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

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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.

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 hydraulic 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.

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).

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

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

species in a particular region, the 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 a clear safety-efficiency tradeoff across 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, studied, and quantified. These traits include the rooting depth, the root to shoot ratio, the vertical and lateral distribution of roots, and the fine root density and diameter , 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 (ET) 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 for 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 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

149 also characterized by the highest forest productivity along an elevation gradient from foothill
150 woodlands to subalpine forest (Kelly and Goulden 2016). This leads us to ask whether strategies
151 associated with high productivity have exposed trees to high mortality risk under prolonged
152 drought.

153 Specifically, here we use the Functionally Assembled Terrestrial Ecosystem Simulator, in
154 a configuration that includes plant hydraulics (FATES-Hydro), to explore the tradeoffs
155 associated with differing hydraulic strategies, and in particular their implications for plant
156 productivity and risk of drought-induced mortality. We conduct a sensitivity analysis, using
157 FATES-Hydro in comparison with observations from the CZ2 eddy covariance site, to
158 investigate how stomatal, xylem and rooting strategies affect the ecosystem and physiologic
159 processes of the forest, and whether that may explain the high rates of both productivity and
160 drought-associated mortality of conifers at CZ2. We note that this is not an exhaustive
161 model parameter sensitivity study. T he main purpose is to use a sensitivity analysis to
162 explore scientific questions around hydraulic trait tradeoffs.

163 **2. Methods**

164 2.1 Study site

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

174 Soils at the Soaproot site are mainly of the Holland (fine-loamy, mesic Ultic Haploxeralfs)
175 and Chaix (coarse-loamy, mesic Typic Dystroxerepts) series, which are representative of soils
176 across a similar elevation band of the western Sierra Nevada (Mooney and Zavaleta 2003). Soils
177 of the Holland series have sandy loam surface texture and underlying Bt horizons with sandy

clay loam textures, while soils of the Chaix series have sandy loam textures throughout the profile. The regolith depth is estimated to be 15m (Holbrook et al., 2014). The total porosity over the whole regolith depth of the site is estimated to be 1620 mm and the total available storage porosity (plant accessible water storage capacity), which is the difference in volumetric water 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 (GPP) 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 at 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. In the model, multiple cohorts grow on the same land unit, share the soil water, and interact with each other through light competition. 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), is coupled to the existing photosynthesis

and soil hydraulic modules. FATES-Hydro is described in more detail by Xu et al., (in review, https://doi.org/10.5194/egusphere-2023-278) and its supplementary material.

Conceptually, plant hydraulic models can be broadly grouped into two types. The first group represents the plant hydraulic system as analogous to an electrical circuit (e.g. Mackay et al. 2011, Huang et al. 2017, 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 and the transpiration from plants at any given time step is considered to come directly 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 various 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

234 regolith depth. The vertical root distribution affects water uptake by the hydrodynamic model by
235 distributing the total amount of root, and thus root resistance, through the soils.

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

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

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

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

240

241 where E is the total transpiration of a tree, LA is the total leaf area (m^2), J is the transpiration per
242 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
243 specific humidity(kg kg^{-1}), q_s is the atmosphere specific humidity (kg kg^{-1}), g_s is the
244 stomatal conductance per leaf area, r_b is the leaf boundary layer resistance(s m^{-1}), w is a
245 scaling coefficient (unitless), which can vary between 1 and 7, and here we use a value of 3;
246 LWP is the leaf water potential (Mpa), V_{H2O} is the molar volume of water (18×10^{-6} m^3 mol^{-1}), R
247 is the universal gas constant, and T is the leaf temperature (K).

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

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

252

253 where ρ_w is the density of water; z_i is the height of the compartment(m); z_{i+1} is the height
254 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^{-1} m^{-1} s^{-1}). 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 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:

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

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

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.

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):

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

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 ($\mu mol\ CO2\ m^{-2}\ s^{-1}$) 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):

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

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.

2.2.2 Sensitivity analysis and Parameterization

The goal of this analysis is to better understand how coordinated aboveground and belowground hydraulic traits determine plant physiological dynamics and the interplay between ecosystem fluxes and tissue moisture during the extreme 2012-2015 drought at the Soaproot site. We thus conduct a global sensitivity analysis on selected hydraulic parameters to explore the linkages of aboveground and belowground hydraulic strategies. We use a full-factorial design for the parameter sensitivity analysis in order to best investigate the relationships between parameters. Because this design requires a relatively small set of parameters or groups of parameters to vary, we chose parameters that represent the major axes of relatively well-understood stomatal, xylem and rooting mechanisms/strategies that control the hydraulic functioning of trees. We set the values of these parameters within the realistic (allowable biological) range based on online database, and literatures where the species and physical environment are as close to our system as possible. We list other major parameters and their estimates that are not varied in the sensitivity analysis (table 2). We acknowledge that the biggest disadvantage of this study is the lack of sufficient field data to constrain the model. This is a result of using a natural drought as an experiment of opportunity, which because it was not

anticipated, did not allow for as coordinated planning as would be the case in an experimentally-manipulated drought. The trees at that site had all died by the time we started this study.

