Correspondence

Revisiting 'Field plants strategically regulate water uptake from different soil depths by spatiotemporally adjusting their radial root hydraulic conductivity'

A reply to Fu *et al*. (2026) 'Limitations of temporally linearized soil–water flux gradients in estimating root water uptake'

Introduction

The comments of Fu *et al.* (2026) on the paper of Rickard *et al.* (2025a) highlight a critical gap between the complexity of water–root–soil interactions in the field and our current capacity and ability to measure and model them. Given that *New Phytologist* is a plant journal, the focus of Rickard *et al.* (2025a) was the physiological perspective: how plants respond physiologically to spatiotemporal variations in soil water content under field conditions, while the hydrological perspective, including the method for calculating daily root water uptake, was only briefly explained (Rickard *et al.*, 2025a). We take this opportunity to elaborate on this. In this response, in addition to addressing the specific points raised by Fu and co-authors, we discuss the complexity of soil–water–root interactions in the field, as well as their broader implications for what we can measure and model under field conditions. The premise of Fu and co-authors is that the Richards' equation and other methods used in their comments provide error-free solutions, which can then be used as a benchmark to verify our method. This premise is flawed in both theory and practice: the Richards' equation is only an approximation, and its errors for modeling water flow in field soils are unpredictable. Herein, we discuss the mechanisms underlying these errors and clarify why the method proposed by Rickard *et al.* (2025a) represents one of the most practical approaches for calculating daily root water uptake in the field, as noted by Burks & Tumber-Davila (2025). We emphasise that the method of Rickard *et al.* (2025a) is designed to measure and calculate daily root water uptake under real field conditions. The first example in the comments of Fu and co-authors – with constant groundwater depth and constant evaporation – is fictitious and does not exist in the real world.

Roots and soil interact across multiple temporal and spatial scales, shaping soil microbial communities and their functions, while concurrently modifying soil physical and chemical properties. Root–soil–microbe interactions are not static processes but constitute a highly dynamic system (Young & Crawford, 2004). Over the past decades, we have systematically studied root–soil–microbe interactions and their influence on soil structure, water retention and hydraulic conductivity of soils at various scales (Read *et al.*, 2003; Whalley *et al.*, 2004, 2005; Rabbi *et al.*, 2018; Wang *et al.*, 2020), as well as their consequences for root water uptake in three dimensions, with 3D root architecture explicitly resolved (Zhang *et al.*, 2020). We have decades of experience developing and applying numerical solutions of the Richards' equation and were aware of its limitations in modeling water flow under field conditions (Zhang & Ewen, 2000; Zhang *et al.*, 2002, 2020; Huang *et al.*, 2023). The method proposed by Rickard *et al.* (2025a) builds upon this body of work. Since Fu and co-authors used the Richards' equation as a benchmark to assess the method of Rickard *et al.* (2025a), we first discuss this equation and explain its problems in modeling water flow in the field. However, before proceeding further, we identify and address two errors in the comments made by Fu *et al.* regarding the method of Rickard *et al.* (2025a).

The first error is that their comments misinterpret (via their statement 'integration of the Richards' equation over········') eqn (1) in Rickard *et al.* (2025a) as the Richards' equation. In the literature, the Richards' equation specifically refers to the equation derived by Richards (1931), in which Darcy's law, originally formulated for water flow in saturated soils, was extended to unsaturated conditions. Although the Richards' equation conserves mass, it differs fundamentally from eqn (1) in Rickard *et al.* (2025a), which is a general mass-balance equation and does not require water flow to obey Darcy's law. This difference is critical when assessing the suitability of the Richards' equation for modeling water flow under the conditions addressed by Rickard *et al.* (2025a). The second error relates to their claim that there is a dimensional mismatch in eqn (3) in Rickard *et al.* (2025a), without specifying the nature of the alleged mismatch. We have carefully re-examined the derivation of eqn (3) and can confirm that this equation is dimensionally consistent.

