Challenging the maximum rooting depth paradigm in grasslands and savannas

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Summary

1. For many grassland and savanna ecosystems, water limitation is a key regulator of individual plant, community and ecosystem processes. Maximum rooting depth is commonly used to characterize the susceptibility of plant species to drought. This rests on the assumption that deep-rooted plant species would have a greater total volume of soil water to exploit and should be less susceptible to episodic changes in water availability.

2. Independent of maximum rooting depth, rooting strategies based on differences in biomass allocation with depth, uptake plasticity in relation to water availability and variation in water transport capability may all influence growth responses and susceptibility to drought. Many examples from grasslands and savannas reflect these rooting strategies among coexisting grass, forb and woody species.

3. Here, we use a dynamic model of plant water uptake and growth to show how changes in root distribution, functional plasticity and root hydraulic conductivity have the potential to influence aboveground biomass and competitive outcomes, even when maximum rooting depth remains constant. We also show theoretically that shifts in root distribution to surface soils without changes in maximum depth can potentially outweigh the benefits of increased maximum rooting depth.

4. Combining our current reliance on biogeographic descriptions of maximum rooting depth with insights about other, more subtle aspects of root structure and function are likely to improve our understanding of ecosystem responses to dynamic water limitation.

Key-words: drought, hydraulic conductivity, plasticity, root distribution, root function, root length, soil depth

Introduction

Beginning with the origins of modern ecology, the vegetation structure and dynamics of terrestrial ecosystems have commonly been inferred from the maximum rooting depth (MRD) of the species therein (Weaver & Kramer 1932; Walter 1939). The characterization of MRD within ecosystems often provides valuable insight about the role of environmental drivers across global biomes, reflecting differences in climate, edaphic properties and species phenology (Schenk & Jackson 2002a,b, 2005). Over the last decade, Schenk and Jackson's *The Global Biogeography of Roots* has been cited over 400 times, and the ideas in that paper have served as a framework for linking belowground structure (primarily MRD) with community assembly rules (Holdo & Timberlake 2008) and ecosystem function (Schenk & Jackson 2002b). Here, we briefly review current understanding about the role of MRD for ecosystem dynamics in grasslands and savannas—two biomes where soil moisture limitation plays a fundamental role in structuring plant communities (Rodríguez-Iturbe & Porporato 2004). Estimates of MRD provide important insights, but can lead to an incomplete understanding of plant water-use dynamics when used exclusively. Functional water uptake and flux over a wide range of conditions are relevant for describing species coexistence and community dynamics (Ogle, Wolpert & Reynolds 2004; van Wijk 2011; Holdo 2013; Schwinning & Kelly 2013) as well as forecasting responses to novel soil moisture regimes imposed by climate change (Jung *et al.* 2010; Kulmatiski & Beard 2013b).

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Biogeographically, MRD increases as a function of mean annual precipitation, evaporative demand, length of the growing season and deep infiltration (Schenk & Jackson 2002a,b, 2005). For grasslands and savannas, precipitation dynamics (amount and variability of rainfall, infiltration depth and seasonal distribution) are a key predictor of MRD (Schenk & Jackson 2002b). As would be expected, MRD typically varies among growth forms within an ecosystem type and between growth forms when compared across ecosystems (Schenk & Jackson 2002a,b). For example, perennial grasses often have a shallower MRD than woody species (shrubs, subshrubs and trees) (Schenk & Jackson 2002a, 2005), but the zone of overlap can be high among coexisting plant functional types (Weaver & Darland 1949; Nippert & Knapp 2007). It is generally assumed that deep-rooted species in grasslands and savannas benefit during drought and periods with reduced water availability because roots are distributed across a greater portion of the soil profile; water that infiltrates to greater soil depths may be available during drier periods of the growing season (Schenk & Jackson 2002a; Kulmatiski & Beard 2013a; Germino & Reinhardt 2014). This premise is the basis for the two-layer model of tree–grass coexistence, which posits that the greater MRD of trees provides access to subsoil water not available to grasses (Walter 1971; Ward, Wiegand & Getzin 2013). Grasses and other shallow-rooted species (or those with the vast majority of biomass in the top 30 cm of soil) compete for water in a smaller portion of the soil profile and are either better competitors for water when limiting (Schwinning & Kelly 2013), physiologically adapted to survive periods of low water availability (Craine et al. 2013) or both.

