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Coordination of rooting, xylem, and stomatal strategies explains the response of conifer forest stands to multi-year drought in the Southern Sierra Nevada of California

Junyan Ding[1,2], Polly Buotte[3], Roger Bales[4], Bradley Christoffersen[5], Rosie A. Fisher[6,7], Michael Goulden[8], Ryan Knox[1], Lara Kueppers[1,3], Jacquelyn Shuman[6], Chonggang Xu[9], Charles D. Koven[1]

1. Climate and Ecosystem Sciences Division, Lawrence Berkeley National Lab, Berkeley, USA
2. Pacific Northwest National Lab, Richland, WA, USA
3. Energy and Resources Group, University of California, Berkeley, USA
4. Sierra Nevada Research Institute, University of California, Merced, USA
5. Department of Biology, University of Texas, Rio Grande Valley, USA
6. Climate and Global Dynamics Division, National Center for Atmospheric Research, Bold, USA
7. Laboratoire Évolution & Diversité Biologique, CNRS:UMR 5174, Université Paul Sabatier, Toulouse, France
8. Dept. of Earth System Science, University of California, Irvine, USA
9. Earth and Environmental Sciences Division, Los Alamos National Laboratory, Santa Fe, New Mexico, USA

Corresponding author: Junyan Ding (junyan.ding@pnnl.gov)

Key Points:

- We perform a sensitivity analysis using the model FATES-Hydro to explore the co-ordination of leaf, xylem, and root hydraulic traits of pine in Southern Sierra Nevada.
- We find that rooting depth is the major control on water and carbon fluxes, and that deep-rooted pines with risky stomata have the highest GPP but also the highest drought mortality risk.
- Resolving both the plant water sourcing strategies and subsurface processes are critical to represent drought impacts on conifer forests.

https://doi.org/10.5194/bg-2023-16
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Abstract

Extreme droughts are a major determinant of ecosystem disturbance, which impact plant communities and feed back to climate change through changes in plant functioning. However, the complex relationships between above- and belowground plant hydraulic traits, and their role in governing plant responses to drought, are not fully understood. In this study, we use a plant hydraulics model, FATES-Hydro, to investigate ecosystem responses to the 2012-2015 California drought, in comparison with observations, for a site in the southern Sierra Nevada that experienced widespread tree mortality during this drought.

We conduct a sensitivity analysis to explore how different plant water sourcing and hydraulic strategies lead to differential responses during normal and drought conditions.

The analysis shows that:

1) deep roots that sustain productivity through the dry season are needed for the model to capture observed seasonal cycles of ET and GPP in normal years, and that deep-rooted strategies are nonetheless subject to large reductions in ET and GPP when the deep soil reservoir is depleted during extreme droughts, in agreement with observations.
2) risky stomatal strategies lead to greater productivity during normal years as compared to safer stomatal control, but lead to high risk of xylem embolism during the 2012-2015 drought.
3) for a given stand density, the stomatal and xylem traits have a stronger impact on plant water status than on ecosystem level fluxes.

Our study reveals the importance of resolving plant water sourcing strategies in order to represent drought impacts on plants, and consequent feedbacks, in models.

https://doi.org/10.5194/bg-2023-16
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1. Introduction

Understanding plant water use strategies and the resulting ecohydrologic processes in forests is critical for predicting surface water and energy exchange, carbon dynamics and vegetation dynamics of water-constrained ecosystems in a changing climate. Mediterranean-type climates, as in California, are characterized by dry and hot summers and cool, wet winters, resulting in asynchronous supplies of energy and water. In addition to these climatic stresses, plants in California are further subject to high inter-annual variability in precipitation, and periodic severe drought events, such as the recent 2012 – 2015 drought, which led to widespread tree mortality (Fettig et al. 2019). Together, these two climatic constraints bring a unique challenge to the success of forests in California, which are likely to be exacerbated in a warming climate.

On evolutionary timescales, natural selection has led to a wide array of strategies and functional traits that allow plants to both grow and survive under a range of environment conditions (Grime 1977,1979; Coley et al. 1985; Westoby et al. 2002; Craine 2002; Reich et al. 2003). Given the centrality of water sourcing on plant physiology, plant hydraulic traits play an important role in water-constrained ecosystems. Once absorbed by fine roots, water flows through the vascular system via coarse roots, stems, branches, to leaves where it evaporates through stomata. The rate of water flow through stems, and thus the supply to leaves, is determined by the hydraulic conductivity along this pathway. If the water potential of xylem tissue becomes too low, cavitation can occur and cause a loss of conductivity. Because this cavitation can damage the xylem network, trees have developed different strategies to mitigate this effect, all of which come at some cost. These strategies include 1) early stomatal closure or leaf deciduousness to reduce the flow of water, at the cost of reduced carbon intake; 2) building cavitation-resistant xylem, at the cost of increased hydraulic resistance; and 3) growing deep roots to access more moisture, at the cost of higher carbon investment. In this study, we focus on the potential hydraulic strategies that trees in Californian ecosystems use, with a particular emphasis on how the co-ordination of hydraulic functional traits at the leaf, stem, and root levels is critical to carbon assimilation, transpiration, and consequently, the productivity and the response of trees to drought (Matheny, Mirfenderesgi, and Bohrer 2017; Matheny et al. 2017; Mursinna et al. 2018a).

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

87 The traits that regulate stomatal conductivity are the most important hydraulic traits of
88 leaves and the primary ones through which photosynthesis and transpiration are coupled.
89 Stomatal behavior falls along a gradient between two extremes: stomata may close early during
90 water stress to avoid the risk of hydraulic failure, or remain open to maximize carbon uptake
91 while exposing xylem to a higher risk of embolism (Martínez-Vilalta, Sala, and Piñol 2004;
92 McDowell et al., 2008; Skelton, West, & Dawson, 2015, Matheny et al. 2017). The sensitivity of
93 stomata to water stress determines where the stomata operate along the safety-risky gradient,
94 thus the degree that carbon intake is traded for preventing the cavitation of xylem. Where the
95 best stomatal strategy sits along the safety-risky gradient would depend on the physical
96 environment.

97 The maximum hydraulic conductivity and the vulnerability to cavitation are the two key
98 xylem hydraulic traits. Differences in the anatomy and morphology of the conductive xylem cell
99 structure and anatomy (Hacke et al. 2017) lead to differences in maximum conductivity and the
100 water potential at which cavitation starts to occur (Pockman & Sperry, 2000; Sperry 2003).
101 Within the conifers, there are at least three mechanisms that lead to a tradeoff between xylem
102 safety and efficiency. First is the morphology of the xylem conduit. It is widely acknowledged
103 that narrow (or short) tracheid are safer than wider (or longer) tracheid but have lower
104 conductance per sap area (Choat and Pittermann 2009). Second are the intervessel pit
105 membranes. Thicker and less porous membranes prevent the spread of air but increase the
106 hydraulic resistance of xylem (e.g. Li et al., 2016; Pratt & Jacobsen 2017). The third comes from
107 the division of limited space (Pratt and Jacobsen 2017). With the same cross sectional area of
108 conduits, vessels with a thicker cell wall provide stronger mechanical support, so that the
109 conduits are less likely to collapse when xylem water potential becomes more negative, however
110 this reduces the area that can be used for conduits transporting water. While these physiological
111 constraints require that the tradeoff does exist to some extent, in many studies, this tradeoff
112 appears to be weak, and there are certainly species that have both safe and efficient xylem.
113 Further, there are many other plant traits can affect the safety such as wood density (Pratt and
114 Jacobsen 2017), pit anatomy (Sperry & Hacke 2004, Lens et al. 2011), and biochemistry (Gortan
115 et al. 2011). These traits can have large variation among the plant types. The tradeoff will be
116 weakened when grouping plants in coarse scale, e.g by biomass, families and/or across a range of
117 geological and climatic region. But when focusing on certain species in a particular region, the

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

tradeoff becomes stronger, as demonstrated by many local studies (e.g Barnard et al. 2011, Corcuera et al. 2011, Baker et al. 2019). For example, Kilgore et al. (2021) shows that there is clear safety-efficiency tradeoff of the pine trees in a specific location in the western US.Thus, while we acknowledge that there are many exceptions to the xylem safety-efficiency tradeoff, it is a useful framework for examining plant strategies for dealing with drought.

The traits that govern the hydraulic function of plant root systems are also critically important but the least understood and studied. These traits include the rooting depth, the root to shoot ratio, the vertical and lateral distribution of roots, and the fine root density and diameters, all of which are related to water uptake (Canadell et al., 2007, Allen 2009, Reichstein et al., 2014, Wullschleger et al. 2014). In general, species with deeper roots can access water at greater depths that is unavailable to more shallowly rooted species (Jackson et al., 1996; Canadell et al., 1996). The vertical root distribution can affect the water uptake and thus the evapotranspiration pattern during the dry-down period (Teuling, Uijlenhoet, and Troch 2006). This in turn affects the seasonal distribution of water over the soil depth, and thereby the resilience of plants to seasonal droughts (Yu, Zhuang, and Nakayamma 2007). The vertical root distribution is also a means of belowground niche differentiation (Ivanov et al. 2012; Kulmatiski and Beard 2013), whereas the extent of the lateral root distribution dictates the competition of water (Agee et al. 2021). Whether a plant can benefit from having deep roots is related to the plant's leaf and xylem hydraulic traits (e.g. Johnson et al. 2018, Mackay et al. 2020), thus requiring coordination of rooting and hydraulic traits.

Given the strength of the Mediterranean-type climate of California, the coordination of rooting and hydraulic strategies will play a critical role for the forest dynamics. However, the interplay of rooting and hydraulic strategies and their impact on ecosystem processes haven't been well understood. In this study, we address this question at the Soaproot site (CZ2) of the southern Sierra Nevada of California as the study area. The CZ2 site was strongly affected by the 2012-2015 drought, with extremely high tree mortality rates (~90% of the pine died) (Fettig et al. 2019). While the 2012 - 2015 drought was widespread across California, the highest rates of tree mortality occurred in the southern Sierra Nevada, centered around an elevation similar to this site (1160 m to 2015 m, Asner et al. 2016, Goulden and Bales 2019). This mid-elevation region is also characterized by the highest forest productivity along an elevation gradient from foothill

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

148 woodlands to subalpine forest (Kelly and Goulden 2016). This leads us to ask whether strategies
149 associated with high productivity exposed trees to high mortality risk under prolonged drought.

