

Effect of vertical resolution on predictions of transpiration in water-limited ecosystems

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Abstract

Water-limited ecosystems are characterized by precipitation with low annual totals and significant temporal variability, transpiration that is limited by soil-moisture availability, and infiltration events that may only partially rewet the vegetation root zone. Average transpiration in such environments is controlled by precipitation, and accurate predictions of vegetation health require adequate representation of temporal variation in the timing and intensity of plant uptake. Complexities introduced by variability in depth of infiltration, distribution of roots, and a plant's ability to compensate for spatially heterogeneous soil moisture suggest a minimum vertical resolution required for satisfactory representation of plant behavior.

To explore the effect of vertical resolution on predictions of transpiration, we conduct a series of numerical experiments, comparing the results from models of varying resolution for a range of plant and climate conditions. From temporal and spatial scales of the underlying processes and desired output, we develop dimensionless parameters that indicate the adequacy of a finite-resolution model with respect to reproducing characteristics of plant transpiration over multiple growing seasons. These parameters may be used to determine the spatial resolution required to predict vegetation health in water-limited ecosystems.

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1. Introduction

Ecohydrology is the investigation of the hydrologic mechanisms that underlie ecologic patterns and processes [1–3]. This broad definition includes a variety of interactions among hydrologic processes and plant and animal communities. An important aspect is the quantitative prediction of the linkages among climate, soil-moisture dynamics, and vegetation in natural water-limited ecosystems. Vegetation health in such environments depends on a complex interplay among the timing and amount of precipitation and the dynamics of infiltration and evapotranspiration. Effective models of these interactions enable us to predict the responses of these sensitive ecosystems to a changing global environment. To be useful tools, such predictive models

must appropriately address the interconnections among modeling objectives, characterization of spatial and temporal variability of parameters, representation of the chemical, biological, and physical processes, and the amount and quality of available information. As articulated by Rodriguez-Iturbe [3], one must avoid models that are unrealistically oversimplified as well as those that are so complex that they provide little insight to a unifying picture. The goal of an efficient model is to represent accurately those processes and characteristics of a system that affect the particular behavior of interest and to simplify or omit those that have little impact. The objective is not necessarily the precise and accurate representation of all processes and variables, but rather the generation of reliable results with regard to questions of interest. This paper demonstrates that characteristic temporal and spatial scales of plant, soil, and climate conditions can be used to create parameters that indicate a minimum level of vertical resolution required to adequately predict transpiration in water-limited ecosystems.

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Nomenclature

b	soil parameter for retention curve and relative permeability [-]	α	average storm depth [cm]
I	depth of infiltration (volume/area) [cm]	β	relative root density [-]
$I_{\text{req}}^{\Delta z}$	depth of infiltration required such that predicted transpiration meets demand just following infiltration for a model with layers of thickness Δz [cm]	γ	plant compensation parameter [-]
I_{seas}	average infiltration rate over a growing season [cm/day]	Δ	depth of interception [cm]
n	porosity [-]	η	fraction of the growing season for which $T_{\text{act}} = T_{\text{pot}}$ [-]
S	saturation [water volume/pore volume]	λ	storm arrival rate [1/day]
S_{avg}	average saturation over the entire root zone [-]	λ'	infiltration-producing storm arrival rate [1/day]
S_{fc}	saturation at field capacity [-]	ξ	longest number of continuous days with $T_{\text{act}} < T_{\text{pot}}$ [day]
S_{h}	saturation at the hygroscopic point [-]	τ_{inf}	characteristic time between rain events that provide enough water to a dry soil such that predicted transpiration meets demand just following infiltration for a model with no vertical discretization [day]
S_{w}	saturation at the wilting point [-]	$\tau_{\Delta z}$	characteristic time between rain events that provide enough water to a dry soil such that predicted transpiration meets demand just following infiltration for a model with layers of thickness Δz [day]
S^*	uniform saturation for which the plant can just meet T_{pot} [-]	Ψ	water potential [cm]
T_{act}	actual transpiration [cm/day]	Ψ_{e}	air entry potential [cm]
T_{pot}	potential transpiration [cm/day]	Ψ_{w}	minimum plant potential [cm]
T_{seas}	average transpiration rate over a growing season [cm/day]	Ψ^*	uniform soil–water potential for which the plant can just meet T_{pot} [-]
u	local root-water uptake [1/day]		
U	total uptake from the root zone [cm/day]		
Δz	uniform layer thickness [cm]		
Z_{r}	depth of root zone [cm]		
Z_{x}	wetting-front depth for a characteristic infiltration event [cm]		

1.1. Water-limited ecosystems

In water-limited ecosystems the dominant control on vegetation is the availability of water. Often, precipitation in such environments is characterized not only by low annual totals, but also by extreme temporal variability [4]. Such environments include savannas, steppes, and scrublands, and they have been the focus of recent attention [4–11]. The intermittent and variable nature of rainfall coupled with the non-linear processes of infiltration, evaporation, transpiration, and drainage lead to rich and complex variability in soil moisture. The dynamics of soil moisture, in turn, have a significant impact on vegetation stress and the suitability of various plant species to particular climate and soil conditions. While many factors such as grazing, fire, and nutrient limits impact the growth and persistence of plants, these are secondary to water stress for a water-limited ecosystem. Another defining characteristic of these environments is that the average transpiration over a growing season is modulated by the availability of soil moisture rather than atmospheric demand. Actual transpiration will be significantly less than potential

transpiration, and if runoff and changes in storage are negligible, actual transpiration will equal precipitation. Also, unlike irrigated fields, natural ecosystems may experience rain events that only partially rewet the root zone. All of these characteristics have implications for choices of model structure and scale.

1.2. Models of plant uptake

Water flows through the soil–plant–atmosphere continuum along a path of decreasing water potential. The rate of flow is determined by the steepness of the potential gradient and the resistance to flow. When the water content in a soil is high, evapotranspiration is limited by the atmospheric demand for water vapor and resistance to flow along the plant–atmosphere pathway. At low soil saturations, however, the resistance to water flow along the soil–plant pathway becomes significant. The stomata of the plant will then begin to close to maintain a minimum water potential and prevent runaway cavitation in the xylem conduits. The cumulative effect is a reduction in uptake and transpiration in response to soil drying [12–14].

Most models of root-water uptake that are commonly used in hydrology do not consider the details of water flow within the plant or changes in plant water content. Rather, the plant is represented as a valve between the supply of moisture in the soil and the demand for water vapor in the atmosphere. In some representations, total uptake by the plant is fixed based on atmospheric demand, and this total uptake is partitioned throughout the soil column [15]. Such models are not applicable to water-limited ecosystems where total uptake is controlled by available soil moisture. Most representations of plant uptake that incorporate the effects of soil-moisture depletion can be separated into two categories: Type I and Type II models [16,17]. In Type I models, water transport through the soil–atmosphere–plant continuum is driven by a difference in water potential from the soil to the leaf surface [5,18–22]. Such models are consistent with the soil–plant–atmosphere continuum representation, but particular values for the parameters of these models are often difficult to determine. Type II models use an empirical reduction factor to limit transpiration below the potential rate when soil moisture is low [10,23–28]. While less mechanistic than the Type I models, the Type II models rely on parameters that are perhaps more readily identifiable from field experiments. In both representations, the spatial distribution of water over the root zone can have a significant impact on total uptake by the plant. Therefore, it is essential to understand how vertical resolution affects predictions of evapotranspiration in water-limited ecosystems and to know what levels of resolution are appropriate under different conditions.