Theoretical limitations of the Richards' equation

In their comments, Fu and his co-authors use the MOIST model they developed based on the Richards' equation (Fu *et al.*, 2025) to demonstrate what they interpret as errors in the results of Rickard *et al.* (2025a). The Richards' equation is an approximation rather than an exact description of the processes that govern water flow in soil; it was derived based on two key assumptions (Richards, 1931). The first one is that air pressure is spatially uniform across the soil profile, such that air flow and water flow can be decoupled and do not affect each other; this assumption may fail during rainfall events, during which infiltrating water isolates air into air bubbles or traps air into poorly connected pores, thereby influencing liquid water flow. This is a common phenomenon in water infiltration and can be easily tested using soil column experiments. The second one is that the Richards' equation requires soil water retention curve and soil hydraulic conductivity functions. These two parameters are typically measured in the laboratory under conditions in which water distribution in the pore space reaches an equilibrium state. Physically, this means that when wetting a dry soil, water cannot fill pores unless all smaller connected pores are already filled, while when drying a wetted soil, water in pores cannot drain unless all larger connected pores have already drained. Furthermore, the water retention curve obtained during drainage differs from that obtained during wetting, a phenomenon known as hysteresis (Basile *et al.*, 2003). This equilibrium assumption breaks down during rainfall or irrigation events, during which infiltrating water flows preferentially through large and interaggregate pores, while bypassing smaller intra-aggregate pores, even when these pores remain air-filled. This nonequilibrium flow, also known as preferential flow and macropore flow in the literature, has been well-documented (Gerke & van Genuchten, 1993; Ewen, 1996; Beven & Germann, 2013), and cannot be described by the Richards' equation used by Fu *et al.* (2026).

Practical limitations of the Richards' equation

In addition to the theoretical issues discussed previously, the practical limitations of the Richards' equation under field conditions are substantial. First, field soils are vertically stratified, and the soil science community uses O, A, B and C horizons to describe this stratification. Therefore, soil hydraulic properties vary with depth. Accurately measuring the spatial variability of all soil hydraulic parameters *in situ*, without disturbing the soil, is extremely challenging, if not impossible. At best, what we can currently do *in situ* is install soil moisture sensors and tensiometers at multiple depths to simultaneously measure soil water content and matric potential changes over a rainfall or irrigation event; this allows the derivation of average water retention curves for soils at different depths. However, due to technological limitations, current tensiometers cannot measure soil matric potential more negative than −300 kPa (Whalley *et al.*, 2007). Second, soil physical properties are not static but highly dynamic, varying with time. Biologically, as plants grow, roots and root-associated processes, such as root exudation and microbial and faunal activity, reshape soil structure and alter the surface tension and viscosity of soil water over timescales of days (Crawford *et al.*, 2012); these changes in turn modify the soil water retention curve and hydraulic conductivity (Read & Gregory, 1997; Whalley *et al.*, 2004, 2005; Kroener *et al.*, 2014; Schwartz *et al.*, 2016; Choudhury *et al.*, 2018; Rabbi *et al.*, 2018; Helliwell *et al.*, 2019). Physically, wetting and drying cycles caused by rainfall, irrigation and root water uptake result in soil shrinking and swelling, further modifying soil structure and the capacity of soils to retain and transmit water (Utomo & Dexter, 1982). Microbiologically, microbial decomposition of soil organic matter reshapes soil structure and alters soil physical properties (Rabbi *et al.*, 2020). Such spatiotemporal variability in soil physical properties induced by multiple processes is practically impossible to measure *in situ*. Although there is increasing recognition of the need to integrate these processes for a better description of soil water dynamics (Pelosi *et al.*, 2026), progress is slow due to their complexity.

These theoretical and practical limitations mean that the Richards' equation provides only an approximate description of water flow under field conditions and is subject to unpredictable uncertainties. While Fu *et al.* might disagree, arguing that their MOIST model reasonably reproduced soil water dynamics in a lysimeter (Fu *et al.*, 2025, 2026), this apparent agreement likely reflects curve-fitting in a chosen framework rather than a robust model validation for several reasons.