150 Specifically, here we use the Functionally Assembled Terrestrial Ecosystem Simulator, in
151 a configuration that includes plant hydraulics (FATES-Hydro), to explore the tradeoffs
152 associated with differing hydraulic strategies, and in particular their implications for plant
153 productivity and risk of drought-induced mortality. We conduct a sensitivity analysis, using
154 FATES-Hydro in comparison with observations from the CZ2 eddy covariance site, to
155 investigate how stomatal, xylem and rooting strategies affect the ecosystem and physiologic
156 processes of the forest, and whether that may explain the high rates of both productivity and
157 drought-associated mortality of conifers at CZ2.

158 **2. Methods**

159 2.1 Study site

160 The Soaproot site is a 543-ha headwater catchment at 1100m elevation (37°2.4' N,
161 119°15.42' W), which is at the lower boundary of the rain–snow transition line with warm, dry
162 summers and cool, wet winters (Geen et al. 2018). The mean annual temperature is about 13.8°C
163 (Goulden et al., 2012). Under normal conditions, the annual precipitation is about 1300 mm, but
164 during a dry year, the precipitation can drop to 300-600mm. (Bales et al. 2018). The site is a
165 ponderosa pine (*Pinus ponderosa*) dominated conifer ecosystem exhibiting high productivity
166 (Kelly and Goulden (2016) reported 2.1 tC/ha/year average annual gross stem wood production
167 averaged). Other species include California black oak (*Quercus kelloggii* Newberry), and incense
168 cedar (*Calocedrus decurrens*).

169 Soils at the Soaproot site are mainly of the Holland (fine-loamy, mesic Ultic Haploxeralfs)
170 and Chaix (coarse-loamy, mesic Typic Dystroxerepts) series, which are representative of soils
171 across a similar elevation band of the western Sierra Nevada (Mooney and Zavaleta 2003). Soils
172 of the Holland series have sandy loam surface texture and underlying Bt horizons with sandy
173 clay loam textures, while soils of the Chaix series have sandy loam textures throughout the
174 profile. The regolith depth is estimated to be 15m (Holbrook et al., 2014). The total porosity over
175 the whole regolith depth of the site is estimated to be 1620 mm and the total available storage
176 porosity (plant accessible water storage capacity), which is the difference in volumetric water

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

content between field capacity and permanent wilting point (~ -6Mpa) to be 1400 mm (Klos et al. 2017). The available water storage capacity is approximately 0.20 cm^3 cm^{-3} in the upper regolith (0–5 m depth) which decreases to 0.05 cm^3 cm^{-3} or less in the lower regolith (below 5 m depth) (Holbrook et al., 2014).

An eddy-covariance flux tower was installed at this site in September 2010. The elevation of the tower is 1160 m above sea level. Instruments on the flux tower track changes in carbon dioxide, water vapor, air temperature, relative humidity, and other atmospheric properties. We compare the simulated gross primary productivity and latent heat flux with the flux tower measurements over the period from 2011 to 2015 (Goulden and Bales 2019). We computed the Root Mean Square Error (RMSE) of the hourly mean diurnal cycle of each month. This allows us to examine the capacity of FATES-Hydro to predict the carbon and water fluxes. The transpiration of the site contributed to the majority of the ET as indicated by the measurements from an adjacent catchment, as well as the fact that the site is fully vegetated with an annual LAI around 3 to 4.

2.2 FATES-Hydro model and parameterization

2.2.1 The FATES-Hydro model

FATES is a cohort-based, size- and age-structured dynamic vegetation model, where long-term plant growth and mortality rates and plant competition emerge as a consequence of physiological processes. FATES is coupled within both the CLM5 (Lawrence et al., 2019) and the ELM (Golaz et al., 2020) land surface models (LSMs). In this study, FATES is coupled with the CLM5. FATES-Hydro is a recent development of the FATES model (Fisher et al., 2015; Koven et al., 2020), in which a plant hydro-dynamic module, originally developed by Christoffersen et al. (2016), was coupled to the existing photosynthesis and soil hydraulic modules.

Conceptually, plant hydraulic modules can be broadly grouped into to two types. The first group represents plant hydraulic system as analogous to an electrical circuit (e.g. Mackay et al. 2011, Eller et al. 2018, Kennedy et al. 2019). The total resistance of the plant is calculated from the resistance of each compartment using Ohm's law. There is no storage of water in the plants

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

and the transpiration from plants at any given time step is considered to be completed from soil storage. The second group represents plant hydraulics by a series of connected porous media, corresponding to each plant compartment (e.g. Bohrer et al. 2005), Janott et al. 2011, Xu et al., 2016, Christoffersen et al., 2016). The porous media model takes into account the water storage in the plant. The flow between two adjacent compartments is driven by the difference in the water potential, mediated by the hydraulic conductivity. FATES-Hydro falls in the second group. The models in the second group differ in the exact formulas used to describe the pressure-volume and pressure-conductivity relations, as well as different numbers and arrangement of nodes within the soil-plant-atmosphere system.

In FATES-Hydro, for each plant cohort, the hydraulic module tracks water flow along a soil–plant–atmosphere continuum of a representative individual tree based on hydraulic laws, and updates the water content and potential of leaves, stem, and roots with a 30 minute model time step. Water flow from each soil layer within the root zone into the plant root system is calculated as a function of the hydraulic conductivity as determined by root biomass and root traits such as specific root length, and the difference in water potential between the absorbing roots and the rhizosphere. The vertical root distribution is based on Zeng's (2001) two parameter power law function which takes into account the regolith depth:

$$Y_i = \frac{0.5(e^{-r_a z_{li}} + e^{-r_b z_{li}}) - 0.5(e^{-r_a z_{ui}} + e^{-r_b z_{ui}})}{1 - 0.5(e^{-r_a z} + e^{-r_b z})}, \qquad \text{(Eq 1)}$$

where Y_i is the fraction of fine or coarse roots in the ith soil layer, r_a and r_b are the two parameters that determine the vertical root distribution, Z_{li} is the depth of the lower boundary of the ith soil layer, and Z_{ui} is the depth of the upper boundary of the ith soil layer, and Z is the total regolith depth. The vertical root distribution affects water uptake by the hydrodynamic model by distributing the total amount of root, and thus root resistance, through the soils.

The total transpiration of a tree is the product of total leaf area (LA) and the transpiration rate per unit leaf area (J). In this version of FATES-Hydro, we adopt the model developed by Vesala et al. (2017) to take into account the effect of leaf water potential on the within-leaf relative humidity and transpiration rate:

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

$$E = LA \cdot J \quad \text{(Eq 2a)}$$

$$J = \rho_{atm} \frac{(q_l - q_s)}{1/g_s + r_b} \quad \text{(Eq 2b)}$$

$$q_l = \exp\left(\frac{k_{LWP} \cdot LWP \cdot V_{H2O}}{R \cdot T}\right) \cdot q_{sat} \quad \text{(Eq 2c)}$$

where E is the total transpiration of a tree, LA is the total leaf area (m^2), J is the transpiration per unit leaf area (kg s^{-1} m^{-2}), ρ_{atm} is the density of atmospheric air (kg m^{-3}), q_l is the within-leaf specific humidity(kg/kg), q_s is the atmosphere specific humidity (kg/kg), g_s is the stomatal conductance per leaf area, r_b is the leaf boundary layer resistance(s m^{-1}), k_{LWP} is a scaling coefficient (unitless), which can vary between 1 and 7, and here we use a value of 3; LWP is the leaf water potential (Mpa), V_{H2O} is the molar volume of water (18×10^{-6} m^3 mol^{-1}), R is the universal gas constant, and T is the leaf temperature (K).

The sap flow from absorbing roots to the canopy through each compartment of the tree along the flow path way (absorbing roots, transport roots, stem, and leaf) is computed according to Darcy's law in terms of the plant sapwood water conductance, the water potential gradient:

$$Q_i = -K_i[\rho_w g(z_i - z_{i+1}) + (\Psi_i - \Psi_{i+1})] \quad \text{(Eq 3)}$$

where ρ_w is the density of water; z_i is the height of the compartment(m); z_{i+1} is the height of the next compartment down the flow path (m); Ψ_i is the water potential of the compartment(Mpa); Ψ_{i+1} is the water potential of the next compartment down the flow path(Mpa); and K_i is the hydraulic conductivity of the compartment (kg/Mpa/m/s). The hydraulic conductivity of the compartments is by the water potential and maximum hydraulic conductivity of the compartment through the pressure-volume (P-V) curve and the vulnerability curve (Manzoni et al. 2013, Christoffersen et al. 2016).

The plant hydrodynamic representation and numerical solver scheme within FATES-HYDRO follows Christoffersen et al. (2016). We made a few modifications to accommodate the multiple soil layers and to improve the numerical stability. First, to accommodate the multiple soil layers, we have sequentially solved the Richards' equation for each individual soil layer, with each layer-specific solution proportional to each layer's contribution to the total root-soil

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

conductance. Second, to improve the numerical stability, we have an option to linearly extrapolate the PV curve beyond the residual and saturated tissue water content to avoid the rare cases of overshooting in the numerical scheme under very dry or wet conditions. Third, Christoffersen et al. (2016) use three phases to describe the PV curves: 1) dehydration phases representing capillary water (sapwood only), 2) elastic cell drainage (positive turgor), and 3) continued drainage after cells have lost turgor. Due to the possible discontinuity of the curve between these three phases, it leads to the potential for numerical instability. To resolve this instability, FATES-HYDRO added the Van Genuchten model (Van Genuchten 1980, July and Horton 2004) and the Campbell model (Campbell 1974) as alternatives to describe the PV curves.