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

The safety-efficiency tradeoff of xylem has been widely discussed in the literature (e.g. Gleason et al. 2016; Hacke et al. 2006, 2017; Martnez-Vilalta, Sala, and Piol 2004). Given that we don't have any measurements that can be used to a generate vulnerability curve at our study site, we consult the literature (Domec et al. 2004, Barnard et al. 2011, Corcuera et al. 2011, Anderegg and Hillerislambers 2016 , Baker et al. 2019, Kilgore et al. 2021) for observed curves from sites that are as similar both in climate (e.g mean annual precipitation and temperature) and in the set of conifer species (P. Ponderosa) to our study site as possible, as well as 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 shown in Fig1b and 1c. It is worth noting that with the same K_{max} and $P50$, the exact shape of the vulnerability can differ depending on the formula used and parameter values. However, this should not be an issue in our study because the vulnerability curve is mainly constrained by P50 and Kmax. Second, given that there is a large range of variation in the 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 to catch the safe vs. risky strategies as described by Skelton et al., rather than to exhaust the parameter space within 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 $P50_{gs}$ for a given Pxylem value, controls the degree of embolism risk, from a 'risky' strategy, where $P50_{gs}$ is equals to or lower than P_{xylem}, to a 'conservative' strategy, where $P50_{gs}$ is higher than 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 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. Here, we wanted to first understand the direct trait control in the absence of structural differences. To overcome complication of the dynamic structure, we use a reduced complexity configuration for running the model which we refer to as 'static stand structure' mode. To investigate dynamic competitive effects when growth and mortality will be the next step. 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) and thus includes multiple cohorts of different sized trees. 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) . We set the initial soil water content to be 75% of saturated water content, close to field capacity. We believe this is a realistic value because the model is initialized in January, when the study area has high precipitation and trees are all in a dormant status, and in a year when there is not drought. We also tried to initialize the soil with higher water content (e.g. saturation), but did not find any differences, as the extra water drained quickly in the winter when transpiration is low.

3. Results

3.1 Sensitivity of GPP and ET to parameter perturbations

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 from 2011 to 2015. The deep-rooted cases also match fairly well the observed ET. The simulated GPP of shallow-rooted cases are higher than observed values during wet seasons (Dec. to Mar.), but much lower than the observed values during dry season of the pre-drought period. The simulated ET of shallow-rooted cases are overall lower than the observed values. To quantify this assessment, we computed Root Mean Square Error (RMSE) from the hourly mean GPP and

ET of each month each year of all the 40 cases (Fig. S2). We choose RMSE as it is a common and compact metric of assessing model performance, though we note that other metrics could in principle be used, each of which has different advantages and disadvantages (e.g. Collier et al., 2018). The RMSE of GPP and ET decreases with both effective rooting depth and P50gs for both xylem strategies (Fig. 3). The P50gs has less impact on the RMSE of GPP for the case with safe xylem than on that of the case with efficient xylem. In terms of GPP, the effective rooting depth of 6.5m gives the best fit, as indicated by the darkest color (RMSE of GPP = 1.12gC/m^2/s, RMSE of ET = 250 W/m^2), underscoring the importance of deep roots in maintaining transpiration and photosynthesis during the dry season, as well as the role of deep roots in increasing the relative decline in these fluxes during the drought.

Among the parameters we varied in the sensitivity analysis, the vertical root distribution has the largest impact on GPP and ET at CZ2. Figures 2a-2b show the monthly mean GPP and ET of the end members of the sensitivity analysis (see Fig. S1 for the complete set of outcomes). We acknowledge that the variation in rooting depth across the ensemble is large, but point out that so is uncertainty in plant rooting depth, and moreover that the uncertainty in rooting depth is less well-quantified than other plant traits such as P50, such that this wide variation reflects a real and deep uncertainty in plant rooting profiles. Deep roots result in substantially higher GPP and transpiration during normal years (2011 and 2012). During long-term droughts, when deep soil moisture is depleted, the relative advantage of deep roots over shallow roots is reduced. Shallow roots result in substantially lower GPP and transpiration during the dry season (Aug. to Oct.), with seasonal maximum occurring earlier, in May, as compared to July with the deep-rooted cases. The shallow-rooted cases also have much lower GPP and ET during the dry seasons of the pre-drought period. During the late stage of drought (2014 and 2015), the GPP and ET of the different cases become more similar between the shallow- and deep-rooted cases.

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

strategy has the smallest effect on GPP and ET of the parameters we varied (e.g., RMSEs of ET are both around 260 W/m^2 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 wides 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, the strength of 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 Sensitivity of plant water status to parameter perturbations

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 root 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 differently-sized cohorts are negligible (Fig. S3). Therefore, we present the outcome of all cohorts 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-extreme loss of xylem conductivity than shallow roots. A deep rooting strategy is also able to maintain xylem conductivity with very little seasonal loss 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 in 2012 is 0.4, but is lower than 0.2 with shallow 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 the very late stage of the drought, deep-rooted cases have a lower fraction of xylem conductivity than shallow-rooted cases (e.g., in Jan. 2015).

In general, risky stomata allow 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 result 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.

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 Sensitivity of subsurface hydrology to parameter perturbations

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

4. Discussion

4.1 Vertical root distribution as the first order control

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

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

598 drought, the deep-rooted trees were able to operate at the high end of the vulnerability curve in
599 the wet season, when the rainfall recharged the surface layer. As the surface layers dry, water
600 potential then gradually falls to the lower end of the vulnerability curve; consequently the
601 photosynthesis and transpiration start to drop as the dry season progresses. With risky stomata,
602 trees can drive the soil moisture to lower values . This is why we see the difference in the
603 effect on GPP and transpiration between different stomatal strategies during the dry season when
604 the drought progresses.

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

613 Rooting strategies greatly control the spatial pattern of vertical soil water content (Figure
614 5). With deep roots, the vertical soil moisture variation is more homogeneous due to the
615 extensive root distribution. With shallow roots, the soil becomes extremely dry at the surface
616 (<1m) and extremely wet in deep layers (>5m) resulting from the aggregated root distribution in
617 the upper layers. Our finding is similar to a recent study conducted by Agee et al. (2021),
618 where the authors found that the extensive lateral root spreading results in homogeneous soil
619 moisture distribution. The homogeneous soil moisture pattern may contribute to a more energy
620 efficient system that reduces plant water stress (Agee et al. 2021) because that minimizes the
621 energy dissipation loss through water transport (Hildebrandt et al. 2016). Both Agee et al (2021)
622 and our studies emphasize the importance of the means by which the root distributions determine
623 how the subsurface storage is utilized.