Despite the systematic variation in MRD among growth forms and ecosystems as a function of environmental constraints, we propose that *quantifying MRD alone is insufficient to predict community dynamics in water-limited systems*. To explore this claim, we highlight existing evidence from grasslands and savannas to show that root morphology (size, density and length), root distribution as a function of depth (e.g. logarithmic, bimodal, etc.) and functional plasticity influence water uptake independent of MRD (Fig. 1). To quantify the role of root traits beyond MRD, we use an existing theoretical model to illustrate how variation in root distribution, plasticity in water uptake as a function of depth and changes in root hydraulic conductance by depth may affect community dynamics even when MRD is held constant. Finally, we provide model simulations of differences in aboveground biomass when root growth is allocated to surface soils versus increases in maximum rooting depth.

Root morphology, physiology and plasticity

The coexistence of grasses, forbs and woody plants in grasslands and savannas provides a rich template of potential interactions and evolutionary adaptations among varying growth forms. These ecosystems are ideal for exploring how varying root attributes (Fig. 1) have the potential to influence aboveground ecosystem dynamics. For many species (both herbaceous and woody), root biomass and total root length are unevenly distributed throughout the soil profile, with the majority of roots concentrated in the shallowest soil layers (Weaver & Darland 1949). The architectural constraints of root production (radiating growth
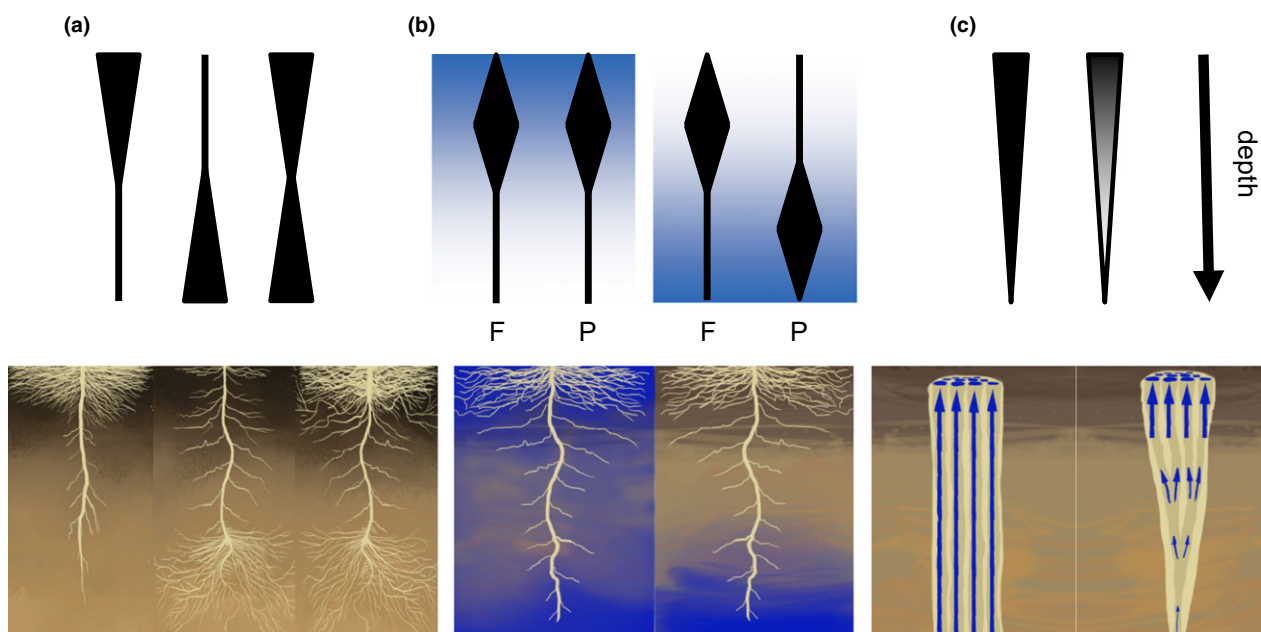

