

Soil-moisture limits on plant uptake: An upscaled relationship for water-limited ecosystems

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Abstract

Transpiration in water-limited ecosystems is controlled by the availability of soil moisture. Rain events in these natural environments may only partially wet the root zone, leading to a heterogeneous distribution of available water. This spatial variability coupled with the non-linearity of the function relating local uptake to local saturation produces a non-unique relationship when these quantities are scaled up. This work proposes a simple multi-valued relationship between plant transpiration and average root-zone saturation predicated on the distinct spatial patterns of wetting and drying. Predictions of daily transpiration from an upscaled model that uses this relationship match closely those from a vertically resolved model that employs an Ohm's law analogy for plant uptake.

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1. Introduction

Water-limited ecosystems are characterized by low annual precipitation, infiltration events that may only partially wet the vegetation root zone, and transpiration that is limited by the availability of soil moisture. Such environments include savannas, steppes, and scrublands, and have been the focus of recent ecohydrologic studies (e.g., [32,27,23,36,21,15,28,31,16]). The intermittent and variable nature of rainfall coupled with the non-linear character of infiltration and evapotranspiration creates a complex dynamical system. Under conditions in which the root zone is only partially wet by precipitation events, Federer [10] and Guswa et al. [15] demonstrated that vertical variability in soil moisture affects plant uptake and vegetation health, and Guswa et al. [16] suggested dimensionless groups of environmental

parameters that could be used to determine appropriate model resolution.

In some cases, however, a vertically resolved representation of the soil column may not be desirable or feasible. Such applications require a function that captures the limiting effects of low soil moisture on transpiration without resolving vertical variations in saturation or uptake. Celia and Guswa [4] propose that local non-linear functions lead to multi-valued relationships when represented at larger scales. The present work builds on this idea along with the recognition that vertical patterns of infiltration and uptake are distinct: water infiltrates the soil column from the top down; soil moisture is removed from those regions that contain water and roots. Based on these ideas, an efficient relationship between daily transpiration and average root-zone saturation is presented. No vertical variability is included; the entire soil column is treated as a homogeneous bucket. Instead, average saturation along with the knowledge of whether the root zone is getting wetter or drier is used to determine daily transpiration. Since this work focuses

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on representations of soil-moisture dynamics with no vertical resolution, bare-soil evaporation is not treated separately from transpiration.

In Section 2 of this paper, some background is provided on models of plant uptake and the effects of vertical resolution on predictions of transpiration. More detail on these subjects can be found in Guswa et al. [15] and Guswa et al. [16]. Section 3 presents the theoretical and conceptual development of a new multi-valued relationship between daily transpiration and average root-zone saturation. Section 4 presents a comparison of daily transpiration predicted by three models: a vertically resolved representation; a model with no vertical resolution for which the function relating plant uptake to saturation is the same as used in the vertically resolved case; a model which also does not resolve the soil column but which uses the new multi-valued relationship to predict daily transpiration as a function of average root-zone saturation. The goal is to reproduce the uptake behavior of the fully resolved model without resolving any vertical variations in soil-moisture dynamics.

2. Background

In water-limited ecosystems, transpiration can be determined from two limiting conditions: uptake limited by available energy when soil moisture is plentiful and by available water under water-stressed conditions. Thus, plant transpiration can be represented as the minimum of a demand function determined by energy conditions and a supply function that depends on soil-moisture availability [5,10,24,15,11]. This conceptual model can be represented by the following function:

$$T_{\text{act}} = \min(T_{\text{pot}}, U_{\text{max}}) \quad (1)$$

In Eq. (1), T_{act} represents total plant uptake as volume per area per time, T_{pot} is the potential rate of daily transpiration, and U_{max} is the maximum uptake possible by the plant. In this work, Eq. (1) is used to represent transpiration and plant uptake on the time scale of a day; therefore, T_{act} , T_{pot} , and U_{max} represent daily rates.

The representation of plant uptake in water-limited ecosystems requires a function that accounts for the reduction in transpiration caused by depletion of soil moisture in the root zone. One common approach is to use a Type I model based on an Ohm's law analogy (e.g., [34,13,5,17,9,10,35,22,15,18]). With this formulation, uptake is driven by a difference in water potential between the soil and plant. This difference is required to overcome a network of resistances: resistance to flow in the soil and resistance to flow across the root surface and through the roots. Local uptake from a soil layer of thickness Δz is given by

$$u(z, t) = \frac{\psi(z, t) - \psi_p}{R_1(S(z, t)) + R_2} \Delta z \quad (2)$$

where $u(z, t)$ is local uptake as volume of water per area per time, Ψ is the soil–water potential as a function of depth and time, and Ψ_p is the plant potential (note: since Ψ and Ψ_p are represented as potentials rather than suction, their values will be negative). R_1 is a saturation-dependent resistance that depends on soil and root characteristics (saturation is defined as volume of water per volume of void space), and R_2 is vegetation dependent [15]. Because Eq. (2) is applied at the daily scale, $u(z, t)$ is restricted to be greater than or equal to zero (see below for a discussion of diurnal hydraulic lift and redistribution).

