., 1998; Phillips et al., 2003; Bohrer et al., 2005). The daily PWS consumed can be computed by integrating the differences between F_e and $q_{p, sb}$ when $F_e > q_{p, sb}$. Fig. 3b shows a larger diurnal variation in predicted θ_p near the tree crown suggesting that the use of PWS can be primarily attributed to water depletion from xylem tissues closer to the transpiring sites. *In situ* experiments (Schulze et al., 1985; Loustau et al., 1996) on coniferous species also reported a pattern consistent with the modeled results here. Since the sap flow velocity within tree species is low (Granier, 1987; Dye et al., 1996; Zang et al., 1996), this finding may not be surprising especially when the water stored in the upper part of the plant can be immediately accessible for crown transpiration. The modeled daily PWS usage normalized by daily F_e and the modeled 'actual' PWS usage without normalizing are presented in Fig. 4a,b, respectively. When soil water status cannot be recovered (i.e., continued loss of soil water through transpiration and drainage) during the dry-down, the increasing reliance on PWS with respect to F_e is inevitable. This finding appears consistent with sap flow measurements reported elsewhere (Loustau et al., 1996; Phillips et al., 2003). When the soil water availability is not limited due to the presence of a shallow groundwater table (i.e., S5), the depleted water by F_e in the soil column and plant xylem tissues can be completely recovered to its previous state within a single diurnal cycle. This explains why the use of PWS as well as HR (shown later) for S5 remains constant during the dry-down. The modeled average daily PWS usage across all scenarios ranges from 1.1 to 23.3 % when normalized by daily F_e and from 0.07 to 1.61 kg m⁻² (ground) day⁻¹ without normalization.

3.2 General features of the modeled HR

The modeled diurnal variations in θ_s and Q_r profiles across L_R are respectively shown in Fig. 5a,b for S6, the largest HR across all eight scenarios. Although the overall θ_s decreases with progressively drying soil conditions, HR can partially refill θ_s in the upper layers when a finite ψ_s gradient across L_R is maintained and F_e recedes to minimum at night. In the presence of PWS and $F_{e,night}$, daily HR can be computed using the total Q_r^- across each layer on a daily

basis. For all runs, modeled daily HR normalized by daily F_e and modeled daily HR without normalization are shown in Fig. 6a,b, respectively. With the exception of S5, a bell-shaped HR cycle during the dry-down process emerges and reaches a maximum value when largest ψ_s vertical gradient across L_R occurs. In the early phases of the dry-down, θ_s and ψ_s in the upper soil layers are reduced rapidly when compared to θ_s in the deeper layers thereby generating a continuously increasing ψ_s gradient across L_R resulting in an increasing HR. After ψ_s gradient reaches a maximum across L_R , the water located within the upper soil layers become difficult to extract by roots and most of the contribution from Q_r^+ to F_e is shifted to deeper soil layers. As a result, the ψ_s gradient is gradually 'evened out' resulting in a decreasing trend in HR. This dynamic drying process across the soil layers explains the bell-shaped HR cycle reported in the literature (Meinzer et al., 2004; Warren et al., 2005; Scholz et al., 2008; Prieto et al., 2010). The modeled average and maximum magnitudes of HR across all scenarios are respectively in the range of 6.3 to 16.7 % and 0.63 to 22.9 % when normalized by daily F_e , and in the range of 0.43 to 1.08 kg m⁻² day⁻¹ and 0.47 to 1.56 kg m⁻² day⁻¹ without normalization, a result more comparable to previous empirical estimates of HR (e.g., 20 % of F_e and 0.42 kg m⁻² day⁻¹ on average with maximum of 1.1 kg m⁻² day⁻¹ for loblolly pine) summarized elsewhere (Neumann and Cardon, 2012). While previous modeling studies tended to provide higher HR estimates (Neumann and Cardon, 2012), the proposed approach here ameliorates such high modeled HR by accounting for the possible use of PWS and $F_{e,night}$ (i.e., g_{res}) that increase residual water potential gradient at night ($\Delta\psi_{p,night}$) and reduce the magnitude of HR.