Fig. 1. Root attributes with the potential to affect patterns of water uptake: (a) variation in root distribution; (b) plasticity (F = fixed response, P = plastic response) in response to soil moisture distribution as a function of depth (shaded blue background); (c) variation in hydraulic conductivity as a function of root length. In all cases, MRD is assumed to be constant.

from crown tissue at the above/belowground interface) typically result in the highest proportion of root biomass being present in the shallowest soil layers, but can also result in a variety of root distributions and densities as a function of soil depth. Alterations in root density and distribution by depth impact transpiration (van Wijk 2011), and the vascular capacity to transport water (Sperry, Stiller & Hacke 2002). In other words, root architecture and distribution may be more important for water uptake and eventual transpiration than MRD.

Rooting profile (size and shape) and functional plasticity determine the zone of influence from which a plant forages and competes with neighbouring individuals (Casper, Schenk & Jackson 2003). In grasslands and savannas, 'zones of influence' are commonly noted between grasses and woody plants, as grasses are more effective at water uptake from shallow soils than shrubs and trees (Nippert & Knapp 2007; Kulmatistki *et al.* 2010). The 'shallow-rooting strategy' is common among many species in grasslands and savannas, where most biomass is concentrated in the top 30 cm of soil (Weaver & Darland 1949; Schenk & Jackson 2002a; Nippert *et al.* 2012). Thus, a strategy to allocate a majority of root biomass to the uppermost layers may facilitate competitive exclusion of species with roots that are less effective at resource uptake (either by root size, length or surface area) or that are more susceptible to physiological stress during periods of low soil moisture.

Beyond MRD and root distribution, plant species exhibit variation in root traits associated with anatomical structure (Wahl & Ryser 2000) and architecture (Pagès & Picon-Cochard 2014). Vessel architecture and root hydraulic conductivity may vary by species, root type and distribution within the soil profile (McElrone *et al.* 2004). As a consequence, the occurrence of roots in deep soil layers does not necessarily imply deep water use if the vessel size, number of vascular conduits and amount of functional root biomass are small (Nippert *et al.* 2012). The types of roots produced (fine versus coarse roots) impacts water uptake and transport capacities (Eissenstat 1992). Wahl & Ryser (2000) showed robust correlations between plant height and root relative growth rate and axial root conductance in grasses. Xylem cross-sectional area of roots (a surrogate for transport capacity) increased with growth rate and plant height, suggesting a role of root anatomy for meeting overall water supply (Wahl & Ryser 2000). Thus, the cumulative transport capacity of fine versus coarse roots likely varies, even if the total root biomass is similar at a given depth. Grassland species can have high spatial variability in root length density (Kuchenbuch, Gerke & Buczko 2009) with higher root length density compared to forest ecosystems (Pärtel & Wilson 2002) as well as temporal variability in response to short-term changes in water availability (Padilla *et al.* 2013). In all, more research is needed to examine how root traits vary among coexisting grasses, forbs and woody plants in grasslands and savannas and identify how these differences relate to patterns of resource availability and long-term coexistence.

Finally, source-water plasticity in response to changes in soil water availability illustrates the critical disconnect that can exist between root function and root structure. Empirical research from grasslands and savannas has shown interactions among spatial and temporal ecohydrological niche among functional groups (Dodd, Lauenroth & Welker 1998; Hipondoka *et al.* 2003). Functional plasticity in water uptake facilitates the use of surface soil water following rainfall events, but allows the possibility to switch to deeper sources as soils dry (Schulze *et al.* 1996; Ogle, Wolpert & Reynolds 2004; Asbjornsen *et al.* 2008). For example, grasses frequently rely on soil water from upper layers regardless of maximum rooting depth or water availability at depth, while coexisting forbs and/or woody species typically have plastic source-water strategies based on water availability (Nippert & Knapp 2007; Kulmatiski *et al.* 2010; Kulmatiski & Beard 2013a). A plastic strategy would be most advantageous for species with greater sensitivity to drought and subsequent cavitation allowing for water uptake from varying soil layers based on changes in water availability.