624 Given the shape of the vulnerability curves, in all these simulations, plants will stop
625 transpiring when their leaf water potential reaches around -10Mpa with efficient xylem or -
626 15Mpa with safe xylem, depending on their stomatal strategy (Fig 7). Because we are here
627 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 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 indicator of the degree of canopy desiccation. With no or very little leaves , 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. Further, the unrealistic leaf water potential from the shallow root simulations indicates that the trees at that site must have really deep roots to exist at this site, which is in agreement with the conclusions of Goulden and Bales (2019).

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,

659 the difference in the xylem traits of conifers do not cause significant impacts on the ecosystem
660 level fluxes under the Mediterranean-type climate of CZ2, where the ecosystem fluxes are
661 constrained by energy during the wet season (Goulden et al., 2012). In addition, the maximum
662 rate of GPP and ET are co-constrained by the stand density, the total leaf area, the maximum
663 stomatal conductance, and VPD. In this study, we used the static stand structure mode of
664 FATES-Hydro, whereby the stand density and the total leaf biomass (so as total leaf area) of the
665 trees are held constant. This further limits the effect of xylem traits on GPP and ET.

666

667 4.2 Balancing productivity and mortality risk

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

674 To better understand the tradeoff between productivity and mortality risk, we plot the
675 simulated annual average GPP for each year against the fraction of conductivity (K/Kmax) of a
676 55cm DBH cohort for two scenarios: deep roots (Fig. 8a) and shallow roots (Fig. 8b), with
677 different combination of xylem and stomatal strategies. In both scenarios, for each pair of xylem
678 and stomatal strategies, the GPP per tree increases almost linearly with the K/Kmax. But, with
679 increasing the safety of the stomata, the GPP declines faster with loss of conductivity. This
680 response is stronger in deep-rooted scenarios. Having e fficient xylem only slightly increases
681 the steepness of the lines. The stomatal strategies thus represent points along a gradient of the
682 tradeoff between growth and mortality risk - the safer the stomata, the more GPP is traded for
683 reducing the mortality risk.

684 Along this tradeoff space, where trees can maximize their net carbon gains likely depends
685 on the xylem traits. Studies have shown that trees may temporarily lose xylem conductivity
686 during mild drought, which can recover once the soil water becomes available. However, under
687 an extreme drought, their xylem could collapse and permanently damage the xylem conduits. In

this case, trees rely on new sapwood growth to support the transpiration (Brodribb et al. 2010, Anderegg et al. 2013). At one extreme, if the stomatal behavior is too safe, it will give low GPP and the tree will be outcompeted for light due to faster-growing neighbors, but at the other extreme, if the stomata behave very aggressive (risky), it will give high GPP but also empty the subsurface storage quickly, consequently leading to a prolonged dry period of soil moisture. This would lead to substantial xylem damage (and/or root death), and then the carbon needed to grow new sapwood (or roots) can exceed the benefit of getting the additional GPP. So, the optimal location along the gradient would probably be located slightly below the K/Kmax associated with that critical xylem water potential. Currently, the xylem refilling and associated carbon cost are not incorporated in FATES-Hydro. These two processes should be implemented in the model to better understand the water-carbon balance, and thus remains as future work.

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

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

718 The model outcome indicates that under drier root zone soil conditions, if pines were to
719 follow a shallow rooting strategy, they would benefit from a safer stomatal strategy, with more
720 conservative water use; but if they follow a deep rooting strategy, pines would benefit from
721 riskier stomata. This is consistent with Anderegg et al.'s (2016) finding on the relative stomatal
722 conductance (gs) across elevation. They found that at low elevation (lower precipitation) site,
723 Ponderosa pine has lower relative stomatal conductance and less loss of xylem conductivity,
724 equivalent to safer stomata in our study, while at mid elevation (higher precipitation) site, pine
725 has higher relative stomatal conductance and greater loss of xylem conductivity, equivalent
726 to risky stomata in our study. The simulation results are consistent with the idea that the CZ2
727 region is dominated by deep-rooted trees. This is supported by previous studies. In situ
728 measurements of regolith structure (particularly the porosity) indicates that at CZ2, there is a
729 layer of thick semi-weathered bed rock that allows the trees to grow deep roots (Holbrook et
730 al., 2014). Growing deep roots to access rock moisture to support plant water use has also been
731 observed in the Eel River CZO catchment (Rempe et al., 2018), another Mediterranean-type
732 ecosystem along the west coast. Observed net CO_2 exchange and ET during the pre-drought
733 period suggest that during a wet year, deep moisture supported summer transpiration and
734 productivity when the upper layer moisture was low (Goulden et al. 2015). Because the deep
735 rooting strategy is sufficient in most cases to avoid the main effects of dry seasons and short
736 droughts, and that, conditional on having deep roots, the risky stomatal strategy confers a
737 productivity advantage at little increased risk of vulnerability, then we would expect that plants
738 with these traits would dominate. However, under extreme cases such as the 2012 - 2015
739 drought, which ranked as one of the most severe in California in the last 1200 years (Lu et al.
740 2019), we would expect that plants with this deep-rooted, risky stomatal strategy would be
741 highly vulnerable to drought, which is consistent with the ~90% mortality of the pine observed at
742 CZ2 during the drought (Fettig et al. 2019). The water balance of the catchment based on the
743 long-term observation from precipitation, stream flow, and ET (Bales et al. 2018, Goulden and
744 Bales 2019) also support that it was the slow depletion of deep moisture that caused tree
745 mortality in the late stage of the prolonged 2012 – 2015 drought.

746 The finding of our study indicates that the future drought mortality would likely occur in
747 the ecosystems which are co-limited by water and other factors. In those ecosystems, trees can
748 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.