4 Discussion

4.1 Model analysis for PWS usage

The modeled results here indicate that the use of PWS tends to diminish under two conditions: a smaller $C_{p,total}$ by reducing C_p or H and a smaller F_e due to a reduced g_{res} or LAI. PWS usage is interpreted as the ensemble effect of water flux gradient along the transpiration stream from stem base to leaf lamina. Hence, reductions in F_e with a smaller g_{res} or LAI (i.e., S3 and S7) promotes a smaller water flux gradient that then suppresses the use of PWS. Both daytime F_e and $F_{e,night}$ are reduced by a smaller g_{res} . It can be expected that a smaller C_p or H (i.e., S2 and S8) provides less 'available' stored water for F_e given that $C_{p,total}$ represents an effective measure of whole-plant water storage. Since the contribution of PWS to F_e is reduced by a smaller $C_{p,total}$, the water flux gradient is further reduced resulting in a smaller use of PWS for S2 and S8. The increasing trend in the use of PWS with increasing tree size appears consistent with field experiments conducted for different tree sizes across different species or within the same species (Goldstein et al., 1998; Phillips et al., 2003). Unlike above-ground plant attributes, the vertical heterogeneity in root distributions may exert only minor impact on the use of PWS but potentially significant impact on RWU_{net} and F_e . The comparison for different root distributions (i.e., S4 and S6) suggest that less PWS is used for the case of a power-law root distribution (i.e., S6). Hence, RWU_{net} (i.e., $q_{p,sh}$) is reduced if the majority of root density is concentrated within the upper dry soil layers. Due to the reduction in RWU_{net} , daytime F_e appears to decrease as well. As a result, the more rapid reduction in daytime F_e when compared to RWU_{net} can be used to explain the smaller use in PWS in S6 when compare to S4. Taken together, a larger use of PWS implies a more efficient RWU_{net} to mitigate against drought conditions (i.e., maintain highest leaf photosynthesis at a given f_e), especially when roots are competing with drainage losses (shown later). The modeled results also indicate that more PWS usage occurs in less sandy soils (i.e., S4) or shallower groundwater level (i.e., S5). In contrast to the sandier soil type, higher soil water availability conditions can be maintained

in finer-textured soil (i.e., less conductive) even though drainage is allowed. It is for this reason that the more rapid increase in F_e than RWU_{net} generates a larger PWS usage for S4. When a shallow groundwater table is imposed on the soil system, the diurnal recovery of soil water status through HR or Darcian redistribution explains why the use of PWS for S5 can be maintained constant.

4.2 Model analysis for HR

In Fig. 7, the partitioning between nighttime HR and RWU_{net} (i.e., nocturnal refilling) normalized by total root water influx at night over the dry-down period shows how increases in nocturnal refilling suppress HR across all scenarios. Unlike the use of PWS, HR is impacted by $C_{p,total}$ and F_e in opposite ways. The above-ground sink strength can be reduced by a smaller $C_{p,total}$ (i.e., S2 and S8) or F_e (i.e., S3 and S7) that potentially enhance HR differently as drought progresses. When compared to S1, the ψ_s gradient driving HR for S2 and S8 is approximately the same, given a similar daytime F_e for these three scenarios. However, the ψ_s gradient for S1 is compensated for by a larger above-ground competing sink strength that directly suppresses HR. It can be stated that the soil water drawn by the rooting system at night in S1 contributes more to recharging θ_p depleted by previous daytime F_e but not θ_s in the drier and shallower soil layers. When $\Delta\psi_{p,night}$ induced by $F_{e,night}$ is ruled out, a pattern similar to what has been reported elsewhere (Hultine et al., 2003) emerges. Although the above-ground competing sink strength for S3 and S7 is smaller than S1, their ψ_s gradients driving HR cannot rapidly develop due to a reduced daytime F_e but can be retained with a longer duration when compare to S1. It is for this reason that a wider but shallower bell-shaped HR cycle is formed for cases S3 and S7, implying a larger amount of HR in total but smaller intensity of HR during the dry-down process. If nighttime evaporative demand (averaged overnight vapor pressure deficit is 0.07 kPa computed from the atmospheric forcing shown in Supporting Information; not g_{res}) is set to zero to suppress only $F_{e,night}$, an immediate increase in the intensity of HR is predicted (not shown here) consistent with a number of experiments manipulating $F_{e,night}$ (Hultine et al., 2003; Scholz et al., 2008; Howard et al., 2009; Prieto et al., 2010). Over a dry-down, the increase in modeled HR with zero $F_{e,night}$ is approximately 10% across all scenarios. However, the model calculations suggest that the reduction in HR due to the presence of $F_{e,night}$ may be less significant when compared to larger $C_{p,total}$ (i.e., more than 22% reduction in HR). Among the many plant attributes affecting HR, the variation in root distribution can directly alter the pattern of ψ_s gradient along L_R even when the above-ground competing sink strength is maintained the same. If the root density is concentrated in the upper soil layers as reflected by S6 especially for coniferous species (Jackson et al., 1996; Finér et al., 1997; Andersson, 2005), significant daytime depletion of soil water in the upper layers (Fig. 5) produces a much larger ψ_s gradient that increases the magnitude of HR. A larger HR corresponding to a vertically asymmetric root distribution has been reported by other experiments and model calculations (Hultine et al., 2003; Scholz et al., 2008; Siqueira et al., 2008; Volpe et al., 2013) lending some support to the model results here.

Regarding soil texture, the comparison between S1 and S4 suggests that sandy soils result in smaller intensity and duration (i.e., frequency) of HR (Yoder and Nowak, 1999; Wang et al., 2009) when compared to their clay counterpart. Rapid drainage in coarse-textured soils impedes the development of ψ_s gradient required for the onset of HR (Burgess et al., 2000; Scholz et al., 2008). Moreover, the loss of soil-root contact (i.e., a larger l is expected here) at low θ_s can further diminish the ability to exude water by roots (i.e., Q_r^-) even when the ψ_s gradient is well developed (Wang et al., 2009). Since l is held constant here with a pre-specified B for any θ_s condition, this reduction in Q_r^- is only possible through reductions in K_s and k (see Equation 8).