As a soil dries, plant stomata close to prevent runaway cavitation and maintain turgor. The uniform saturation and corresponding potential at which stomatal closure begins are defined as S^* and Ψ^* . In the model presented here, the functioning of plant stomata and the associated vulnerability curve are not represented explicitly; rather a critical plant potential is determined, herein referred to as the wilting potential, Ψ_w , and the plant potential, Ψ_p , is constrained to remain above this value. Note that no water will be taken up by the plant if the soil-moisture potential falls to the wilting potential, Ψ_w . Since this potential is the minimum for the plant, it also represents the plant potential at which the most water will be pulled from the soil for a given soil-moisture potential; i.e., such conditions provide the maximum rate of plant uptake. Therefore, integrating Eq. (2) over the root zone (depth = Z_R) with Ψ_p set equal to Ψ_w and combining with Eq. (1) gives an expression for daily transpiration:

$$T_{\text{act}}(t) = \min \left(T_{\text{pot}}, \int_0^{Z_R} \frac{\psi(z, t) - \psi_w}{R_1(S(z, t)) + R_2} dz \right) \quad (3)$$

Because of the branching nature of roots, water flows from the soil to the plant via a number of parallel pathways. With multiple paths for uptake, the root system compensates for spatial variations in soil moisture by extracting water from wet regions at a high rate when some of the roots are water stressed. The extent of this behavior is a consequence of the hydraulic architecture of the roots and the relative magnitudes of R_1 and R_2 . In this paper, this compensating ability is quantified by a parameter, γ , which is defined as the maximum uptake per unit of roots relative to what is needed to meet the daily demand; thus, $1/\gamma$ indicates the minimum fraction of roots that must be wetted to field capacity in order to meet T_{pot} . Since Eqs. (1)–(3) are applied at the daily scale, the compensation parameter can also represent the effects of diurnal hydraulic redistribution or hydraulic lift in which wet roots continue to extract water throughout the night, infusing dry areas with soil moisture that is taken up during the day [7,2,3,24]. Note

that this compensating ability is not something added to the representation given by Eqs. (1)–(3), but comes naturally from the Ohm’s law formulation. Split-root experiments have indicated that values of the parameter γ can range from one to more than two (e.g., 26,19,1,14,6, 12,37).

Fig. 1 presents the maximum rate of local uptake versus local saturation for a woody species (*Burkea africana*) in an African savanna [32]. The y-axis presents the local rate of plant uptake per unit of roots relative to what is required to reach T_{pot} . Curves are presented for three values of plant compensation ($\gamma = 1.3, 2,$ and 4), and each passes through the points $(S_w, 0)$ when transpiration shuts down completely and $(S^*, 1)$ when soil moisture limits plant uptake. When soil water is plentiful (i.e., when saturation is near field capacity), relative local uptake approaches γ (total daily uptake is, of course, constrained to be less than or equal to T_{pot}). The strong non-linearity in the function indicates that local uptake is relatively insensitive to changes in saturation when saturation is high, but quite sensitive when saturation is near S^* .

2.1. Effect of vertical distribution of soil moisture on plant uptake

The non-linearity in Fig. 1 indicates that whole-plant transpiration as a function of available water within the root-zone will depend on the distribution of soil moisture. To illustrate this behavior, Fig. 2 shows the relationship between average root-zone saturation and total plant uptake as a soil dries out. Curves are presented for five different initial conditions, ranging from the entire root zone being at field capacity to just the top 20% of the roots being wetted. Comparison of these

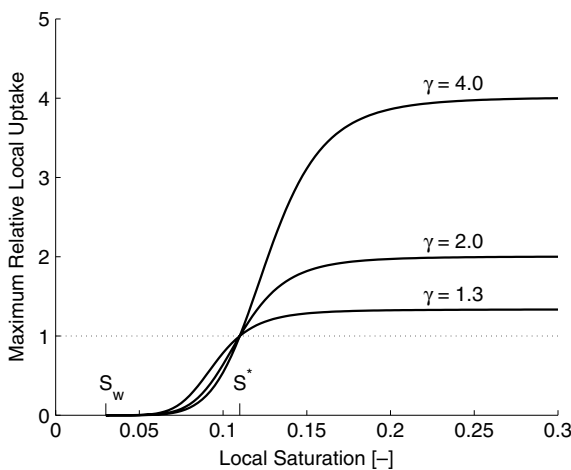


Fig. 1. Local uptake, relative to T_{pot} per unit of roots, as a function of local saturation in the soil when $\Psi_p = \Psi_w$. The three curves represent plants with varying degrees of compensation ability. For this sandy soil, $S_w = 0.03$, $S^* = 0.11$ and $S_{fc} = 0.30$.