5. Conclusions

Our analysis indicates that root distribution can affect the most competitive stomatal traits. 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 with low mortality risk, 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. In contrast , shallow roots with risky stomata leads to high mortality even during non-drought years, thus an uncompetitive combination at the site. 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, and JD wrote the code. PB, RB, BC, RF, MG, RK, LK, JS, CX edited the MS.

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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-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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Tables

Table 1 Parameters used in FATES-Hydro sensitivity analysis

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

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

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

Figures

Figure 1

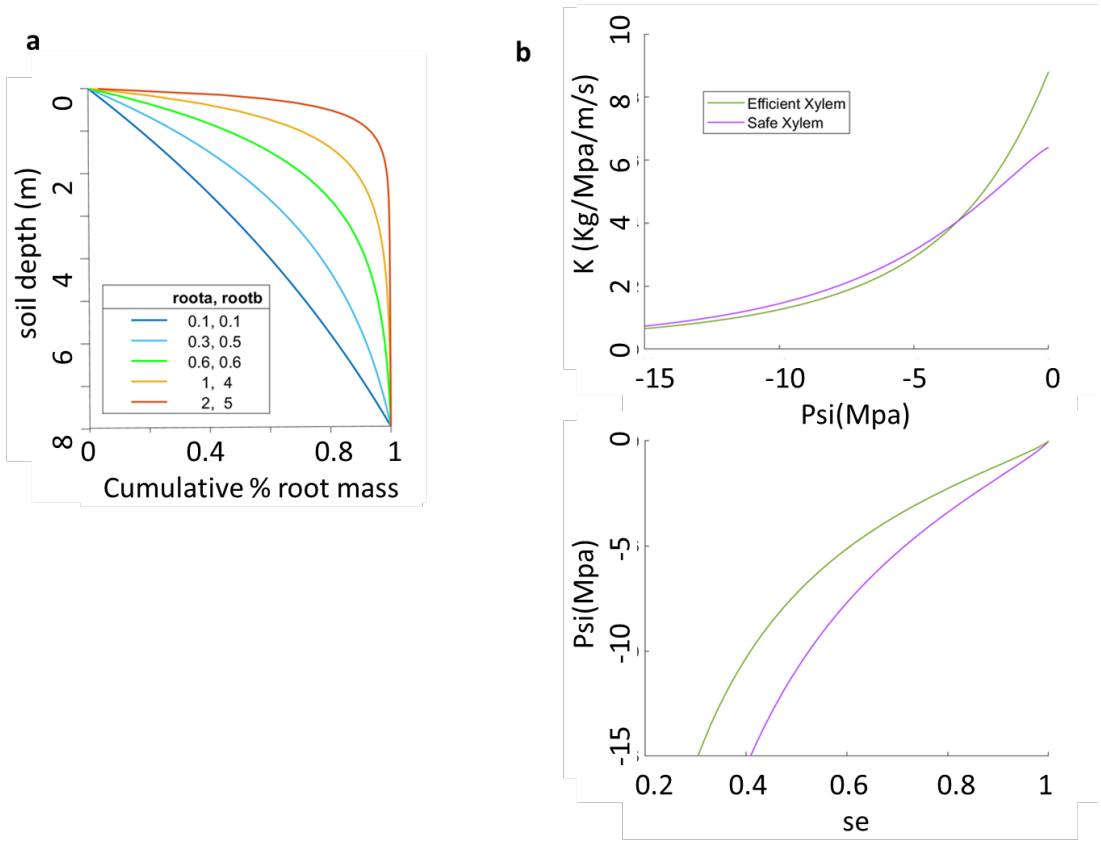

Figure 1. Sensitivity analysis set up for: a) root parameters that give five root distribution scenarios with effective rooting depths of 1m, 3m, 5m, 6.5m, and 8m , and b) two xylem scenarios for safe xylem (P50x=-4.8, Kmax=0.64), and efficient xylem (P50x=-2.5, Kmax=0.88).

