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The Influence of Climate on Root Depth: A Carbon Cost-Benefit Analysis

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The influence of climate on root depth: A carbon cost-benefit analysis

A. J. Guswa[1]

[1] The depth of the active root zone identifies the portion of the subsurface that exchanges soil water with the atmosphere. The depth of this zone is determined by a number of factors, and this work focuses on the drivers related to water and climate. An analytical expression for a water-optimal root depth is developed by equating the marginal carbon cost and benefit of deeper roots. Soil-moisture dynamics are driven by stochastic rainfall, and the predicted root depth is a function climate, soil, and vegetation characteristics. Consistent with results from the field, deep roots coincide with environments for which precipitation and potential evapotranspiration are approximately equal. For water-limited ecosystems, increases in the wetness of the climate produce deeper roots, and root depth is more sensitive to changes in the depth of rain events than to their frequency. In wet environments, the opposite is true; root depth generally decreases with increasing wetness and shows greater sensitivity to changes in rainfall frequency than intensity.

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1. Introduction

[2] The active root zone has the potential to return water to the atmosphere via evapotranspiration, and the depth of this zone affects the extent of the exchange between soil-moisture and water vapor. Therefore just as variations in climate may result in changes in vegetation and root-zone depth, so too can changes in root depth affect the global water cycle [*Milly and Dunne*, 1994]. Thus understanding the impacts of changes to precipitation and temperature on water resources requires an understanding of the response of the root-zone depth to climate. In addition to genetic predisposition, multiple environmental factors affect the growth and extent of plant roots including soil composition and heterogeneity, nutrient distribution, and water availability [e.g., *Waisel et al.*, 2002; *Caldwell and Pearcy*, 1994; *Stone and Kalisz*, 1991]. The importance of soil strength and nutrient availability notwithstanding, this work focuses on the role of climate, and precipitation in particular, in determining the depth of plant roots.

[3] A typical half-life for roots ranges from a few weeks up to a year [*Fitter and Hay*, 2002]. This timescale is long enough so that the hourly to daily dynamics of infiltration are not important, and it also is short enough to enable plant roots to respond plastically to the environment. Thus climate should have power to explain root depth around the globe. Indeed, *Stephenson* [1990] correctly classified vegetation type for 60% of 241 sites in North America on the basis of the timing and intensity of water supply and potential evapotranspiration. A number of scholars have reported on the plastic response of plant roots, and *Schenk* [2005] asserts that roots should be shallow in both cold environments and wet environments (the former because of lack of demand for water and the latter because of the abundance of supply), and deep in warm and seasonally dry environments. Much of the empirical literature supports this assertion.

1.1. Field Measurements of Root Depth

[4] While more difficult to examine than aboveground biomass, roots and their distributions have been the subject of many investigations over the past decade [e.g., *Waisel et al.*, 2002]. In an early comprehensive review, *Jackson et al.* [1996] reported on 250 root studies; they found that tundra, boreal forests, and grasslands have the shallowest roots. *Canadell et al.* [1996] report a maximum root depth of 68 m for *Boscia albitrunca* in the central Kalahari, but values of only 0.3 m for some tundra species. Figure 2 from *Cairns et al.* [1997] indicates that tree-root biomass is greater for temperate forests than for tropical or boreal forests. In an extensive analysis, *Schenk and Jackson* [2002a] examined data on 475 root profiles for 209 different geographic locations and found that climate explained the greatest proportion of variability in rooting depth, more so than plant or soil type. Mean root depth increases with decreasing latitude outside of the tropics, and annual potential evapotranspiration and rainfall account for the largest percent of variance in root depth; the deepest roots are found under Mediterranean climates [*Schenk and Jackson*, 2002a]. For water-limited ecosystems, *Schenk and Jackson* [2002b] examined 1300 records of root depth; they report an increase of root depth with annual precipitation and deeper roots for climates in which evapotranspiration demand and precipitation are out of phase. *Schenk and Jackson* [2005] built an empirical model to predict the probability of deep

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roots based on climate and soil, and they calculated the highest probabilities of deep roots for seasonal tropical climates. Consistent with this prediction, *Nepstad et al.* [1994] found very deep roots (18 m) in an Amazonian forest for the purpose of maintaining transpiration throughout the seasonal drought. While not denying the importance of variability among species, nutrients, and soil properties, these observational results indicate a primary role for climate in the determination of root depth.

1.2. Models of Root Depth

[5] In light of the hydrologic and ecologic importance of roots, and coupled with the difficulty of field measurements, a number of researchers have proposed models to predict and describe root depth and distribution. *Protopapas and Bras* [1987] employed a numerical model to simulate root growth and development in which the objective of the root system was to maximize plant uptake of water. With this model, they found that differing irrigation and salinity scenarios led to differences in the distributions of root biomasss with depth. In an effort to develop a global data set for use in climate models and terrestrial biosphere models, *Kleidon and Heimann* [1998] and *Kleidon* [2004] predicted root depth by maximizing net primary productivity with a simple hydrologic model. In their work, the cost and benefit of deeper roots were incorporated implicitly in the formulation for water uptake. The results indicate that the seasonality and synchronicity of precipitation and potential evapotranspiration have a significant effect on root depth [*Kleidon and Heimann*, 1998; *Kleidon*, 2004].

[6] Both *Laio et al.* [2006] and *Collins and Bras* [2007] investigated water-limited ecosystems (i.e., those with precipitation less than potential evapotranspiration) with stochastic rainfall forcing. *Laio et al.* [2006] developed an analytical expression for the vertical distribution of roots under the imposed principle that roots will be distributed such that the long-term mean soil moisture will be vertically homogeneous. Under this condition, the authors found that the shape of the root profile is a direct function of the probability distribution of precipitation depths and that the deepest roots are predicted in the environments for which precipitation and potential evapotranspiration are approximately equal [*Laio et al.*, 2006]. *Collins and Bras* [2007] employed a numerical model to determine the vertical distribution of roots that would maximize mean annual transpiration for a variety of plant, soil, and climate conditions. They found deeper roots on coarser soils and in wetter and cooler environments, especially those for which evapotranspiration and precipitation were out of phase [*Collins and Bras*, 2007]. In all of these modeling efforts, the objective functions used to determine root depth and distribution were formulated in terms of water uptake or soil moisture.

1.3. Objectives of This Work

[7] This work develops an analytical framework to relate climate, soil, and vegetation characteristics to root depth via carbon costs and benefits. Unlike some other efforts, the goal is not to predict root depth from a few readily measurable parameters. Rather, the intent is to incorporate the relevant variables into a mechanistic model and to focus on the response of root depth to changes in precipitation patterns. What happens to root depth if a climate becomes wetter? Drier? What if rainfall is less intense but more frequent? Under what circumstances would a plant invest in deeper roots? In answering these questions, the goal is to understand better how roots might respond to changes in climate.