1.3. Objectives

In this work, we seek to quantify the impact of spatial scale on predictions of plant transpiration and to develop parameters that may indicate an appropriate level of vertical resolution. Plant uptake as a fraction of transpiration demand depends not only on the volume of water available within the root zone, but also on the distribution of that water. Therefore, a coarse resolution that homogenizes soil moisture and does not allow for an adequate representation of its spatial variability may lead to erroneous predictions of transpiration and vegetation health. However, the dependence of uptake on the variability of soil moisture is complex. Water uptake is a self-limiting process that directs extraction to wet locations, and some plants have an ability to compensate for spatial variations in soil moisture by extracting water from wet regions at particularly high rates. Therefore, the appropriate spatial scale for representing uptake is not obvious and will depend not only on the soil, plant, and climate parameters, but also on the output variables of interest. Through a conceptual analysis coupled with numerical experiments, we seek to

develop dimensionless groups of characteristic parameters that can indicate appropriate levels of vertical resolution. Our goal is not to present a new model for plant uptake; rather it is to explore the effects of vertical resolution on predictions of transpiration with a mathematical representation that provides reliable results and is simple enough to facilitate insight to the governing processes.

2. Methods

We present a series of numerical experiments and theoretical calculations that demonstrate the dependence of transpiration on spatial resolution. Included among these are determinations of transpiration as a function of average root-zone saturation, the change in transpiration rate immediately following an infiltration event as a function of vertical resolution, and the response of plant transpiration to intermittent precipitation events for models of varying resolution. For the last set of experiments, we compare the results to determine how a coarsening of vertical resolution affects predictions of a variety of temporal characteristics of transpiration. To generalize the results, we use dimensionless groups of parameters related to the desired output and pertinent soil, plant, and climate processes.

2.1. Model structure and scale

2.1.1. Spatial and temporal resolution

We consider an areally homogeneous patch of vegetation for which lateral inflows can be neglected. While previous work has shown that such a simplification is justifiable for some environments [29,30], it does limit the scope of this work, as lateral fluxes can be significant components of the local water balance in areas of moderate to high topographic relief. Nonetheless, this simplification allows us to focus this work on issues of scale and representation related to vertical variations in parameters and processes and to develop a methodology that can be brought to bear on the interesting questions of horizontal variability in future endeavors.

Soil-moisture dynamics are represented with a one-dimensional volume-balance equation applied over the root zone of a plant

$$\frac{\partial(nS(z, t))}{\partial t} = -\frac{\partial q(z, t)}{\partial z} - u(z, t) \quad (1)$$

where S is local saturation, n is the porosity, q is vertical soil-moisture flux, and u is the local rate of uptake for evapotranspiration with dimensions of depth (volume per horizontal area) per depth per time. For solution, Eq. (1) must be coupled with boundary conditions, an expression for plant uptake, and a relationship (or set of relationships) between flux and saturation (see below).

In the vertical direction, we consider a wide range of model resolutions, from fine layers (2 cm) to a very coarse scale in which the entire root zone is represented as a single layer. Because of the greater interest in the limitations of water availability than atmospheric demand, sub-daily variations in processes are not resolved. Rather, the results are to be interpreted at the daily time scale.

2.1.2. Infiltration

Coarsening vertical resolution can affect not only the spatial distribution of soil moisture, but also the temporal characteristics of infiltration. If the root zone is represented with a single layer, infiltrating water instantly reaches all of the roots; this is in contrast to a vertically resolved model in which the infiltrating front must make its way downward over time. For clarity of the effects caused by spatial variability in soil moisture, we represent both infiltration and drainage as instantaneous for all levels of vertical resolution. Given a volume of infiltration, the soil column fills from the top down, and each layer is saturated to field capacity until either all infiltrating water is accommodated or the entire root zone is saturated to field capacity. The movement of soil moisture between layers is neglected, except for infiltration during precipitation events. This representation is the same as that employed by Scholes and Walker [11]. Making these simplifications preserves the intermittency of rainfall events and allows us to isolate the effects of spatial variation of soil moisture and uptake while facilitating theoretical analysis. Despite these simplifications, comparison of this piston-type model to a full Richards representation showed the two to give very similar predictions of daily transpiration for the environmental conditions discussed in Section 2.2.

2.1.3. Plant uptake

Plant uptake is represented by a Type I model, following the early work of Gardner [20] and Cowan [18] and subsequent extensions [5,19,21,22,27,31,32]. These works represent water uptake as being driven by a difference in water potential between the soil and the plant. Movement of water is limited by a network of resistances through the soil to the roots, through the roots and into the shoots, and from the plant to the atmosphere (see Fig. 1). Since the soil-to-plant and plant-to-atmosphere pathways are in series, the total flux will be controlled by the dominant resistance: the atmosphere when soil moisture is plentiful and the soil when water availability is limited. As a result, the mathematical representation of this system can be simplified to focus solely on the soil-to-plant pathway with the caveat that total uptake will not exceed a specified maximum rate of transpiration [18,33,34].

Local uptake is described mathematically by

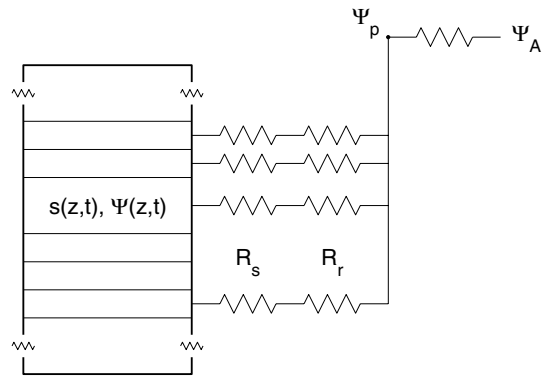


Fig. 1. Schematic representation of resistance to water flow through the soil–plant–atmosphere continuum. The resistance between Ψ_p and Ψ_A incorporates shoot and stomatal resistance and is dominant when soil–water is not limiting.

$$u_i(t) = \frac{\Psi_i(t) - \Psi_p(t)}{R_{s,i}(t) + R_{r,i}} \quad (2)$$

where $R_{s,i}$ represents the soil resistance in layer i and $R_{r,i}$ represents the root resistance; Ψ_i is the soil–water potential in layer i , Ψ_p is the potential in the plant, and the dimensions of $u_i(t)$ are depth per depth per time. Local uptake is constrained to be greater than or equal to zero (see the discussion of hydraulic lift below), and the rate of total uptake is given by the sum of $u_i(t)$ over the root zone:

$$U(t) = \sum_{i=1}^{nz} u_i(t) \cdot \Delta z \quad (3)$$

where dimensions of $U(t)$ are depth per time, Δz is the uniform layer thickness, and nz is the number of layers.

As the soil dries, the plant potential will decrease in order to maintain uptake. However, to prevent runaway cavitation and cell embolism a plant will close its stomata to reduce transpiration and keep the plant potential above a minimum value, Ψ_w , referred to as the wilting potential. For given soil–moisture conditions, the maximum rate of water uptake will occur when the plant potential is at this minimum value:

$$U_{\max}(t) = \sum_{i=1}^{nz} \frac{\Psi_i(t) - \Psi_w}{R_{s,i}(t) + R_{r,i}} \cdot \Delta z \quad (4)$$

The actual transpiration rate of the plant is taken as the lesser of the transpiration demand (potential transpiration, T_{pot}) and the maximum rate of uptake, similar to Federer et al. [34]:

$$T_{\text{act}} = \min(U_{\max}, T_{\text{pot}}) \quad (5)$$

Like many prior efforts, the local root and soil resistances are inversely proportional to the local root density (length of roots per volume of soil), and the soil resistance is also inversely proportional to the unsatu-

rated hydraulic conductivity, K , which is a function of saturation [20,22,32,35]:

$$R_{r,i} = \frac{C_r}{\beta_i} \quad (6)$$

$$R_{s,i}(t) = \frac{C_s}{\beta_i K(S_i(t))} \quad (7)$$

where β_i is a local relative root density, and C_r and C_s are constants.