In this study, we use the Van Genuchten model because of two advantages: 1) it is simple, with only three parameters needed for both curves, and 2) it is mechanistically based, with both the P-V curve and vulnerability curve derived from a pipe model, and thus connected through three shared parameters:

$$\Psi = \frac{1}{-\alpha} \cdot \left(\frac{1}{Se^{1/m}} - 1 \right)^{1/n} \quad \text{(Eq 4a)}$$

$$FMC = \left(1 - \left(\frac{(-\alpha \cdot \Psi)^n}{1 + (-\alpha \cdot \Psi)^n} \right)^m \right)^2 \quad \text{(Eq 4b)}$$

where Ψ is the water potential of the media (xylem in this case) (Mpa); FMC is the fraction of xylem conductivity, K/K_{max}, (unitless); α is a scaling parameter for air entry point (Mpa^{-1}), Se is the dimensionless standardized relative water content as $Se=(\theta-\theta_r)/(\theta_{sat}-\theta_r)$ with θ, θ_r, θ_{sat} are volumetric water content ($m^3\ m^{-3}$), residual volumetric water content, and saturated volumetric water content correspondingly; and m and n are dimensionless (xylem conduits) size distribution parameters. The model assumes that xylem conductance can be restored as xylem water content increases due to increased water availability after a dry period without any hysteresis in the FMC curve.

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

The stomatal conductance is modelled in the form of the Ball-Berry conductance model (Ball et al. 1987, Oleson et al. 2013, Fisher et al. 2015):

$$g_s = b_{slp} \frac{A_n}{c_s / P_{atm}} \frac{e_s}{e_i} + b_{opt} \beta_t \ , \qquad \text{(Eq 5)}$$

where b_{slp} and b_{opt} are parameters that represent the slope and intercept in the Ball-Berry model, correspondingly. These terms are plant strategy dependent and can vary widely with plant functional types (Medlyn et al. 2011). The parameter b_{opt} is also scaled by the water stress index β_t. A_n is the net carbon assimilation rate (μmol CO2 m^{-2} s^{-1}) based on Farquhar's (1980) formula. This term is also constrained by water stress index β_t in the way that the $V_{cmax,25}$ is scaled by β_t as $V_{cmax,25}\beta_t$ (Fisher et al. 2018). c_s is the CO_2 partial pressure at the leaf surface (Pa), e_s is the vapor pressure at the leaf surface (Pa), e_i is the saturation vapor pressure (Pa) inside the leaf at a given vegetation temperature when $A_n = 0$.

The water stress index β_t, a proxy for stomatal closure in response to desiccation, is determined by the leaf water potential adopted from the FMC_{gs} term from Christoffersen et al. (2016):

$$\beta_t = \left[1 + \left(\frac{\Psi_l}{P50_{gs}} \right)^{ags} \right]^{-1} \qquad \text{(Eq 6)}$$

where Ψ_l is the leaf water potential (MPa), $P50_{gs}$ is the leaf water potential of 50% stomatal closure, and a_{gs} governs the steepness of the function. For a given value of a_{gs}, the $P50_{gs}$ controls the degree of the risk of xylem embolism (Christoffersen et al. 2016, Powell et al. 2017). A more negative $P50_{gs}$ means that, during leaf dry down from full turgor, the stomatal aperture stays open and thus allows the transpiration rate to remain high and xylem to dry out, which thus can maintain high photosynthetic rates, at the risk of exposing xylem to embolism and thus plant mortality. Conversely, a plant with a less negative $P50_{gs}$ will close its stomata quickly during leaf dry down, thus limiting transpiration and the risk of xylem embolism and mortality associated with it, at the cost of reduced photosynthesis.

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

306 2.2.2 Sensitivity analysis and Parameterization

307 The goal of this analysis is to better understand how coordinated aboveground and
308 belowground hydraulic traits determine plant physiological dynamics and the interplay between
309 ecosystem fluxes and tissue moisture during the extreme 2012-2015 drought at the Soaproot site.
310 We thus conduct a global sensitivity analysis on selected hydraulic parameters to explore the
311 linkages of aboveground and belowground hydraulic strategies. We use a full-factorial design for
312 the parameter sensitivity analysis in order to best investigate the relationships between
313 parameters. Because this design requires a relatively small set of parameters or groups of
314 parameters to vary, we chose parameters that represent the major axes of relatively well
315 understood stomatal, xylem and rooting mechanisms/strategies that control the hydraulic
316 functioning of trees. We set the values of these parameters within the realistic range based on
317 online database, and literatures where the species and physical environment are as close to our
318 system as possible. We list other major parameters and their estimates that are not varied in the
319 sensitivity analysis (table 2).

320 The parameters that we vary here are 1) the pair of r_a and r_b , which control vertical root
321 distribution as deep vs shallow roots, 2) two sets of xylem parameters (P_{50x}, K_{max}, *m, n, and* α)
322 that represent two distinct xylem strategies: efficient/unsafe and inefficient/safe xylem within the
323 range observed for temperate conifer trees, and 3) the stomatal parameter $P50_{gs}$, which represents
324 the stomatal strategy along a risky to safe gradient (Table 1). The ranges of root parameters are
325 chosen so that the effective rooting depth, above which 95% of root biomass stays, varies from
326 1m to 8m which is the possible range at the Soaproot site, as indicated by current knowledge of
327 the subsurface structure (see Klos et al., 2017). Note, here we refer to a higher proportion of
328 roots in deep subsurface layers as 'deep rooting' (e.g effective rooting depth = 8m; r_a=0.1,r_b=0.1)
329 as compared to 'shallow rooting' (e.g effective rooting depth = 2; r_a=1,r_b=5) which represents a
330 larger proportion of fine roots in upper layers (Figure 1a).

331 The safety-efficiency tradeoff of xylem has been widely discussed in the literature (e.g.
332 Gleason et al. 2016; Hacke et al. 2006, 2017; Martnez-Vilalta, Sala, and Piol 2004). Given that
333 we don't have any measurements that can be used to generate vulnerability curve at our study
334 site, we consult the literature (Domec et al. 2004, Barnard et al. 2011, Corcuera et al. 2011,
335 Anderegg and Hillerislambers 2016 , Baker et al. 2019, Kilgore et al. 2021) for observed curves

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

from sites that have as similar climate (e.g mean annual precipitation and temperature) and conifer species (P. Ponderosa) to our study site as possible and the values of xylem traits (K_{max} and $P50_x$) of Ponderosa pine in temperate regions of the TRY database (Kattge et al. 2020) to determine the two hypothetical vulnerability curves representing the safe/inefficient and unsafe/efficient xylem strategies. We set the parameters of the van Genuchten model to represent these two sets of P-V and vulnerability curves as showing in Fig1b and 1c. It is worth noting that with the same K_{max} and $P50$, the exact shape of the vulnerability can be different depends on the formula used and parameter values. However, this should not be an issue in our study because vulnerability curve is mainly constrained by P50 and Kmax. Second, given there is a large range of variation of the observed/measured values, the effect caused by the exact shape of the curves is minor. Third, since the objective of our study is not to accurately predict mortality, but rather to examine the effect of different combination of stoma, xylem, and root strategies, even if the shape of our vulnerability curve is not the most accurate, as long as the curve captures the overall pattern of the pressure-conductivity relation, it will not affect the relative outcome of this study.

We follow the theory of Skelton et al. (2015) to define safe vs. efficient stomatal strategy. In FATES-Hydro, there are two key stomatal parameters: $P50_{gs}$ and a_{gs}. Here, we only vary $P50_{gs}$ while keeping a_{gs} as a constant because the objective here is to choose the parameters that are relatively well understood and catch the safe vs. risky strategies as described by Skelton et al., rather than to exhaust the parameter space throughout the model. In essence, the different combinations of $P50_{gs}$ and the shape parameter (a_{gs}) can generate similar stomatal response curves. For example, a small negative $P50_{gs}$ with small a_{gs} would result in a flat stomatal response curve, which is similar to a large negative $P50_{gs}$ combined with a large a_{gs}. Further, $P50_{gs}$ is well understood and has more observed data, while a_{gs} is less studied and barely has any observed data. With a given a_{gs}, the variance of $P50_{gs}$ along a vulnerability curve controls the degree of embolism risk, from a 'risky' strategy, where $P50_{gs}$ equals to a lower P_{xylem}, to a 'conservative' strategy, where $P50_{gs}$ equals a higher P_{xylem}. The P_{xylem}s in Skelton et al.'s (2015) are for Fynbos species, therefore are not appropriate for our study because our species are pine trees, a woody plant. Trees have woody tissue which contribute to strengthen the conduits and make them less easy to collapse when embolized, hence allow their stomata to be riskier than herbaceous plants. From the observed $P50_{gs}$ and xylem traits of closely related pine species in the TRY database (Kattge et al. 2020) and elsewhere in the literature (Bartlett et al. 2016), as

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

well as the observed soil water potential at the study site, we choose to vary $P50_{gs}$ between $P50_{xylem}$ and $P20_{xylem}$, (correspondingly the point at which xylem have lost 50% and 20% of their maximum conductivity).

The emergent behavior of FATES or any model with dynamic ecosystem structure can make analysis of physiological rate variation difficult, as the stand structure will respond and thus also vary when parameters are changed. To overcome this complication, we use a reduced complexity configuration for running the model which we refer to as 'static stand structure' mode. In this mode, the stand structure is initialized from observed forest census data, and subsequently is fixed, i.e. the model does not permit plant growth or death to change the vegetation structure. This allows the direct assessment of hydraulic and physiological parameter variation in the model without the consequent feedback loops associated with varying ecosystem structure. The stand structure is initialized with census data from the CZ2 site (Table S1). Because this type of model configuration ignores prognostic plant mortality, in the interest of being able to compare across simulations where mortality rates might otherwise be very high, we use the loss of xylem conductivity as a measure of mortality risk of conifer trees at CZ2, which has widely been used as an indicator of drought mortality of forest (e.g. Hammond et al., 2019).

To force the model with an atmospheric upper boundary, we use the Multivariate Adaptive Constructed Analogs (MACA) climate data (Abatzoglou and Brown 2012) from 2008 – 2015 of a 4km x 4km grid covers the study area. The daily average MACA data are disaggregated to 3-hourly climate data (see Appendix S2 in Buotte et al. 2018 for detail) . To assess the credibility of model predictions, we compare the model to observations of gross primary productivity (GPP) and ET, both as inferred from eddy covariance (Goulden and Bales 2019). Here, we use the Latent Heat Flux (LH) is used as a proxy of ET.

