Effect of plant uptake strategy on the water−optimal root depth

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[1] The depth of plant roots depends on a variety of conditions, including soil properties, vegetation type, nutrient availability, and climate. A water-optimal root depth is determined by equating the marginal carbon cost of deeper roots with the benefit of those roots to continued transpiration. This work compares the effect of two bounding strategies of plant uptake, conservative and intensive, on the water-optimal root depth and the response of that depth to changes in precipitation. While there are some differences between the models, both indicate similar responses of root depth to climate. The deepest roots are found in climates for which precipitation and potential transpiration are approximately equal, and root depths are more sensitive to changes in precipitation depth than frequency under dry conditions and more sensitive to rainfall frequency when the climate is wet. For all climate conditions, the water-optimal root depth is deeper and mean transpiration is lower when plant uptake is represented by the conservative model. These results highlight the explanatory power of water with respect to root depth and identify potential effects of a changing climate.

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1. Introduction

[2] The depth of plant roots depends on a variety of factors, including climate, soil, and vegetation characteristics. From a water perspective, rooting depth strikes a balance between the benefits of water storage to maintain transpiration between rain events and the cost of constructing and maintaining the roots. *Guswa* [2008] developed an analytical model for a water-optimal root depth, predicated on the simplification that water acquisition drives root morphology. The water-optimal root depth is the depth for which the marginal carbon cost and benefit of deeper roots are equal, i.e., the depth that maximizes the net carbon profit for the plant [*Schymanski et al.*, 2008, 2009].

[3] This paper extends the work of *Guswa* [2008] by considering two uptake strategies. Under the intensive strategy, roots take up water at a potential rate independent of soil saturation until the wilting point when transpiration goes to zero [*Guswa*, 2008; *Milly*, 1993]. This behavior is contrasted with a conservative strategy under which transpiration is proportional to the plant-available soil moisture [*Porporato et al.*, 2004]; the plant reduces transpiration and, thus, assimilation in response to soil drying. This conservative model represents a balance between carbon assimilation and stress avoidance [*Caylor et al.*, 2009], whereas the intensive strategy provides no mechanism for reducing uptake in response to water stress. These two models represent bounding strategies, and the behavior of most vegetation will fall between these limiting cases (Figure 1).

[4] The intent of this work is not to predict root depth per se, as in the works of *Kleidon and Heimann* [1998], *van Wijk and Bouten* [2001], and *Schymanski et al.* [2009]. Rather, the goal is to provide insight to potential root zone adaptations to changes in precipitation and to identify differences between intensive and conservative water use strategies.

2. Theory

[5] A water-optimal root depth is determined by equating the marginal carbon cost of adding deeper roots to the marginal benefit due to increased transpiration as a result of deeper roots [*Guswa*, 2008]:

$$\left.\frac{\gamma_r \cdot RLD}{SRL}\right|_{Z_r} = WUE \cdot f_{seas} \cdot \frac{d\langle T\rangle}{dZ_r}. \quad (1)$$

On the left-hand side, γ_r is the root carbon cost, incorporating both construction and respiration [mmol C per g roots per day], *SRL* is the specific root length [cm of roots per g], and *RLD* is the root length density [cm of roots per cm^3 of soil], all evaluated at the depth of the advancing root front. On the right-hand side, *WUE* is water use efficiency [mmol C per cm^3 of H_2O], f_{seas} is the length of the growing season expressed as a fraction of a year, and $\langle T\rangle$ is the average rate of transpiration during the growing season [mm of H_2O per day]. Solution of equation (1) for a water-optimal root depth, Z_r, requires an expression for transpiration as a function of root depth.

[6] A stochastic model of soil moisture dynamics is employed to highlight the effects of rainfall intensity and frequency. Rainfall events are considered independent and arrive randomly with a mean frequency, λ. Precipitation depths are exponentially distributed with mean, α. Infiltration and redistribution are presumed to occur rapidly, and precipitation first fills the root zone to a maximum field capacity saturation before excess water is lost to drainage or runoff.