Note that this representation of the plant roots as a network of parallel and series resistances leads to some intriguing behavior. If soil moisture is distributed non-uniformly over the root zone, additional water will be extracted from a wet region to compensate for some of the roots being dry [5,16]. Split root experiments have indicated that plants may require from less than 50% to nearly 100% of their roots to be wetted in order to meet transpiration demand, depending on the species [25,36–39]. Because the model results are interpreted at the daily scale, this compensating behavior could also be used to represent the redistribution of water from wetter to drier regions at night, and its subsequent uptake during the day, i.e., hydraulic lift [33,40–42].

This representation of the plant–soil–atmosphere continuum can represent many observed behaviors of water-limited ecosystems. The determination of the constants C_s and C_r , however, presents a significant challenge. In this work, the values are determined from two behavioral constraints:

- (1) From field data, we select a minimum value of soil suction, Ψ^* , or the corresponding saturation, S^* , uniform over the entire root zone, for which the plant can just meet daily transpiration demand.
- (2) We choose a value for γ , the maximum possible uptake per unit of roots relative to what is needed to meet transpiration demand if all roots are contributing equally. The inverse, $1/\gamma$, indicates the minimum fraction of roots needed to meet demand, if the soil around those roots is wetted to field capacity and extraction from all other roots is zero. For plants with large values of γ , even a small amount of infiltration may be enough to bring evapotranspiration to its potential rate, and the water will be depleted quickly. A plant with a smaller value of γ , however, may not meet transpiration demand for the same amount of infiltrated water, and the supply will be used more slowly.

These two constraints enable the determination of C_s and C_r .

While explicit relative permeability and retention functions are not needed for infiltration and soil-moisture redistribution (see Section 2.1.2), they are required to compute plant uptake according to the representation

we have outlined here. We use functional forms similar to those used by Clapp and Hornberger [43]

$$\Psi(S) = \Psi_e(S - S_h)^{-b} \quad (8)$$

$$K(S) = K_{\text{sat}}(S - S_h)^{2b+3} \quad (9)$$

where Ψ_e is the air-entry potential, K_{sat} is the saturated hydraulic conductivity, b is a soil texture parameter, and S_h is the hygroscopic saturation, i.e., the saturation at which the conductivity is zero and no water can be extracted from the soil.

Fig. 2 presents examples of the rate of local uptake, given by Eq. (2), normalized by relative root density, as a function of local soil moisture when the plant potential is at Ψ_w . Parameter values are for a woody species on a sandy soil from an African savanna [11] discussed below (Section 2.2) and given in Table 1. Because the compensation parameter is not known, we use three values of γ , representing vegetation that requires 25%, 50%, and 75% of the roots to be wet to meet transpiration demand.

2.2. Plant, soil, climate, and model parameters

The particular water-limited ecosystem that we use to demonstrate the impact of spatial resolution on predictions of transpiration is a savanna from South Africa as described in Scholes and Walker [11]. The climate is characterized by two seasons: one hot and wet (the growing season) from October through April, and one warm and dry from May through September. Average annual rainfall is 620 mm, and we allocate approxi-

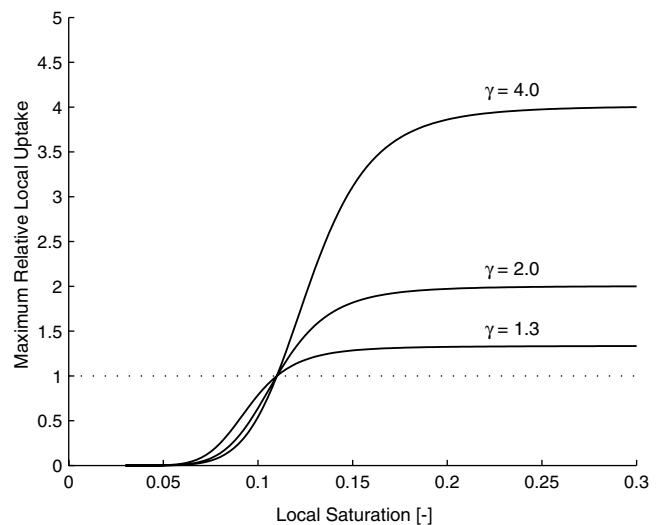


Fig. 2. Maximum relative local uptake versus local saturation for varying degrees of plant compensation. The ordinate represents the maximum local uptake per unit of roots relative to the uptake per unit of roots needed to meet transpiration demand. Note that all three curves pass through the point $(S^*, 1)$. Soil and plant parameters are given in Table 1.

Table 1
Parameter values for an African savanna used in numerical experiments

Variable	Values
α	1.2, 1.5, 1.8 cm
$\alpha \cdot \lambda'$	0.219 cm/day
γ	1.33, 2.0, 4.0
Δ	0.2 cm
Δz	2, 5, 10, 25, 50, 100 cm
Z_r	100 cm
n	0.42
K_{sat}	109.8 cm/day
b	1.7
Ψ_e	-11.6 cm
Ψ_w	-31,600 cm (-3.1 MPa)
S_h	0.02
S_w	0.03
S^*	0.11
S_{fc}	0.30
T_{pot}	0.475 cm/day

mately 500 mm of this total to the 200-day growing season. Rainfall events are dominated by short convective storms of high intensity. Because the duration of a rainfall event is shorter than the daily time scale, storm events over the growing season are modeled as shots of water concentrated in time, arriving as a Poisson process with rate λ . The depth of precipitation is modeled as an exponentially distributed random variable with mean, α , and the depth of interception, Δ , is taken to be a fixed quantity. This implies that the depths of infiltration are exponentially distributed with mean, α , and the rate of arrival of storms that generate infiltration is $\lambda' = \lambda e^{-\Delta/\alpha}$ [10].

For vegetation, we focus on the common woody species, *Burkea africana*, which grows on a very sandy soil. Mean potential evapotranspiration during the growing season is 4.75 mm/day. To simplify the interpretation of results, the distribution of active roots is taken to be uniform, which is very similar to the root distribution reported for *Burkea africana* [11]. Data on the plant compensation parameter, γ , however, are not available. Consequently, we choose three values: 1.33, 2.0, and 4.0, corresponding to plants that require 75%, 50%, and 25% of their roots to be taking up water in order to meet potential transpiration, respectively. This range allows us to investigate how an ability to compensate for spatial variations in soil-moisture affects the needed level of model resolution. All other parameter values are given in Table 1.

2.3. Transpiration characteristics of interest

The degree of vertical resolution appropriate for a particular ecohydrologic application depends not only on the soil, plant, and climate parameters, but also on one's questions and objectives. To explore this, we

consider the effect of resolution on a number of transpiration characteristics. First, we investigate the impact of spatial upscaling on predictions of soil drying between storms. Second, we consider the effect of resolution on predictions of transpiration immediately following an infiltration event. Third, we explore seasonal characteristics of transpiration in response to intermittent rain events. Through these investigations, we elucidate the interconnections among modeling objectives, parameter values, and spatial and temporal resolution.