3. Results

3.1 Impact on GPP and ET

The parameter sensitivity analysis shows that in a monthly-mean flux comparison, the simulations with deep roots give a better match to the overall observed pattern of GPP and ET (Fig. 2). The simulated transpiration contributes to 90% of the ET in general. The deep-rooted cases better capture the seasonality (e.g. the peak time) and the declining trend of observed GPP

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

396 from 2011 to 2015. The deep-rooted cases also match fairly well the observed ET. The simulated
397 GPP of shallow-rooted cases are higher than observed values during wet seasons (Dec. to Mar.),
398 but much lower than the observed values during dry season of the pre-drought period. The
399 simulated ET of shallow-rooted cases are overall lower than the observed values. To quantify
400 this assessment, we computed Root Mean Square Error (RMSE) from the hourly mean GPP and
401 ET of each month each year of all the 40 cases (Fig. S2). The RMSE of GPP and ET decreases
402 with effective rooting depth and P50gs for both xylem strategies (Fig. 3). The P50gs has less
403 impact on RMSE of GPP of the safe xylem than on that of the efficient xylem. In terms of GPP,
404 the effective rooting depth of 6.5m gives the best fit, as indicated by the darkest color (RMSE of
405 GPP = 1.12gC/m^2/s, RMSE of ET = 250 W/m^2), suggesting the importance of deep roots in
406 maintaining transpiration and photosynthesis during the dry season, as well as increasing the
407 relative decline in these fluxes during the drought.

408 Among the parameters we varied in the sensitivity analysis, the vertical root distribution
409 has the largest impact on GPP and ET at CZ2. Figures 2a-2b show the monthly mean GPP and
410 ET of the end members of the sensitivity analysis (see Fig. S1 for the complete set of outcomes).
411 Deep roots result in substantially higher GPP and transpiration during normal years (2011 and
412 2012). During long-term droughts, when deep soil moisture is depleted, the relative advantage of
413 deep roots over shallow roots is reduced. Shallow roots result in substantially lower GPP and
414 transpiration during the dry season (Aug. to Oct.), with seasonal maximum occurring earlier, in
415 May, as compared to July with the deep-rooted cases. The shallow-rooted cases also have much
416 lower GPP and ET during the dry seasons of the pre-drought period. During the late stage of
417 drought (2014 and 2015), the GPP and ET of the different cases become more similar between
418 the shallow- and deep-rooted cases.

419 The second set of parameters in importance to rooting depth for controlling carbon and
420 water fluxes is the stomatal strategy. The simulations with a more risky strategy ($P50_{gs}$=$P50_x$)
421 gives higher GPP and ET than the simulations with a safer strategy ($P50_{gs}$=$P20_x$) during pre-
422 drought periods and the early stage of the drought (2011 to 2013), but slightly lower GPP and ET
423 at the late stage of the drought (2014 and 2015) for the deep-rooted cases. However, risky
424 stomata gives slightly higher GPP and ET at all times for shallow-rooted cases. The xylem
425 strategy has the smallest effect on GPP and ET of the parameters we varied (e.g RMSEs of ET

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

are both around 260 W/m2 for safe and efficient xylem respectively, with P50gs = P20x and 8m effective rooting depth). In deep-rooted cases, the safe xylem and efficient xylem strategy result in almost the same GPP and ET, which can be seen via the widespread overlap between the dashed and solid lines in figure 1. In shallow-rooted cases, with safe stomata, safe xylem generates slightly higher GPP and ET than efficient xylem. In addition, how strong the effects of stomatal and xylem strategy also depend on the rooting depth. The deeper the effective rooting depth, the less significant the impacts of stomatal strategy (Fig. S1).

3.2 Impact on plant water status

We examine the impact of vertical root distributions, stomatal and xylem strategies on the seasonal variation of three plant physiologic variables that serve as indices of plant water stress (fig. 4): the fraction loss of xylem conductivity of stem (SFL), leaf water potential (LWP), and an overall absorbing roots water potential (AWP). In the model, absorbing roots in different soil layers have different water potentials, associated with the soil water potential of that layer. We calculate a cohort-level effective AWP as the root-fraction weighted average of water potential in absorbing root across all soil layers. In this way, the AWP represents the overall rhizosphere soil moisture condition that is sensed by the tree. These physiological variables are tracked for each cohort. For any given case, the differences in these variables among cohorts are negligible (Fig. S3). Therefore, we present the outcome of the cohort class with a diameter at breast height (DBH) between 50 – 60cm, the size class that is most abundant at CZ2.

Stomatal and rooting strategies together control the loss of xylem conductivity during the dry season of the pre-drought period and the whole period of the long-term drought (Fig 4a). In all cases, the xylem conductivity reaches a maximum during the wet season (Dec. to Jan.), starts to decline during the growing season (Apr. to Jun.), then reaches its minimum in the dry season. With the same stomatal strategy, deep roots lead to less loss of xylem conductivity than shallow roots. A deep rooting strategy is also able to maintain very little loss of xylem conductivity during the pre-drought period, but as deep soil moisture is depleted, this effect is reduced. With a shallow rooting profile, the xylem conductivity starts to decline earlier and the minimum is much lower than that of a deep rooting profile. For example, with risky stomata, the minimum fraction of xylem conductivity of deep-rooted cases at 2012 is 0.4, but is lower than 0.2 with shallow

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

roots. Unlike deep-rooted cases, in shallow-rooted cases, the seasonal variation of the loss of xylem conductivity does not differ too much during pre-drought and drought periods. During very late stage of drought, deep-rooted cases have a lower fraction of xylem conductivity than shallow-rooted cases (e.g. Jan. 2015).

In general, risky stomata cause a greater loss of xylem conductivity (K/Kmax) than safe stomata, but the extent depends on the vertical root distribution. The effect of the stomatal strategy is more obvious in shallow-rooted cases. Risky stomata combined with shallow roots results in increasing the duration of 50% loss of xylem conductivity, as well as the maximum loss of xylem conductivity during the dry season. With a deep rooting strategy, the difference in the percentage loss of xylem conductivity between safe stomatal and risky stomatal cases increases with the progression of the drought, but with a shallow rooting strategy this difference remains more or less the same over time. In addition, in 2011, a very wet year, with deep roots, a safe xylem strategy is able to maintain the maximum xylem conductivity even during dry season (Fig 4a). The impact of xylem strategy on the percentage loss of xylem conductivity is relatively weak. For both deep- and shallow-rooted cases, trees with safe xylem lose less xylem conductivity during the wet season but lose more conductivity during the dry season.

The safe stomata & safe xylem cases for both deep- and shallow-rooted trees experience greater declines in stem conductivity as compared to the safe stomata and efficient xylem for the corresponding rooting depths (Fig. 4a). This is because with safe stomata, trees operate at the right end of the vulnerability curve shown in fig. 1b, where the hydraulic conductivity of efficient xylem is much higher than that of the safe xylem. Thus, when transpiring the same amount of water, the efficient xylem will lose less water potential as compared to safe xylem. This keeps the xylem water potential of a plant with efficient xylem higher than one with safe xylem, and consequently also keeps the xylem conductivity, K, higher. This is also because we set $P50_{gs}$ based on P_{xylem}, thus the $P50_{gs}$ of safe stomata for plants with efficient xylem is higher (less negative) than that of plants with safe xylem, thus resulting in lower transpiration rates, which in term reduces the loss of xylem water potential. As a result, plants with both safe stomata and efficient xylem not only transpire less water but also lose less water potential per volume of water transpired. Together, these two mechanisms contribute to keep the xylem conductivity of the efficient xylem cases higher.

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

Stomatal, rooting, and xylem strategies have similar impacts on the seasonal variation of both leaf and fine root water potentials (Fig4c and 4d). Leaf and fine root water potentials peak during the winter, then start to decline in early spring and reach their lowest point in the dry season. Deep roots, safe stomata, and safe xylem traits all contribute to the maintenance of higher leaf and fine root water potentials during the growing and dry seasons. With deep roots, there is less difference in leaf and fine root water potential between stomatal and xylem strategies in the very wet year 2011. Plants that combine safe stomata and/or safe xylem with deep roots can keep the leaf and fine root water potentials relatively high (less than -5 Mpa) during the dry season of the drought period. However, while plants that combine risky stomata or efficient xylem with deep roots can keep the dry season leaf water potential above -5 Mpa during the pre-drought period, their traits lead to the dry season leaf water potential dropping below -8 Mpa or even below -10 Mpa during the drought period. In both deep-rooted and shallow-rooted cases, safe xylem leads to much lower leaf and fine root water potentials during the dry season. The seasonal and inter-annual variation of fine root water potentials are almost identical to the leaf water potential, except that the water potential of fine roots is slightly higher (~ 0.5 Mpa) than the leaf water potential.

3.3 Impact on subsurface hydrology

In the simulation outcomes, the vertical root distributions again have the largest impact on hydrologic processes and subsurface water content and the way that they change over the drought. With deep roots, there is less drainage loss from surface and subsurface runoff as compared to shallow roots, especially during the growing season (Figure 5a,c,e,g). The subsurface water content shows different vertical and temporal patterns between the cases with different vertical root distributions. In the deep-rooted cases, during the pre-drought period, the water content in the deepest layers fluctuates between wet and dry seasonally; during the first year of the drought, the water content of the deepest layers (6 to 8m) slightly increases during the wet season, but with the progression of the drought, the soil water content becomes consistently depleted in the middle and deep layers (between 5 and 8 m depth) and only the shallow layer (<0.16 m) water content increases during wet season. In the shallow-rooted cases (Figure 5b,d,f,h), soil moisture in the surface layers (top 2m) shows seasonal variation, but this seasonal

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

variation becomes weaker over depth and the soil moisture at 6-8m depth stays consistently high throughout the year during pre-drought period, and remains slightly low through the entire drought period; while the water content of the middle and upper layers of the shallow-rooted case have a similar pattern of seasonal variation before and during the drought.

