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Root water potential explains logarithmic variations of soil matric potential

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ABSTRACT: Changes in soil matric suction (or matric potential; ψ_S) due to plant transpiration affect shallow soil stability. Understanding water transport within the soil-plant-atmosphere continuum (SPAC) is the key to quantify the transpiration-induced changes in ψ_S, but this is often challenging due to the difficulties in measuring water potential in all components of the SPAC. Handheld tools are readily available to measure leaf water potential (ψ_L), but they only partially explain variations in ψ_S. Although root water potential (ψ_R) is known to be much more closely associated with ψ_S, data on ψ_R is very scarce. This study presents findings obtained from soil columns cultivated with vetiver grass (*Chrysopogon zizanoides L.*). The vegetated columns were subjected to a drought period typical to a tropical climate region, during which various water potential terms, including ψ_S and ψ_R, as well as relevant root traits, were measured to understand water transport in this SPAC. Our findings showed a logarithmic increase in the gradient between ψ_S and ψ_R. Specific leaf area significantly decreased with ψ_R, indicating hydraulic continuity between roots and leaves. We propose a new power-law correlation between root diameter and ψ_R to facilitate a trait-based understanding of root water uptake.

Keywords: Soil matric potential; Root water potential; Specific leaf area; Transpiration; Root diameter

1 INTRODUCTION

Vegetation plays a crucial role in stabilising shallow soil slopes under rainfall. Plant roots penetrate the soil matrix, providing mechanical reinforcement to resist against shear stress. In practical environments where soil water conditions affect root water uptake, the root hydromechanical properties may be altered and hence affect the reinforcement effects. Over the past decades, studies have focused on investigating this kind of root hydromechanical reinforcement, such as the variations in root tensile strength and Young's modulus with root moisture contents (Boldrin et al., 2018; Wu et al., 2021). In particular, Boldrin et al. (2018) introduced a term called 'root water retention curve' (RWRC, relating root moisture content with root water potential) by viewing roots as a porous medium that can retain certain amount of water. Later, Leung et al. (2019) conducted a theoretical study to highlight the role and importance of RWRC when assessing the effects of varying root moisture content (hence root water potential) on the unsaturated shear strength of soil. Thus, quantifying root hydraulic status is important and relevant to assess the effects of root hydromechanical reinforcement to unsaturated soils. However, existing studies often test roots that have been severed / cut-off from their plants, not accounting for the water transport between soil and roots. Also, it is crucial to understand the inherent relationship between soil and root water potential to explain the mechanisms of plant water relation and root reinforcement in soils in engineering applications.

Water transport through a soil-plant-atmosphere continuum (SPAC) is imperative and governed by the spatiotemporal distribution of water potential (ψ) in the system. Gradients in ψ of soil (ψ_S), roots (ψ_R) and leaves (ψ_L) form the energetic basis to govern the water transport (Novick et al., 2022). However, interpretation of root water potential (ψ_R) is often challenging due to a complex interplay between soil and roots (Doussan et al., 2006), and tortuous root anatomical structure with various hydraulic pathways in SPAC (Zarebanadkouki et al., 2016). Given these constraints, several studies have attempted to replace ψ_R with above-ground plant functions. Leaf phenological parameters such as stomatal conductance (Sperry et al., 2002), ψ_L (Dainese and Tarantino, 2020) and some normalised root-shoot traits have been quantified to estimate ψ_R. In particular, 'sink term' has been often adopted to implicitly model the effects of root-water uptake in soil, instead of through ψ_R, by relating transpiration rate with soil water content (or matric suction), micrometeorological parameters and other root empirical functions (Feddes et al., 1974). Although leaf-based traits seemed viable, the sensitivity of ψ_R is still yet to be verified with any actual measurements.

Existing works have made attempts to make direct measurements on root hydraulic conductivity (k_{root}; Zarebanadkouki et al., 2016) and they found significant influence of k_{root} on ψ_R. k_{root} does not only explain the root hydraulic property, but also were found to have significant correlation with leaf phenotypic responses. Despite a wealth of research focused on measuring k_{root}, the dataset is still sparse, limiting our ability to characterise ψ_R and gradient of ψ between soil and roots. Even if such gradients are reported in some existing studies (Ball & Oosterhuis 2005; Puértolas et al. 2015), continuous observations do not exist.