2.3.1. Non-unique relation between transpiration and root-zone saturation

An interesting observation in the work of Guswa et al. [5] is that the relationship between total evapotranspiration and average saturation can be non-unique. This behavior may be explained by soil-moisture variation within the root zone and the nature of local extraction. For example, total uptake for a plant with all of its roots in soil at 50% saturation will be different from a case where half of its roots are in fully saturated soil and half are dry, even though the average root-zone saturation is the same in both cases. A number of split-root and localized irrigation experiments support this result [36,38,39,44–47].

This non-uniqueness may preclude the use of a simple relationship between total plant uptake and average saturation over the root zone. If the entire root zone is consistently rewetted to field capacity, as in agricultural applications or natural ecosystems with wet climates, such an upscaled relationship may appear to be one-to-one, since the spatial pattern of drying will be similar from event to event. As noted by Federer [19,35], however, the non-uniqueness becomes significant under conditions of partial rewetting of the root zone. For some plant species, the effect of spatial variability in soil moisture may be mitigated by significant plant compensation ability (either through hydraulic lift or differential uptake). To explore the relationship between average root-zone saturation and plant uptake, we simulate soil drying for *Burkea africana* (parameters given in Table 1). Initial conditions range from the entire root zone being at field capacity to just the top 20% of the roots being wetted in order to highlight the effect of spatial variability in soil moisture on uptake. Water is extracted from the soil column according to the representation described in Section 2.1.3, and plots of total uptake versus average root-zone saturation are presented for two levels of plant compensation ability.

2.3.2. Effect of vertical resolution on transpiration immediately following precipitation

The non-linear behavior depicted in Fig. 2 indicates that the spatial distribution of soil moisture over the root zone will affect total plant uptake. Because varia-

tions in soil moisture cannot be resolved beyond model resolution, the choice of resolution will affect predictions of total plant uptake. To demonstrate the effect of resolution, we consider a plant with a uniform root distribution in a dry soil ($S = S(\Psi_w) = S_w$) subjected to infiltration events of variable magnitude, I . According to our simplified representation of infiltration, after soil-moisture redistribution the resulting soil-moisture profile should be a step function. Water saturations at depths less than or equal to the depth of the wetting front, $Z_I = I / ((S_{fc} - S_w) \cdot n)$, should be at field capacity; deeper in the soil, the saturation should equal the initial saturation, S_w . For a model with finite resolution, however, the depth Z_I may not correspond precisely to the boundary of a model layer. Therefore, the saturation in the cell at the edge of the wetting front will have a saturation between S_{fc} and S_w . The resulting distribution of soil moisture will lead to a particular intensity of plant uptake as described by the representation outlined in Section 2.1.3. Thus, without doing any simulation, we can calculate the uptake that would be predicted immediately following an infiltration event for models with varying vertical resolution. Correspondingly, we can calculate the depth of infiltration which will supply enough water to a dry soil such that transpiration is predicted to just reach the potential rate immediately following the infiltration event.

For example, for infinite resolution in the vertical, the depth of water required is given by the amount of water that will cover $1/\gamma$ of the roots. For a uniform root distribution, this corresponds to a wetting-front depth of Z_r/γ . In such a case, the required volume of infiltration per unit area is given by

$$I_{\text{req}}^{\text{inf}} = \frac{Z_r \cdot n \cdot (S_{fc} - S_w)}{\gamma} \quad (10)$$

where the superscript on I denotes vertical resolution. If the root-zone is represented by a single layer, however, the detail of the spatial distribution of soil moisture is lost. In this case, predicted uptake will equal potential transpiration if the average root-zone saturation is brought to S^* . The depth of infiltration needed to achieve this is given by

$$I_{\text{req}}^{\text{one}} = Z_r \cdot n \cdot (S^* - S_w) \quad (11)$$

To generalize these results for models with multiple finite layers, we first determine the number of layers, N , of thickness, Δz , needed to meet or exceed Z_r/γ . We then approximate the local uptake function (presented in Fig. 2) by a step function: zero for $S < S^*$ and γ for $S \geq S^*$. With this simplification, the required volume of water is estimated by

$$I_{\text{req}}^{\Delta z} = \Delta z \cdot n \cdot [(N - 1)(S_{fc} - S_w) + (S^* - S_w)] \quad (12)$$

Eq. (12) indicates that potential transpiration will be reached when $N - 1$ layers are filled to field capacity,

and the N th layer, which contains the wetting front, reaches an average saturation of S^* . Note that while all of these calculations were performed presuming a uniform root distribution for the sake of clarity, the extension to a non-uniform distribution is straightforward.

To demonstrate the effect of resolution on predicted uptake immediately following an infiltration event, we present a plot of total uptake as a function of the amount of infiltrating water for three levels of vertical resolution: infinite vertical resolution, a model with 10 layers, and a model with no vertical resolution for which the entire root zone is represented by a single layer. Relevant soil and plant parameters are given in Table 1.

2.3.3. Transpiration response to intermittent rainfall

As articulated in the introduction, the utility of a model must be judged with respect to the particular behaviors of interest to be reproduced. Here the goal is to predict accurately plant vitality in water-limited ecosystems. While vegetation responses to water stress are quite complex and plant specific, and not completely understood, there are some common features. As the availability of soil moisture declines, a plant begins closing stomata with the goal of maintaining cell turgor and relative water content. Due to this tight coupling between water stress and evapotranspiration, the latter can be used to indicate vegetation health. The significance of water stress is strongly time dependent and increases in intensity the longer it lasts [48–50]. Given all this, three characteristics of transpiration are used to indicate plant health over a growing season:

- (1) T_{seas} , the average transpiration rate over the growing season.
- (2) η , the fraction of the growing season for which actual transpiration equals the potential daily rate.
- (3) ξ , the longest number of continuous days during a growing season for which actual transpiration is below potential.

These variables are not intended to indicate the onset of particular physiological damage; rather, they characterize the suitability of a particular plant to given soil and climate conditions and can be used to compare models of varying resolution.

We consider three sets of climate parameters that vary in the timing and intensity of rainfall, but share the same mean seasonal infiltration, and three levels of plant compensation ($\gamma = 1.33, 2.0, \text{ and } 4.0$). For each of the nine combinations of climate and plant parameters, we represent the root zone with six degrees of vertical resolution, ranging from 1 to 50 layers (Δz ranges from 2 to 100 cm). For each of these 54 scenarios, soil-moisture dynamics and evapotranspiration are simulated over 100 growing seasons, each 200 days long. Because of the

dry nature of the winter, the initial saturation at the start of each simulation is set to S^* uniformly over the root zone. From these 5400 realizations, we investigate the impact of vertical resolution on predictions of T_{seas} , η , and ξ .

2.4. Characterization of scenarios

As noted above, water-limited ecosystems are characterized by uptake that is limited by soil-moisture availability, actual transpiration significantly less than potential transpiration, and rain events that may only partially rewet the root zone. For these ecosystems, we would like to determine what model resolution is required to adequately represent various characteristics of transpiration dynamics. Doing so on a case-by-case basis is laborious and offers no advantage. Instead, we would like to develop simple indicators that represent key characteristics of these environments and would enable us to determine appropriate levels of resolution a priori. Guswa et al. [5] proposed that dimensionless groups of relevant time and space scales may prove successful in this regard.