Stomatal strategy, as quantified by $P50_{gs}$, has a weak impact on hydrologic processes and soil moisture. In both the deep- and shallow-rooted cases, riskier stomata lead to a slightly lower total subsurface water content (Figure 6a). The effect of $P50_{gs}$ is less significant during the pre-drought period for both the deep-rooted and shallow-rooted cases, and becomes more significant as the drought progresses. The effect of $P50_{gs}$ on total subsurface water content is less significant in shallow-rooted cases. Figure 5c shows the effect of $P50_{gs}$ on the water content of shallow and deep soil layers. In both the shallow- and deep-rooted cases, increasing $P50_{gs}$ has a negligible impact on the water content of the shallow layers during both the pre-drought and drought periods (Figure 5c left). For deeper layers, in the shallow-rooted case, $P50_{gs}$ has no impact on the water content at all times; in the deep-rooted cases, a risky $P50_{gs}$ results in lower dry season water content of deep layers (7-8m) during the pre-drought period (indicated by the red cycles of Figure 5a and 5c), but decreases the water content of those layers year round during the drought period (Figure 5a and 5e). In deep-rooted cases, safe stomata with efficient xylem lead to a slightly higher water content in deep layers (5m to 8m) during the pre-drought period, and in shallow layers (0 to 3m) during the drought period (Figure 6a). Risky stomata with safe xylem in deep-rooted cases are most effective in accessing soil water. Though the soil water contents are generally high in shallow-rooted cases, stomatal and xylem strategies show a similar impact on the soil water storage as those in the deep-rooted cases (Fig S4).

Simulations with deep roots have almost no loss of soil water to drainage during the dry season in normal years, or during the whole drought period; while with shallow roots, the drainage loss is high during the pre-drought period and decreases through the drought period, but still with some runoff even at the end of the drought period (Figure 6a). The observed total annual runoff from the 2008 to 2011 pre-drought period was about 250 mm/year, but was zero during the 2012 – 2015 drought period (from figure 4, Bales et al. 2018). This observed difference in runoff between the pre-drought (~290mm/year, 2011 - 2012) and drought periods (~0 mm/year) from the deep-rooted case is consistent with the predicted pattern. During the pre-

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

546 drought period, the wet season total subsurface water contents from Dec. to Feb. are similar
547 between the cases with deep and shallow roots, but during the dry season (from June to Sep.) the
548 total subsurface water content with shallow roots is substantially higher than the case with deep
549 roots (Figure 6b).

550 **4. Discussion**

551 4.1 Vertical root distribution as the first order control

552 The outcome of our simulations indicates that the vertical root distribution exerts the first
553 order control over both ecosystem level fluxes and plant physiology at CZ2. This dominance of
554 rooting strategy over other hydraulic traits is related to the nature of the rainfall pattern of the
555 Mediterranean-type climate of that region. The CZ2 site receives effectively all of its rain during
556 winter. This water is stored in the soil column and slowly released through the growing season.
557 The root zone soil moisture has strong seasonal variation, which constrains plant water use and
558 gas exchange as a function of the gradual drying of the soil column (Bales et al., 2018). In the
559 model, the stomatal behavior is controlled by the leaf water potential, which itself is strongly
560 affected by the root zone soil moisture. In our simulations, the daytime average leaf water
561 potential of a 55cm DBH cohort is well correlated with the fine root water potential and is
562 always about 0.5 Mpa lower (fig S5). This offset is consistent with the relationship between mid-
563 day leaf water potential and pre-dawn leaf water potential found by Martínez-Vilalta et al. (2014)
564 at the global scale.

565 With deep roots, trees use more subsurface storage capacity at the CZ2 site, and thus a
566 higher amount of total rainfall. In a wet year such as 2011, the root zone water potential of deep-
567 rooted trees is kept relatively high (Figure 4b) and the trees operate at the upper end of their
568 vulnerability curve through the year, with typical loss of conductivity < 10% (Fig 7). Therefore,
569 we don't see much effect of the stomatal strategy on GPP and transpiration in a wet year. At the
570 upper end of the vulnerability curve, stomata are fully open regardless of the stomatal strategy
571 (either to be safe or risky). When the drought began in late 2012, annual rainfall fell below the
572 total root zone storage, thus the deep storage remained depleted throughout the year. During the
573 drought, the deep-rooted trees were able to operate at the high end of the vulnerability curve in
574 the wet season, when the rainfall recharged the surface layer. As the surface layers dry, water

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

potentials then gradually falls to the lower end of the vulnerability curve; consequently the photosynthesis and transpiration start to drop as the dry season progresses. With risky stomata, trees can drive the soil moisture a little further down. This is why we see the difference in the effect on GPP and transpiration between different stomatal strategies during the dry season when the drought progresses.

With shallow roots, trees only use surface soil moisture storage. As a result, the surface water storage is quickly used up after the wet season, and the root zone water potential drops near the low end of the vulnerability curve during the dry season. Thus, the shallow-rooted trees operate along the full extent of the vulnerability curve year-round, both during the pre-drought and drought periods. Therefore, as for the deep-rooted cases, we don't see a strong effect of stomatal strategy on GPP and transpiration during the wet season, but unlike the deep root cases, the effect of stomatal strategy on GPP and transpiration during the dry season can be seen throughout the whole simulation period.

Rooting strategies greatly control the spatial pattern of vertical soil water content (Figure 5). With deep roots, the vertical soil moisture variation is more homogeneous due to the extensive root distribution. With shallow roots, soil becomes extremely dry at the surface (<1m) and extremely wet in deep layers (>5m) resulting from the aggregated root distribution at upper layers. Our finding is similar to a recent study conducted by Agee et al. (2021), where the authors found that the extensive lateral root spreading results in homogeneous soil moisture distribution. The homogeneous soil moisture pattern may contribute to a more energy efficient system that reduces plant water stress (Agee et al. 2021) because that minimizes the energy dissipation loss through water transport (Hildebrandt et al. 2016). Both Agee et al (2021) and our studies emphasize the importance of the means by which the root distributions determine how the subsurface storage is utilized.

Given the shape of the vulnerability curves, in all these simulations, plants will stop transpiring when their leaf water potential reaches around -10Mpa with efficient xylem or -15Mpa with safe xylem, depending on their stomatal strategy (Fig 7). Because we are here holding the stand structure and leaf area constant to allow comparison between cases, the simulated leaf water potential of the shallow rooted, risky stomata combination can get as low as -15Mpa (Figure 4b) during dry seasons even during pre-drought period, which is well below the

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

lowest possible leaf water potential observed (-10Mpa) (Vesala et al., 2017). Leaves will likely be wilted before the water potential drops below -10Mpa and the tree would have already shed the leaves due to canopy desiccation. But we specifically do not permit that to occur in these simulations, so as to keep the different cases comparable. Although it might be unrealistic, the leaf water potential can serve as an indicate of the degree of canopy desiccation. With no or very little leaf, trees would rely on the storage carbon to support respiratory demand until the wet season comes to regrow leaves. Depending on the duration of the dry season, trees may exhaust the stored carbon and die from carbon starvation. Risky stomata can generate higher GPP (Figure 1a), but also result in longer duration of more negative leaf water potential (Figure 4b). This suggests that shallow rooted pines at CZ2 with risky stomata will benefit from allocating more net primary productivity to their storage pools rather than growth in order to reduce the carbon-starvation mortality. Therefore, even though the model generates unrealistically low leaf water potentials, the extent and the duration of the simulated very low leaf water potential allows us to gain some insight on the interaction of plant hydraulic strategy and the life history strategy of conifer trees under a Mediterranean-type climate.

In this simulation, the impacts of xylem traits on GPP and ET are weak and subtle. This is the result of the relative position of the two vulnerability curves, in particular, the intersection of the two vulnerability curves in absolute conductivity. When the absolute conductivity is plotted as a function of pressure (fig. 1b and solid lines in fig. S6), it can be seen that, on the left side of the intersection, the safe xylem is not only safe but also efficient, and a safety-efficiency tradeoff of xylem thus only occurs on the right side of the intersection point. Therefore, in shallow-rooted cases, when the root zone water content—and hence plant water status—is low, safe xylem can generate slightly higher GPP and ET than unsafe xylem. Furthermore, the two pressure-conductivity curves diverge mainly at the wet end (corresponding to the wet season). This is likely because the xylem structures of conifers are very similar, and the range of variation of xylem traits in the sensitivity analysis are limited to the dominant species at the site. Therefore, the difference in the xylem traits of conifers do not cause significant impacts on the ecosystem level fluxes under the Mediterranean-type climate of CZ2, where the ecosystem fluxes are constrained by energy during the wet season (Goulden et al., 2012). In addition, the maximum rate of GPP and ET are co-constrained by the stand density, the total leaf area, the maximum stomatal conductance, and VPD. In this study, we used the static stand structure mode of

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

636 FATES-Hydro, whereby the stand density and the total leaf biomass (so as total leaf area) of the
637 trees are held constant. This further limits the effect of xylem traits on GPP and ET.

638

639 4.2 Balancing productivity and mortality risk

640 The hydraulic traits that contribute to high carbon fixation rates often make trees more
641 susceptible to drought. Stomatal strategy ($P50_{gs}$) can have both positive and negative impact on
642 the trees, creating a tradeoff in the balance between productivity and physiological stress. The
643 risky stomata ($P50_{gs} = P50_x$) can generate higher GPP but also result in a greater loss of xylem
644 conductivity and lower leaf water potential. The tradeoff varies depending on the plant's root
645 strategy—i.e. having a deep vs. a shallow root distribution—and the moisture state.

646 To better understand the tradeoff between productivity and mortality risk, we plot the
647 simulated annual average GPP against the fraction of conductivity (K/Kmax) of a 55cm DBH
648 cohort for two scenarios: deep roots (Fig. 8a) and shallow roots (Fig. 8b), with different
649 combination of xylem and stomatal strategies. In both scenarios, for each pair of xylem and
650 stomatal strategies, the GPP per tree increases almost linearly with the K/Kmax. But, with
651 increasing the safety of the stomata, the GPP declines faster with loss of conductivity. This
652 response is stronger in deep-rooted scenarios. Efficient xylem only slightly increases the
653 steepness of the lines. The stomatal strategies thus represent points along a gradient of the
654 tradeoff between growth and mortality risk - the safer the stomata, the more GPP is traded for
655 reducing the mortality risk.