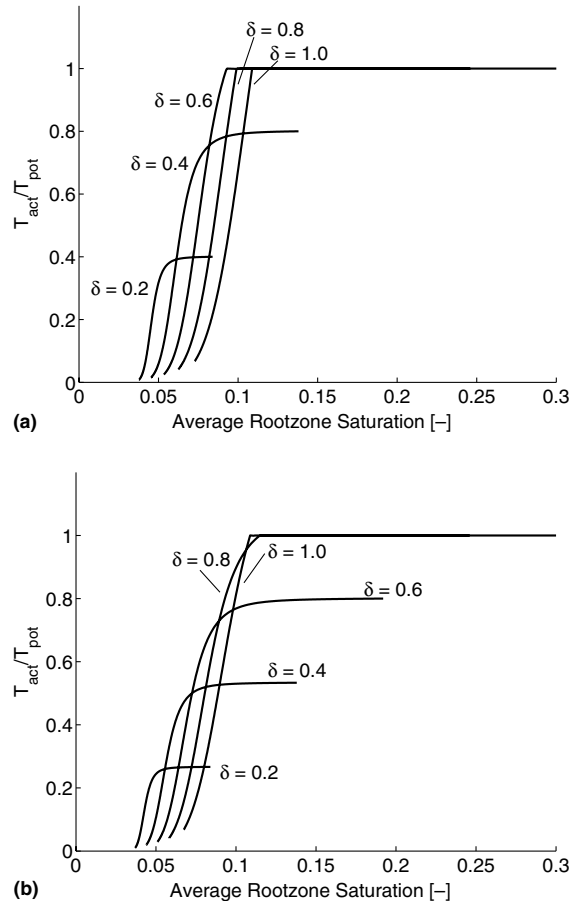


Fig. 2. Relationships between transpiration and average root-zone saturation. δ is the fraction of the soil column initially wetted to field capacity. (a) Drying curves for vegetation with $\gamma = 2.0$, (b) drying curves for vegetation with $\gamma = 1.33$.

curves demonstrates the non-unique character of the relationship between T_{act} and S_{avg} when the root zone is variably wet and the effect of the compensation parameter, γ , on the degree of non-uniqueness. For example, Fig. 2b shows that daily transpiration could range from 60% to 100% of potential when the average root-zone saturation is 0.15. Note that I intentionally refrain from using the word hysteresis to describe these patterns so as not to confuse this behavior with the hysteresis commonly seen in the relationship between capillary pressure and saturation, which is not included here. The non-uniqueness arises as a result of spatial upscaling. A detailed discussion of these results can be found in [16].

3. Theory: proposed upscaled function

Section 2.1 highlighted the effects of vertical variations in soils moisture on the relationship between transpiration and saturation. This implies a minimum vertical resolution necessary to accurately represent

total plant uptake with Eq. (2), and Guswa et al. [16] discusses how to determine the required resolution as a function of dimensionless groups of characteristic environmental parameters. In some instances, however, increasing vertical resolution may not be feasible or desirable, and one may wish to characterize the water content of the entire root zone with a single value (e.g., [30,29,20]). In such cases, a relationship is required to relate total transpiration to average water saturation over the root zone. To do so requires a function that incorporates implicitly the effects of vertical variability in soil moisture on transpiration. In this work, a multi-valued but simple relationship between daily transpiration and average root-zone saturation is proposed. The suggested relationship comes from the premise that infiltration and water uptake are processes with distinct but repeated spatial characteristics.

Infiltration occurs from the top down. In the limiting case, this drives soil moisture toward a binary distribution—wet in the upper layers, dry below. The process of drying extracts soil moisture from the locations with water and roots. This process is self-limiting since uptake drops sharply as saturation falls below S^* . Thus, drying drives the distribution of soil moisture to a state of uniform dryness. Because of these distinct and repeated spatial patterns, this work seeks to use knowledge of whether the soil column is getting wetter or drier in place of an explicit representation of vertical variations in soil moisture.

Consider first the case of water infiltrating into a dry soil with a uniform initial saturation of S_w , corresponding to a soil–water potential of Ψ_w . The soil column will wet from the top down, and the depth of infiltration can be approximated by

$$Z_i = \frac{i}{n(S_{fc} - S_w)} \quad (4)$$

where i is the volume of infiltrating water per unit area and n is porosity. With this approximation of a sharp wetting front, roots shallower than Z_i will be supplied with water at field capacity (defined as the saturation for which gravity drainage becomes negligible relative to potential transpiration) and roots deeper than Z_i will remain dry. The resulting average root-zone saturation is given by

$$S_{avg} = \frac{Z_i}{Z_R} S_{fc} + \left(1 - \frac{Z_i}{Z_R}\right) S_w \quad (5)$$

Since the soil water at depths below Z_i has a potential of Ψ_w , no water will be extracted from that region. The pores shallower than Z_i are filled to field capacity, and local relative uptake can be as high as γ , as indicated by Fig. 1. Thus, immediately following the infiltration event, transpiration is given by

$$\frac{T_{act}}{T_{pot}} = \min \left[\gamma \cdot F \left(\frac{Z_i}{Z_R} \right), 1 \right] \quad (6)$$

where F is the cdf of the root distribution as a function of relative depth, Z_i/Z_R , and $F(Z_i/Z_R)$ gives the fraction of active roots at relative depths shallower than Z_i/Z_R . Solving Eq. (5) for Z_i/Z_R and substituting that expression into Eq. (6) provides a limiting curve for transpiration as a function of average saturation immediately following an infiltration event (i.e., following an increase in average root-zone saturation):

$$\frac{T_{act}}{T_{pot}} = \min \left[\gamma \cdot F \left(\frac{S_{avg} - S_w}{S_{fc} - S_w} \right), 1 \right] \quad (7)$$