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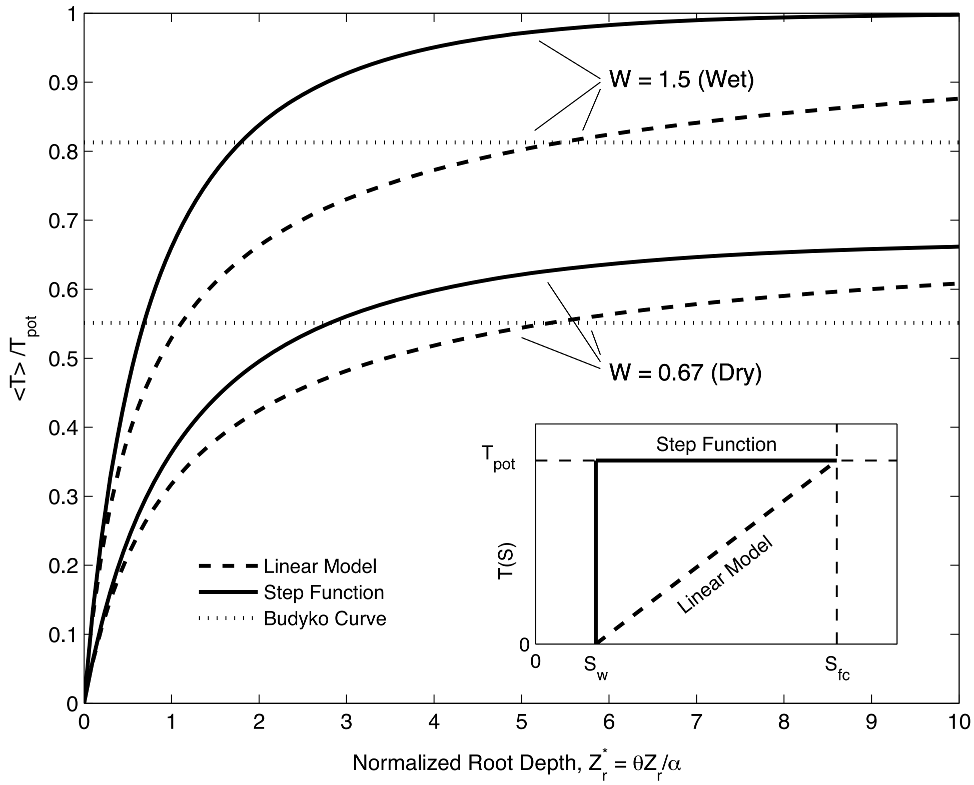

Figure 1. Normalized transpiration versus normalized root depth for a wet and dry climate ($W = 1.5$ and 0.67, respectively). Solid lines represent the intensive strategy (step function), while dashed lines indicate results for the more conservative approach (linear model). Corresponding values from the Budyko curve [*Budyko*, 1974] are included for comparison. The inset indicates the dependence of transpiration on root zone soil moisture for the two bounding uptake strategies.

[7] The effect of root zone soil moisture on transpiration is represented by two bounding curves. Under the conservative strategy, transpiration varies linearly from zero at the wilting point to the potential rate at field capacity:

$$T(S) = T_{pot} \cdot \frac{S - S_w}{S_{fc} - S_w}, \tag{2}$$

where T_{pot} is the potential rate of transpiration, S_w is the wilting point saturation, and S_{fc} is the field capacity (which is also the maximum saturation for the simplified infiltration model). Bare soil and interception evaporation are not included explicitly, and *Guswa* [2008] shows how they may be incorporated through modification of λ and T_{pot}.

[8] With the intensive representation, transpiration proceeds at the potential rate for all saturations above the wilting point:

$$T(S) = \begin{cases} T_{pot} & S > S_w \\ 0 & S = S_w \end{cases}. \tag{3}$$

This model could represent vegetation that uses water intensively and then goes dormant when the soil dries out. In contrast, the linear model (equation (2)) scales the transpiration flux in proportion to the water in storage; such a strategy might be employed by plants seeking to reduce water stress [*Caylor et al.*, 2009].

[9] The relationships discussed here are between average root zone soil moisture and total uptake by the plant, not layer-by-layer applications as in the works of *Feddes et al.* [2001] and *Van Dam et al.* [1997]. When the root zone is only partially rewet by infiltration events (often the case in nonirrigated systems), the relationship between uptake and average saturation becomes more intensive as root resistance decreases [*Guswa et al.*, 2004; *Guswa*, 2005]. In such cases, the vegetation is able to use the available water wherever it may be within the root zone.

[10] Solutions for mean transpiration, $\langle T \rangle$, are provided by *Milly* [1993] for the step function strategy and *Porporato et al.* [2004] for the linear model. Both are functions of only two dimensionless variables: Z_r^* and W. Z_r^* represents root depth as the number of mean precipitation events that can be stored within the root zone:

$$Z_r^* = \frac{n(S_{fc} - S_w)Z_r}{\alpha}, \tag{4}$$

where n is the soil porosity. W is similar to the aridity index [*U.N. Environment Programme*, 1997] and the inverse of the index of dryness [*Budyko*, 1974]:

$$W = \frac{\alpha\lambda}{T_{pot}}. \tag{5}$$

This measure of climate wetness differs from the aridity index in that the potential rate of transpiration (not evapotranspiration) appears in the denominator, and *Guswa* [2008] presents a discussion of the difference.