656 Along this tradeoff space, where trees can maximize their net carbon gains likely depends
657 on the xylem traits. Studies have shown that trees may temporarily lose xylem conductivity
658 during mild drought, which can recover once the soil water becomes available. However, under
659 an extreme drought, their xylem could collapse and permanently damage the xylem conduits. In
660 this case, trees rely on new sapwood growth to support the transpiration (Brodribb et al. 2010,
661 Anderegg et al. 2013). At one extreme, if the stomatal behavior is too safe, it will give low GPP
662 and the tree will be outcompeted for light due to faster-growing neighbors, but at the other
663 extreme, if the stomata behave very aggressive (risky), it will give high GPP but also empty the
664 subsurface storage quickly, consequently leading to a prolonged dry period of soil moisture. This

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

665 would lead to substantial xylem damage (and/or root death), and then the carbon needed to grow
666 new sapwood (or roots) can exceed the benefit of getting the additional GPP. So, the optimal
667 location along the gradient would probably be located slightly below the K/Kmax associated
668 with that critical xylem water potential. Currently, the xylem refilling and associated carbon cost
669 are not incorporated in the FATES-Hydro. These two processes should be implemented in the
670 model to better understand the water-carbon balance.

671 In the deep-rooted scenario, the values of the pre-drought period and early drought stage
672 are clustered at the upper-right corner, above K/Kmax of 0.6. (Fig. 8a). In this region, the stress
673 from the loss of xylem conductivity likely won't be high enough to cause severe consequences, if
674 using 50 percent loss of xylem conductivity as the threshold for mortality and/or permanent
675 xylem damage. The deep-rooted tree can thus benefit by trading less GPP for maintaining xylem
676 conductivity with a risky/more-productive stomatal strategy during normal years. But, during the
677 late stage of the drought (2014 and 2015), the conductivity values become much lower. If this
678 mega drought stopped earlier, e.g. if it were a mild drought that only lasted for two years, the
679 additional GPP obtained from risky stomata may overweight the carbon cost for repairing xylem
680 damage. This suggests that, if the 2012 – 2015 drought was not common in California, natural
681 selection might favor the risky/more-productive stomatal strategy for deep-rooted trees.
682 However, this same strategy also exposes trees to high mortality risk under severe droughts.

683 In the shallow-rooted case (Fig. 8b), the values are all clustered lower and to the left, as
684 compared to deep rooted scenario, irrespective of the drought status. Thus, for shallow roots,
685 risky/more-productive stomatal behavior results in a similarly high mortality risk during both the
686 pre-drought and drought period. Thus, under the long-term climate conditions seen at CZ2,
687 whether or not severe droughts were frequent, the only shallow-rooted trees that could persist
688 would have to follow the safe and less-productive stomatal strategy. And, this safe and less-
689 productive stomata also protects the shallow-rooted tree plant from mortality risk during drought.

690 The model outcome indicates that under drier root zone soil conditions, if pines were to
691 follow a shallow rooting strategy, they would benefit from a safer stomatal strategy, with more
692 conservative water use; but if they follow a deep rooting strategy, pines would benefit from
693 riskier stomata. This is consistent with Anderegg et al.'s (2016) finding on the relative stomatal
694 conductance (gs) across elevation. They found that at low elevation (lower precipitation) site,

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

Ponderosa pine has lower relative stomatal conductance and less loss of %xylem conductivity, equivalent to safer stomata in our study, while at mid elevation (higher precipitation) site, pine has higher relative stomatal conductance and more loss of %xylem conductivity, equivalent to risky stomata in our study. The simulation results are consistent with the idea that the CZ2 region is dominated by deep-rooted trees. This is supported by previous studies. In situ measurements of regolith structure (particular the porosity) indicates that at CZ2, there is a layer of thick semi-weathered bed rock that allow the trees to grow deep roots (Holbrook et al., 2014). Growing deep roots to access rock moisture to support plant water use has also been observed in the Eel River CZO catchment (Rempe et al., 2018), another Mediterranean-type ecosystem along the west coast. Observed net CO_2 exchange and ET during the pre-drought period suggest that during a wet year, deep moisture supported summer transpiration and productivity when the upper layer moisture was low (Goulden et al. 2015). Because the deep rooting strategy is sufficient in most cases to avoid the main effects of dry seasons and short droughts, and that, conditional on having deep roots, the risky stomatal strategy confers a productivity advantage at little increased risk of vulnerability, then we would expect that plants with these traits would dominate. However, under extreme cases such as the 2012 - 2015 drought, which ranked as one of the most severe in California in the last 1200 years (Lu et al. 2019), we would expect that plants with this deep-rooted, risky stomatal strategy would be highly vulnerable to drought, which is consistent with the ~90% mortality of the pine observed at CZ2 during the drought (Fettig et al. 2019). The water balance of the catchment based on the long-term observation from precipitation, stream flow, and ET (Bales et al. 2018, Goulden and Bales 2019) also support that it was the slow depletion of deep moisture that caused tree mortality in late stage of the prolonged 2012 – 2015 drought.

The finding of our study indicates that the future drought mortality would likely occur in the ecosystems which are co-limited by water and other factors. In those ecosystems, trees can benefit from having more efficient but less safe hydraulic traits, which allow them to be more competitive for water, and bring in higher GPP. The extra carbon gain can be used to develop measures to deal with other constraining factors, such as increase storage carbon to lower the risk of carbon starvation, or build thicker bark to resist fire, and to grow more roots which further enhance their capacity to compete for water.

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

5. Conclusions

Our analysis indicates that, in a Mediterranean-type climate where the supply of energy and water is desynchronized and accessible subsurface water storage capacity is close to annual precipitation, deep roots combined with risky stomata represent a beneficial strategy for high productivity in normal years, but exposes trees to high mortality risk during multi-year droughts. While such a strategy enables trees to fully utilize subsurface storage and precipitation for productivity over the regular years, the lack of deep water storage recharge during droughts exposes trees to high drought stress and makes this strategy unfavorable under severe and prolonged drought. In contrast, shallow roots combined with safe stomata represent a strategy for drought resistance, albeit at the cost of considerably reduced productivity, as such a combination only allows trees to use shallow subsurface storage while leaving deep moisture untouched, thus less precipitation is used for productivity. But this strategy leaves trees to be less susceptible to drought-induced mortality should the deep reservoir be depleted. These results suggest that stomatal strategy is controlled by root zone soil moisture and regulated by root distribution in that region. Thus, our study underscores the importance of considering plant rooting and hydraulic strategies within the larger context of plant ecological strategies.

Author contribution

JD and CDK design the study and write the MS. JD conducted the simulation. PB, RB, MG provided model input data. BC, CDK, RF, RK, CX wrote the code. PB, RB, BC, RF, MG, RK, LK, JS, CX edited the MS. CDK provided the funding

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Data availability statement

The FATES code (branch FATEScodeforMS1), parameter files and data that support the findings of this study are openly available at ZENODO: https://zenodo.org/account/settings/github/repository/JunyanDing/Rooting-and-Hydraulic-

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Preprint. Discussion started: 16 February 2023

strategy-of-pine-at-Sierra-CZ2- (DOI 10.5281/zenodo.5504405). The flux tower data can be retrieved from the UC Merced online database (https://www.ess.uci.edu/~california/).

Competing interests

The authors declare no conflict of interest

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1012 **Tables**

1013 **Table 1 Parameters used in FATES-Hydro sensitivity analysis**

1014

Parameters	Biological meaning	Values	Units
r_a, r_b	Root distribution: shallow roots vs. deep roots	(0.1, 0.1) – (2 5)	unitless
$P50_{gs}$	Leaf xylem water potential at half stomatal closure stomatal control on safety vs. efficiency	P50x – P20x	Mpa
$P50_x$	Xylem water potential when xylem loss half of the conductance	-3.0[a], -4.8[b]	Mpa
K_{max}	Maximum xylem conductivity per unit sap area	0.88[a], 0.64[b]	kg/MPa/m/s
A	Shape parameter of van Genuchten hydrologic function	0.11855[a], 0.088026[b]	Mpa^{-1}
m, n	Shape parameters of van Genuchten hydrologic function	(0.8, 1.25)[a], (0.8, 1.5)[b]	unitless

1015 a: values for efficient/unsafe xylem
1016 b: values for inefficient/safe xylem

1017

Table 2. List of major parameters

Symbol	Source code name	Value	Units	Description	Source
a_{gs}	fates_hydr_avuln_gs	2.5	unitless	shape parameter for stomatal control of water vapor (slope)exiting leaf	Christoffersen et al., 2016
χ	fates_hydr_p_taper	0.333	unitless	xylem taper exponent	Christoffersen et al., 2016
$\pi_{o,l}$, $\pi_{o,s}$, $\pi_{o,r}$	fates_hydr_pinot_node	-1.47, -1.23, -1.04	MPa	osmotic potential at full turgor of leaf, stem, root	Christoffersen et al., 2016
$RWC_{res,l}$, $RWC_{res,s}$, $RWC_{res,r}$	fates_hydr_resid_node	0.25, 0.325, 0.15	proportion	residual fraction of leaf, stem, root	Christoffersen et al., 2016
$\Theta_{sat,x}$	fates_hydr_thetas_node	0.65	cm^3/cm^3	saturated water content of xylem	Christoffersen et al., 2016
SLA_{max}	fates_leaf_slamax	0.01	m^2/gC	Maximum Specific Leaf Area (SLA)	TRY
SLA_{top}	fates_leaf_slatop	0.01	m^2/gC	Specific Leaf Area (SLA) at top of canopy, projected area basis	TRY
$V_{cmax,25,\ top}$	fates_leaf_vcmax25top	55	umol $CO2/m^2/s$	maximum carboxylation rate of Rub. at 25C, canopy top	TRY
b_{opt}	fates_bbopt_c3	10000	umol $H2O/m^2/s$	Ball-Berry minimum leaf stomatal conductance for C3 plants	Calibrated