As discussed earlier, HR at night can be maintained constant for the case of groundwater level adjacent to L_R (i.e., S5) given a constant ψ_s gradient generated by daytime F_e . It also implies that the magnitude of HR with a shallow groundwater level mainly depends on the magnitude of the previous daytime F_e when below-ground conditions (i.e., soil type, groundwater level and root attributes) are not appreciably varying. However, the ψ_s gradient driving HR in this case does not accumulate with progressively drying soil condition resulting in a smaller HR magnitude.

Interestingly, when combining all the factors that potentially impact the magnitude of HR, plausible explanations can be given for two conflicting empirical studies on HR with rooting system near or in contact with a groundwater table: sugar maple (*Acer saccharum*) with significant HR (Dawson, 1993; Emerman and Dawson, 1996) and three desert phreatophytic plants with insignificant HR (Hultine et al., 2003). Although $F_{e,night}$ for sugar maple is among the largest reported from a literature survey (Dawson et al., 2007), the ψ_s gradient along L_R is not reduced by $\Delta\psi_{p,night}$ when deeper roots are in contact with groundwater. Thus, the significant ψ_s gradient across L_R , which was developed by a large daytime F_e (Dawson et al., 2007), fine-textured soil type (i.e., silt loam) and asymmetric root distribution, can intensify the magnitude of HR in this case. However, the ψ_s gradient for the three desert phreatophytes may be lacking due to the combined effects of sandy soil (up to 84% sand) and small daytime F_e thereby suppressing the occurrence of HR.

4.3 Combined effects of PWS and HR on the plant drought resilience

It can be conjectured that a larger T_c improves the capabilities of a plant to resist drought stress and enhance C_{uptake} over a longer period. T_c varies with different scenarios because the temporal variation in $\bar{\psi}_l$ dictating T_c is impacted by the combined effects of F_e and RWU_{net} as well as PWS and HR. Thus, how RWU_{net} is impacted for different scenarios can be used to explore variations in T_c and C_{uptake} in relation to PWS and HR. The modeled C_{uptake} shown in Fig. 8a features an increasing trend with respect to T_c when leaf-level physiological parameters remain the same across the eight scenarios. It is suggested that T_c during a dry-down period can be used as a direct indicator to examine the extended use of soil water to sustain C_{uptake} for each of the eight scenarios. The coordinated relation between stomatal behavior and plant hydraulics in response to soil-drying is also illustrated in Fig. 9 - showing the modeled time-course of g_s, CO_2 and water potential in each compartment as well as the corresponding $\bar{\psi}_l$. The g_s, CO_2 decreases with decreasing $\bar{\psi}_l$ (not bulk ψ_s) because the cost of water in carbon units (i.e., λ) increases as specified by the hydraulic signal curve. Moreover, the more rapid reduction in ψ_s when compared to the smoothly varying $\bar{\psi}_l$ indicates how PWS impacts this hydraulic signal and subsequent response of leaf-level gas exchange to drought condition.

Fig. 8b shows that the daily RWU_{net} decreases with decreasing bulk θ_s except for S5. A shallow groundwater level can support a constant daily RWU_{net} and F_e preventing $\bar{\psi}_l$ from being reduced to $\bar{\psi}_{l,c}$. This explains why T_c is indefinite unless this ideal balance between demand and supply is discontinued. To contrast the effects of atmospheric demand (i.e., F_e) on T_c when $C_{p,total}$ remains the same, a larger T_c is predicted by the reduction in F_e with a reduced g_{res} (i.e., S3) or LAI (i.e., S7) in comparison to S1. Apparently, RWU_{net} needed for F_e in such cases is reduced, suggesting that a wetter soil condition and a larger $\bar{\psi}_l$ can be maintained for a longer period to support leaf-level gas exchange. When $C_{p,total}$ is reduced by using a smaller C_p (i.e., S2) or H (i.e., S8) compared to S1, a rapid reduction in $\bar{\psi}_l$ was found to diminish T_c for both cases. Although the total HR and RWU_{net} in these two cases are larger than S1, ψ_s still cannot be maintained in a wetter condition when a larger amount of RWU_{net} is required due to a lack of available PWS. Adopting the two-end member for total hydraulic capacitance (i.e., S1 and

S8) as examples (Fig. 9), larger PWS to compensate for the decline in bulk θ_s and ψ_l enhances T_c (and C_{uptake}) as drought progresses thereby delaying the incipient reduction in $\bar{\psi}_l$.

Examining the model results for S4 and S6, it is evident that the magnitude of RWU_{net} is suppressed by the case of root density concentrated in the upper soil layers (i.e., S6). Unlike previous $C_{p,total}$ comparisons, $\bar{\psi}_l$ can be less negative (i.e., larger T_c) due to a larger RWU_{net} provided $C_{p,total}$ for the two cases differing in root distributions is the same. Again, a larger HR promoted by asymmetric root distribution overnight cannot directly contribute to RWU_{net} mainly occurring during daytime. Regarding soil texture, more RWU_{net} can be supported by less sandier soil (i.e., S4). Similar to the comparison for the two-end members of root distribution, T_c is increased by a larger RWU_{net} if $C_{p,total}$ is held constant. Hence, the finer-textured soil type can prevent a rapid decline in $\bar{\psi}_l$ and yield larger T_c .