For clarity of discussion, the first term inside the brackets will be denoted $W(S_{avg})$:

$$W(S_{avg}) = \gamma \cdot F \left(\frac{S_{avg} - S_w}{S_{fc} - S_w} \right) \quad (8)$$

Following an infiltration event, if fewer than $1/\gamma$ of the roots are wetted, transpiration will be less than potential. For example, if $\gamma = 2$ and only 25% of the roots are wetted to field capacity, actual daily transpiration will be half of T_{pot} . Transpiration will just reach T_{pot} when $W(S_{avg}) = 1$; the average saturation at this point is defined as S' and is given by:

$$S' = F^{-1} \left(\frac{1}{\gamma} \right) \cdot S_{fc} + \left(1 - F^{-1} \left(\frac{1}{\gamma} \right) \right) \cdot S_w \quad (9)$$

where F^{-1} is the inverse of the cumulative distribution of roots; $F^{-1}(1/\gamma)$ gives the relative depth (Z/Z_R) above which $1/\gamma$ of the roots are found. If a precipitation event raises the average saturation above S' , transpiration will meet potential. If the volume of rain is too small, however, daily transpiration will remain below potential at least until the next rain event.

The spatial patterns of drying are distinct from the infiltration fronts of wetting events. As the root zone dries out, water is removed preferentially from those locations where it is readily available—a function of Ψ and the distribution of roots. Fig. 1 indicates that the decrease in local uptake due to a decrease in local saturation from S_{fc} to S^* is minimal. Therefore, local uptake from a layer of soil wetted to field capacity remains nearly constant until the local water content approaches S^* . It is the spatial distribution of water, not the total amount, that governs total uptake at this time. Indeed, the plateaus in Fig. 2 indicate that the rate of transpiration is maintained over a range of average saturations as the readily available water from wet layers is depleted. The average root-zone saturation at which plant transpiration drops from this plateau is a complex function of S^* , γ , and the fraction of the root zone from which water is being extracted. A simple empirical curve for normalized transpiration as a function of average saturation that captures the essence of this range of behaviors is a line that decreases from one to zero as the average saturation drops from S^* to S_w :

$$D(S_{avg}) = \frac{S_{avg} - S_w}{S^* - S_w} \quad (10a)$$

$$\frac{T_{act}}{T_{pot}} = \min[D(S_{avg}), 1] \quad (10b)$$

Note that this relationship is the same as or similar to that of many other empirical representations of plant uptake (e.g., [25,33,30,8]).

$D(S_{avg})$ and $W(S_{avg})$ are two functions that describe the variation of transpiration with average root-zone saturation under conditions of decreasing and increasing soil moisture, respectively. The two functions differ because of the distinct vertical patterns associated with root uptake and infiltration. Fig. 3 presents these two curves for the case of vegetation with a uniform root distribution and $\gamma = 1.33$. For comparison, $D(S_{avg})$ and $W(S_{avg})$ are superposed on top of the curves from Fig. 2b.

Key features of this figure are that $W(S_{avg})$ intersects the right-most points of the drying curves from Fig. 2b and that those curves are close to horizontal between $W(S_{avg})$ and $D(S_{avg})$. These observations and conceptual considerations lead to an upscaled relationship between transpiration and root-zone soil moisture that can be expressed as two rules: one for conditions of decreasing S_{avg} , and one for increasing S_{avg} . As drying removes root-zone soil moisture, T_{act} remains constant until (S_{avg}, T_{act}) intersects the line given by $D(S_{avg})$; at this point, T_{act} decreases as S_{avg} decreases, following the relationship given by $D(S_{avg})$. Under wetting conditions, T_{act} remains constant as S_{avg} increases until (S_{avg}, T_{act}) intersects $W(S_{avg})$; at this point, T_{act} increases with S_{avg} , following $W(S_{avg})$ until $T_{act} = T_{pot}$, where it remains constant despite any further increases in S_{avg} . This algorithm is expressed graphically in Fig. 4; the heavy

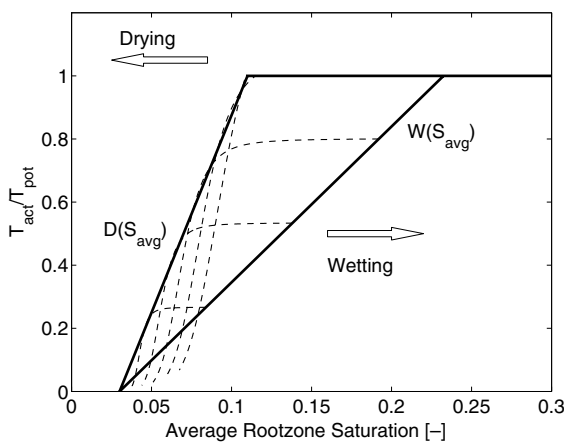


Fig. 3. Relationships between transpiration and root-zone saturation, $D(S_{avg})$ and $W(S_{avg})$, for a plant with a uniform root distribution and $\gamma = 1.33$ (solid lines). These curves are laid over the set of relationships from Fig. 2b (dashed lines). In this example, $S_w = 0.03$, $S^* = 0.11$, $S' = 0.23$, and $S_{fc} = 0.30$.