In addition to the neglect of water retention hysteresis, which has a significant impact on the soil water capacity parameter (the derivative of soil water content with respect to soil matric potential) and accuracy of their modeling, Fu *et al.* (2025, 2026) overlooked at least three other key processes. The first one is the dynamics of soil properties. Over a four-year experimental period in their lysimeter example, plant roots underwent repeated growth, senescence and decay, which, along with the concurrent changes in soil microbial communities and fauna, inevitably reshaped soil structure and modified soil physical properties. Thus, the use of static soil hydraulic properties over years in their modeling framework is difficult to justify. As an illustration, Fig. 1 shows the saturated hydraulic conductivity measured at different times at our experimental site using an infiltrometer (Rickard *et al.*, 2025b), which varies by more than an order of magnitude, from 0.05 to 0.6 m d^{-1}. Second, Fu *et al.* (2025, 2026) used a constant saturated hydraulic conductivity in their hydrothermal model, apparently unaware the strong temperature dependence of water viscosity and water surface tension. When temperature increased from close to 0°C to 27°C in their lysimeter example, the kinetic viscosity (ν) of water decreased from 0.0179 to 0.0085 $\mathrm{cm}^2\,\mathrm{s}^{-1}$. Since soil saturated hydraulic conductivity (K) is inversely proportional to ν ($K = k/\nu$, where k is permeability), this temperature increase enhanced soil hydraulic conductivity by *c.* 100%. Such temperature-dependent variations in soil hydraulic conductivity were not considered by Fu *et al.* (2025). Third, Fu *et al.* (2026) assumed root water uptake is proportional to root length density, overlooking major advances in our understanding of root water uptake since Feddes' work in the 1970s (Feddes *et al.*, 1976). It has been well-established that root water uptake is a compensatory process, whereby plants increase water uptake from wetter zones when other zones become dry (Thomas *et al.*, 2020; Müllers *et al.*, 2023). Recent discovery by Rickard *et al.* (2025a) and others (Müllers *et al.*, 2023) that plants take up the topsoil water preferentially adds further complexity to this process. All of these observations indicate that root water uptake is not solely determined by root length, as assumed in Fu *et al.* (2025, 2026), but emerges from a complex root–soil interaction (Vadez, 2014), which cannot be described by the Feddes' model used by Fu *et al.* (2025).

Mathematically, Fu *et al.* also overlooked that their MOIST model is formulated using the *h*-form of the Richards' equation, where the matric potential is used as the dependent variable. It has been well-established that numerical solutions of the Richards'

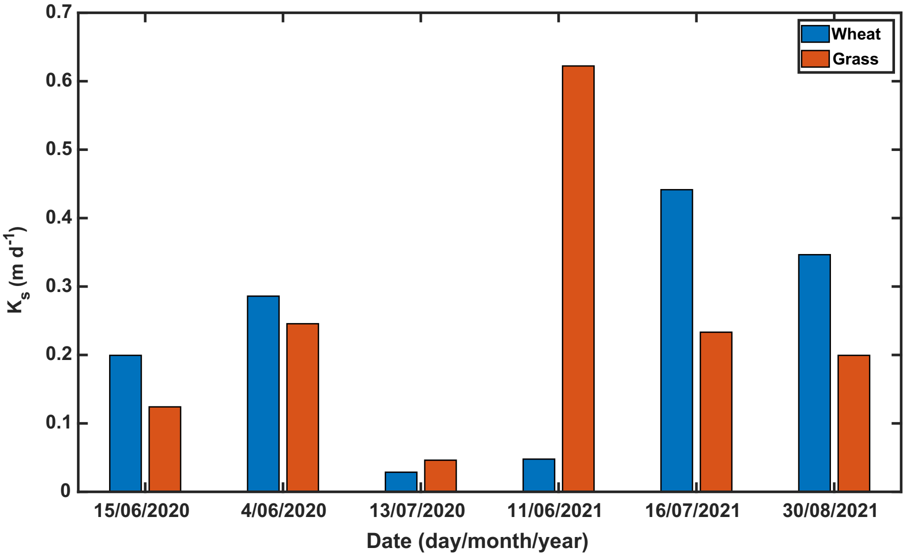

Fig. 1 Temporal variation in saturated hydraulic conductivity of the surface soil measured at the experimental site at Rothamsted (Rickard *et al*., 2025b).