A simulation-based example

To illustrate how root morphology, physiology and plasticity may influence community dynamics, we used a published model that couples plant water uptake and biomass dynamics with soil moisture dynamics as a function of depth (Holdo 2013). This model illustrates how variation in root distribution, uptake plasticity and hydraulic conductivity might influence competitive outcomes among individuals when MRD is held constant. We ran three 100-year scenarios with competing rooting strategies. (i) Four root distributions generated from a Beta distribution rescaled to the interval 0–70 cm (when 70 cm is the MRD). The Beta distribution is flexible and captures a wide range of root distributions (exponential, Normal, uniform) including one that allocates root biomass preferentially to shallow and deep soils over intermediate depths (Fig. 2a). (ii) A fixed vs. plastic uptake strategy where the root profile with Beta parameters $a = 1$, $b = 5$ was used as a default profile and generated two very similar alternatives. The contrasting strategies allocate relatively more water uptake capacity to shallow ($a = 1$, $b = 5.5$) and deeper soils ($a = 1$, $b = 4.5$), respectively (Fig. 2c). In this case, the model was modified within each daily time step such that the plastic strategy was allowed to adopt the profile that maximizes daily transpiration. (iii) We compared changes in root hydraulic conductivity with depth (Fig. 2e). The default model assumes no change in conductivity by root depth, while the contrasting strategy shows a linear decline in hydraulic conductivity with depth, from the maximum value at the surface to 50% of maximum at 70 cm deep. In all cases, we conducted 10 model runs
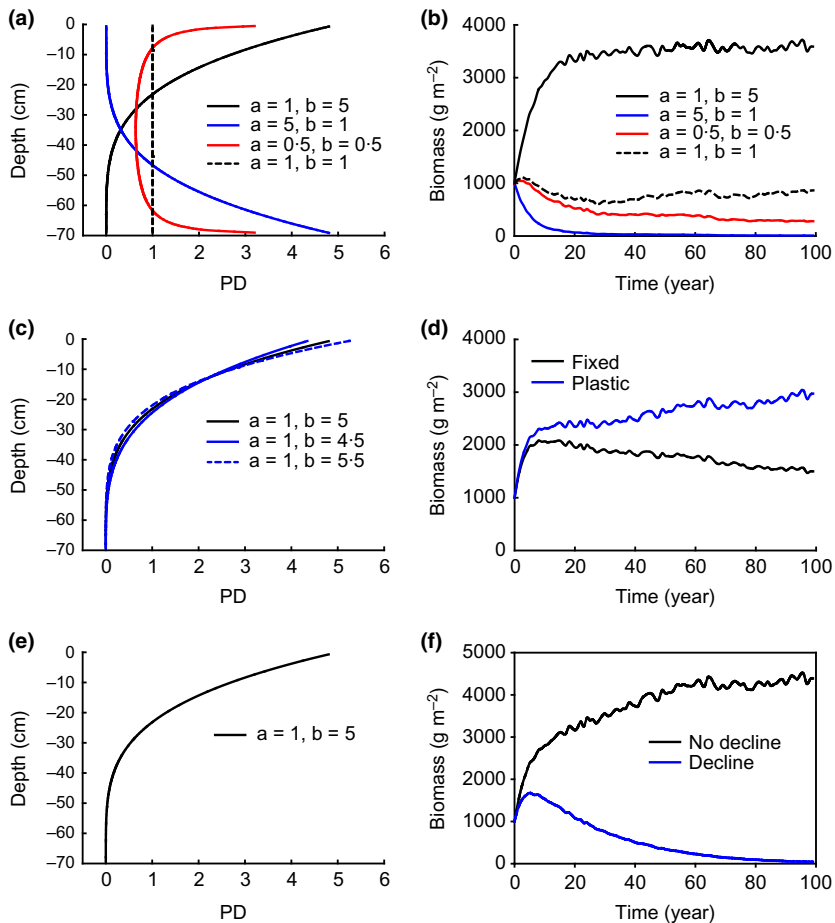
Fig. 2. Simulated rooting strategies (left panels) and their competitive outcomes (right panels): (a) four distributions with equal maximum root depth and root biomass, generated by Beta distributions with parameters a and b and (b) competitive outcome; (c) fixed and plastic root distribution strategies and (d) the outcome of competition between them; the default distribution (black line) never changes in the 'fixed' scenario, but can shift to be slightly shallow- or deep-biased (dashed lines) depending on environmental conditions in the 'plastic' scenario. (e) Fixed distribution for two strategies differing in hydraulic conductance with depth, and (f) outcome of competition between strategies with and without a decline in conductance (to 50% of the default value at maximum depth) as a function of root length. Simulation plots show means for 10 runs conducted over 100 years, assuming stochastic rainfall (mean annual precipitation = 650 mm) and equal maximum rooting depth.