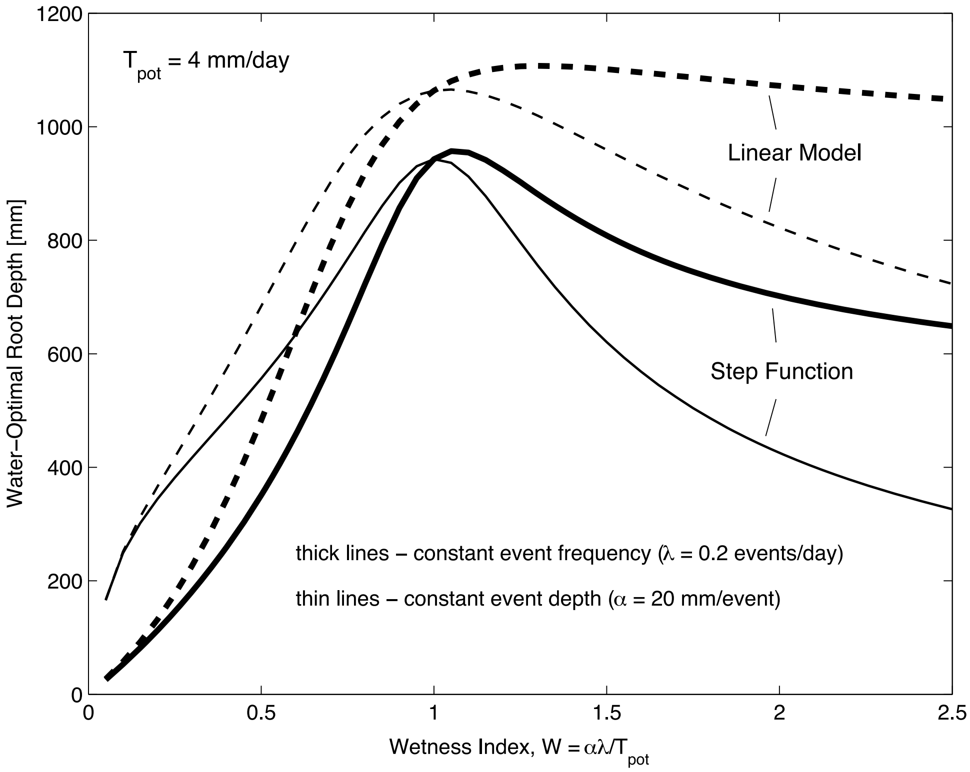

Figure 2. Dependence of the water-optimal root depth on climate wetness. Solid lines represent the intensive strategy, while dashed lines indicate results for the more conservative approach. Thicker lines represent changes in climate wetness due to variation in event depth; thinner lines indicate changes to event frequency.

[11] For the step function strategy, the long-term average rate of transpiration is provided by equation (36) in the work of *Milly* [1993]:

$$\frac{\langle T \rangle}{T_{pot}} = W \cdot \frac{\exp\left[Z_r^*(1-W)\right] - 1}{\exp\left[Z_r^*(1-W)\right] - W}. \tag{6}$$

Mean transpiration under the linear model is derived from equations (3) and (4) in the work of *Porporato et al.* [2004]:

$$\frac{\langle T \rangle}{T_{pot}} = W - \frac{\exp\left(-Z_r^*\right) \cdot \left(Z_r^*\right)^{WZ_r^*-1}}{\Gamma\left(WZ_r^*\right) - \Gamma\left(WZ_r^*, Z_r^*\right)}, \tag{7}$$

where $\Gamma(\cdot)$ is the gamma function [*Abramowitz and Stegun*, 1964, equation 6.1.1] and $\Gamma(\cdot,\cdot)$ is the incomplete gamma function [*Abramowitz and Stegun*, 1964, equation 6.5.3]. Figure 1 presents mean transpiration as a function of normalized root depth for both a wet and dry climate.

[12] Differentiating equations (6) and (7) with respect to root depth, Z_r, and combining with equation (1) enables the determination of a water-optimal root depth as a function of climate, soil, and vegetation characteristics.