To sum up, routing available soil water into PWS instead of HR can be more advantageous as a strategy when drought progresses and soil water availability is the main limiting factor (even in the absence of competing species). However, the significance of HR associated with enhancement of nutrient uptake through maintaining soil-root contact, rendering water to neighboring species and maintaining microbial activities cannot be overlooked (Prieto et al., 2012). Other environmental factors and plant traits can also exert positive or negative effects on T_c depending on the duration that can sustain higher ψ_l as drought progresses. Fig. 10 summarizes the conditions promoting enhancement or suppression of modeled T_c as well as HR. Despite all the simplification made in the proposed modeling approach, the framework here can serve as a 'hypothesis generator' to assess how exogenous environmental conditions and endogenous soil-root-stem-leaf hydraulic and eco-physiological properties shape plant responses to droughts. Testing such hypothesis requires coordinated field and laboratory experiments that measure water movement in all compartments of the soil-plant system.

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Author Contribution

Cheng-Wei Huang, Gabriel G. Katul and Jean-Christophe Domec developed the model. Cheng-Wei Huang and Gabriel G. Katul wrote the manuscript. Tomer Duman, Gabriele Manoli and Anthony J. Parolari analyzed the model results. Eric J. Ward provided sap flux data for model evaluation.

Table 1: Eight scenarios (S1-S8) set up to explore the use of plant water storage (PWS)

	S1	S2	S3	S4	S5	S6	S7	S8
H (m)	20	20	20	20	20	20	20	10
C_p (kg m ⁻³ MPa ⁻¹) ^a	L	S	L	L	L	L	L	L
LAI (m ² m ⁻²)	6	6	6	6	6	6	4	6
g_{res} (mol m ⁻² s ⁻¹)	0.04	0.04	0.02	0.04	0.04	0.04	0.04	0.04
Lower boundary condition ^b	FD	FD	FD	FD	WT	FD	FD	FD
Root distribution ^c	U	U	U	U	U	PW	U	U
Soil type	sand	sand	sand	sandy clay loam	sand	sandy clay loam	sand	sand

^a Two plant hydraulic capacitance: larger (L) and smaller (S) C_p ’s (see Supporting Information).

^b Two lower boundary conditions for the soil column: free drainage (FD) and water table (WT) at 2 m depth.

^c Two vertical root distributions: Uniform (U) and power-law (PW) rooting profiles. Note that the power-law reduction function provides a more realistic description for coniferous species (Jackson et al., 1996; Finér et al., 1997; Andersson, 2005).