assuming a stochastic mean annual precipitation of 650 mm (Holdo 2013).

Next, we compared differences in aboveground biomass produced when root distribution was altered versus increasing MRD (Fig. 3). Starting with a simple default profile with equal biomass allocation across 50 cm depth, the model could take two forms: new root biomass was allocated to deeper soil layers ('deepen'), versus allocation of new root biomass to the most superficial soil layer without changes in MRD ('reshape') (Fig. 3a). It is not geometrically feasible to independently manipulate maximum depth and distribution while retaining constant biomass (*i.e.* cross-sectional area in our model): increasing MRD for a fixed root biomass implies moving to a longer, thinner distribution (Fig. 3a). For this reason, this analysis is a preliminary approximation comparing altered root distributions versus altered MRD.

Our model runs suggested strong effects of root distribution, the occurrence of plasticity and variation in root hydraulic conductivity on aboveground biomass production independent of MRD. Fig. 2a shows that a root strategy that preferentially distributes biomass to the top 30 cm (black line, Fig. 2a, b) produces more aboveground biomass than one that allocates more biomass at depth (blue line, Fig. 2a, b), at least for this precipitation regime. The outcome that even subtle differences in root distribution

can lead to highly divergent outcomes in plant biomass over time has already been demonstrated (Holdo 2013). Here, we emphasize two key points: first, these effects can become apparent over relatively short periods (<20 years). Second, while performance is strongly influenced by root distribution, it is not necessarily predictable: allocation to shallower soil is an advantage in this particular case, but excessive allocation to deep soil is predicted to be more deleterious than insufficient