3. Results

[13] The intent of this paper is to provide insight to the explanatory power of water with respect to root depth, more so than to predict root depth (especially given the data requirements). Nonetheless, a check on the reasonableness of the predictions is valuable. Data on root depth, respiration rates, and plant, soil, and climate characteristics are available for *Burkea Africana*, a woody species, in the savanna of Nylsvley, South Africa [*Scholes and Walker*, 1993], and *Guswa* [2008] showed that the water-optimal root depth is very close to the observed root depth of one meter.

[14] Figure 2 presents the dependence of the water-optimal root depth on climate and plant uptake strategy. Climate wetness, W, is varied by changing either the frequency, λ, or mean depth, α, of precipitation events, with other characteristics held constant (values provided in Table 1). This paper focuses on the effect of changes in precipitation regime, and the sensitivity of the water-optimal root depth to other variables is discussed in detail in the work of *Guswa* [2008].

[15] As can be seen in Figure 2, both representations of plant uptake predict the deepest roots for climates with a wetness index near one, i.e., when precipitation and transpiration demand are approximately equal. For the same climate, plants with a more conservative uptake strategy will have deeper roots than those with a more intensive uptake behavior. Both strategies lead to similar responses to changes in precipitation: root depth is more sensitive to changes in rainfall frequency for wet climates and to changes in rain

Table 1. Vegetation and Soil Parameters Used in the Creation of Figures 2 and 3

Parameter	Value	Units
T_{pot}	4	mm/d
θ	0.18	–
$\frac{\gamma_r RLD}{SRL \cdot f_{seas} \cdot WUE}$	0.0004	1/d

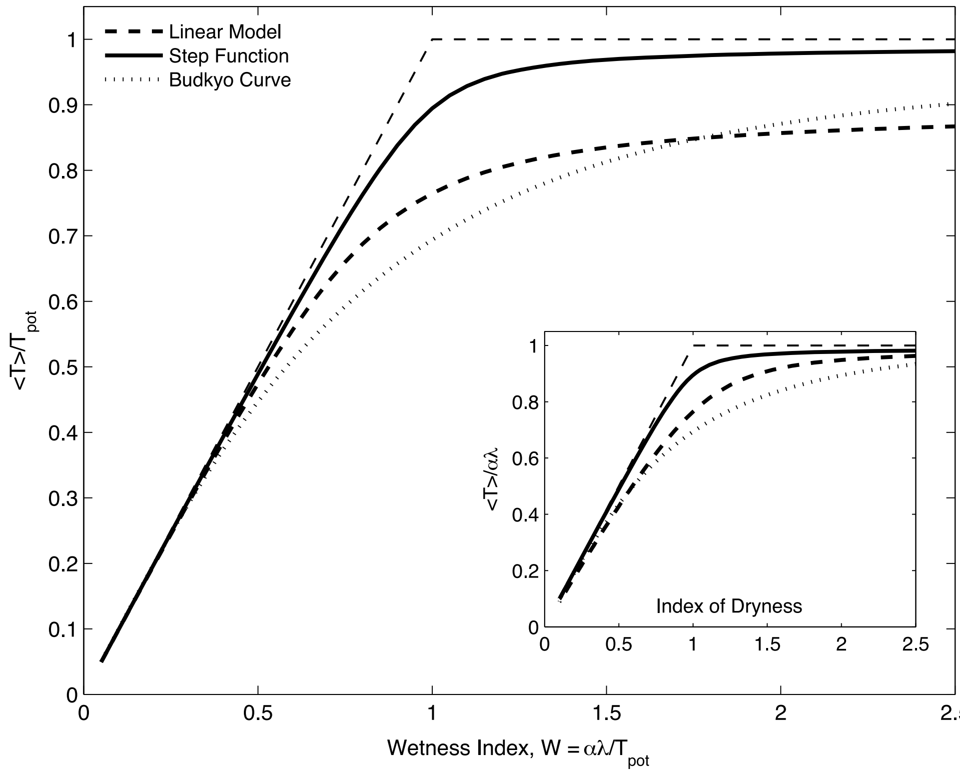

Figure 3. Dependence of mean transpiration, normalized by the potential rate, on climate wetness with roots at their water-optimal depth. The inset presents the same data; in this case, however, transpiration is normalized by mean precipitation, and the *x* axis indicates the index of dryness, i.e., the inverse of *W*. Solid lines represent the intensive strategy, while dashed lines indicate results for the more conservative approach. The dotted lines represent the Budyko curve [*Budyko*, 1974].

depth for dry climates. The sensitivity of root depth to climate wetness differs slightly between the two strategies.