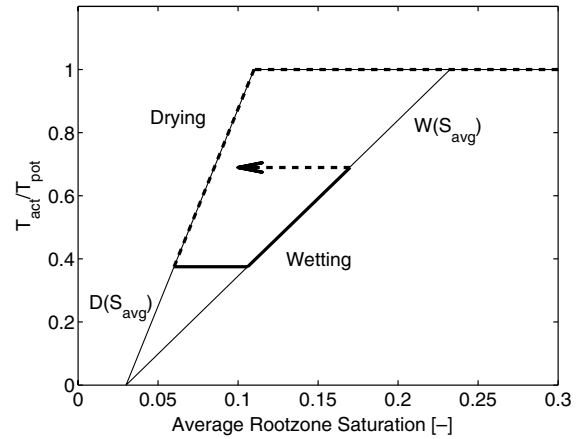


Fig. 4. Graphical representation of the multi-valued upscaled relationship between transpiration and average root-zone saturation. The heavy dashed lines represent examples of paths followed when soil moisture is decreasing; the heavy solid line represents an example of a path traced in response to increasing saturation.

dashed lines represent examples of paths traveled as soil moisture is decreasing, and the heavy solid line indicates a potential path when soil moisture is increasing.

If T_0 represents an initial rate of daily transpiration, then transpiration at some later time is given by one of two functions depending on whether the soil is drying or wetting:

$$\text{Drying : } T(S_{avg}) = \min[T_0, D(S_{avg}) \cdot T_{pot}] \quad (11)$$

$$\text{Wetting : } T(S_{avg}) = \min[\max[T_0, W(S_{avg}) \cdot T_{pot}], T_{pot}] \quad (12)$$

It is important to remember that since the entire root-zone is characterized by a single saturation, the terms wetting and drying are pseudonyms for increasing and decreasing saturation, respectively. Also, the above development says nothing about the time spent on each type of path (wetting versus drying). Rain events drop a significant amount of water in a short time; therefore, the dynamical system of soil and plant spends almost no time on the wetting curve defined by Eq. (12). Rather, that curve is used to determine the point of departure for the drying cycle following a rain event.

The non-linear nature of plant uptake as a function of local saturation indicates that daily transpiration is a function not only of total root-zone soil moisture but also of the distribution of that water throughout the soil column. Because of the distinct and regular spatial patterns of infiltration and uptake, however, a simple multi-valued relationship between daily transpiration and average root-zone saturation can capture the soil-moisture dynamics.

The need for a multi-valued relationship between transpiration and root-zone saturation arises as a consequence of partial rewetting of the root zone and the resulting spatial variability in soil moisture. If this

condition does not exist, the need for a multi-valued relation is obviated. Thus, a multi-valued function would not be required for irrigated or well-watered environments in which infiltration events regularly saturate the entire root zone. More precisely, if rain events regularly bring the average saturation above S' , there would be no need for the multi-valued function. In such cases, the curve, $W(S_{\text{avg}})$, would not play a role, and a one-to-one relationship between transpiration and root-zone saturation, given by Eq. (10b), would suffice.

For a given environment, the potential need for a multi-valued function can be characterized by an updated version of the spatial infiltration index presented by Guswa et al. [15]:

$$I_{I,z} = \frac{\alpha}{(S' - S_w)nZ_R} \quad (13)$$

where α is a characteristic volume of infiltration per unit area and Z_R is the depth of the root zone. A value of $I_{I,z}$ greater than one indicates that a typical rain event will provide enough water to a dry soil to raise the average saturation above S' and correspondingly to raise transpiration to its potential rate. In such a case, a multi-valued relation between transpiration and saturation is not needed. If $I_{I,z}$ is less than one, however, this indicates that a characteristic rain event does not provide sufficient water to a dry soil to bring transpiration up to potential, and a multi-valued function may be required.

4. Numerical experiments

To examine the efficacy of the proposed upscaled relationship between daily transpiration and average root-zone saturation, the results from a set of numerical experiments are presented. Three models predict daily transpiration over 100 growing seasons for a woody species from an African savanna. In one model, the root zone is resolved into 50 vertical layers, each two centimeters in thickness, and Eqs. (1) and (2) are used to simulate uptake from the soil column. This highly resolved representation (hi-res model, hereafter) stands as a surrogate for truth to which results from two other models are compared, each of which represents the root zone with a single layer and a single value of saturation. The first of these, the direct model, employs Eq. (2) directly to the entire root zone to calculate uptake by the plant, as would happen if one simply coarsened the resolution of the hi-res model. The second single-layer model, the upscaled model, uses the new multi-valued function presented in Section 3 for the relationship between plant transpiration and saturation.