Appropriate spatial resolution depends upon the relevant processes, scales of parameter heterogeneity, and the desired spatial and temporal scales of the output. Since we simplify this analysis by considering a homogeneous soil column with a uniform root distribution, spatial variability is driven by the stochastic nature of infiltration events. For output, this work focuses on temporal characteristics of daily transpiration (see Section 2.3). The spatial scale of the output is the root zone, and the temporal scales range from daily to seasonal.

Transpiration rate, the variable of interest in this work, can be described by the following root-zone balance equation:

$$T_{\text{act}} = i - q - nZ_r \frac{dS_{\text{avg}}}{dt} \quad (13)$$

where i is infiltration rate, and q is the rate of drainage and runoff. Seasonal transpiration is determined by integration of Eq. (13) over a growing season:

$$\int_{\text{season}} T_{\text{act}} dt = \int_{\text{season}} i dt - \int_{\text{season}} q dt - nZ_r \Delta S_{\text{season}} \quad (14)$$

Runoff in this water-limited ecosystem is expected to be negligible, as the soil is very sandy; according to our representation of infiltration, Hortonian runoff is identically zero. The index of dryness, $D_I = T_{\text{pot}}/(\alpha \cdot \lambda')$, is 2.2, indicating that little water will be lost to drainage [5,51]. Also, the change in root-zone water content over a growing season is small compared to total transpiration and precipitation. This will not be the case for all environments, especially those which receive most of the annual precipitation during a period of vegetation

dormancy. For this ecosystem, however, Eq. (14) indicates that average transpiration over a growing season will be approximately equal to infiltration. This result is independent of vertical resolution as well as the expression for uptake as a function of saturation. Therefore, we expect that model resolution will have no impact on predictions of seasonal transpiration.

For transpiration over shorter time scales, however, the change in root-zone saturation may not be negligible. Thus, we need to investigate the functional relationship between local saturation and uptake, specifically Eq. (4). In this expression, uptake depends on the number and size of the vertical layers from which water is being extracted. Because the spatial variability of soil moisture is driven by infiltration, one might expect that a model need be resolved enough to adequately capture the spatial heterogeneity of infiltration. For a typical infiltration event of depth α (see Section 2.2), the resulting wetting front will reach a depth of

$$Z_\alpha = \frac{\alpha}{n(S_{\text{fc}} - S_w)} \quad (15)$$

This formulation is based on the premise that the soil column dries to the wilting saturation between rain events. Given that the index of dryness for this soil is 2.2, this is reasonable. Presumably, model resolution of this scale will be adequate to describe soil-moisture dynamics, and the dimensionless ratio $Z_\alpha/\Delta z$ can be used to characterize different scenarios. Values of $Z_\alpha/\Delta z$ greater than one indicate adequate resolution, while models with values less than one may not be resolved enough. This ratio is a more general version of the spatial infiltration index used in Guswa et al. [5].

Note, however, that while the dimensionless ratio $Z_\alpha/\Delta z$ accounts for climate, soil, and model characteristics, it does not adequately represent plant behavior. Given that plants may compensate for spatial variations in soil moisture (see Section 2.1.3), the above criterion for model resolution may be overly conservative, i.e., sufficient, but not necessary. Thus, we would like a better dimensionless parameter that includes characteristics of soil, plant, climate, model, and study objectives.

Both η and ξ are temporal statistics that depend on the frequency with which plant uptake meets transpiration demand. The discussion in Section 2.3.2 above indicates that the amount of infiltration required to supply a dry soil with enough water such that actual transpiration reaches potential is a function of model, plant, and soil parameters (see Eqs. (10)–(12)). This required volume is independent of climate, however. Therefore, to develop a parameter that also incorporates climate characteristics, we consider the return period between storms that generate enough infiltration to bring transpiration up to potential. Given our stochastic representation of infiltration events as a Poisson process

with rate λ' and exponentially distributed depths with mean α , the return period for an event with depth I is

$$\tau = \frac{1}{\lambda' \cdot \exp(-I/\alpha)}$$

This time scale provides us with a diagnostic parameter that incorporates characteristics of the climate, soil, plant, and model. Calculation of this time scale for the cases of infinite and finite vertical resolution gives

$$\tau_{\text{inf}} = \frac{1}{\lambda' \cdot \exp(-I_{\text{req}}^{\text{inf}}/\alpha)} \quad (16)$$

$$\tau_{\Delta z} = \frac{1}{\lambda' \cdot \exp(-I_{\text{req}}^{\Delta z}/\alpha)} \quad (17)$$

where $I_{\text{req}}^{\text{inf}}$ and $I_{\text{req}}^{\Delta z}$ are given by Eqs. (10) and (12), respectively. We hypothesize that the closer $\tau_{\Delta z}$ is to τ_{inf} , the better the predictions of η and ζ will be. Thus, the ratio, $\tau_{\Delta z}/\tau_{\text{inf}}$, can be used to indicate the appropriateness of a given resolution.

3. Results

3.1. Non-unique relation between transpiration and root-zone saturation

Fig. 3 presents a set of relationships between average saturation over the entire root zone and total plant uptake as a soil dries from a range of initial conditions. The left-hand plot shows the results for a plant with $\gamma = 1.33$, i.e., one that requires uptake from at least 75% of its roots in order to meet demand. The impact of the spatial distribution of soil moisture is evident. An average saturation of 0.13 corresponds to actual transpiration equal to potential if the water is spread over most of the root zone ($\delta = 0.8$ or 1.0). If the water is concentrated over a smaller fraction of the root zone, however, total uptake can be significantly less for the same average saturation.

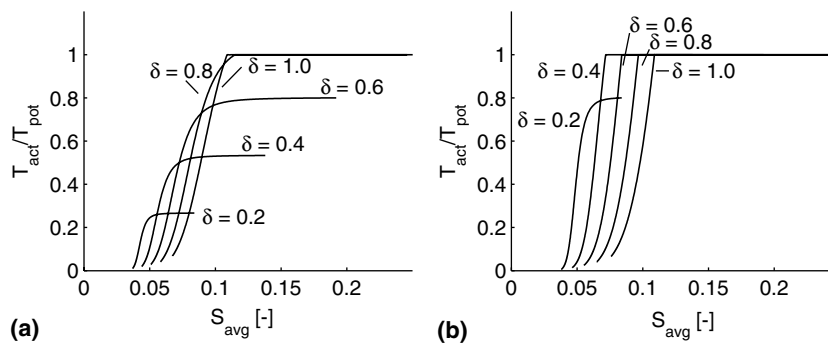


Fig. 3. Total plant uptake versus average root-zone saturation under drying conditions for vegetation with a compensation ability of (a) $\gamma = 1.33$ and (b) $\gamma = 4.0$. δ represents the fraction of roots wetted to field capacity before drying begins; other soil and plant parameters are given in Table 1.

The right-hand figure presents a similar set of relationships, but for a plant with $\gamma = 4.0$. In this case, the plant has a stronger ability to compensate for soil-moisture heterogeneity, and transpiration demand can be met with as few as 25% of the roots taking up water. This behavior manifests itself in the result that, at the onset of drying, transpiration is at the potential rate for all cases except $\delta = 0.2$. The left-right shift in the location of the drop-off in transpiration results from the fact that as δ decreases, larger and larger fractions of the root zone are dry, which pushes the average saturation to the left for the same level of saturation over the wetted roots. These curves demonstrate the non-unique character of the relationship between T_{act} and S_{avg} when the root zone is variably wet, especially when the vegetation has little ability to compensate.