equation in this form are not mass-conservative. Depending on spatial and temporal discretization in numerical solution and soil hydraulic properties, it can give rise to substantial errors (Celia *et al*., 1990). Taken together, these numerical errors, methodological oversights, inherent uncertainties and numerous processes that the Richards' equation cannot describe seriously undermine the suitability of the model of Fu *et al.* (2026) for mechanistically describing water flow in field soils.

Mathematical accuracy and modeling accuracy

Fu *et al.* criticize our method for using night-time $\partial Q/\partial z$ to estimate daytime $\partial Q/\partial z$, labelling it a 'major assumption'. Mathematically, this is an approximation rather than an assumption; it is an approach used in all numerical modeling. In fact, when formulating their numerical solution, Fu *et al.* (2025, 2026) also assume that soil matric potential varies linearly within each time step, just as in our method, thereby introducing truncation errors. The only difference is that the time-step size in the method of Rickard *et al.* (2025a) is *c.* 12 h. Because such truncation errors depend on time-step size, Fu *et al.* might argue that their numerical solution can use smaller time steps (e.g. 10^{-8} s) to reduce such errors. While this is mathematically correct, field data, such as rainfall and other meteorological data (required for calculating evapotranspiration), are typically recorded daily or collected on event basis (as in the archived Rothamsted meteorological data used by Fu *et al.* in their comments). Disaggregating these recorded values into shorter intervals (e.g. 10^{-8} s) is purely a mathematical manipulation rather than a physically meaningful representation of rainfalls in the field. The errors induced by such approaches are uncertain and unpredictable. Consider a recorded daily rainfall event as an example. If the rainfall occurs during the preceding night of a sunny day, the rainfall enhances plant transpiration in the following day due to increased soil moisture; by contrast, if the same amount of rainfall occurs during the day rather than at night, the rainfall suppresses plant transpiration due to reduced sunlight and decreased vapor pressure deficit. That is, although the recorded daily rainfall in the two scenarios is identical, its consequences for soil water dynamics differ markedly. Therefore, when comparing with measured data, using a time step of 10^{-8} s instead of 12 h does not necessarily improve modeling accuracy. In other words, mathematical refinement of a numerical solution does not necessarily translate into improved modeling accuracy when limitations of available field data are considered. While rain gauges in modern weather stations can record a rainfall event at fine temporal resolutions, these measurements cannot be directly extrapolated to other locations due to spatial variability of rainfall intensity (will be discussed later).

Combination of Richards' equation and Bayesian inference

Fu *et al.* suggest combining the Richards' equation with Bayesian inference to estimate root water uptake, apparently unaware that we have done this (Huang *et al*., 2023). Calculating root water uptake using the Richards' equation and measured soil water data is an inverse problem, which is ill-posed, meaning that a small error in soil water measurements could lead to large errors in the calculated root water uptake. Due to the unmeasurable spatiotemporal variability of soil physical properties and the inherent inaccuracies of soil moisture measurement devices, inverse modeling is extremely challenging. In fact, Guderle & Hildebrandt (2015) systematically studied this and demonstrated that when measured data are prone to small errors, methods based on the Richards' equation cannot yield satisfactory results; the outcome deteriorates further when soil physical properties are not accurately known. While all models require high-quality data, inverse models based on the Richards' equation tend to amplify measurement errors in the estimated root water uptake.