The particular plant that is simulated is *Burkea africana*, a prevalent woody species from an African savanna [32]. This species has a wilting point of 3.1 MPa, and the potential transpiration rate is 4.75 mm/day [21]. The

roots reach to a depth of one meter, and the fine root distribution is represented as triangular with 75% of the roots concentrated in the top 50% of the root zone. The plant grows on a sandy soil with a porosity of 0.42 and a saturated hydraulic conductivity of 109.8 cm/day. Field capacity is reached at a water content of 0.13 (saturation of 30%), and the water content at the wilting point is 0.013 (saturation of 0.03). More important than the absolute values of these last two numbers is the difference between them, which defines the available water content. For the 21 soils analyzed by Federer et al. [11], available water contents ranged from 0.06 to 0.26; the value for the sandy soil of the African savanna is 0.11, which corresponds to 110 mm of water available for uptake or more than 3 weeks of potential transpiration if the soil of the root zone is filled to capacity. Water stress in this environment arises from a lack of precipitation not a lack of capacity.

For each 200-day growing season, rainfall events arrive as a Poisson process with a mean frequency of one event every 6 days. The depth of precipitation is modeled as an exponentially distributed random variable with a mean of 1.5 cm. Interception is fixed at 0.2 cm, which implies that the depths of infiltration remain exponentially distributed with a mean of 1.5 cm, but the frequency of infiltration-producing events drops to 0.146 days⁻¹ [30]. Because of the high permeability of the soil and the short duration of rain events relative to the daily time scale at which these models apply, infiltration is represented as instantaneous. In the single-layer models, average saturation increases until it reaches field capacity or all of the infiltrating water is used up. In the hi-res model, water moves down through the soil column as piston flow, filling each layer to field capacity from the top down until all infiltrating water is allocated.

There is no seasonal variation in parameters; daily transpiration demand and the distribution of roots are held constant over the growing season. These simplifications enable a focus on the effects of vertical variability in soil moisture on plant uptake. Table 1 presents a summary of the parameter values used in the simulations.

Table 1
Parameter values used in the numerical experiments

Parameter	Value
Storm frequency	0.167 days ⁻¹
Storm depth	1.5 cm
Interception depth	0.2 cm
T_{pot}	0.475 cm/day
γ	1.33
Ψ_w	-3.1 MPa
S_w	0.03
S^*	0.11
S_{fc}	0.30
n	0.42
Z_R	100 cm

Fig. 5 presents the upscaled multi-valued relationship between transpiration and root-zone saturation for this set of parameters. The saturation at which $W(S_{avg})$ reaches a value of one, S' , is 0.165, and the slight curvature in $W(S_{avg})$ arises as a result of the non-uniform distribution of roots. The spatial infiltration index presented in Section 3, $I_{l,z}$, is significantly less than one; its value of 0.26 indicates that a characteristic precipitation event supplies a dry soil with only 26% of the water necessary to raise transpiration to T_{pot} .

Since all three of the models conserve mass and there is little runoff or recharge in this environment (potential transpiration is more than twice as large as the mean infiltration rate), predictions of mean transpiration over a growing season are the same for all three—approximately equal to the average rate of infiltration. It is in the timing and intensity of transpiration that the models differ. Two variables are used to characterize succinctly the effects of transpiration timing and intensity on vegetation health: (1) the number of growing-season days for which daily transpiration is at potential and (2) the longest number of consecutive days during a growing season that daily transpiration is below potential.

5. Results

Fig. 6 presents an illustrative comparison of daily transpiration predictions over a single growing season from the hi-res, direct, and upscaled models. The solid line represents the time history of daily transpiration as given by the vertically resolved model. The dotted and dashed lines represent predictions of daily transpiration for the single-layer models; the dotted line gives the result from the direct model, and the dashed line represents the result from the upscaled model. As can be seen in this example, the results from the upscaled model

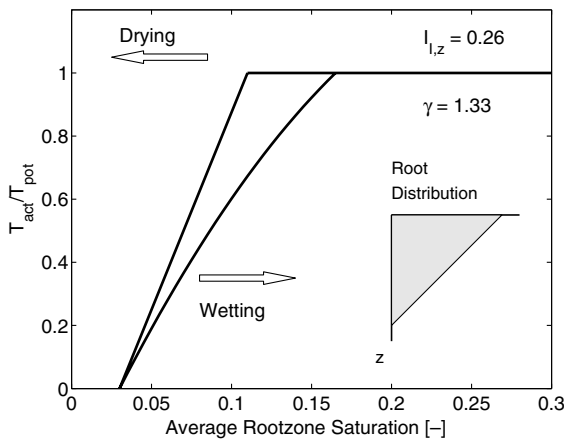


Fig. 5. Upscaled relationship between transpiration and root-zone saturation for vegetation with a root-density profile given by the inset image. For this sandy soil, $S_w = 0.03$, $S^* = 0.11$, and $S_{fc} = 0.30$.