[8] A number of key features distinguish the approach presented in this work. First, precipitation is represented as a stochastic process characterized by both frequency and intensity, and the analysis spans both dry and wet environments. Thus the work highlights the role of the intermittency of precipitation and encompasses environments for which transpiration is and is not limited by precipitation. Second, the solution is analytical. In contrast to more complex numerical models, an analytical solution enhances insight by making transparent the dependencies among variables. This choice necessitates some simplification, and this paper focuses on an areally homogeneous process with no lateral inflows of water and no interaction with a water table. Third, root depth is driven explicitly by carbon costs and benefits stemming from the acquisition of soil moisture. This makes clear the biophysical strategy that drives root morphology, which facilitates the use of the model as an interpretive tool. For example, a match between field data and model results lends credence to the interpretation that root depth is driven by water acquisition in that case. Similarly, a mismatch may point to other important factors worthy of investigation, e.g., nutrient availability, the presence of a water table. The contributions of this work are in both the presentation of an analytical and mechanistic model for root depth and in the interpretation of the dependence of root depth on changes to precipitation.

2. Theory

2.1. Cost and Benefit of Deeper Roots

[9] The construction and maintenance of root tissue costs a plant carbon, carbon that could otherwise be used for shoot tissue, reproductive organs, etc. At the same time, deeper roots may enable a plant to access additional soil moisture that allows it to keep its stomata open for a longer period of time. In this case, the construction of deeper roots may result in a net carbon gain. One growth strategy a plant might employ is to add deeper roots only if the incremental carbon cost is outweighed by the associated carbon benefit. This is the fundamental premise that underlies this work; i.e., that a water-optimal root depth can be determined by equating the marginal carbon cost and benefit of deeper roots. This approach does not account for other strategies that plants may employ, such as sending out deep exploratory roots in search of the water table. The results and conclusions are to be interpreted within this context.

[10] The average carbon cost of plant roots per unit area of ground surface as a function of the depth of the root zone can be written as

$$C(Z_r) = \int_0^{Z_r} \frac{\gamma_r \cdot RLD}{SRL} dz \qquad (1)$$

where γ_r is the rate of root respiration [mmol C per g roots per day], *SRL* is the specific root length [cm of roots per g], *RLD* is the root-length density [cm of roots per cm^3 of soil], and the units for $C(Z_r)$ are mmol C per cm^2 per day. Note

that the quantities, γ_r, *SRL*, and *RLD*, are taken to be annual averages, and the respiration rate groups together both the construction and maintenance costs of the roots. The marginal cost of deeper roots is thus

$$\frac{dC(Z_r)}{dZ_r} = \left(\frac{\gamma_r \cdot RLD}{SRL}\right)_{Z_r} \tag{2}$$

where γ_r, *SRL*, and *RLD* are evaluated at the depth of the advancing root front. Equation (2) represents the incremental increase in carbon cost associated with an incremental increase in root depth. It requires knowledge of root characteristics at the advancing front only and presumes nothing about the entire root distribution.

[11] The carbon benefit of all roots to the plant on a per area basis can be determined from the average rate of transpiration:

$$B(Z_r) = WUE \cdot f_{seas} \cdot \langle T \rangle \tag{3}$$

where *WUE* is water-use efficiency [mmol C per cm^3 of H$_2$O per day], 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$_2$O per day] and is a function of the depth of roots. By setting the marginal cost equal to the marginal benefit, the root depth at which the cost of deeper roots begins to outweigh the benefit can be determined:

$$\frac{\gamma_r \cdot RLD}{SRL} = WUE \cdot f_{seas} \cdot \frac{d\langle T \rangle}{dZ_r} \tag{4}$$

[12] Since the average transpiration rate, $\langle T \rangle$, depends on a plant's access to soil moisture, and thus on the depth of roots, equation (4) can be solved for a water-optimal root depth. Such a solution requires the determination of the average rate of transpiration during the growing season as a function of climate, soil, and vegetation characteristics. Many models could be used for this; this work uses a simple model based on the work of *Milly* [1993, 2001] and *Rodriguez-Iturbe et al.* [1999] to represent the response of soil moisture and transpiration to the stochastic nature of precipitation.

2.2. Representation of Soil-Moisture Dynamics

2.2.1. Precipitation

[13] Precipitation is represented as a Poisson process with rain events arriving instantaneously with rate, λ^* [events per day]. The rainfall depth of an event, h, is represented as an exponentially distributed random variable, H, with mean, α [mm]:

$$f_H(h) = \frac{1}{\alpha} \exp\left(-\frac{h}{\alpha}\right) \tag{5}$$

This rainfall model captures variability in the occurrence and depth of rainfall with two parameters (λ^* and α) and has been used in many ecohydrologic investigations in recent years [e.g., *Rodriguez-Iturbe et al.*, 1999; *Laio et al.*, 2001; *Guswa et al.*, 2002]. This precipitation model is intended to represent the rainfall dynamics during the growing season when there is a transpirational demand for

water. Mediterranean or other climates for which rainfall and potential evapotranspiration are out of phase can be modeled by choosing α and $1/\lambda^*$ to be very large. For example, a choice of $\lambda^* = 1/180$ days and $\alpha = 500$ mm could approximate an environment in which soil moisture is depleted by transpiration over the growing season and is replenished by winter rains.

2.2.2. Interception and Soil Evaporation

[14] In response to each rain event, losses due to interception evaporation and soil evaporation are given priority over transpiration. That is, precipitation is first partitioned to interception and soil evaporation, up to maximum depths, Δ_{IE} and Δ_{SE}, respectively, and the remainder is potentially available for transpiration. Given the Poisson nature of rain events, the effect of these losses is then to decrease the rate of arrival of storms that produce enough rain to overcome soil and interception evaporation [*Rodriguez-Iturbe et al.*, 1999]:

$$\lambda = \lambda^* \exp\left(-\frac{\Delta_{IE} + \Delta_{SE}}{\alpha}\right) \tag{6}$$

Since soil and interception evaporation are treated in a similar way, the depths, Δ_{IE} and Δ_{SE}, are combined into a single evaporative depth, Δ. For example, if $\Delta = 3$ mm, then all of the water in a light mist that delivers 2 mm would be lost to interception and evaporation, while a rain of 15 mm would make 12 mm of water potentially available for transpiration.