3.2. Effect of vertical resolution on transpiration immediately following precipitation

Fig. 4 presents the rate of plant uptake immediately following a rain event onto a previously dry soil as a function of the volume of infiltration for three levels of spatial homogenization. Note that the x-axis is labeled as volume of infiltration per horizontal area to avoid confusion between depth of infiltration and depth of penetration of the wetting front. The curves are generated for a plant with $\gamma = 2.0$ and a uniform distribution of roots with other soil and plant parameters given in Table 1. The solid line shows the intensity of predicted uptake if vertical resolution is infinite, i.e. if there is no spatial discretization. In this limiting case, saturation at a point above the wetting front is at field capacity, and adding more water has the effect of moving the front downward. This is in contrast to the opposite case of a single layer, in which the water instantly penetrates to cover the entire root zone, and adding more water results in an increase in saturation. For the former, because of the uniform root distribution, increases in wetting front depth result in a linear increase in plant

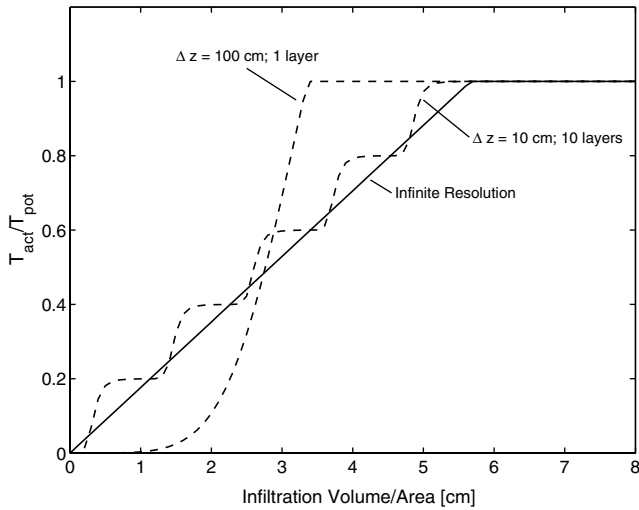


Fig. 4. Effect of vertical resolution on predicted plant uptake immediately following an infiltration event into dry soil for a plant with $\gamma = 2$. Other soil and plant parameters are given in Table 1.

uptake until 50% of the roots are covered. At that point, plant uptake meets demand, and it no longer increases with additional infiltration. For this fully resolved case, the depth of infiltration required to bring transpiration up to T_{pot} , given by Eq. (10), is 5.7 cm. The curve for the single-layer case mimics that of Fig. 2 up to $T_{act} = T_{pot}$. In this case, the depth of infiltration required, given by Eq. (11), is 3.4 cm. An intermediate case with 10 vertical layers is also shown for comparison.

3.3. Transpiration response to intermittent rainfall

Fig. 5 presents an example of the simulated behavior of *Burkea africana* over a single growing season in an African savanna. The thin solid line represents daily evapotranspiration, which fluctuates between T_{pot} and values approaching zero. The dark bars indicate infiltration normalized by the root-zone pore volume, and the response of the vegetation to these events is clear. The interpretation of the output variables, η and ξ , is also shown on this figure. η is the fraction of the growing season with transpiration equal to potential, and ξ is the longest number of continuous days for which transpiration is less than potential.

Based on the analysis presented in Section 2.4, we expect the ratio of average transpiration to infiltration over a growing season to be close to one and independent of vertical resolution. Indeed, we find this to be the case. Over all 5400 realizations, the average ratio of T_{seas} to I_{seas} is 0.992, and the season to season variation is greater than that caused by changes in resolution. For example, for the realizations with $\alpha = 1.5$ cm, $\lambda = 0.167$ days⁻¹, and $\gamma = 2$, the average values of T_{seas}/I_{seas} are presented in Table 2 as a function of Δz . An analysis of variance shows that the variance of T_{seas}/I_{seas} within each

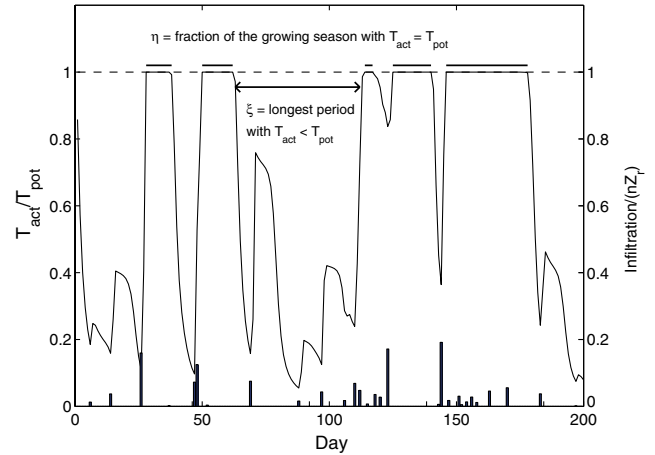


Fig. 5. Example trace of plant transpiration and infiltration over a growing season. The left-hand ordinate shows actual transpiration normalized by potential; the right-hand ordinate presents infiltration depth normalized by root-zone pore volume. η indicates the fraction of the growing season for which $T_{act} = T_{pot}$. The variable ξ indicates the longest number of continuous days for which $T_{act} < T_{pot}$.

Table 2

Variation of the ratio of seasonal transpiration to infiltration as a function of model resolution for realizations with $\alpha = 1.5$ cm, $\lambda = 0.167$ days⁻¹, and $\gamma = 2$

Δz [cm]	T_{seas}/I_{seas}
2	1.007
5	1.002
10	0.999
25	0.996
50	1.000
100	0.995

level of resolution is 0.0036, while the variance between levels of resolution is 0.0019, indicating that spatial resolution has no effect on the seasonal value of transpiration. Results from the other climate and plant scenarios are similar. This result is as expected and the same as that found by Federer et al. [34] for dry ecosystems.

While mean transpiration is independent of resolution, spatial scale does affect other temporal characteristics of transpiration. Fig. 6 presents histograms of η and ξ over 100 growing seasons for two of the 54 scenarios. The two left-hand histograms show results from a highly resolved model ($\Delta z = 2$ cm), and the right-hand plots present results from a model with the same climate, soil, and plant, but for which the entire root zone is represented with a single vertical layer. There are clear differences in both the shape of the histograms and mean values of η and ξ for models with differing levels of spatial resolution.

To succinctly characterize the results from all scenarios, Figs. 7–10 present the mean values of η and ξ determined over 100 growing seasons: $\langle \eta \rangle$ and $\langle \xi \rangle$.