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

Figures

Figure 1

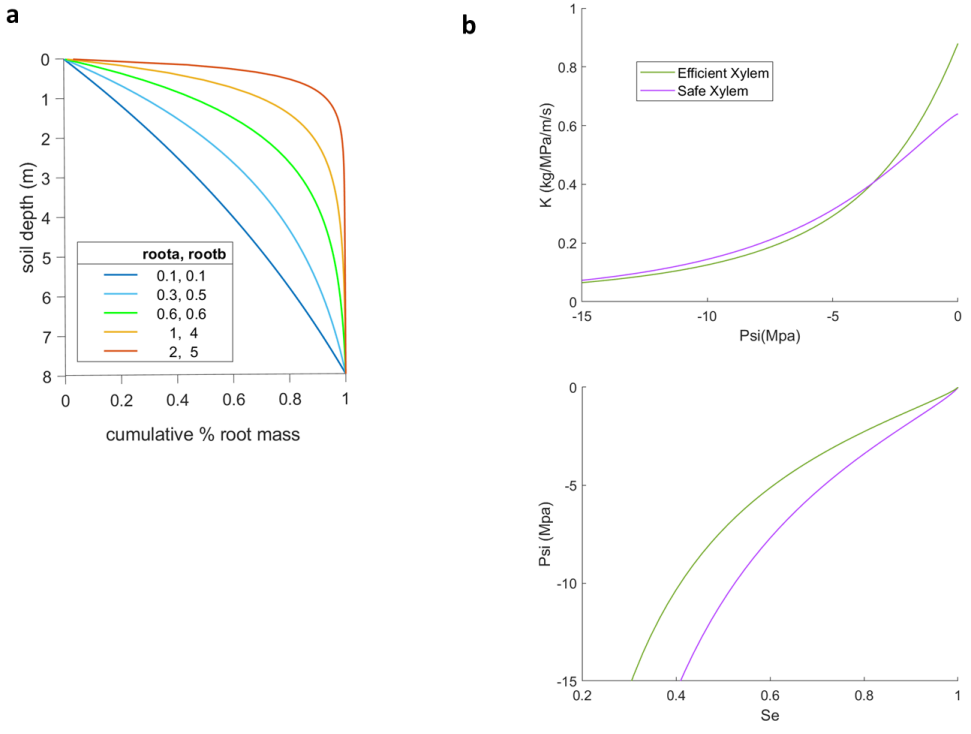

Figure 1. Sensitivity analysis set up for: a) root parameters that give five root distribution scenarios with effective rooting depths of 1m, 3m, 5m, 6.5m, and 8m , and b) two xylem scenarios for safe xylem (P50x=-4.8, Kmax=0.64), and efficient xylem (P50x=-2.5, Kmax=0.88).

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

Figure 2

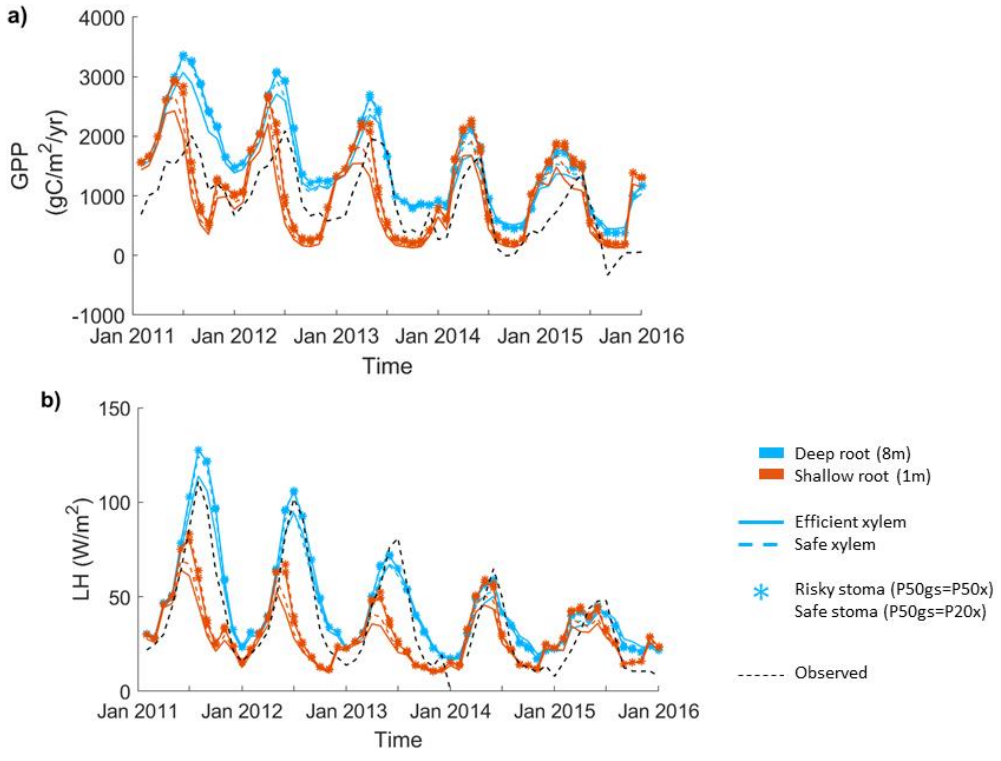

Figure 2. Impact of hydraulic strategies on ecosystem water and energy fluxes: a) monthly mean gross primary productivity, and B) monthly mean latent heat flux, of the end member cases.

https://doi.org/10.5194/bg-2023-16
Preprint. Discussion started: 16 February 2023

Figure 3

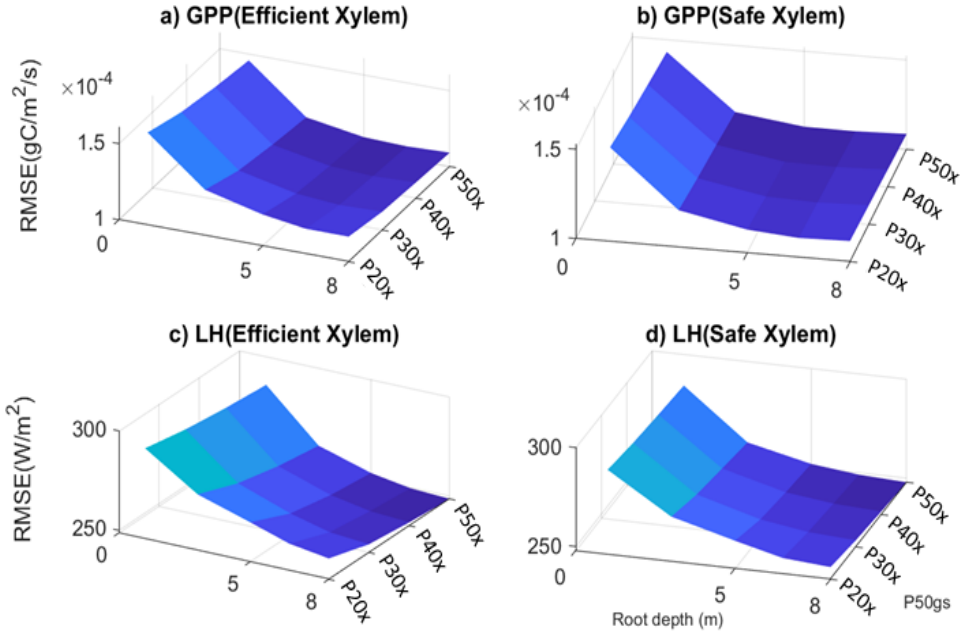

Figure 3. Root mean square error of GPP (a-b), and latent heat flux (c-d) with respect to variation in input parameters.

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Preprint. Discussion started: 16 February 2023

Figure 4

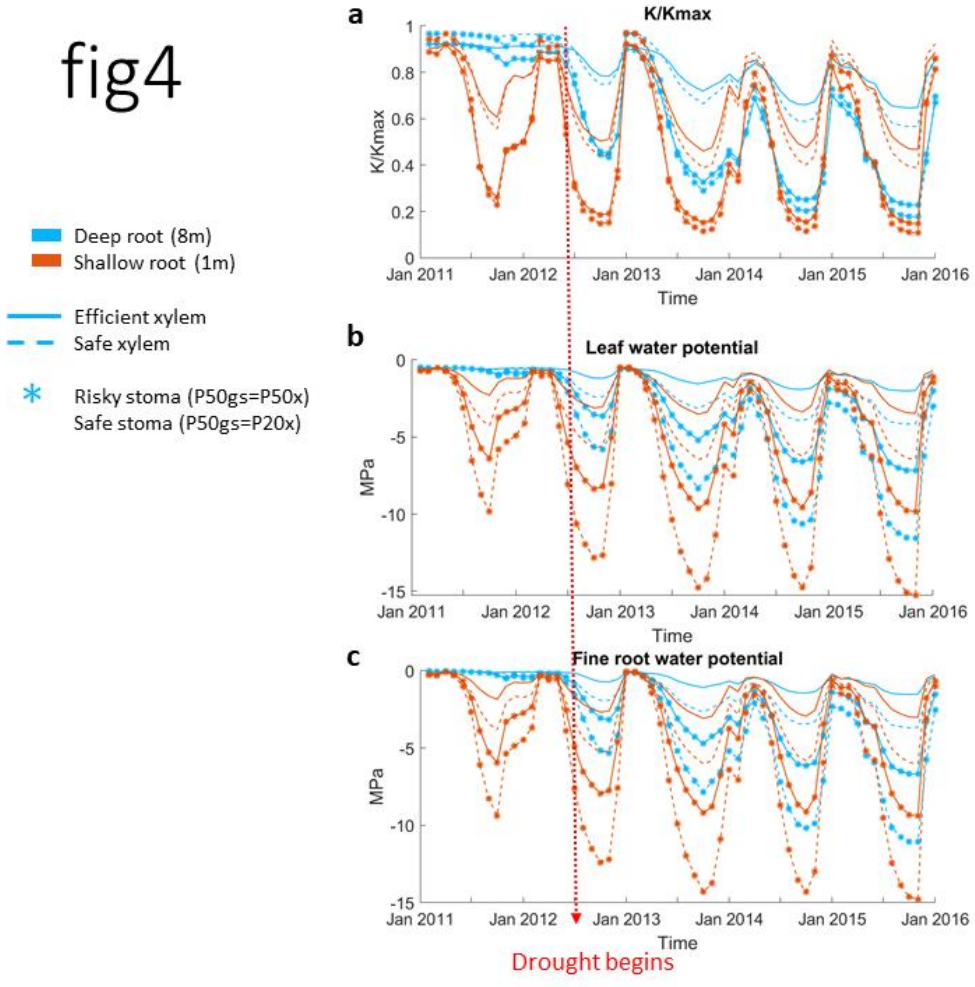

Figure 4. Seasonal and inter-annual variation of plant physiologic characteristics: a) monthly mean stem fraction of conductance K/K_{max} (a), monthly mean leaf water potential, and c) monthly mean overall absorbing roots water potential, of the 55cm DBH cohort throughout the 2011-2015 period.