[15] While numerous studies have employed this representation [e.g., *Rodriguez-Iturbe et al.*, 1999; *Laio et al.*, 2001; *Guswa et al.*, 2002], the effect of these losses on the potential rate of transpiration is usually neglected. As another approach, potential transpiration could be reduced in response to this partitioning of available energy:

$$T_{pot} = \max\left[0, PET - \lambda^* \cdot \overline{\Delta}\right] \tag{7}$$

where *PET* is the potential rate of evapotranspiration, T_{pot} is the average rate of potential transpiration, and $\overline{\Delta}$ is the average depth of evaporation per event. This average can be determined from the maximum evaporative depth, Δ, and the distribution of precipitation depths:

$$\overline{\Delta}(\Delta) = \int_0^{\Delta} xf(x)dx + (1 - F(\Delta)) \cdot \Delta \tag{8}$$

where $F()$ and $f()$ are the cdf and pdf of the rainfall-depth distribution, respectively. For an exponential distribution of precipitation depths, the average evaporation depth per storm is given by the following expression:

$$\overline{\Delta} = \alpha\left(1 - \exp\left(-\frac{\Delta}{\alpha}\right)\right) \tag{9}$$

2.2.3. Infiltration

[16] Beyond the stochastic nature of storm arrivals, the temporal and spatial dynamics of infiltration are not resolved. The root zone is represented as a single unit, and it absorbs all incoming rain up to field capacity, at which point any additional water is lost to drainage and runoff. This model

could represent the upscaled result of piston-flow behavior in which each soil layer is filled instantaneously to field capacity as a wetting front advances. It could also represent the effects of macropore flow with water being channeled along roots. Following a rain event, the average saturation of the root zone is given by the following expression (see also *Milly* [1993]):

$$S^+ = \min\left(S_{fc}, S^- + \frac{h}{nZ_r}\right) \tag{10}$$

where S^+ is the saturation of the root zone following a rain event, S^- is the saturation just prior to the event, S_{fc} is the saturation of the soil at field capacity, h is the depth of rain [mm], n is porosity, and Z_r is the depth of the root zone [mm]. Following infiltration, there is no further redistribution of soil moisture.

2.2.4. Actual Transpiration

[17] Between infiltration events, soil moisture is depleted by plant uptake, and transpiration is represented as the minimum of a supply and demand function. Throughout the literature, there are many representations of transpiration supply as a function of soil moisture [e.g., *Molz*, 1981; *Federer*, 1979, 1982; *Feddes et al.*, 1988; *Milly*, 1993; *Rodriguez-Iturbe et al.*, 1999; *Laio et al.*, 2001]. This work employs the representation of *Milly* [1993]. With this formulation, the rate of uptake is constant and equal to a potential rate until soil moisture drops to a threshold value, S_w, the saturation at which the vegetation can no longer remove water from the soil. Thus the uptake of water as a function of root-zone saturation is given by the following:

$$T(S) = \begin{cases} 0 & S = S_w \\ T_{pot} & S > S_w \end{cases} \tag{11}$$

where T_{pot} is the potential rate of uptake when water is not limiting [mm of H_2O per day]. This formulation makes no assumptions about the distribution of roots and implies that the plant has an ability to compensate for a heterogeneous distribution of soil moisture within the root zone [*Guswa et al.*, 2004; *Guswa*, 2005]. In other words, if there is water somewhere in the root zone, the plant will find it and use it. This representation of plant uptake is a simplification of a more complex set of processes, but *Milly* [2001] has shown that the soil-moisture dynamics that result from this simplified model are similar to those cases when a more gradual decline of transpiration with decreasing soil moisture is modeled explicitly [e.g., *Rodriguez-Iturbe et al.*, 1999].

[18] With this stochastic model, the long-term average rate of evapotranspiration is a function of the climate and soil characteristics (see equation (36) by *Milly* [1993]):

$$\langle T \rangle = \alpha\lambda \cdot \frac{\exp\left[\frac{\theta Z_r}{\alpha}(1-W)\right] - 1}{\exp\left[\frac{\theta Z_r}{\alpha}(1-W)\right] - W} \tag{12}$$

where θ is the plant-available water content:

$$\theta = n(S_{fc} - S_w) \tag{13}$$

W is the ratio of the mean rainfall rate to the mean rate of potential transpiration and is similar to the aridity index

[*UNEP*, 1997] and the inverse of the index of dryness [*Budyko*, 1974; *Milly*, 1993]:

$$W = \frac{\alpha\lambda}{T_{pot}} \tag{14}$$

This quantity differs from the aridity index and the index of dryness in that it uses potential transpiration rather than the potential rate of evapotranspiration (see section 2.2.2 above), and it uses the modified rainfall rate to account for the loss of water to interception and soil evaporation. Thus W and the aridity index, AI [*UNEP*, 1997], are only equivalent when $PET = T_{pot}$ and the transpiration demand is not affected by soil or interception evaporation. For the representation of soil-moisture dynamics employed in this work, a simple relationship can be derived to relate the two indices by combining equations (14), (6), and (7):

$$W = \frac{\alpha\lambda}{T_{pot}} = \frac{\alpha\lambda^*}{PET} \cdot \frac{\exp\left(-\frac{\Delta}{\alpha}\right)}{\max\left[0, 1 - \frac{\alpha\lambda^*}{PET} \cdot \frac{\overline{\Delta}}{\alpha}\right]} = AI \cdot \frac{\exp\left(-\frac{\Delta}{\alpha}\right)}{\max\left[0, 1 - AI \cdot \frac{\overline{\Delta}}{\alpha}\right]} \tag{15}$$

Figure 1 presents W/AI for a range of values of the normalized precipitation loss, Δ/α, and the aridity index, AI. From Figure 1, one can see that the wetness index, W, is a stretched version of the aridity index. W is larger than AI when AI is greater than one (i.e., in wet climates), and W is less than AI when AI is less than one (i.e., in dry climates).