allocation to shallow soil, as shown by the better performance of the uniform root distribution over the distribution with preferential allocation to shallow and deep soils over intermediate depths (Fig. 2a, b). These model results also suggest that functional plasticity in the depth of water uptake increases aboveground biomass compared to a fixed strategy (Fig. 2d). As previously discussed, this model result mirrors a strategy common to woody plants in savannas (e.g. Kulmatiski & Beard 2013a). Our simulation results also suggest dramatic aboveground effects (competitive exclusion) when roots display a 50% reduction in hydraulic conductance at maximum soil depth (Fig. 2f). This scenario illustrates that reductions in root vasculature corresponding with changes in soil depth severely reduce the capacity of deep roots to transport water. Finally, under the model conditions tested here, we show that allocation of belowground biomass to produce roots in surface soils
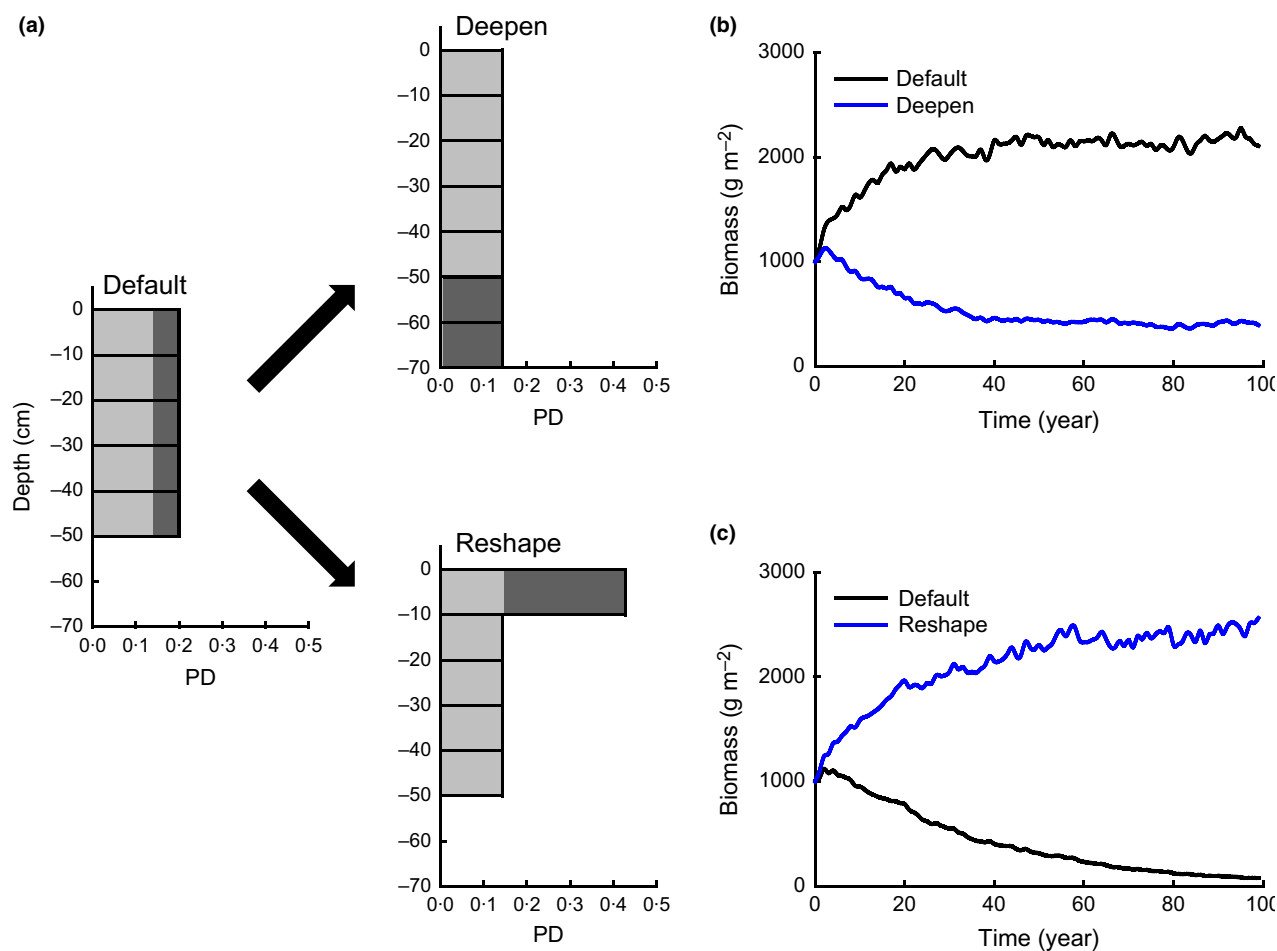
Fig. 3. Simulated outcomes of competition between a 'default' rooting profile and two derived ones of equal root mass: (a) default profile and two alternative strategies based on an increase in MRD ('deepen') or a change in distribution ('reshape'); (b) outcome of competition between the default and deepen strategies and (c) between the default and reshape strategies. The shaded portions of the profiles denote the root biomass that is reallocated. Simulation plots show means for 10 runs conducted over 100 years, assuming stochastic rainfall (mean annual precipitation = 650 mm).

without changes in MRD (Fig. 3c) has a larger increase (though roughly comparable in magnitude) in aboveground biomass than the strategy where new root production is used to increase MRD without changes in root distribution (Fig. 3b), at least for this particular set of environmental conditions.