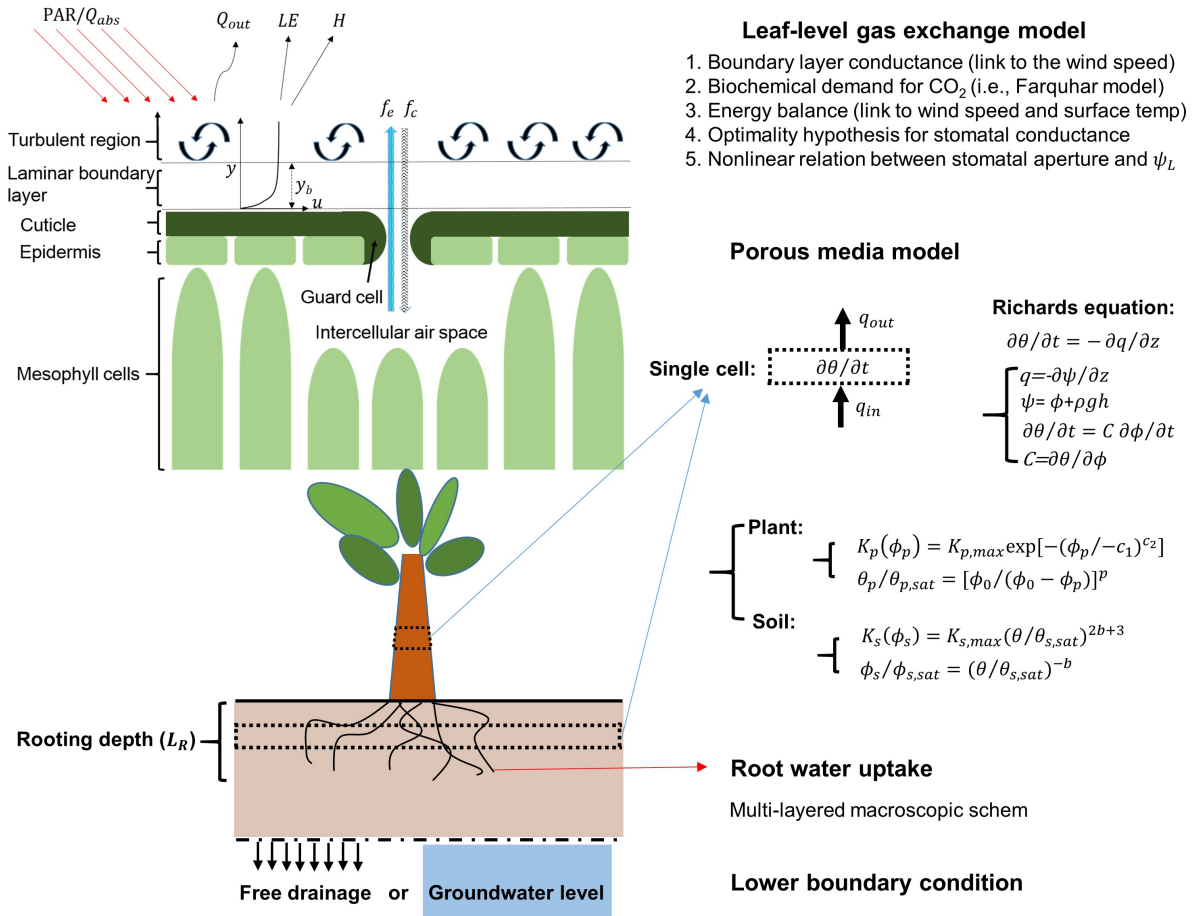


Figure 1: Schematic of the modeling approach describing the water movement through each compartment of the soil-plant-system with a summary of the porous media flow equations used, the lower boundary conditions and the upper boundary conditions represented by the leaf-gas exchange equations.

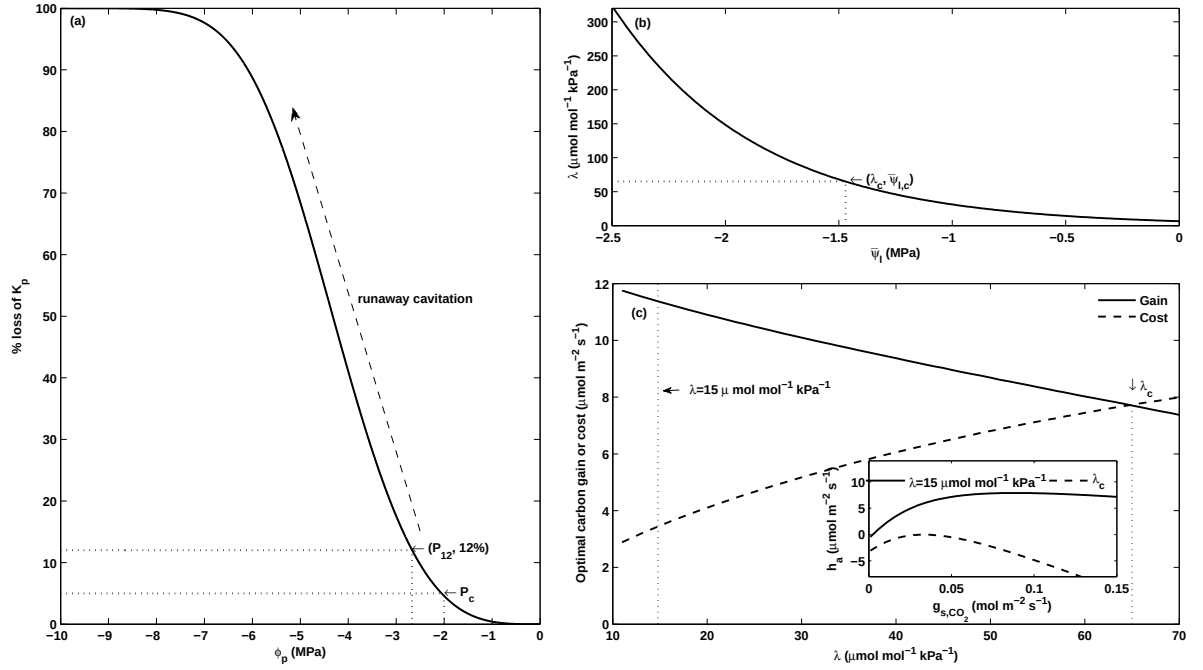


Figure 2: (a) Xylem vulnerability curve with indication of water potentials at 12% loss of K_p (P_{12}) and at complete stomatal closure (P_c). (b) The λ values as a function $\bar{\psi}_l$ using the relation proposed elsewhere (Manzoni et al., 2011). (c) The two components (i.e., carbon gain and water loss in carbon unit) of the optimal 'net' carbon gain (h_a) as a function of λ . Inset: the 'net' carbon gain (h_a) as a function of given g_{s,CO_2} for $\lambda = 15 \mu\text{mol mol}^{-1} \text{kPa}^{-1}$ and λ_c . Note that λ_c , $\bar{\psi}_{l,c}$ and P_c are determined at the condition where optimal the 'net' carbon gain is identical to zero (i.e., optimal $h_a = 0$). $\lambda = 15 \mu\text{mol mol}^{-1} \text{kPa}^{-1}$ is arbitrarily selected to illustrate that $h_a > 0$ when $\lambda < \lambda_c$.