Given the state-of-the-art by existing studies on water flow in SPAC, two scientific challenges exist: (1) proper experimental quantification on ψ_R in a heterogenous soil conditions is not properly defined; and (2) the hydraulic continuum in the root-leaf system is not experimentally studied hitherto. This study aims to (1) tackle these challenges by continuously mapping and searching for correlations between ψ_S and ψ_R using a thermodynamic equilibrium method (i.e., dew-point potentiometer); and (2) seek correlations between measured ψ_R with leaf traits to explain the hydraulic continuum and water transport in a SPAC.

2 METHODS

Grass rhizomes of *Chrysopogon zizanioides* L. was transplanted in a 1 m-long clayey sand columns at a glasshouse. To avoid cluster of roots impeding the ψ measurements, only single grass was fed in each pot. A total of 54 soil-plant columns were then equally split into three sets and propagated for three different growth periods of 3, 4 and 5-months (i.e. 18 columns per growth period). All the columns were regularly irrigated with tap water to the field capacity and sufficient natural light was provided during their growth. Spatiotemporal variations of soil moisture content and matric suction was monitored by three pairs of moisture content sensors (SM-150 T, Decagon Devices) and mini-tip tensiometers, respectively, at 0.25 m, 0.55 m and 0.85 m depths. Once the grass reached the desired growth period, irrigation was stopped and the grass in each column was subjected to a prolong drying period to introduce drought stress to the grass. The grasses were subsequently sampled at various time intervals, covering almost the full spectrum of soil water conditions from field capacity to near the wilting point.

During the experiments, the leaves were first cut and then scanned to obtain the leaf surface area by using an image analysis software. The scanned leaves were kept in a 55 °C oven until a constant weight was achieved to obtain the dry leaf biomass. The specific leaf area (SLA) was then calculated by dividing the leaf area by the dry biomass. After measuring the leaf traits, the 1-m column was cut into three equal sections for easier segregation of roots. The collected roots were cleaned with a brush to remove any soil adhered to them and then placed in a WP4C dew-point potentiometer for the direct measurements of ψ_R. It is known that this device can measure ψ_S above -1 MPa, but its application for root samples is limited due to challenges in maintaining transient water status and the inability to directly observe xylem exudation or dew-point formation. However, this limitation was addressed by verifying the sensitivity of ψ_L measurements and their agreement with existing tools like the pressure chamber. Furthermore, recent studies have suggested the use of potentiometer beyond its traditional soil-focused applications (Novick et al., 2022), encouraging its potential use for measuring ψ in plant samples. Consequently, we aimed to measure ψ_R using the dew-point potentiometer, considering that values measured by the device are deemed accurate after -1 MPa, which typically is the magnitude of ψ in plant cells during soil drying.

Thereafter, the root diameter was obtained by taking the average values of five root fragments. In addition, the experimental protocol followed several precautions to preserve the innate moisture content of the roots and soil: (1) cut sections of the columns were wrapped and kept in a dry ice chamber until the experiments of the first cut section was complete; (2) all the root samples were carefully handled by a clean forceps to avoid moisture loss from direct hand contact; and (3) the potentiometer chamber was wiped with distilled water and calibrated with a standard 0.5 M KCl solution (-2.19 MPa at 24 °C) before each ψ_R measurement, in order to eliminate any impurities existed in the chamber and hence to ensure high measurement accuracy.