[16] With roots at their water-optimal depth, the two strategies result in differences in the dependence of mean transpiration on climate wetness (Figure 3). Results are shown for variations in wetness due to changes in precipitation depth, and the results (not shown) for changes in frequency are nearly identical. Though the optimal root depth is shallower with the step function strategy (Figure 2), mean transpiration is greater than for the linear model (Figure 3). The Budyko curve is included for comparison [*Budyko*, 1974], and the position of the model results relative to this curve is a strong function of the carbon cost of roots. As the cost goes up, the water-optimal root depth and the corresponding mean transpiration rate decrease for both strategies (results not shown).

4. Discussion and Conclusions

[17] In this work, a water-optimal root depth is determined as a function of climate characteristics by equating the marginal carbon cost and benefit of deeper roots. Both representations of plant uptake, conservative and intensive, give rise to the same general shape for root depth as a function of climate (Figure 2); roots are deepest when potential transpiration and mean precipitation are approximately equal. In wetter climates, deep roots are not needed as water is regularly available near the surface, and there is no water to be found at depth in drier climates. These theoretical findings are consistent with the field data of *Schenk and Jackson* [2002a]. They show that precipitation and potential evapotranspiration account for the greatest proportion of variation in plant rooting depth and that root depths increase as one moves from arid to semiarid to subhumid regions; rooting depths decrease moving to more humid environments, and root depths are negatively correlated with annual precipitation in the humid tropics [*Schenk and Jackson*, 2002a].

[18] This work considers two bounding responses of transpiration to soil drying, the linear model and the step function. As indicated in section 2, the intensive strategy corresponds to plants with higher root conductivities [*Guswa et al.*, 2004; *Guswa*, 2005]. In general, root conductivities are larger for herbaceous plants than for woody species [*Larcher*, 2003], and the theoretical results presented in Figure 2 are consistent with empirical evidence that herbaceous plants are more shallowly rooted than woody species [*Schenk and Jackson*, 2002a, 2002b].

[19] In dry climates, mean transpiration is limited by precipitation, and it is advantageous (from a carbon perspective) to ensure that little water is lost to drainage. Consequently, root depth is positively correlated with the wetness index (i.e., with increasing precipitation), a result that is consistent with the modeling results from *Laio et al.* [2006] and *Collins and Bras* [2007] and the field data from [*Schenk and Jackson*, 2002b]. In comparing the two bounding uptake strategies, roots are deeper under the more conservative behavior, as discussed above. Since soil moisture depletion is slower under the conservative strategy, antecedent soil moisture will

be higher, and deeper roots will ensure that little water is lost to drainage below the root zone during an infiltration event. With a more intensive water use strategy, the root zone is depleted of water more quickly, creating space to absorb the next rain. The same volume of effective storage can be achieved with shallower roots. This advantage comes at the expense of drier soils, and the vegetation must be able to withstand periods of reduced soil moisture.

[20] For wet climates, transpiration is limited by the potential rate more so than by available water. Under the step function strategy, the plant transpires at the potential rate independent of the soil moisture status; for the linear model, transpiration is maximized if saturation is kept close to field capacity. Thus, under the conservative strategy there is an additional advantage to having a large soil moisture reservoir (i.e., deep roots), not to capture more water but to minimize changes in soil saturation and suction head as water is lost to transpiration. Therefore, even though water becomes more and more abundant as the wetness increases, the water-optimal root depth is rather insensitive to these changes under the conservative strategy. This is especially true when the increase in climates wetness results from changes in precipitation depth and not frequency.

[21] Figure 3 shows that when roots are at their optimal depth, the intensive strategy always results in greater transpiration than the conservative strategy. The conservative strategy may represent a trade-off between increased transpiration and reduced water stress [*Caylor et al.*, 2009], and one could imagine the coevolution of deep roots and a conservative water use strategy. Just as deeper roots provide the storage required for the conservative uptake behavior (Figure 2), so might that uptake strategy help preserve the larger carbon investment in the root system by limiting water stress.

[22] Both the linear and step function strategies indicate a response of transpiration to climate wetness that is sharper than indicated by the Budyko curve (Figure 3). This deviation is similar to that shown in the field data presented by *Szilagyi and Jozsa* [2009]. It is also worth remembering that the results presented in Figures 2 and 3 are generated by holding plant and soil characteristics constant, and these quantities will likely also vary with climate [e.g., *Bell et al.*, 2010].

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