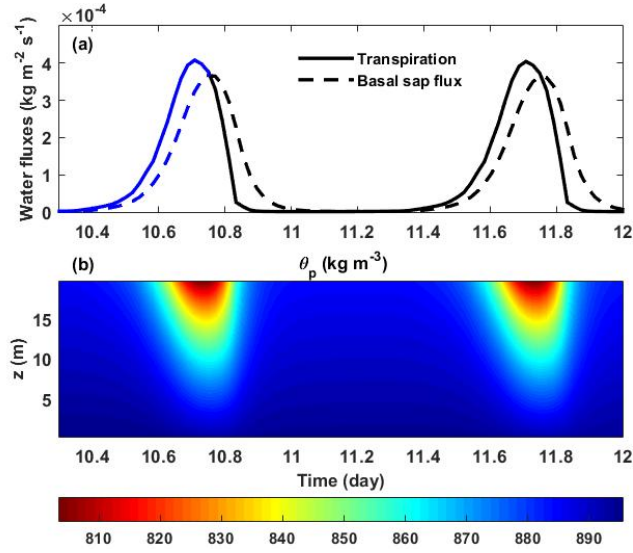


Figure 3: (a) Modeled transpiration rate (F_e) and basal sap flux ($q_{p, sb}$) on a per unit ground area basis and (b) modeled profile of plant xylem water content (θ_p) with a unit of kg m⁻³ for S1 (see Table 1 for model setup). Note that daily PWS usage is determined by the area within the solid and dashed blue lines)

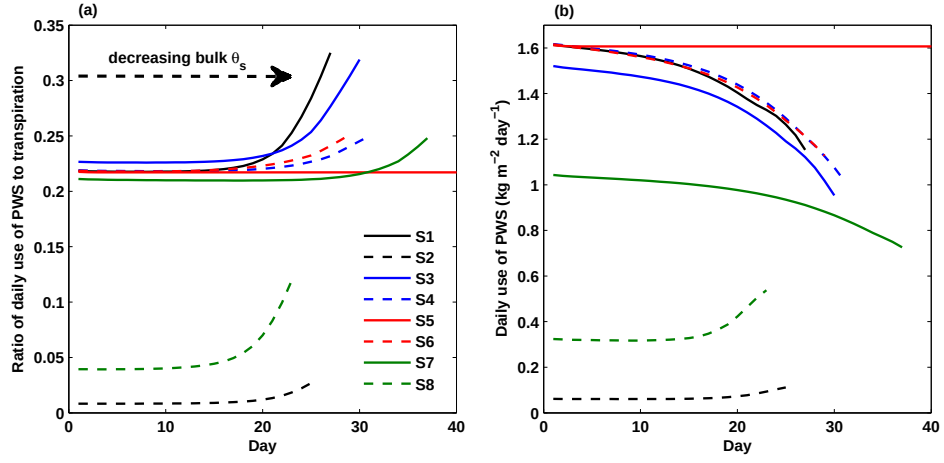


Figure 4: (a) Modeled daily use of plant water storage (PWS) normalized by daily transpiration and (b) modeled daily use of PWS on a per unit ground area basis for the eight scenarios (see Table 1 for the model setup).

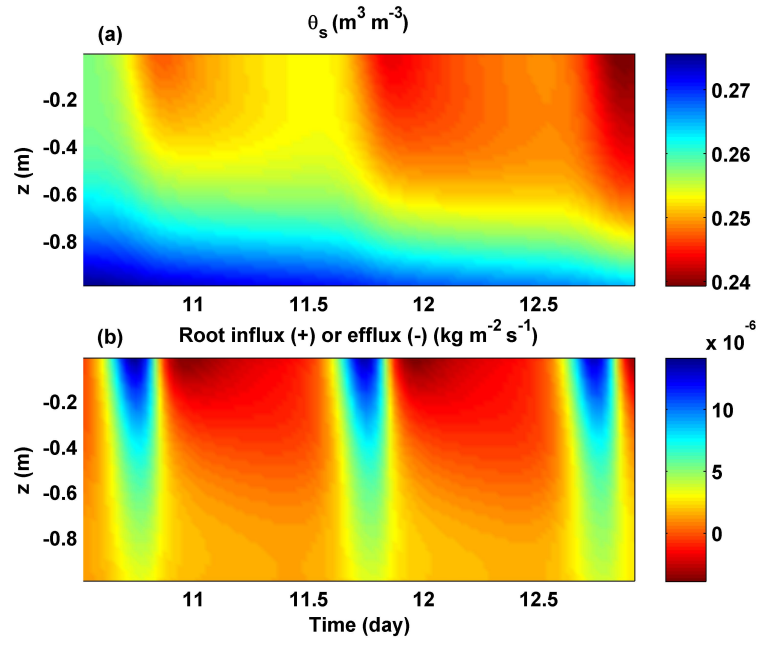


Figure 5: (a) Modeled profiles of soil water content (θ_s) and (b) root water influx (Q_r^+) or efflux (Q_r^-) on a per unit ground area basis for S6 (see Table 1 for model setup)