Misapplication of bounds in root water uptake estimation

Fu *et al.* attempted to estimate the upper and lower bounds of root water uptake in the 0- to 50-cm soil layer, but their approach contains flaws. We explicitly stated (Rickard *et al.*, 2025a) that our method cannot distinguish between evaporation and root water uptake. Accordingly, we carefully selected time periods during which evaporation was negligible and provided photographic evidence in the Supporting Information (Rickard *et al.*, 2025a) to illustratively support this.

In estimating the upper bound using rainfall and soil water storage changes, Fu *et al.* failed to account for canopy interception and overlooked that mounds formed by root expansion and soil fauna at different locations and times can induce surface run-off at spatial scales relevant to our experimental measurements. They also implicitly neglected (due to the assumption of zero matric-potential gradient at the bottom end) upward water flow from the subsoil (> 50 cm), which could become significant when the topsoil is dry. In their lower bound calculation, they included an evaporation term that did not exist and did not clarify how water percolation out of the 0- to 50-cm soil layer was calculated when the topsoil was wet. Since the leaf area index during the selected period is > 3, canopy interception is substantial. Indeed, because of canopy interception, not all rainfall events during this period resulted in measurable changes in soil water content. Furthermore, soil water content was measured at three depths (15, 30 and 45 cm), and Fu *et al.* did not give the inter- and extrapolation methods they used to estimate soil water storage changes in the 0- to 50-cm profile, which could significantly influence results.

Beyond these issues, there is an additional problem in their use of the archived rainfall data in Rothamsted. The weather station at Rothamsted is located *c.* 200 m east of the experimental site. Although we do not have direct evidence of spatial variability of these rainfalls at Rothamsted, data we observed from other locations show significant variability. As an illustrative example, Fig. 2 shows the spatial variation of a rainfall event measured by twelve 2 m × 2 m weighing lysimeters at the Experimental Station of the Chinese Academy of Agricultural Sciences.

All these factors contributed to the discrepancies reported by Fu *et al.* Importantly, not all root water uptake values in the 0- to 50-cm soil layer calculated using our method exceed the upper bounds estimated by Fu *et al.*, further supporting that these discrepancies arise from natural variability and other uncertainties discussed previously, rather than from our method.

Revisit the method for calculating daily root water uptake

The method proposed by Rickard *et al.* (2025a) is based on mass balance and is thus theoretically sound. It requires only soil moisture data and thus naturally accounts for the combined influence of numerous physical and biological processes, as discussed previously, that cannot be measured *in situ* and cannot be described by the Richards' equation. It is thus more reliable than the Richards' equation for calculating daily root water uptake in the field (Burks & Tumber-Davila, 2025). To distinguish the effect of water redistribution from the influence of root water uptake on daytime soil moisture changes, we propose estimating daytime $\partial Q/\partial z$ using night-time soil moisture changes. Like all numerical solutions, this approach is an approximation. All numerical solutions introduce errors, and the errors of our method depend on the temporal variability of $\partial Q/\partial z$, as Fu *et al.* correctly noted.

Eqn (3) in Rickard *et al.* (2025a) performs well under most conditions during the main crop growing season, but special care and treatments are required during and immediately after rainfall events, when soil water movement is rapid. These considerations, outlined later, were not detailed in the previous work because the focus of Rickard *et al.* (2025a) was the physiological perspective, elucidating the physiological response of field plants to spatiotemporal variations in soil water.

The method of Rickard *et al.* (2025a) is designed to calculate daytime root water uptake. Therefore, when root water uptake is absent, for example, during a continuous daytime rainfall event, in which sunlight is low and vapor pressure deficit is small, there is