3 RESULTS AND DISCUSSION

3.1 $\psi_S - \psi_R$ *correlation*

An apparent decline in ψ_R was observed as available soil water depleted during the drought, with a decrease in ψ_S correspondingly (Fig. 1). Cai et al. (2022) reported similar decrease in k_{root} with decreasing ψ_S for six different crop species, attributable to several reasons including the downregulation of aquaporin (Caldeira et al. 2014), abscisic acid (ABA) signalling (Maurel and Nacry 2020) and/or root shrinkage. We similarly hypothesise that one of these underlying mechanisms may have contributed to the observed decline in ψ_R in the present study. As the plants approached the perceived permanent wilting point (approximately -1.5 MPa of ψ_S), the ψ_R value approached an asymptote of -4 MPa. The measurements of ψ_R in excised roots, spanning from field capacity to the near wilting condition, revealed a nonlinear, or specifically logarithmic, correlation between ψ_S and ψ_R, regardless of the plant growth period. The non-linearity in the $\psi_S - \psi_R$ response was evident within the ψ_S range of -0.3 to

-0.5 MPa. Cai et al. (2022) found similar nonlinear response for their findings of k_{root} during soil drying. They also established a critical value of ψ_S near -0.4 MPa that marks the onset of nonlinearity in k_{root}, at which point soil water fluxes begin to limit in the soil-plant continuum, leading to stomatal closure (Carminati and Javaux, 2020). Our results also showed that the roots located in shallower soils consistently exhibited less negative ψ_R compared to those at greater depths, which essentially should drive water along the root system.

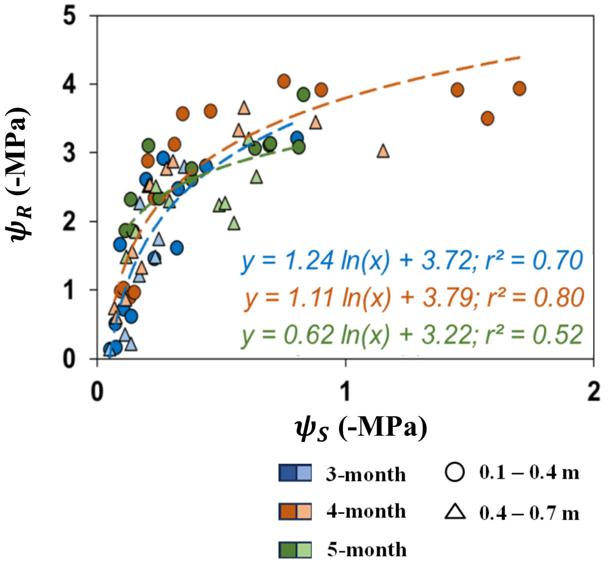

Figure 1. Logarithmic correlation between ψ_S and ψ_R under drought (after Ganesan et al. 2024)

3.2 Leaf responses to varying ψ_R

The significance of direct measurements of ψ_R was validated against SLA to substantiate the hydraulic continuum between roots and leaves. SLA demonstrated a clear decline trend with ψ_S (Fig. 2a) and exhibited a similarly significant nonlinear (logarithmic) correlation, as shown in Fig. 1. The onset of nonlinearity in SLA was observed at ψ_S values ranging from -0.3 to -0.5 MPa, which is consistent with the range identified for the onset of nonlinearity in ψ_R. As grass species (used in this study) are known for their lack of strong stomatal control (Bollig and Feller 2014), the decline in SLA may represent the phenotypic adjustment to the applied drought (Wellstein et al. 2017). Despite well capturing the general response, SLA did not show any significant difference among different plant growth periods (p-value > 0.05). To examine the linkage between root and leaf hydraulics, we observed that SLA reduced with reducing ψ_R, meaning that the dry matter in the leaves increased as ψ_R dropped. The ψ_R and SLA (Fig. 2b) was found to be negatively linearly correlated. Because the reduction in SLA likely reflects the phenotypic adaptation of the grass species, we hypothesise that the observed negative linearity may be linked to stomatal regulation following drought stress experienced by the plants.