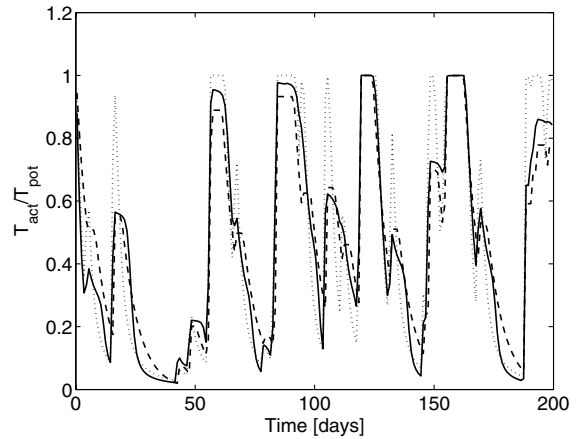


Fig. 6. Comparison of transpiration predictions over a single growing season. The solid line represents the result from the high-resolution model with 50 vertical layers; the dashed line represents the prediction from a single-layer model employing the new multi-valued upscaled function; the dotted line represents the prediction from a model that applies Eq. (2) directly to the entire root zone.

match those from the hi-res model better than the results from the direct model do. The direct model predicts fluctuations in transpiration whose amplitude and frequency are too high; daily transpiration rates reach potential too often and decay too quickly. The fit of the upscaled model is quite good but not perfect; the model sometimes underpredicts peak transpiration values, and the hi-res model shows a faster drop off to very low transpiration values. Nonetheless, predictions from the single-layer upscaled model generally match those from the hi-res model with 50 vertical layers.

To better quantify the performance of the upscaled and direct models, Fig. 7 presents scatter plots of predictions from the single-layer models relative to the predictions from the hi-res model for 100 growing seasons. Each point represents the result from a single growing-season realization. Fig. 7a presents a comparison of predictions of the number of days during a growing season for which daily transpiration meets the potential. This plot shows that the predictions of the upscaled model closely match those from the hi-res model, falling almost exactly on the one-to-one line. All of the predictions from the direct model overestimate this quantity. Fig. 7b shows the comparison for predictions of the longest number of consecutive days during which the plant does not reach T_{pot} . The upscaled model does a reasonable job of reproducing this variable but overestimates it in a few instances. The direct model, however, underestimates this quantity for nearly all of the realizations, in some cases missing quite significantly.

The higher frequency responses of the direct model seen in Fig. 6 result from transpiration rising to potential when S_{avg} increases to S^* rather than S' . For the environmental conditions considered here, such a difference corresponds to a 40% reduction in the amount of

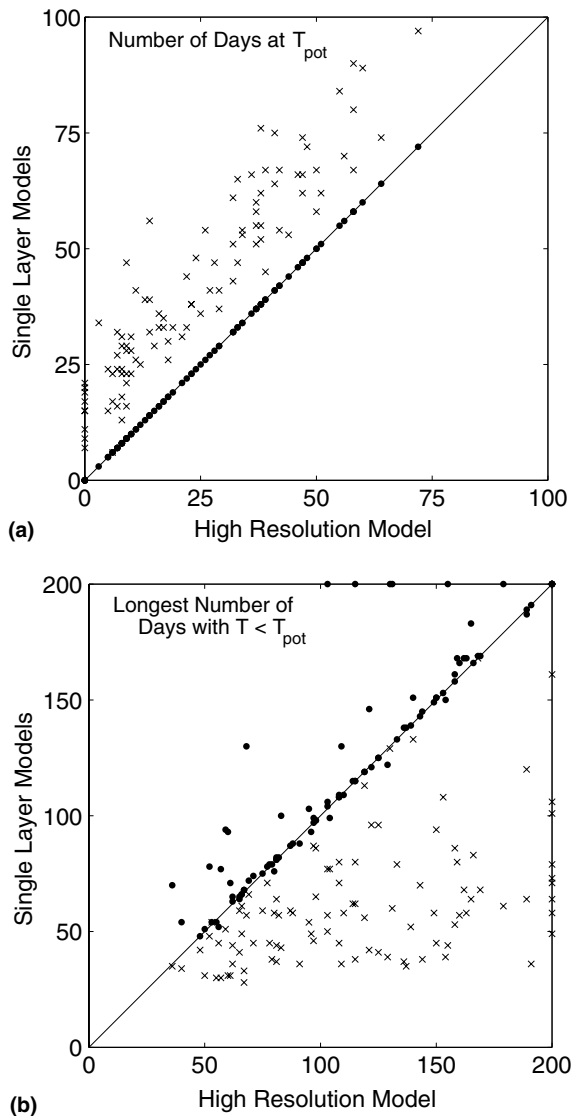


Fig. 7. Comparison of one hundred predictions of (a) the number of growing season days for which transpiration is at potential, and (b) the longest number of consecutive days for which daily transpiration is less than potential. The solid circles represent the predictions from the upscaled model relative to the hi-res model; x's represent predictions from the direct model relative to the hi-res model.

infiltration needed to raise transpiration to T_{pot} when compared to the hi-res and upscaled models. Thus, the direct model overpredicts the number of days that plant transpiration is at potential and underpredicts the longest number of days during which actual transpiration is less than potential.

As mentioned above, the upscaled model misses some of the peaks in transpiration. This error can be explained by examining the behavior of the uptake functions at low saturations. Fig. 1 shows that while transpiration is theoretically non-zero all the way to a saturation of 3%, uptake effectively ceases at a saturation close to 5% or 6%. In contrast, Fig. 5 shows that transpiration predicted by the upscaled representation

is positive until the root-zone saturation is very close to 3%. Thus, the upscaled model brings the soil to a lower saturation between rain events than the hi-res model does. This drier antecedent condition means that the average root-zone saturation following an infiltration event is slightly lower for the upscaled model as compared to the hi-res model, and the corresponding transpiration will also be lower. These lower peaks lead to the upscaled model tending to overpredict the longest number of days for which actual daily transpiration is below T_{pot} (see Fig. 7b). Additionally, this difference in the behavior of the uptake functions at low saturations accounts for the quicker drop-off in transpiration for the hi-res model relative to the upscaled model. These inconsistencies could be eliminated by moving S_w in the upscaled model closer to 0.05 or 0.06, matching the operational value for zero uptake from Fig. 1.