3. Results

3.1. Water-Optimal Root Depth

[19] Combining the equation for the marginal cost and benefit of roots, equation (4), with the expression for mean transpiration, equation (12), gives a solution for the water-optimal root depth. The detailed solution steps are provided in Appendix A, and the result is given here:

$$Z_r = \frac{\alpha}{\theta(1-W)} \ln(X) \tag{16}$$

$$X = \begin{cases} W\left[1 + \frac{\theta}{\alpha}\frac{(1-W)^2}{2A} - \sqrt{\frac{\theta}{\alpha}\frac{(1-W)^2}{A} + \left(\frac{\theta}{\alpha}\frac{(1-W)^2}{2A}\right)^2}\right] & \text{if } W > 1 \\ W\left[1 + \frac{\theta}{\alpha}\frac{(1-W)^2}{2A} + \sqrt{\frac{\theta}{\alpha}\frac{(1-W)^2}{A} + \left(\frac{\theta}{\alpha}\frac{(1-W)^2}{2A}\right)^2}\right] & \text{if } W < 1. \end{cases} \tag{17}$$

$$A = \frac{\gamma_r \cdot RLD}{SRL \cdot WUE} \cdot \frac{1}{T_{pot} \cdot f_{seas}} \tag{18}$$

Equations (16)–(17) indicate that root depth, Z_r, is a function of just three variables: W, α/θ, and A. W is a measure of the wetness of the climate; values greater than one indicate climates for which infiltration exceeds transpiration demand; α/θ is a characteristic depth to which rainwater infiltrates [mm], and it integrates both climate and soil characteristics. The parameter, A, which has dimensions
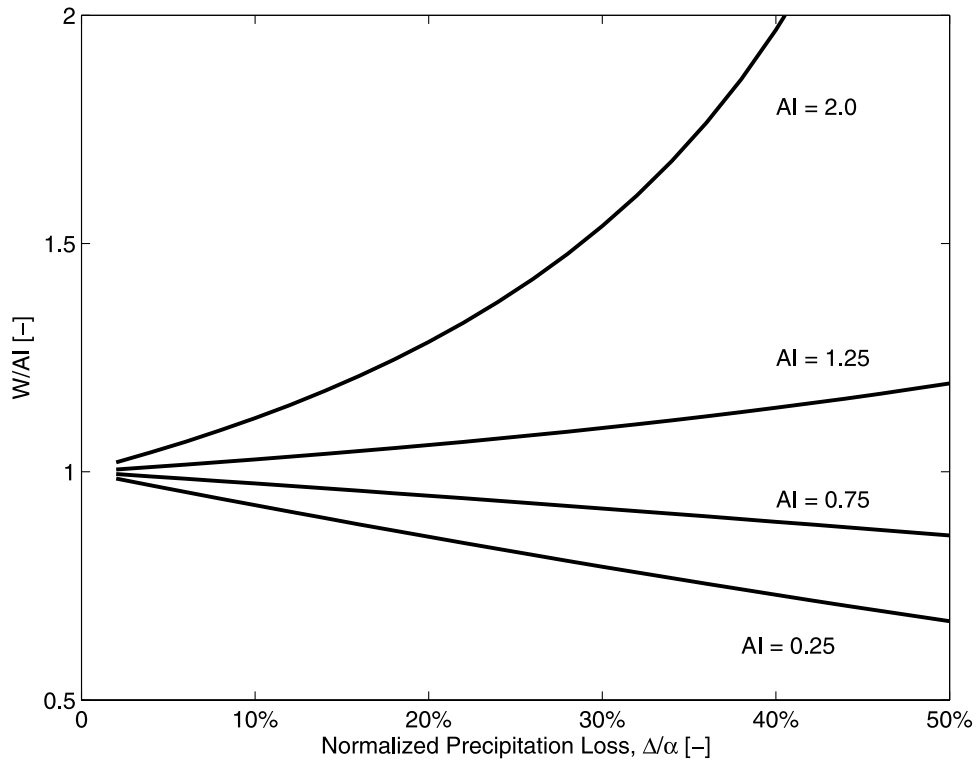
Figure 1. Ratio of the wetness index, $W = \alpha \lambda / T_{pot}$, to the aridity index, $AI = \alpha \lambda^* / PET$, as a function of the aridity index and the normalized loss of precipitation to interception and bare-soil evaporation, Δ/α.

of inverse length [mm^{-1}], represents the cost of deeper roots relative to the potential benefit; the first term on the right-hand side of equation (18) represents the increase in transpiration needed to justify a unit depth increase in the rooting depth. As a whole, A represents the transpiration cost per unit length of increase in root depth, expressed as a fraction of the potential transpiration rate. Larger values of A indicate roots that are more expensive to maintain.

[20] The case of $W = 1$ represents an interesting singularity. For values of W less than one, the plant cannot meet transpiration demand, independent of root depth; i.e., transpiration, and, therefore, carbon assimilation and root depth, are fundamentally limited by the availability of water. Indeed, when $W \rightarrow 0$, there are no positive solutions for Z_r. For $W > 1$, the plant has the potential to meet transpiration demand given deep enough roots; in this case, adding roots at depth may be a waste of resources if the transpiration demand can be met with shallower roots.

3.2. Illustrative Example: Nylsvley, South Africa

[21] The analytical model presented herein is intended to provide insight to the dependencies of root depth on climate, soil, and vegetation characteristics if water acquisition were the only function driving the morphology of roots. The large number of parameters and variables that appear in equations (16)–(18), however, limits the predictive utility of this model when compared to the more parsimonious models of *Holdridge* [1947], *Budyko* [1974], *Stephenson* [1990], etc. Nonetheless, the model results can be compared to some field data to verify the reasonableness of the predictions. Such a comparison requires extensive data on soil, vegetation, and climate, and also requires an environment subject to the simplifications articulated above

(e.g., no interaction with a water table, relatively homogeneous soils, flat topography, root morphology driven by water acquisition). The Nylsvley savanna in South Africa is a well-studied ecosystem [*Scholes and Walker*, 1993] that meets these requirements.

[22] The climate in Nylsvley is characteristic of a savanna — a warm, dry winter (April through September) followed by a hot, wet summer (October through March). The soils are sandy, and land-cover is approximately one-third woody, one-third grass and forbs, and one-third bare soil [*Scholes and Walker*, 1993]. Annual rainfall is approximately balanced by evapotranspiration (586 and 581 mm, respectively), and evapotranspiration is partitioned to interception (90 mm), bare-soil evaporation (275 mm), and transpiration (215 mm). A dominant tree is *Burkea Africana*, and detailed data for this plant, along with climate and soil parameters, are taken from *Scholes and Walker* [1993] and are reported in Table 1. All parameters for the model are measured directly, with the exception of the depth of bare-soil evaporation from beneath the canopy of *Burkea Africana*. This is estimated by presuming that transpiration comes from the vegetated two-thirds of the land-surface (i.e., that the transpiration rate for vegetated areas is 215 mm/66% = 326 mm per year), and selecting the value for Δ such that the predicted transpiration matches this value. This results in a value of Δ equal to 5 mm per event, of which 2 mm is due to interception [*Scholes and Walker*, 1993] and 3 mm results from under-canopy soil evaporation.