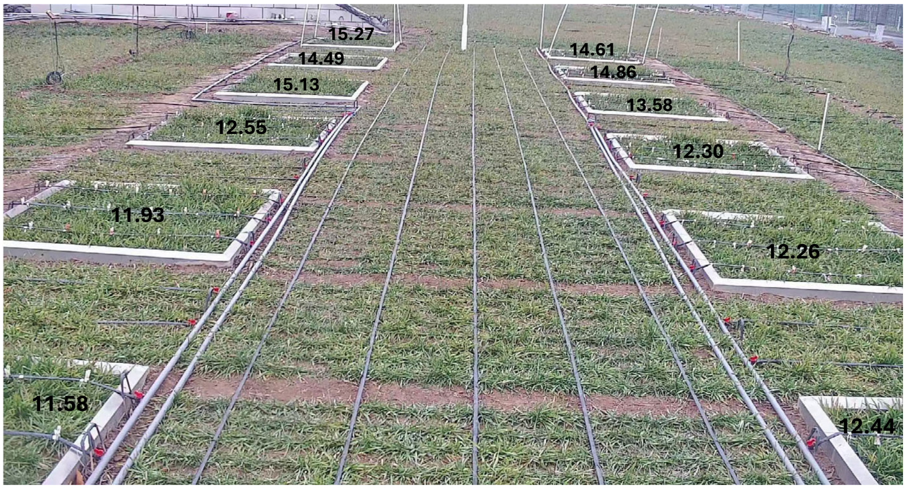

Fig. 2 Spatial variation of a rainfall event (mm) from 16:00 h to 17:00 h on 23 August 2025, measured using twelve 2 m × 2 m weighing lysimeters at the Experimental Station of the Chinese Academy of Agricultural Sciences, Qiliying (35.16° N, 113.79° E). Courtesy of Ni Song, Chinese Academy of Agricultural Sciences.