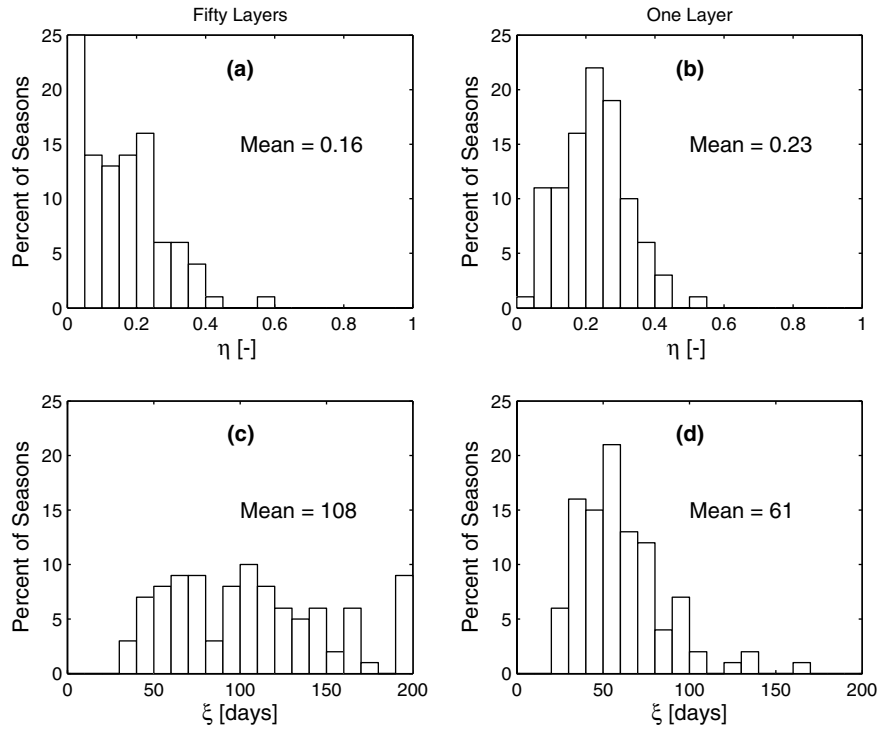


Fig. 6. Comparison of predictions of vegetation health between models with one vertical layer and 50 vertical layers for 100 growing seasons. Plots *a* (50 layers) and *b* (one layer) compare histograms of the fraction of the growing season for which $T_{act} = T_{pot}$. Plots *c* (50 layers) and *d* (one layer) compare histograms of the maximum number of continuous days during a growing season for which $T_{act} < T_{pot}$.

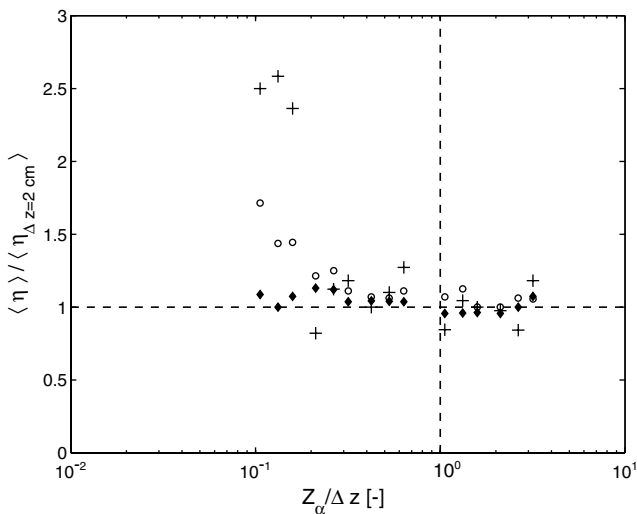


Fig. 7. Effect of vertical resolution on predictions of the mean fraction of a growing season for which $T_{act} = T_{pot}$. The ordinate is the mean of η over 100 growing seasons for vertical resolutions ranging from 1 to 20 layers, normalized by the mean of η for a model with 50 vertical layers. The x-axis presents the ratio of the characteristic depth of an infiltration event to the thickness of a model layer. Plus symbols represent those scenarios with $\gamma = 1.3$; open circles are those with $\gamma = 2$; and diamonds are those with $\gamma = 4$.

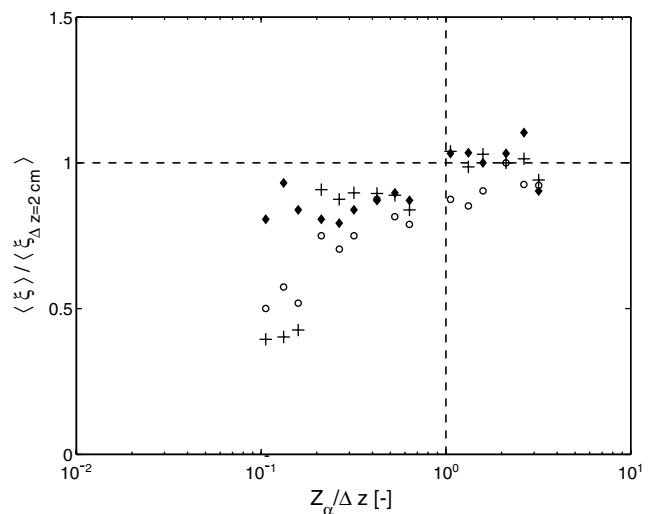


Fig. 8. Effect of vertical resolution on predictions of the longest number of continuous days during a growing season for which $T_{act} < T_{pot}$. The ordinate is the mean of ξ over 100 growing seasons for vertical resolutions ranging from 1 to 20 layers, normalized by the mean of ξ for a model with 50 vertical layers. The x-axis presents the ratio of the characteristic depth of an infiltration event to the thickness of a model layer. Plus symbols represent those scenarios with $\gamma = 1.3$; open circles are those with $\gamma = 2$; and diamonds are those with $\gamma = 4$.

Additionally, we choose to show not the absolute values of $\langle \eta \rangle$ and $\langle \xi \rangle$, but rather the values normalized by $\langle \eta \rangle$

and $\langle \xi \rangle$ determined from the models with the highest resolution ($\Delta z = 2$ cm). In this way, the figures show

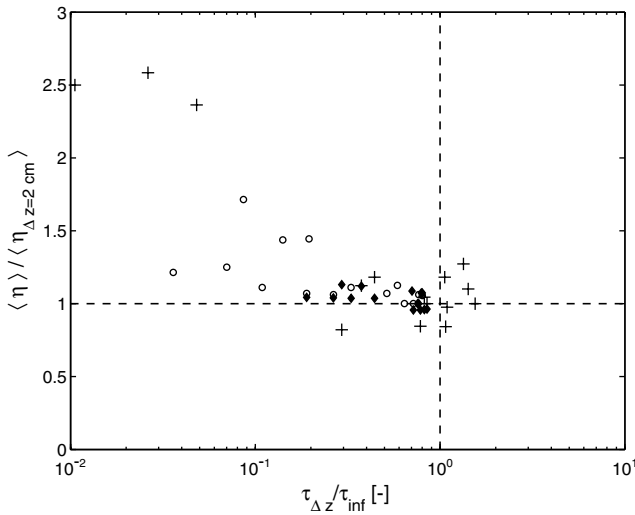


Fig. 9. Effect of vertical resolution on predictions of the mean fraction of a growing season for which $T_{\text{act}} = T_{\text{pot}}$. The ordinate is the mean of η over 100 growing seasons for vertical resolutions ranging from 1 to 20 layers, normalized by the mean of η for a model with 50 vertical layers. The x-axis presents the ratio of the characteristic time between rain events that provide enough water to a dry soil to enable the plant to transpire at T_{pot} for a finite-resolution model to the characteristic time for a model with infinite vertical resolution. Plus symbols represent those scenarios with $\gamma = 1.3$; open circles are those with $\gamma = 2$; and diamonds are those with $\gamma = 4$.