[23] These environmental conditions correspond to $W = 0.36$, $\theta = 0.10$, and $A = 1.5 \times 10^{-5}$ mm^{-1}. For this system, the marginal cost-benefit model predicts a water-optimal root depth of one meter, which matches the observations in

Table 1. Climate, Soil, and Vegetation Parameters for *Burkea Africana* in the Broad-Leaved Savanna of Nylsvley, South Africa [*Scholes and Walker*, 1993]

Variable	Symbol	Value	Units
Event frequency	λ*	0.167	events per day
Mean event depth	α	15	mm per event
Evaporation depth	Δ	5	mm per event
Potential evapotranspiration	PET	5.7	mm/day
Length of growing season	f_{seas}	0.5	fraction of year
Porosity	n	0.42	-
Field capacity saturation	S_{fc}	0.29	-
Wilting point saturation	S_w	0.06	-
Water-use efficiency	WUE	0.0864	mmol C per cm^3 H$_2$0
Mean root respiration rate	γ	0.16	mmol C per g roots per day
Specific root length	SRL	1000	cm per g roots
Root-length density	$RLD|_{Z_r}$	0.02	cm/cm^3
Depth of root zone	Z_r	100	cm

Nylsvley [*Scholes and Walker*, 1993]. The conceptual understanding of this savanna (flat terrain, no water table, roots driven by water acquisition) matches the premise of the carbon cost-benefit model, and the root data match the model results. This is not intended as a full validation of the approach, but these results give confidence that the model may be used to provide insight to the response of vegetation and roots to climate.

[24] Since the measurements of many of the vegetation characteristics (fine root biomass, root respiration) are subject to uncertainty, it is also worth understanding the sensitivity of the water-optimal root depth to these quantities. All show up in the parameter, A, (see equations (16)–(18)), and a doubling and halving of this variable leads to water-optimal root depths of 84 and 120 cm, respectively, for *Burkea Africana*. While a doubling or halving of A is required to achieve this range, the root depth is more sensitive to the plant-available water content (θ) and the precipitation characteristics (α and λ). Root depths of 84 and 120 cm result from a 25% increase and 20% decrease in θ, respectively, or a 30% change in precipitation frequency (increase or decrease). Only a 10% change in the mean rainfall depth, α, is needed to give root depths of 84 and 120 cm.

3.3. Dimensionless Water-Optimal Root Depth

[25] The expression for water-optimal root depth given by equations (16)–(18) can be further simplified by making the variables dimensionless. Normalizing the root depth, Z_r, by the characteristic infiltration depth, α/θ, leads to the following:

$$\frac{Z_r}{\alpha/\theta} = \frac{\ln\left(W\left[1 + \frac{1}{2}\beta(1-W)^2 \pm \sqrt{\beta(1-W)^2 + \left(\frac{1}{2}\beta(1-W)^2\right)^2}\right]\right)}{(1-W)} \tag{19}$$

$$\beta = \frac{\theta}{\alpha A} = \frac{\theta}{\alpha} \cdot \frac{SRL \cdot WUE}{\gamma_r \cdot RLD} \cdot T_{pot} \cdot f_{seas} \tag{20}$$

In its dimensionless form, the water-optimal root depth is a function of two variables: the wetness of the climate, W, and

a variable, β, that incorporates climate, soil, and vegetation characteristics. For a given climate and soil (i.e., constant λ, α, T_{pot}, and θ), an increase in β represents a decrease in the relative cost of roots (see equation (18) above). Alternately, for given soil and vegetation characteristics and a given value of W, an increase in β represents an increase in the frequency of rain events and a decrease in their intensity. In this case, an increase in β can be interpreted as moving to conditions for which the intermittency of events becomes less important, i.e., conditions for which W characterizes the day-to-day weather as well as the long-term climate. Thus overall, increasing β represents a move to more efficient conditions for water acquisition, whether that efficiency comes through cheaper roots or a more constant supply of precipitation.

[26] Figure 2a presents a plot of the normalized root depth versus W and β as both a surface and a contour plot. For reference, the characteristics of the Nylsvley site ($W = 0.36$, $\beta = 440$, and $Z_r\theta/\alpha = 6.5$) are included as the black circle. The normalized root depth, $Z_r\theta/\alpha$, represents the depth of the root zone as a multiple of the characteristic depth of infiltration. Figure 2a shows that this quantity has a peak at a wetness index of one except in the case of very small values of β (low frequency or seasonal rain events).

[27] The normalized root depth increases less than linearly with β for the range of variables presented. Thus while the normalized root depth increases with increasing β, actual root depth decreases if the increase in β is due to a change in θ/α, i.e., due to an increase in plant-available water content or a decrease in precipitation intermittency. Near $W = 1$, the actual root depth, Z_r, increases with the characteristic infiltration depth, α/θ, at a rate that is less than linear. Away from $W = 1$ and at larger values of β, the contour lines turn parallel to the β-axis, indicating that the normalized root depth is less dependent on β. This is synonymous with a near linear dependence of Z_r on the characteristic infiltration depth.

[28] Figure 2b presents the efficiency of plant uptake as a function of W and β. That is, it presents actual transpiration normalized by the available water supply ($\alpha\lambda$) or demand (T_{pot}), depending on which is limiting. These efficiencies are lowest for values of W approaching 1 and 0. The singularity at $W = 1$ represents the transition between supply limiting and demand limiting conditions; as W approaches 0, the climate is too dry to support vegetation. As one might expect, the efficiencies also increase with increasing β, i.e., with increasing efficiency of water acquisition.