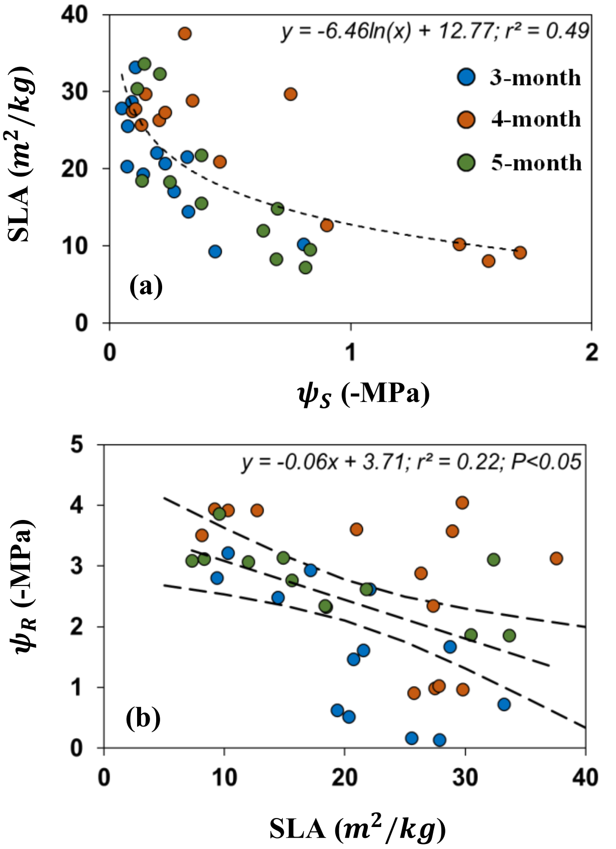

Figure 2. (a) Relationship between ψ_S and SLA fitted with the generalized nonlinear (logarithmic) fitting; (b) Relationship between ψ_R and SLA fitted with a moderate linear regression (after Ganesan et al. 2024)

3.3 Root water potential at varying root diameter

To explore a trait-based relationship with the measured ψ_R, we analysed the correlation between root diameter and ψ_R. The diameters measured in all the columns ranged from 0.3 to 0.6 mm and showed no significant differences across the plant growth periods (p-value > 0.05). Generally, ψ_R was found to be less negative for larger root diameters and more negative for smaller roots (Fig. 3), exhibiting a negative power correlation. The observed trend of reduced ψ_R in roots with smaller diameters may be attributed to several factors: (1) root shrinkage during soil drying (Rodriguez-Dominguez and Brodribb, 2020); (2) increased water uptake demand at later growth periods due to a larger leaf area combined with underdeveloped root diameters; and (3) thicker roots, which typically contain more xylem vessels, and could be the reason larger root diameters measured less ψ_R. A similar observation was reported by Abdalla et al. (2022), where the nonlinearity of transpiration was noted in shorter root systems. Further study is required to generate datasets containing a wider range of root diameters to examine the trait-based correlation.

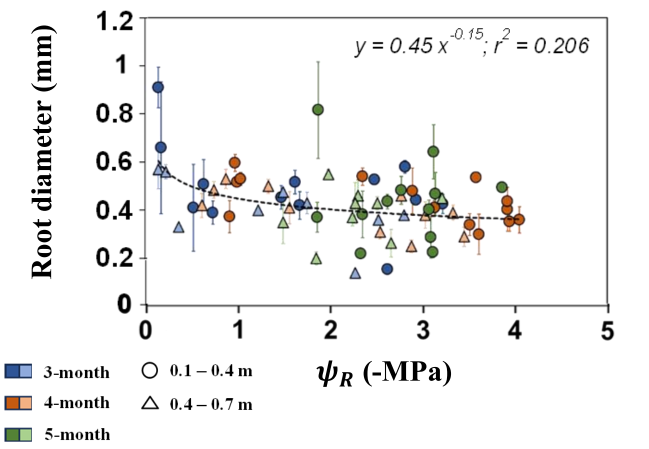

Figure 3. Relationship between ψ_R and root diameter fitted with a nonlinear (second-order power) regression (after Ganesan et al. 2024)

4 CONCLUDING REMARKS

Our study on direct ψ_R measurements captured the ψ gradient between soil and roots during water uptake, highlighting a significant logarithmic correlation under imposed drought stress. Our subsequent investigation into the correlation of leaf hydraulics using SLA revealed similar patterns of nonlinearity. The strong association with existing information on k_{root} and root diameter reinforces our findings and suggests the need for future studies to address the challenges of direct ψ_R measurement using potentiometer.

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