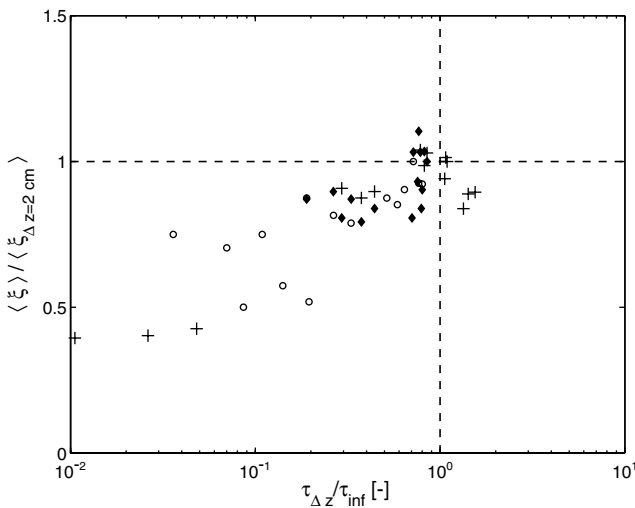


Fig. 10. Effect of vertical resolution on predictions of the longest number of continuous days during a growing season for which $T_{\text{act}} < T_{\text{pot}}$. The ordinate is the mean of ξ over 100 growing seasons for vertical resolutions ranging from 1 to 20 layers, normalized by the mean of ξ for a model with 50 vertical layers. The x-axis presents the ratio of the characteristic time between rain events that provide enough water to a dry soil to enable the plant to transpire at T_{pot} for a finite-resolution model to the characteristic time for a model with infinite vertical resolution. Plus symbols represent those scenarios with $\gamma = 1.3$; open circles are those with $\gamma = 2$; and diamonds are those with $\gamma = 4$.

how a coarsening of model resolution affects predictions of these characteristics of transpiration.

Figs. 7 and 8 present the normalized $\langle \eta \rangle$ and $\langle \xi \rangle$ results versus the ratio of the characteristic infiltration depth to model resolution (see Section 2.4). Results for scenarios with $\gamma = 1.3$ are presented as crosses, those with $\gamma = 2$ are open circles, and those with $\gamma = 4$ are diamonds. Fig. 7 indicates that $\langle \eta \rangle$ increases as Δz increases for some of the scenarios; i.e., models with coarser resolution may overestimate the health of vegetation. This figure also shows that the models with $\Delta z \leq Z_{\alpha}$ all give similar results for $\langle \eta \rangle$, indicating that layers of thickness close to the depth of a typical infiltration event are sufficient. This resolution may be overly conservative, however, as many of the scenarios with $Z_{\alpha}/\Delta z < 1$ also predict values of $\langle \eta \rangle$ close to those from the highest resolution models. The separation of the results for different values of γ in Fig. 7 emphasizes that the ratio $Z_{\alpha}/\Delta z$ does not account for plant behavior. For example, a value of $Z_{\alpha}/\Delta z = 0.1$ may be adequate for $\gamma = 4$, but inappropriate for $\gamma = 1.3$. Fig. 8 shows that $\langle \xi \rangle$ tends to decrease as Δz increases, and the results are qualitatively similar to those presented in Fig. 7.

Figs. 9 and 10 present the same normalized results for $\langle \eta \rangle$ and $\langle \xi \rangle$ as Figs. 7 and 8 but plotted against $\tau_{\Delta z}/\tau_{\text{inf}}$ (see Section 2.4). Scenarios with $\tau_{\Delta z}/\tau_{\text{inf}}$ close to one give good predictions of $\langle \eta \rangle$ and $\langle \xi \rangle$. This dimensionless parameter appears to be a better indicator of appropriate model resolution than $Z_{\alpha}/\Delta z$, especially for predictions of $\langle \xi \rangle$. The ratio $\tau_{\Delta z}/\tau_{\text{inf}}$ incorporates plant behavior, and the separation as a function of γ that is seen in Figs. 7 and 8 is absent from Figs. 9 and 10.

4. Discussion

Figs. 4, 6–10 all show clear effects of model resolution on predictions of evapotranspiration and vegetation health. For models to be effective tools, choices of resolution must be made with full awareness of these implications. For the scenarios considered here, a coarsening of model resolution did not affect predictions of average transpiration, but led to overestimates of η and underestimates of ξ over multiple growing seasons. Figs. 7–10 show that there are many choices of model resolution that lead to similar results for these variables. The parameters, $Z_{\alpha}/\Delta z$ and $\tau_{\Delta z}/\tau_{\text{inf}}$, arising from combinations of relevant climate, soil, plant, and model parameters prove to be reasonable indicators of adequate vertical resolution. The dimensionless group, $Z_{\alpha}/\Delta z$, requires knowledge of the difference in volumetric water content between field capacity and the wilting point and a characteristic depth of rainfall. While simpler to determine than $\tau_{\Delta z}/\tau_{\text{inf}}$, this parameter does not sufficiently incorporate plant behavior and may be overly conservative. A more precise indicator of

appropriate model resolution is $\tau_{\Delta z}/\tau_{\text{inf}}$, but the data requirements are more significant. This parameter requires the same knowledge as for $Z_r/\Delta z$, plus a characteristic rate of storm arrivals and the depth to which plant roots must be wetted to supply enough water to meet the potential evapotranspiration demand.

Underlying the results of this work are a series of modeling choices, the impact of which must be discussed. In simulating soil-moisture dynamics and vegetation uptake, we chose to work at a daily time scale, we neglected bare-soil evaporation, we simplified the representation of infiltration, we limited our analysis to a single soil type, and we employed a Type I model for plant uptake. Diurnal variations in potential evapotranspiration were not included in this work. This precludes analysis of the effects of midday wilting that arise from rate limitations on the movement of water from the soil to the roots [35,52]. We chose to focus instead on the more severe reductions in transpiration that persist from day to day, and our conclusions should be interpreted in this light. Also, we did not separate evaporation and transpiration; the explicit representation of bare-soil evaporation will require a reassessment of adequate spatial resolution, as this process occurs at the soil surface. Infiltration dynamics were simplified by representing the events as instantaneous piston flow. In reality, soil-moisture redistribution will happen over time; consequently, our model reduces the spatial heterogeneity in soil moisture that would be encountered under field conditions. This leads to overpredictions of uptake immediately following a rain event. Because soil-moisture redistribution is rapid for this sandy soil and our results are interpreted at a daily time scale, the simplification of the infiltration dynamics does not have a significant impact on our results or conclusions. For other, less permeable soils, however, the timing of soil-moisture redistribution may be important, as might runoff. In this work, plant uptake was represented with a Type I model in which evapotranspiration was driven by a potential difference between the soil and the plant. Our results can be extended to Type II models, however, by recognizing that such representations are nearly equivalent to Type I models in which the plant has no ability to compensate for spatially varying soil moisture—local uptake is solely a function of local soil moisture. Thus, with a Type II representation, variations in model resolution will have even larger effects on predictions of vegetation health.

The results presented here highlight the importance of spatial scale and point to a couple of dimensionless parameters that can be used to determine appropriate model resolution. To extend the generality of these findings, future work will consider a range of ecosystems (such as the steppes of Colorado and Texas scrublands), increased process, complexity (such as diurnal and seasonal variation in evapotranspiration forcing, root

growth, soil heterogeneity, and lateral inflows), and additional output variables of interest (such as the partitioning of water among evaporation, transpiration, and drainage). Doing so will test the applicability of the parameters defined here under a wider range of conditions, and may lead to the development of new dimensionless groups.

5. Conclusions

The work presented here elucidates the effect of vertical resolution on predictions of transpiration. In water-limited ecosystems, intermittent rainfall may only partially rewet the root zone. Because of this and the non-linear nature of the root-water uptake function, the choice of model resolution can significantly impact predictions of plant health. An ability to determine appropriate model resolution a priori would greatly benefit ecohydrologic studies. The results presented here demonstrate that dimensionless groups of characteristic parameters can be used for this purpose. In particular, we show that ratios of characteristic spatial and temporal scales are reasonable indicators of appropriate vertical resolution for the prediction of transpiration in water-limited ecosystems.

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