3.4. Effect of Climate

[29] The dimensionless nature of equations (19) and (20) provides a compact means of relating root depth to characteristics of climate, vegetation, and soil. This compactness can hinder intuitive interpretation, however. Therefore Figures 3 and 4 present root depth as a function of physically meaningful and intuitive climate variables, while holding soil and vegetation parameters constant (Table 2). The specific parameter choices are not intended to represent any particular ecosystem or plant community but rather are representative of values found in the literature; references for these data are provided in Table 2.
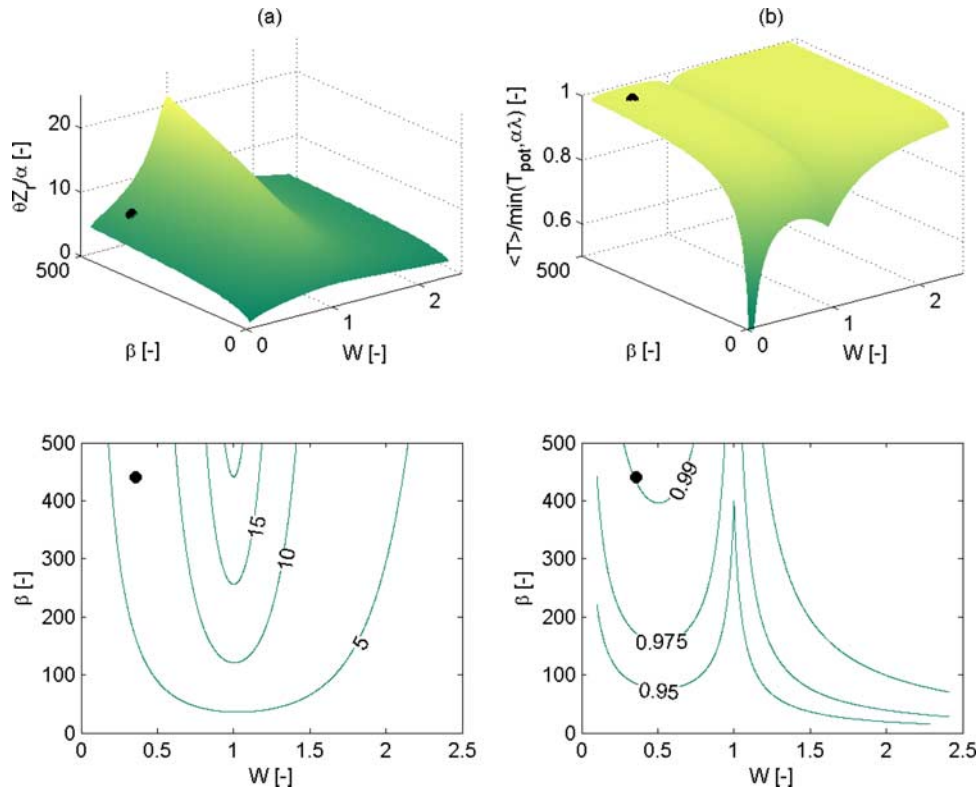
Figure 2. (a) Normalized water-optimal root depth, $\theta Z_r/\alpha$, and (b) efficiency of plant uptake, $\langle T \rangle/\min[T_{pot}, \alpha\lambda]$, as functions of the wetness of the climate, $W = \alpha\lambda/T_{pot}$, and the dimensionless variable, β, representing the efficiency of water acquisition. The conditions for *Burkea Africana* from the Nylsvley savanna are given by the black circle.
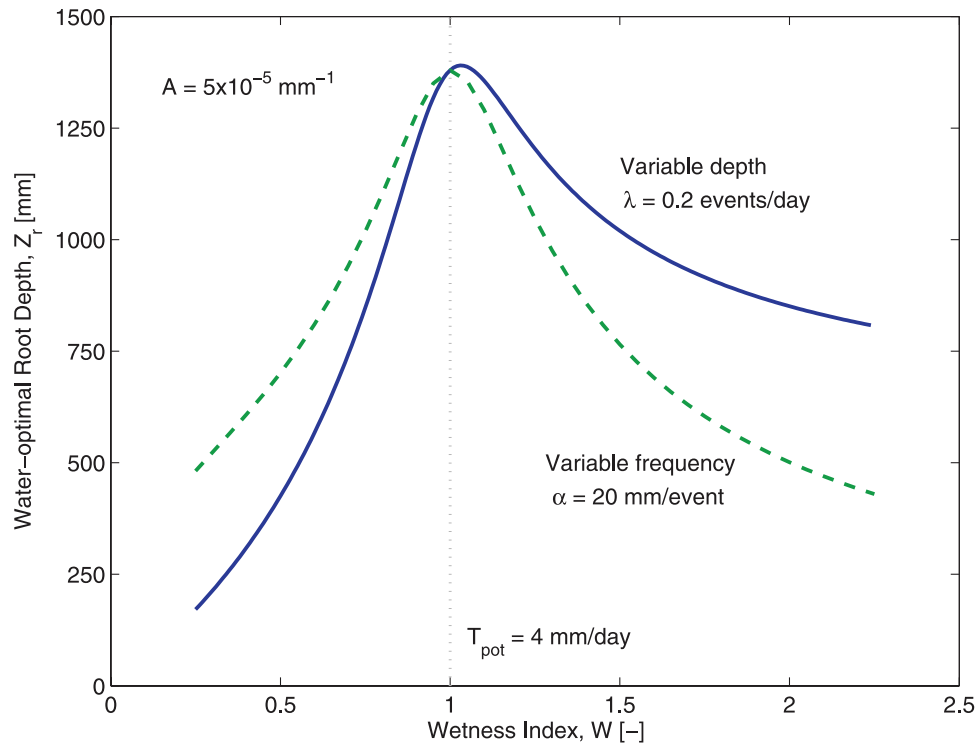

Figure 3. Water-optimal root depth, Z_r [mm], as a function of mean annual precipitation, characterized by the wetness index, $W = \alpha\lambda/T_{pot}$, for constant soil and vegetation parameters (see Table 2). The dashed line represents the effect of changing the frequency of precipitation while the solid line represents the effect of changing the mean depth of events.
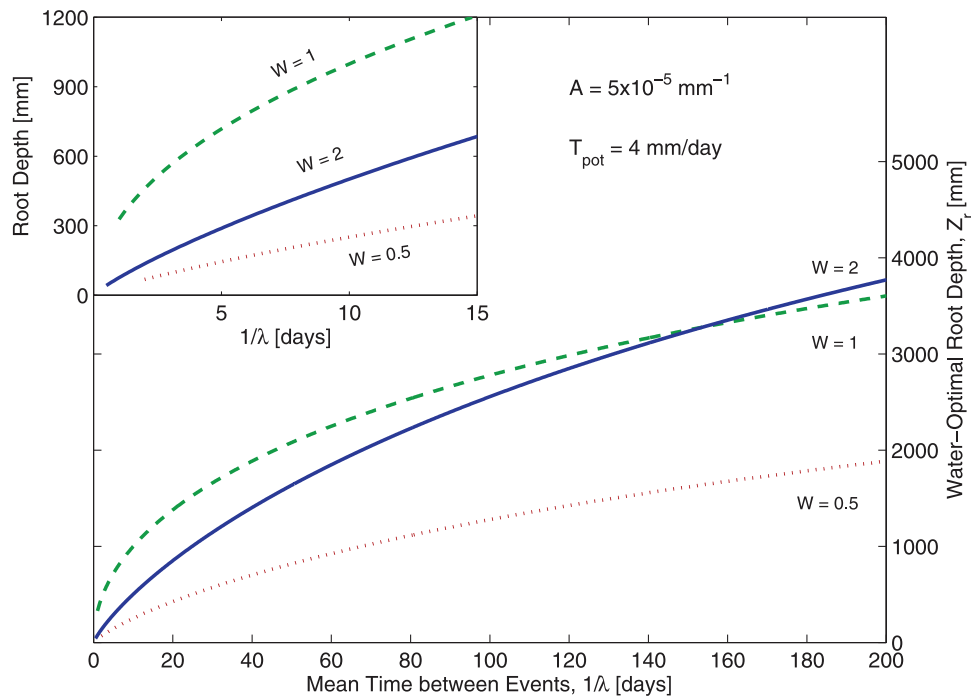
Figure 4. Water-optimal root depth, Z_r [mm], as a function of precipitation frequency, λ [events/day], for constant soil and vegetation parameters (see Table 2). The three curves represent different values of the wetness index (0.5, 1.0, 2.0).