Figure 2

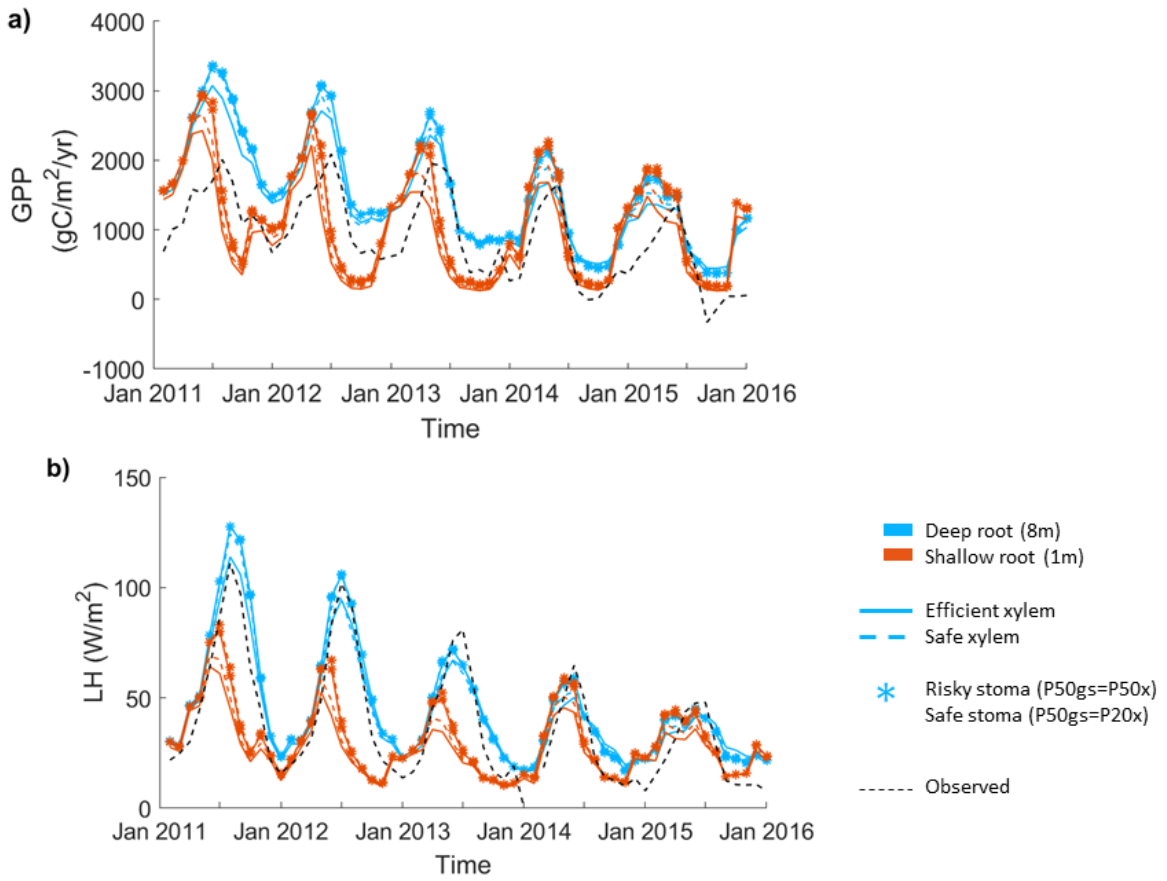

Figure 2. Impact of hydraulic strategies on ecosystem water and energy fluxes: a) monthly mean gross primary productivity, and B) monthly mean latent heat flux, of the end member cases.

Figure 3

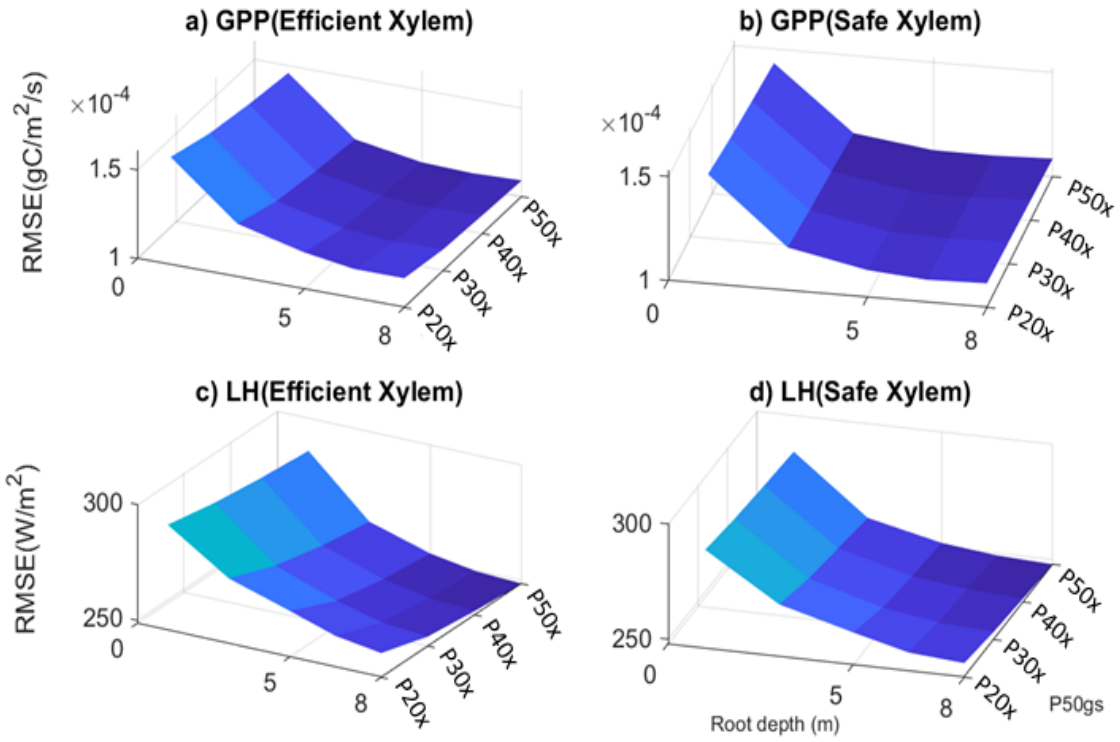

Figure 3. Root mean square error of GPP (a-b), and latent heat flux (c-d) with respect to variation in input parameters.