6. Discussion

Figs. 6 and 7 demonstrate that a model of soil-moisture dynamics with no vertical resolution can do a good job of replicating predictions of daily transpiration obtained from a model highly resolved in the vertical. Such an upscaled representation provides an efficient means of predicting transpiration when knowledge of the distribution of soil-moisture is not needed. For the water-limited conditions presented here, the relationship between transpiration and root-zone saturation is multi-valued with distinct behavior for wetting and drying conditions.

As mentioned in Section 3, however, a multi-valued relationship may not be required in well-watered environments. The need for a multi-valued function can be quantified by the spatial infiltration index given in Eq. (13), which relates the characteristic depth of infiltration to the depth needed to bring plant transpiration up to potential. Even for those situations in which this index is less than one, however, a multi-valued function may not be needed, and a one-to-one relationship between transpiration and saturation may suffice. If S' and S^* are close to each other, the difference between the $D(S_{avg})$ and $W(S_{avg})$ curves may be small. If the plant compensation parameter for the example presented in Sections 4 and 5 had been 2.0 rather than 1.3, S' and S^* would both have been equal to 0.11, and $D(S_{avg})$ and $W(S_{avg})$ would have been nearly indistinguishable. In such a case, the error introduced by combining the two into a single curve will be outweighed by the gains in simplicity. Thus, the need for a multi-valued relationship depends both on $I_{I,z}$ and on the difference between S' and S^* . The latter quantity, in turn, depends on the plant compensation parameter, distribution of roots, plant tolerance for low potentials, and physical properties of the soil. Of these, γ is usually the quantity least

well known, especially for non-agricultural vegetation. While one might speculate that this parameter is large for a plant native to a water-limited ecosystem, there is a need for continued field and laboratory experiments to determine the extent to which plants can compensate for spatially heterogeneous soil moisture.

Underlying the results presented in this work are decisions that warrant some discussion. For clarity of interpretation, the numerical experiments relied on a root distribution and daily transpiration demand that were constant over a growing season. Accounting for the temporal evolution of these quantities would lead to time-varying supply and demand curves but would not affect the principal conclusions of this work.

Additionally, infiltration was represented as instantaneous, and the wetting front in the hi-res model was approximated as a step function with layers saturated to field capacity within the zone of infiltration. In reality, infiltration, while rapid, evolves over time. Thus, the hi-res model leads to zones of infiltration that are more spread out than those arising under field conditions. Given the rapidity of drainage, however, and the interpretation of results at the daily time scale, it is anticipated that the effects of this difference are small. For a soil that drains very slowly, however, the appropriateness of a single layer model must be questioned since soil-moisture distribution throughout the root zone occurs instantaneously for any model without vertical resolution. The emphasis of this work is on the question of how to represent plant uptake provided that one has already committed to representing the root zone as a single layer.

Finally, plant uptake was represented with a model that relies on an Ohm's law analogy, sometimes called a Type I model [18]. For Type II models, such as those used by van Dam et al. [33], Feddes et al. [8] and others, local uptake is given by

$$u(z, t) = \beta(S(z, t)) \cdot \omega(z) \cdot T_{\text{pot}}(t) \quad (14)$$

where β is an empirical reduction factor ranging from zero to one that depends on water content, and ω is a weighting factor dependent on the root distribution and layer thickness. If Eq. (14) is applied layer by layer, the entire root zone must be wet in order for transpiration to reach T_{pot} . This behavior is similar to a Type I model in which the plant compensation parameter is 1.0, and the layer-by-layer application of Eq. (14) also results in a multi-valued relationship between transpiration and root-zone saturation when upscaled. The similarity between $D(S_{\text{avg}})$ and the Type II representation, however, suggests a relationship between the Type I and Type II models that is fundamentally tied to scale. In well-watered environments, the layer-by-layer application of a Type I model results in an upscaled relationship between transpiration and average root-zone saturation that is similar to that obtained from a Type II model applied directly to the entire root zone.

7. Conclusions

The relationship between transpiration and root-zone saturation depends on the distribution of soil moisture. This implies the existence of a minimum spatial resolution required to predict plant uptake accurately for water-limited ecosystems in which the root zone is only partially wet by infiltration events. Because of the distinct and repeated spatial patterns of wetting and drying, however, a simple multi-valued upscaled relationship is proposed that reproduces daily transpiration simulated with a highly resolved model based on an Ohm's law analogy. In well-watered environments, such a multi-valued relationship may not be required, and the dimensionless spatial infiltration index presented as Eq. (13) can indicate whether or not a one-to-one function is adequate. The similarity between the upscaled function presented here and Type II models from the literature suggests that the connection between Type I and Type II representations of plant uptake may be one of scale.

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