[30] Figure 3 presents the water-optimal root depth as a function of mean rainfall, quantified as a change in the wetness index. The dashed line represents the case of changing the mean rainfall rate by changing the frequency of events (and holding the mean depth constant at 20 mm/event), while the solid line shows the effect of changing the average depth of an event (and holding the frequency constant at 0.2 events/day). The two curves intersect at a wetness index of one. For the solid curve, the mean infiltration depth ranges from 10 to 40 mm/event for $W = 0.5-2$. Over the same range of $W = 0.5-2$, the mean time between infiltration events varies from approximately once per week to nearly every other day for the dashed curve. Both curves show a maximum in rooting depth near a wetness index of one. For the solid line, the peak is shifted to a slightly larger value of W. For wet environments ($W > 1$), root depth decreases with increasing wetness and shows a greater sensitivity to precipitation frequency than depth. For dry environments ($W < 1$), root depth increases with increasing wetness and is more sensitive to depth than frequency.

[31] Figure 4 presents the dependence of the water-optimal root depth on the frequency of precipitation events for three values of the wetness index: 0.5 (dotted line), 1.0 (dashed line), and 2.0 (solid line). The inset figure shows behavior at higher frequencies (rain events occurring on the daily to weekly scale), and the deepest roots are predicted for the case with $W = 1$. As the frequency of events decreases, eventually the curve for $W = 2$ overtakes the others. This shift of the peak in root depth to larger values of W as the frequency of precipitation

decreases can also be seen in Figure 2a (small values of β).

4. Discussion

[32] Figures 2 through 4 present water-optimal root-depth results for a variety of soil, plant, and climate characteristics. One should take care in interpreting these figures across the full range of parameter values, however, as the fundamental variables are not wholly independent. For example, it is likely that large changes in annual precipitation or potential transpiration would be accompanied by concomitant changes in soil and vegetation characteristics. Nevertheless, these results provide insight to the effects of

Table 2. Parameter Values Used in the Creation of Figures 3 and 4 and the Range of Values Found in the Literature[a]

Parameter	Value	Range	Units	Sources
θ	0.18	0.06–0.25	-	6
γ_r	0.5	0.15–2	mmol C/(g roots-day)	1, 2, 4, 5, 11
SRL	1500	800–6500	cm/g	4, 7, 10, 11
RLD	0.10	0.02–270	cm/cm^3	3, 4, 11
WUE	0.33	0.05–0.56	mmol C/(cm^3 H$_2$0)	7, 8, 9, 11
T_{pot}	4	0–7.5	mm/day	12
f_{seas}	0.5	0–1	-	
A	5×10^{-5}	-	mm^{-1}	

[a]Note that the range of values reported for root-length density (RLD) applies to the entire root zone not just the advancing root front. The referenced sources are as follows: (1) *Burton et al.* [2002], (2) *Burton and Pregitzer* [2003], (3) *Caldwell* [1994] (4) *Eissenstat* [1997], (5) *Fahey and Hughes* [1994], (6) *Federer et al.* [2003], (7) *Fitter and Hay* [2002], (8) *Kramer and Boyer* [1995], (9) *Larcher* [2003], (10) *Pregitzer et al.* [2002], (11) *Scholes and Walker* [1993], (12) *UNEP* [1997].

climate and how root depth might change in response to perturbations of precipitation intensity and frequency.

[33] Figures 2a, 3, and 4 show that the maximum root depth coincides with a wetness index of approximately one. Drier climates do not have the water to support deep roots, and deeper roots are a waste of resources in wetter climates. This result is consistent with the finding that rooting depth increases with increasing aridity index up to subhumid and then decreases going to humid environments [*Schenk and Jackson*, 2002a]. Decreasing the frequency of precipitation events (and increasing their intensity) generally leads to an increase in root depth when total rainfall, plant and soil characteristics, and evapotranspiration are held constant. The intermittency in precipitation also introduces an inefficiency in the system; for a given value of the wetness index, the ratio of actual transpiration to the maximum possible decreases as precipitation events become less frequent (Figure 2b). The vegetation lets some water escape, as it is not worth constructing roots so deep as to capture all of the rain from rare events. This inefficiency produces a related shift in the peak of the water-optimal root depth to larger values of W as precipitation becomes less frequent (Figures 2 and 4).

[34] For dry climates ($W < 1$), changes to annual precipitation also change the maximum possible evapotranspiration and, therefore, carbon assimilation. For this reason, root depth is quite sensitive to changes in the wetness index (Figure 3); as more water is added to the system, i.e., as W increases, the root depth increases. These results for water-limited ecosystems are consistent with the empirical data from *Schenk and Jackson* [2002b] and the modeling work of *Collins and Bras* [2007] and *Laio et al.* [2006]. Figure 3 also indicates that, for the same change to the wetness index, the water-optimal root depth is more sensitive to changes in precipitation depth than frequency. In these water-limited environments, roots will chase the water down into the soil.

[35] In wet environments with frequent rain, root depth generally decreases with increasing wetness (Figures 2 and 3). Root depth also decreases with increasing frequency of rain events when the wetness is held constant (Figures 2 and 4). Both of these results are consistent with the observational results of *Schenk and Jackson* [2002a], who found that root depth in the tropics is negatively correlated with annual precipitation and positively correlated with the length of the dry season. Unlike dry climates, which always produce deeper roots as the wetness index approaches one, the deepest roots in wet climates shift to larger and larger values of the wetness index as the frequency of precipitation events decreases (Figure 4). Qualitatively, this result is consistent with the existence of very deep roots in the seasonally wet tropics [e.g., *Nepstad et al.*, 1994]. In contrast to dry environments, root depth in wetter climates is more sensitive to changes in precipitation frequency than from changes in depth (Figure 3). Increasing the depth of rain events, but not their frequency, may not be a significant benefit to a plant that already has roots deep enough to meet its long-term transpiration demand. Increasing the frequency of precipitation, however, means that the plant can reduce the size of its storage reservoir (i.e., the depth of its root zone) and still satisfy its transpiration needs.