Next steps

As is evident from the wealth of literature supporting MRD as a predictor of ecosystem processes, this metric is relatively easy to estimate and provides useful insights. The model results shown here do not undermine the value of MRD, but rather highlight that water uptake as a function of depth is impacted by variables other than MRD (e.g. morphological and physiological traits and plasticity in water uptake). Thus, while MRD imposes a lower depth boundary for resource extraction by individual plants, the interplay of multiple traits (physiology, morphology and plasticity in response to resource availability) define

functional root space. Databases of MRD based on physical rooting profiles provide a foundation for our understanding of water uptake as a function of depth, but the results shown here suggest that further exploration of additional root traits may provide insight linking plant responses to environmental variability (*sensu*, Iversen 2014).

Given the difficulty in measuring plant processes belowground, how can we apply these concepts and measure these root traits in a meaningful context? Stable isotopic techniques to identify source-water use have been valuable and common over the past 20 years based on ease of use, minimal impact and relatively low cost (Ehleringer & Dawson 1992). Trace elements have been used less commonly to identify functional plasticity in water uptake (Martin, Snaydon & Drennan 1982), but this technique holds promise (Hoekstra *et al.* 2014). Current models linking root traits to ecosystem function likely oversimplify the true complexity of belowground interactions. Molecular studies detailing root interactions in mixed communities

(Mommer *et al.* 2010) illustrate the complexity of below-ground competition and the potential of resource sharing among roots of varying species. Improving estimates of resource uptake will require more detailed work linking root traits to function in diverse communities as well as tracking the soil-zone specific rates of water flux along the soil–plant–atmosphere continuum (Zarebanadkouki, Kim & Carminati 2013).

Dynamic root traits and processes are likely key regulators of hydraulic redistribution (HR) in grass–shrub–tree systems (Neumann & Cardon 2012; Prieto, Armas & Pugnaire 2012). HR reflects the integration of root form, function and distribution among soil layers with varying water potential gradient (Neumann & Cardon 2012; Prieto, Armas & Pugnaire 2012). Additionally, HR may play important roles for increasing nutrient availability in surface soil layers (Cardon *et al.* 2013). For many grassland systems, nutrient availability is highest in the surface soil layers (Ajwa, Rice & Sotomayor 1998), with mineralization rates correlated with changes in soil moisture (Stanford & Epstein 1974). Grassland species that allocate more roots to surface soils likely have greater nutrient availability, compared to root allocation to deeper soil depths. To date, little evidence of HR exists for live grasses – potentially reflecting grasses' functional reliance on water uptake from shallow soils as well as root architectural differences among monocot grasses and eudicot forbs and trees.

Dynamic root responses and the characterization of biomass and hydraulic architecture by soil depth are largely absent from most terrestrial biosphere models (Warren *et al.* 2014). As a next step, the structural and functional roots traits analysed here can be incorporated into sensitivity analyses of landscape models predicting aboveground biomass. Presently, most landscape models use MRD as the primary belowground descriptor of resource uptake (e.g. Walker & Noy-Meir 1982; Eagleson & Segara 1985; Warren *et al.* 2014). Incorporating dynamic root processes (structure and function) into terrestrial biosphere models has the potential to improve estimates of landscape energy fluxes (Warren *et al.* 2014) as well as improve our ability to forecast ecosystem responses to future climate scenarios (Norby & Jackson 2000).

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Data accessibility

This manuscript does not use new empirical data. Model development, parameterization and the corresponding R scripts used to support the conclusions are available in Holdo (2013), doi: 10.1371/journal.pone.0069625.

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