Figure 4

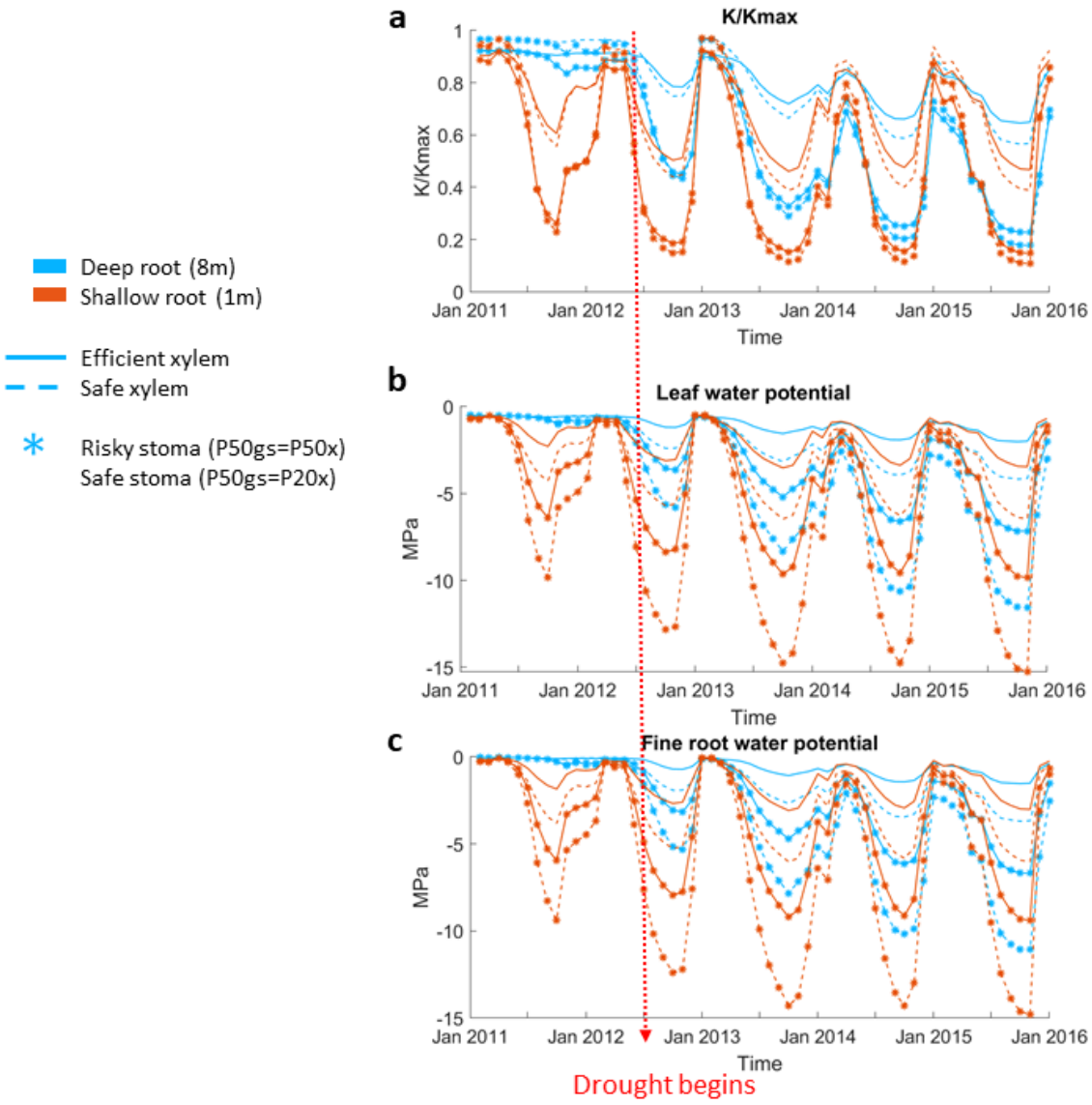

Figure 4. Seasonal and inter-annual variation of plant physiologic characteristics: a) monthly mean stem fraction of conductance K/K_{max} (a), monthly mean leaf water potential, and c) monthly mean overall absorbing roots water potential, of the 55cm DBH cohort throughout the 2011-2015 period.