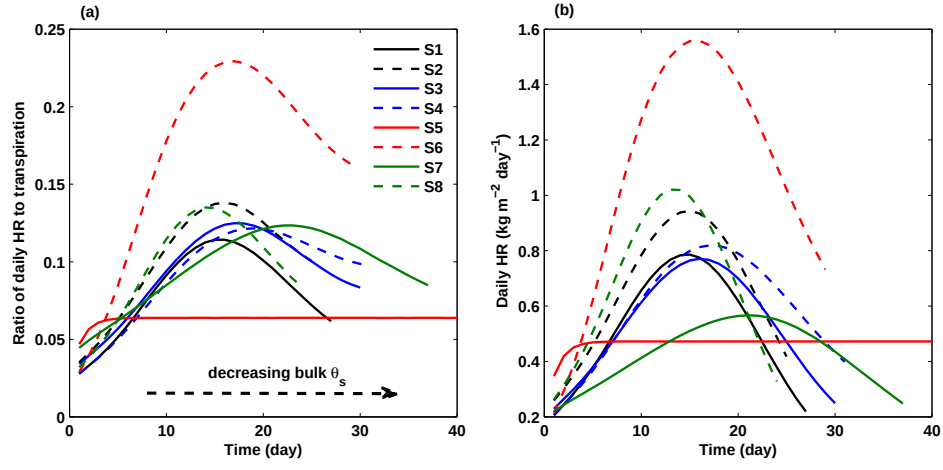


Figure 6: (a) Modeled daily hydraulic redistribution (HR) normalized by daily transpiration and (b) modeled daily HR on a per unit ground area basis for the eight scenarios (see Table 1 for model setup).

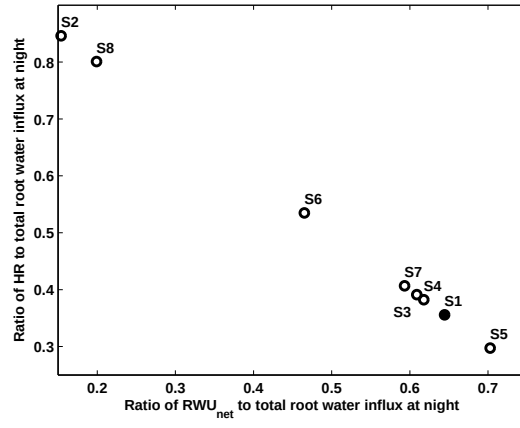


Figure 7: The partitioning between nighttime hydraulic redistribution (HR) and net root water uptake (RWU_{net}) normalized by total root water influx at night over a single dry-down process.

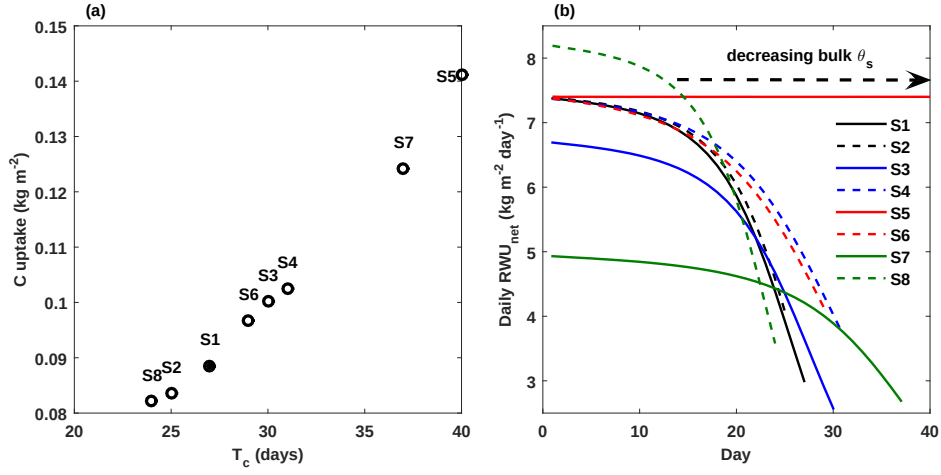


Figure 8: (a) Modeled total carbon uptake (C_{uptake}) on a per unit leaf area basis in relation to the duration before complete stomatal closure (T_c) for each scenario. (b) Modeled daily net root water uptake (RWU_{net}) on a per unit ground area basis for the eight scenarios (see Table 1 for model setup). Note that T_c for S5 is indefinite and is terminated at 40 days for reference.