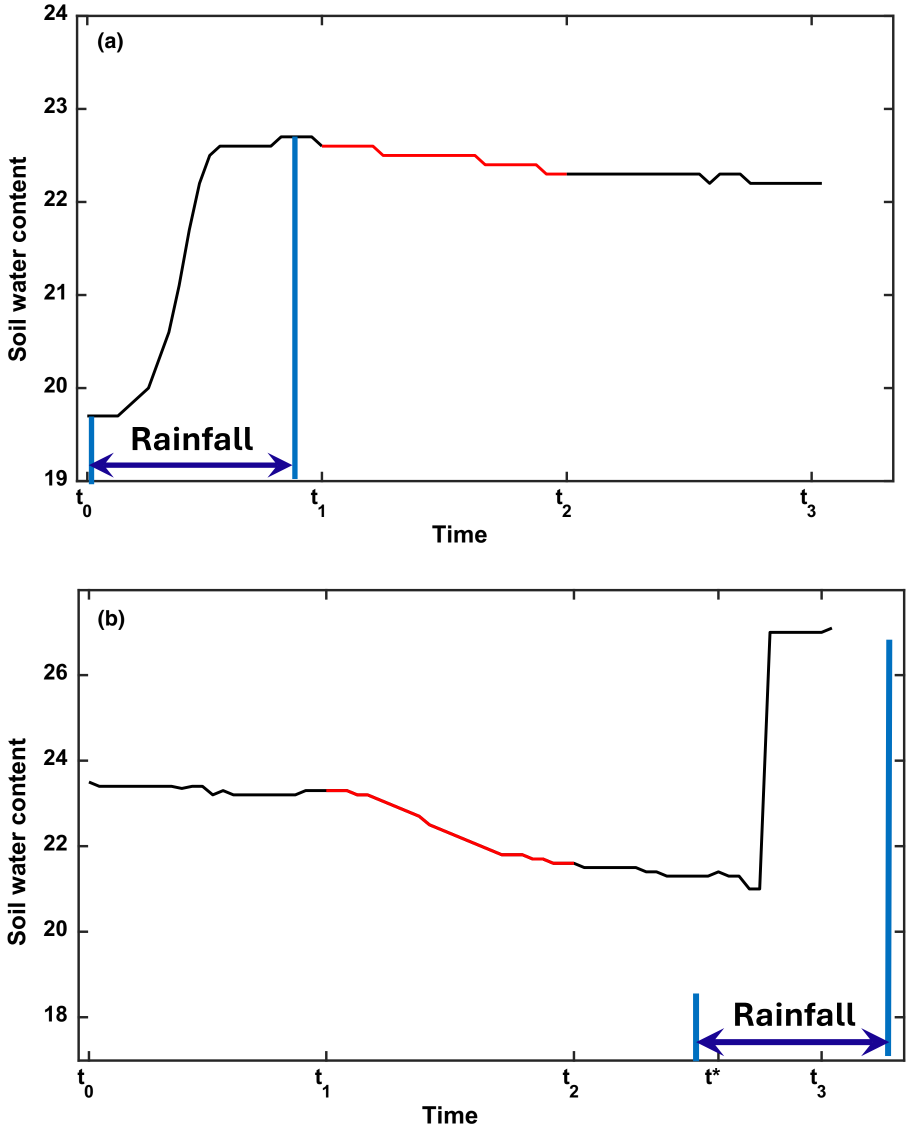

Fig. 3 Calculating daytime $\partial Q/\partial z$ (from t_1 to t_2) using night-time soil moisture changes needs to consider that the forces that drive water flow in the night-time and daytime should be comparable. (a) If rainfall occurs in the preceding night (from t_0 to t_1) and there is no rainfall in the following day (t_1 to t_2) and night (t_2 to t_3), the daytime $\partial Q/\partial z$ should be estimated using soil water change in the second night as: $-\frac{\partial Q}{\partial z}\approx\left[\frac{\Theta(t_3)-\Theta(t_2)}{t_3-t_2}\right](t_2-t_1)$. (b) Conversely, if rainfall occurs in the second night (t_2 to t_3) and there is no rainfall in the daytime and the preceding night, the daytime $\partial Q/\partial z$ should be estimated using soil moisture changes in the preceding night (t_0 to t_1) as: $-\frac{\partial Q}{\partial z}\approx\left[\frac{\Theta(t_1)-\Theta(t_0)}{t_1-t_0}\right](t_2-t_1)$, or by excluding the effect of rainfall after t^*: $-\frac{\partial Q}{\partial z}\approx\frac{1}{2}\left\{\left[\frac{\Theta(t_1)-\Theta(t_0)}{t_1-t_0}\right]+\left[\frac{\Theta(t*)-\Theta(t_2)}{t*-t_2}\right]\right\}(t_2-t_1)$.

little or no root uptake, and calculation is unnecessary. The key principle in using this method is that the forces driving water flow during the daytime and nighttime should be the same or similar. For example, if rainfall or irrigation occurs during the preceding night, while there are no precipitation and irrigation during the following day and night, the daytime $\partial Q/\partial z$ should be calculated using the soil moisture change observed during the second night. Fig. 3 illustrates several scenarios for calculating daytime $\partial Q/\partial z$ based on this principle. In more complex cases, hydrological and biological knowledge is required to reduce errors.

In summary, we agree with Fu *et al.* that the method proposed by Rickard *et al.* (2025a) is an approximation and, like all numerical methods, is subject to truncation errors, as explicitly noted in Rickard *et al.* (2025a). However, the Richards' equation used by Fu *et al.* (2026) cannot serve as a benchmark to verify our method, for the reasons outlined previously. Fu *et al.* substantially underestimated the complexity, uncertainty and limited measurability of water flow and root water uptake under field conditions, implicitly assuming that the Richards' equation can provide an error-free solution for soil water flow and can thus benchmark the method of Rickard *et al.* (2025a). This premise is incorrect. Moreover, in calculating the upper and lower bounds of the transpiration, Fu and co-authors overlooked the errors introduced by various unaccounted-for factors, while taking their calculations as error-free solutions to benchmark our results; such an approach is unjustified. A practical approach to validate our method is through weighing lysimeters, which provide direct daily measurements of transpiration. We are currently conducting such measurements at the Experimental Station of the Institute of Farmland Irrigation, Chinese Academy of Agricultural Sciences.

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Competing interests

None declared.

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