Figure 5

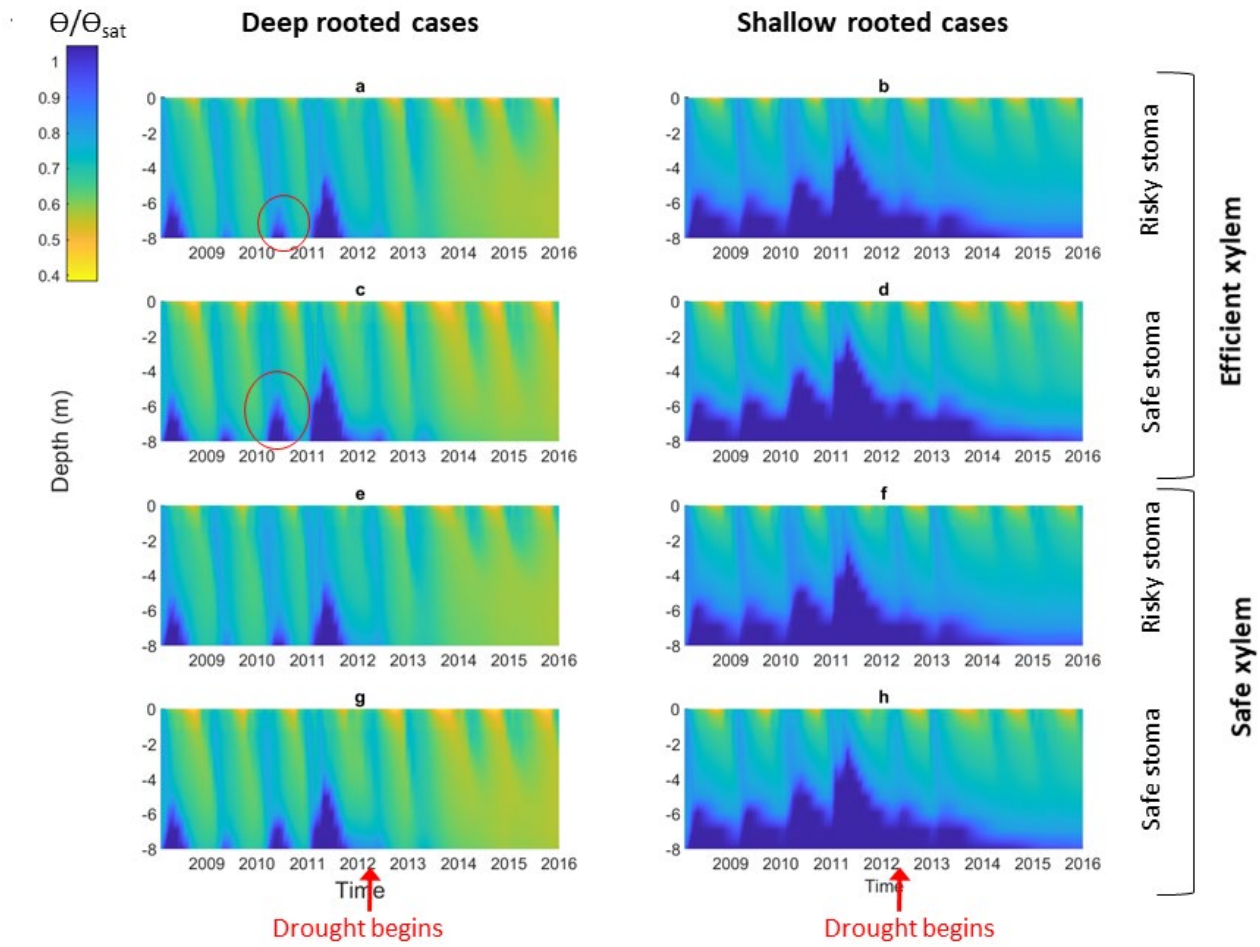

Figure 5. Impact of different combination of rooting depth, xylem and stomatal traits on soil moisture; left column shows deep rooted cases with a) efficient xylem and risky stoma, c) efficient xylem and safe stoma, e) safe xylem and risky stoma, g) safe xylem and safe stoma. Right column shows shallow 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

Figure 6

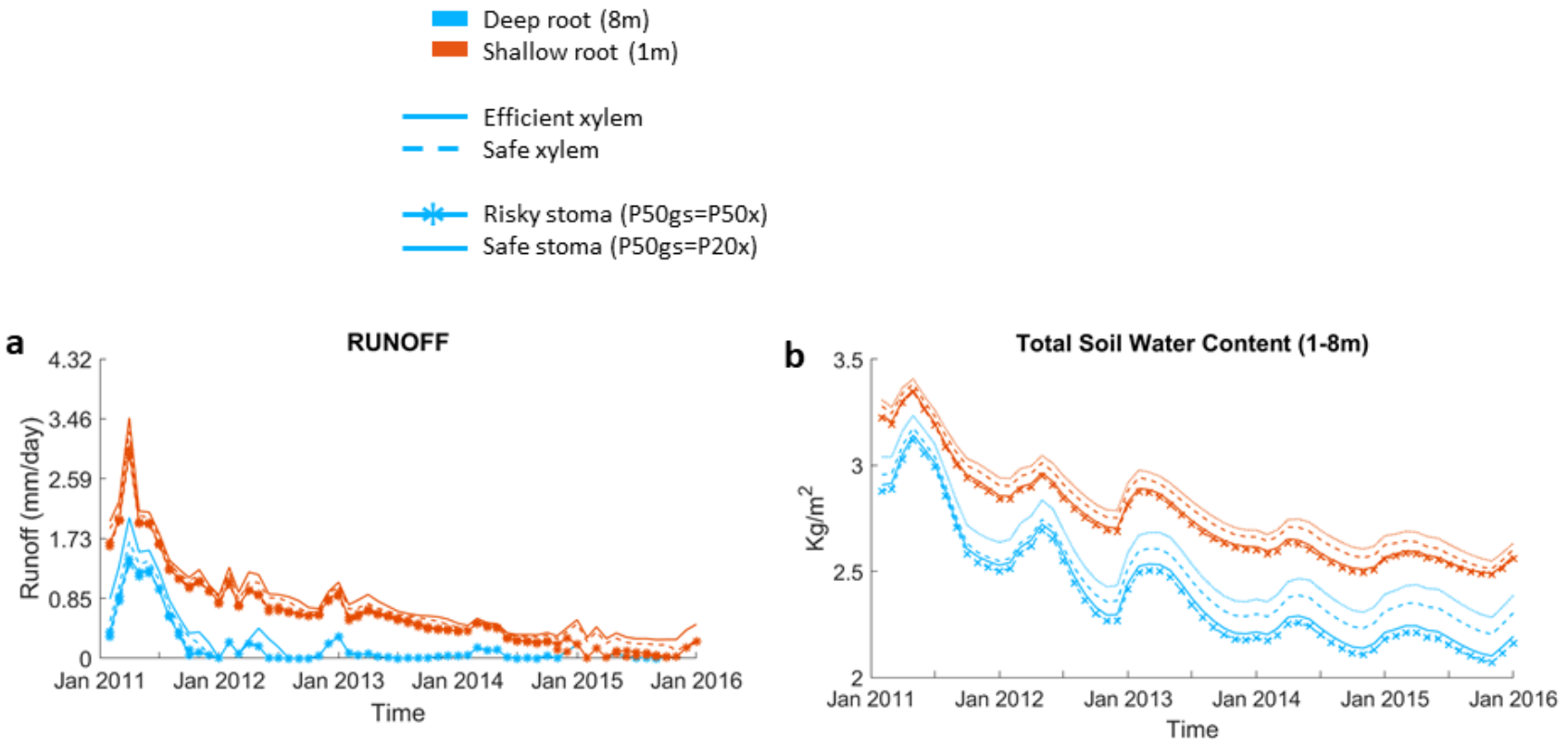

Figure 6. Impact on hydrologic processes: a) mean monthly total runoff, and b) monthly mean total soil water content of the entire soil column.