[36] In addition to the focus on precipitation, the results of this work also provide insight to the role of soil and vegetation characteristics. The effect of soil texture comes through the plant-available water content, θ. A larger value of this quantity indicates that more water is held per unit of soil, and, thus, a plant can access more water with shallower roots. While climate parameters (α, λ, T_{pot}) show up in all three of the dimensionless variables from equations (19) and (20), θ appears in only two of the three. Since it is always paired with the variable, α, increasing θ has the same effect on root depth as making rain events shallower and more frequent (holding W constant). With more water held in the pore space, one might also expect that more water would be lost to soil evaporation, and thus, a change in θ might also warrant a change in Δ_{SE}. For example, if soil evaporation affects the top 3 cm, Δ_{SE} might be 6 mm for $\theta = 0.2$ and 3 mm for $\theta = 0.1$. Therefore the effects of large changes in θ may need to be examined in conjunction with changes to T_{pot}.

[37] In equations (19) and (20), the vegetation parameters (e.g., SRL, WUE) are contained in the dimensionless variable, β. Larger values of β are indicative of vegetation that is more efficient with respect to water uptake and use, e.g., larger WUE or a lower rate of root respiration. Such variations in plant characteristics are reflected in the efficiency of plant uptake (Figure 2b); larger values of β lead to more efficient use of available water. This efficiency is due to a deeper root system that can be constructed at a lower carbon cost.

[38] This analysis has focused on the allocation of carbon to roots and the conditions for which this results in a net carbon benefit. A similar analysis can be performed with respect to aboveground biomass; an increase in leaf area may increase the potential rate of transpiration and result in a carbon gain. This latter process was not represented in the current work, and potential transpiration, T_{pot}, was considered to be a known parameter. Thus as articulated in the opening paragraph of this discussion, care should be taken in interpreting these results across a wide range of precipitation variability. Future efforts could consider allocation of carbon to both roots and shoots in a similar cost-benefit framework.

5. Conclusions

[39] This paper presents an analytical expression for root depth as a function of vegetation, soil, and climate characteristics. The fundamental premise is that the vertical extent of plant roots is determined by the depth at which the marginal carbon cost is equal to the marginal carbon benefit. Additionally, this model presumes that roots respond plastically to the environment at timescales of weeks to months and that plants will find and use the water within their root zones. Infiltration is driven by stochastic rainfall in which precipitation events are characterized by their depth and frequency, and root depth is predicted as a function of these characteristics for wet and dry environments.

[40] Consistent with empirical data, the results of this analysis reveal that root depths are greatest when rainfall and potential evapotranspiration are approximately equal. In dry environments, there is not enough water to justify deep roots; in wet environments, shallow roots may be sufficient to meet the demand. In addition to the total amount, the

intermittency of rainfall also affects root depth. Decreasing the frequency of precipitation, while holding total rainfall constant, leads to deeper roots and decreases the efficiency of the soil-plant-atmosphere system. This inefficiency leads to a shift in the deepest roots to wetter environments ($W > 1$) as the frequency of rain decreases. In water-limited ecosystems, root depth increases with increases in the wetness index, and the water-optimal root depth is more sensitive to changes in precipitation depth than frequency. The opposite is true in wet environments. Root depth generally decreases with increasing W, and root depth is more sensitive to changes in frequency rather than depth. In the context of predicting the effects of climate change, these results highlight the importance of not only changes to total rainfall but also changes to the timing and intensity of precipitation.

Appendix A: Solution Steps for Equations (16)–(18)

[41] From *Milly* [1993], the average rate of transpiration is given as a function of root depth, Z_r, along with climate and soil characteristics:

$$\langle T \rangle = T_{pot} W \cdot \frac{\exp[BZ_r] - 1}{\exp[BZ_r] - W} \tag{A1}$$

$$B = \frac{\theta(1 - W)}{\alpha} \tag{A2}$$

The derivative of $\langle T \rangle$ with respect to depth is thus

$$\frac{d\langle T \rangle}{dZ_r} = T_{pot} W \cdot \frac{(1 - W)B \exp(BZ_r)}{(\exp(BZ_r) - W)^2} \tag{A3}$$

Substituting this expression into the cost-benefit relation given by equation (4) gives

$$\frac{\gamma_r \cdot RLD}{SRL} = WUE \cdot f_{seas} \cdot T_{pot} W \cdot \frac{(1 - W)B \exp(BZ_r)}{(\exp(BZ_r) - W)^2} \tag{A4}$$

Simplifying this equation and solving for root depth, Z_r, results in the following sequence of steps. Rearranging equation (A4) gives

$$A = \frac{\gamma_r \cdot RLD}{SRL \cdot WUE} \cdot \frac{1}{f_{seas} \cdot T_{pot}} = W \cdot \frac{(1 - W)B \exp(BZ_r)}{(\exp(BZ_r) - W)^2} \tag{A5}$$

Letting $X = \exp(BZ_r)$ and substituting into equation (A5) gives

$$X^2 - 2WX + W^2 = \frac{W(1 - W)}{A}BX \tag{A6}$$

Solving for X gives

$$X = W + \frac{W(1 - W)}{2A}B \pm \sqrt{\frac{W^2(1 - W)}{A}B + \left(\frac{W(1 - W)}{2A}B\right)^2} \tag{A7}$$

or

$$X = W\left[1 + \frac{\theta}{\alpha}\frac{(1 - W)^2}{2A} \pm \sqrt{\frac{\theta}{\alpha}\frac{(1 - W)^2}{A} + \left(\frac{\theta}{\alpha}\frac{(1 - W)^2}{2A}\right)^2}\right] \tag{A8}$$

and

$$Z_r = \frac{\alpha}{\theta(1 - W)} \ln(X) \tag{A9}$$

The expression for root depth as a function of climate, soil, and vegetation characteristics requires selection of the two solutions offered in equation (A8). Rewriting equation (A8) gives

$$X = W\left[\sqrt{1 + 2Y + Y^2} \pm \sqrt{2Y + Y^2}\right] \tag{A10}$$

$$Y = \frac{\theta}{\alpha}\frac{(1 - W)^2}{2A} \tag{A11}$$

where Y is always non-negative. If the positive root is taken in equation (A10), the term in brackets will be greater than or equal to one; if the negative root is taken, the term in brackets will lie between zero and one. Consider now equation (A9) for the case of $W < 1$. In this case, $\ln(X)$ must be positive to give a physically meaningful root depth; this can happen only if the positive root in equation (A8) is taken. In the case of $W > 1$, X must be less than one, and thus, the negative root in equation (A8) is taken. Note that these are necessary but not sufficient conditions, as X is further modulated by W, and there is no positive solution for Z_r as $W \to 0$.

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