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Preprint. Discussion started: 16 February 2023

Figure 5

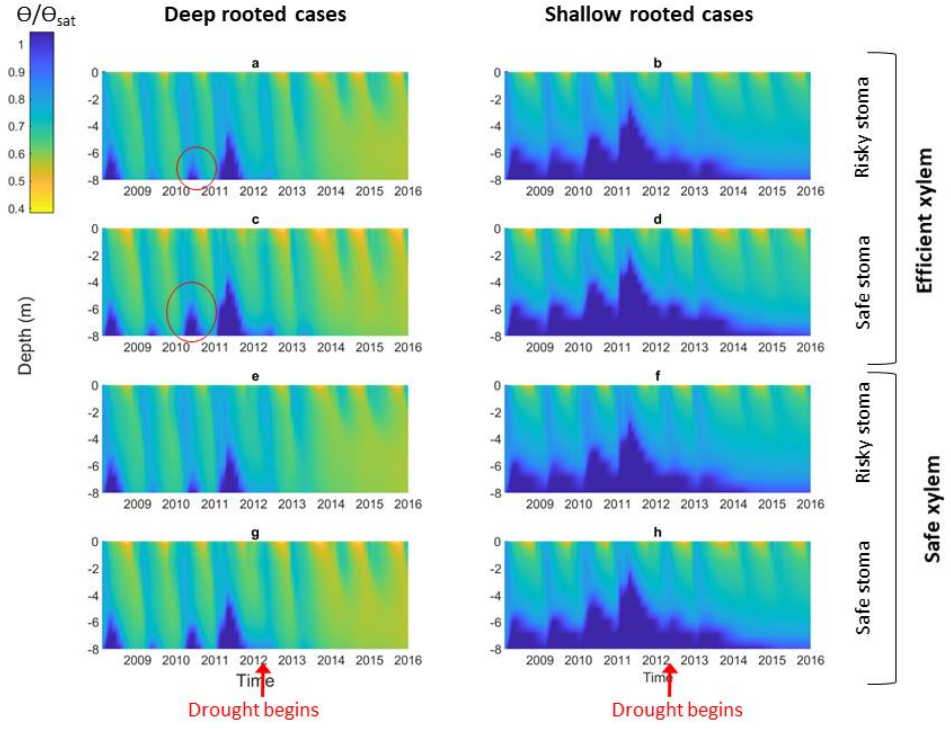

Figure 5. Impact of different combination of rooting depth, xylem and stomatal traits on soil moisture; left column shows deep rooted cases with a) efficient xylem and risky stoma, c) efficient xylem and safe stoma, e) safe xylem and risky stoma, g) safe xylem and safe stoma. Right column shows shallow rooted cases with b) efficient xylem and risky stoma, d) efficient xylem and safe stoma, f) safe xylem and risky stoma, h) safe xylem and safe stoma; red cycle highlights the effect of stomatal traits on deep water storage during the wet season of the pre-drought period

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Figure 6

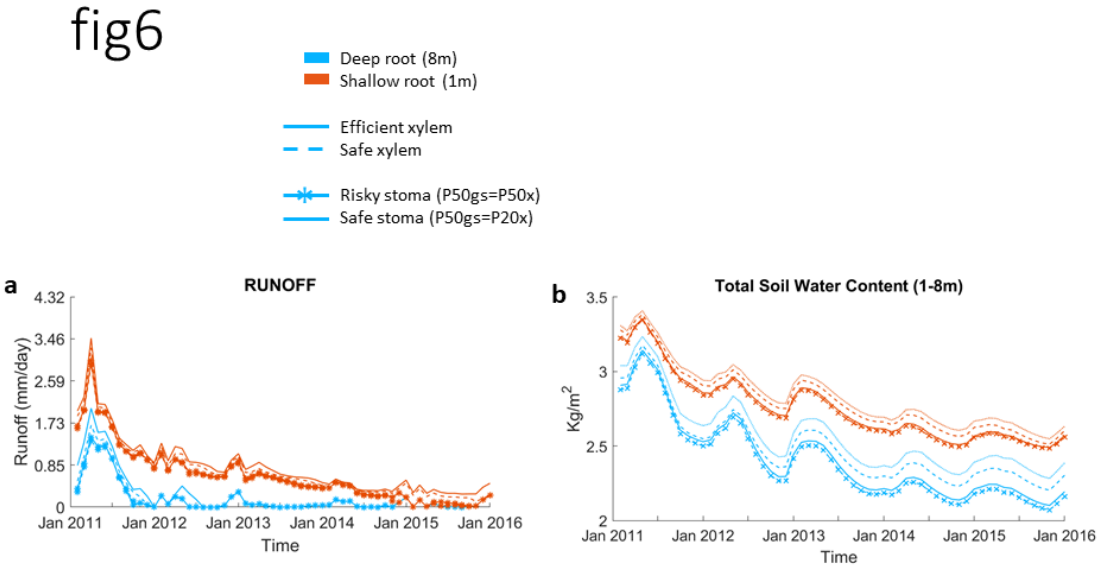

Figure 6. Impact on hydrologic processes: a) mean monthly total runoff, and b) monthly mean total soil water content of the entire soil column.

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Figure 7

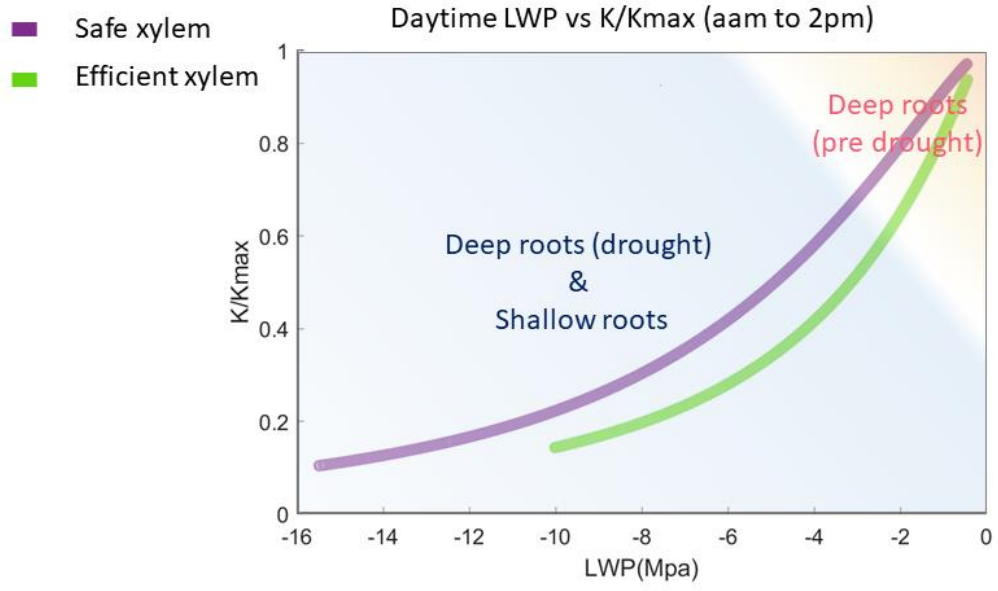

Figure 7. Simulated leaf water potential and fraction loss of conductivity (K/Kmax) of all the cases, which follow the two vulnerability curves.

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Figure 8

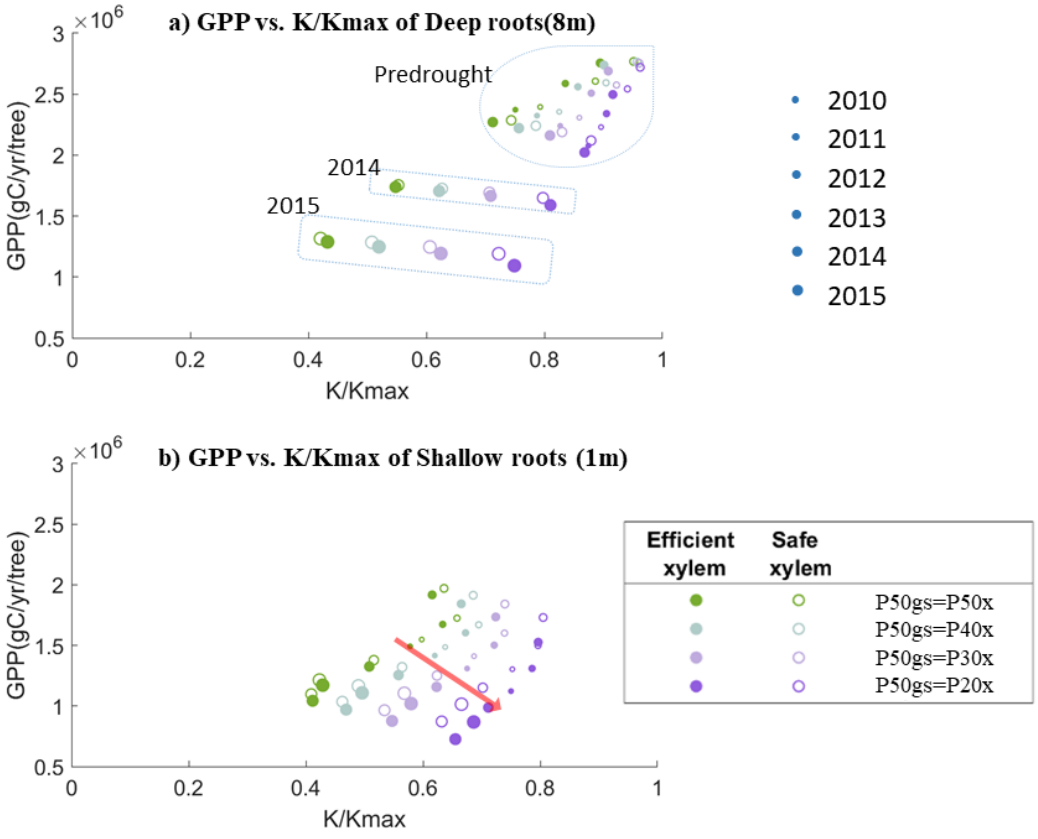

Figure 8. Simulated average annual GPP and fraction of conductance of a 55cm DBH cohort with a) deep roots (effective rooting depth= 8m) and b) shallow roots (effective rooting depth= 1m).