Figure 7

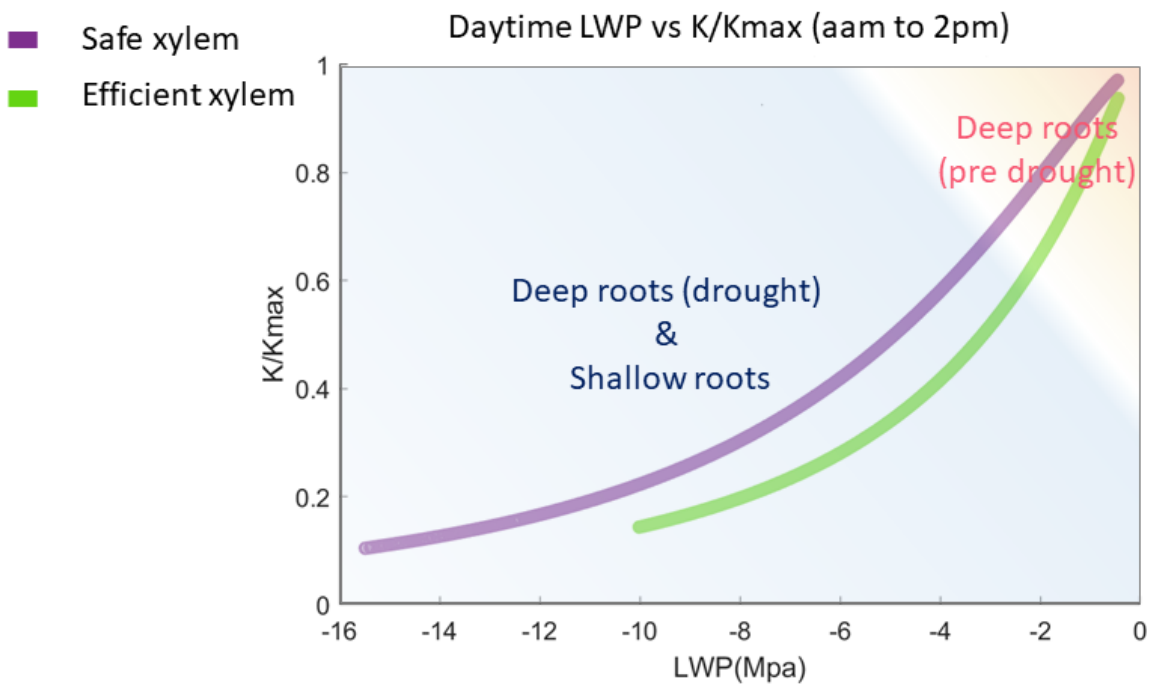

Figure 7. Simulated leaf water potential and fraction loss of conductivity (K/Kmax) of all the cases, which follow the two vulnerability curves.

Figure 8

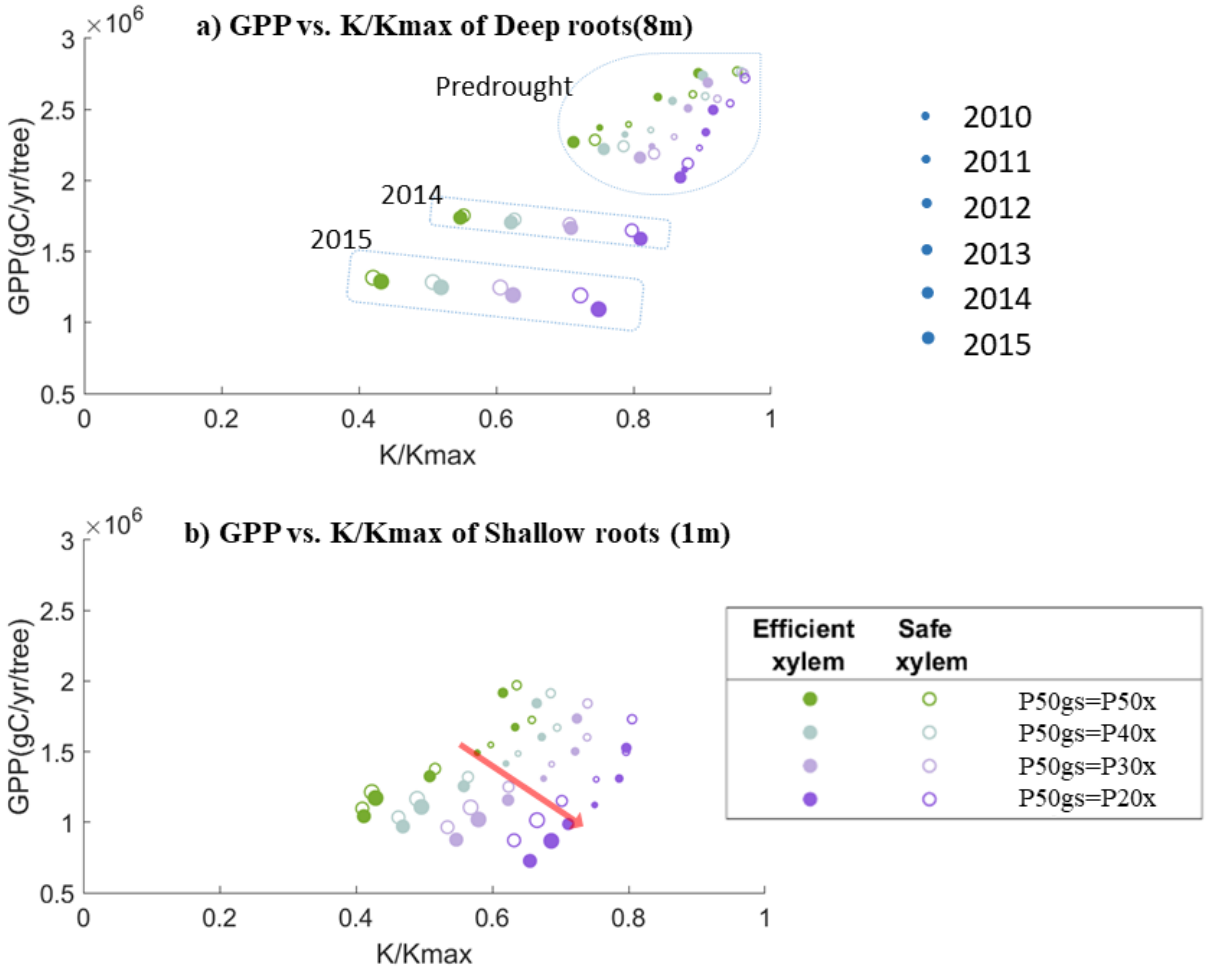

Figure 8. Simulated average annual GPP and fraction of conductance of a 55cm DBH cohort with a) deep roots (effective rooting depth= 8m) and b) shallow roots (effective rooting depth= 1m).