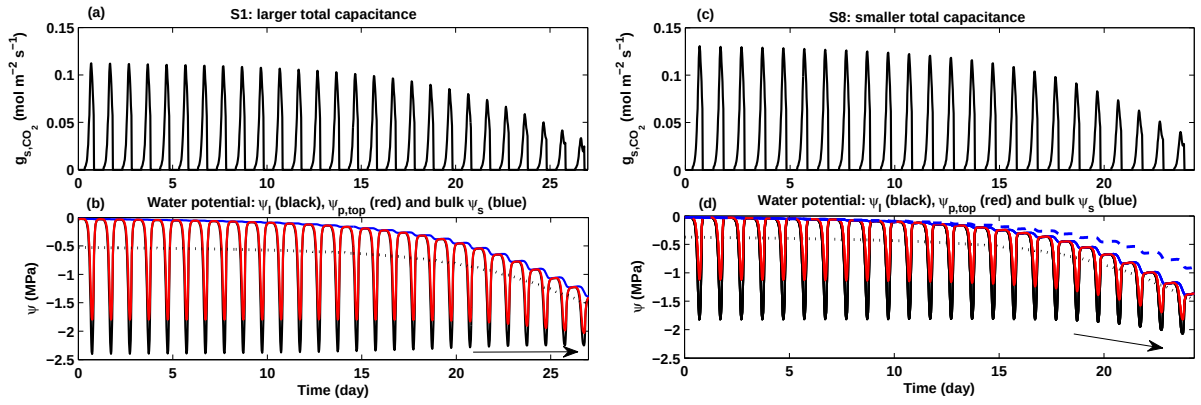


Figure 9: (a) Modeled stomatal conductance (g_{s,CO_2}) and (b) modeled water potential in each compartment for S1. (c) Modeled g_{s,CO_2} and (b) modeled water potential in each compartment for S8. Note that black solid, black dashed, red solid and blue solid lines are used to represent leaf water potential (ψ_l), 24 hours averaged leaf water potential ($\bar{\psi}_l$), distal xylem water potential ($\psi_{p,top}$) and bulk soil water potential (ψ_s) across L_R , respectively. The bulk ψ_s for S1 (blue dashed line) is also included in Fig. 9d for reference. The T_c 's for S1 and S8 are respectively 27 and 23 days (i.e., x-axis range for each scenario).

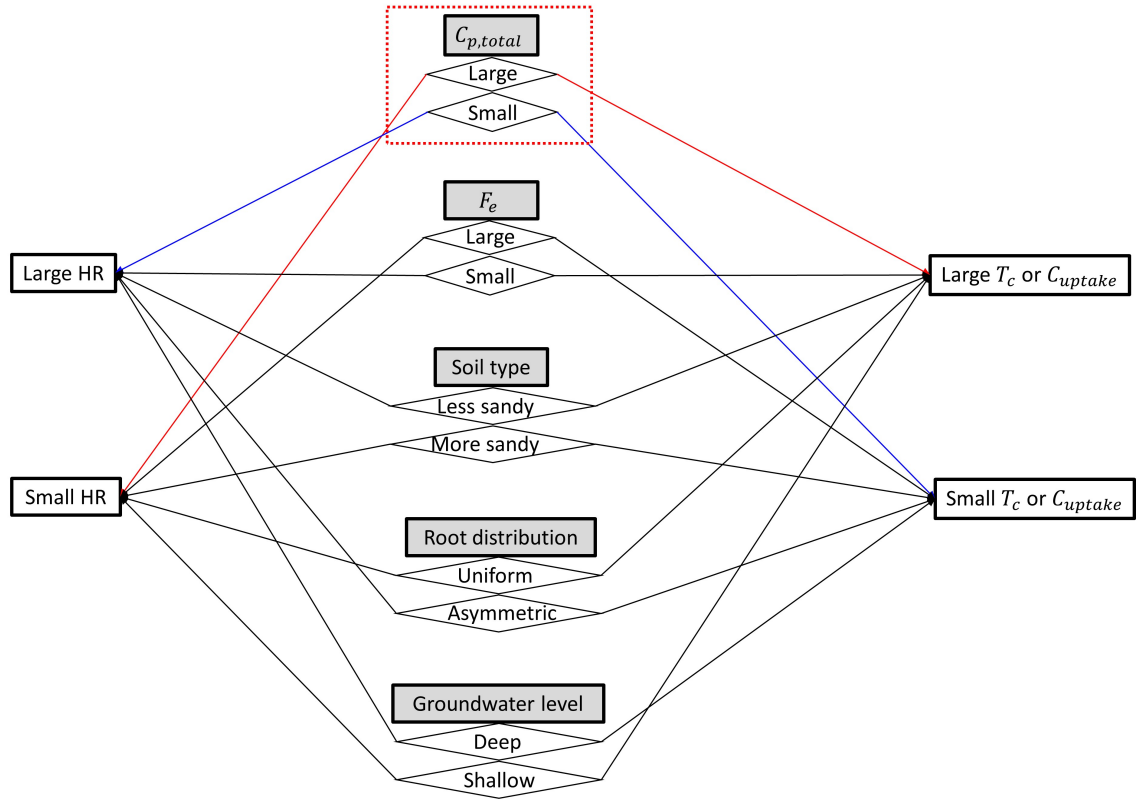


Figure 10: A summary of how exogenous and endogenous factors (i.e., the eight scenarios) impact modeled hydraulic redistribution (HR), duration before complete stomatal closure (T_c) and total carbon uptake (C_{uptake}) during a dry-down period. Note that all the factors explored here have the same positive or negative effects on HR and T_c (or C_{uptake}) except for $C_{p,total}$. Thus, the blue and red lines are used to indicate the opposite trends imposed by $C_{p,total}$ that is enclosed by the dotted box for clarity.

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