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Root uptake under mismatched distributions of water and nutrients in the root zone.

Jing Yan[1], Nathaniel A. Bogie[2], and Teamrat A. Ghezzehei[1]

[1]Life and Environmental Sciences Department, University of California, Merced, CA 95343, USA
[2]Geology Department, San Jose State University, San Jose, CA 95192, USA

Correspondence: Teamrat A. Ghezzehei (taghezzehei@ucmerced.edu)

Abstract. Most plants derive their water and nutrient needs from soils, where the resources are often scarce, patchy, and ephemeral. In natural environments, it is not uncommon for plant roots to encounter mismatched patches of water-rich and nutrient-rich regions. Such an uneven distribution of resources necessitates plants to rely on strategies that allow them to explore and acquire nutrients from relatively dry patches. We conducted a laboratory study to provide a mechanistic understanding of the biophysical factors that enable this adaptation. We grew plants in split-root pots that permitted precisely controlled spatial distributions of resources. The results demonstrated that spatial mismatch of water and nutrient availability does not cost plant productivity compared to matched distributions. Specifically, we showed that nutrient uptake is not reduced by overall soil dryness, provided that the whole plant has access to sufficient water elsewhere in the root zone. Essential strategies include extensive root proliferation towards nutrient-rich dry soil patches that allows rapid nutrient capture from brief pulses. Using high-frequency water potential measurements, we also observed nocturnal water release by roots that inhabit dry and nutrient-rich soil patches. Soil water potential gradient is the primary driver of this transfer of water from wet to dry soil parts of the root zone, which is commonly known as hydraulic redistribution (HR). The occurrence of HR prevents the soil drying from approaching the permanent wilting point, and thus supports root functions and enhance nutrient availability. Our results indicate that roots facilitate HR by increasing root-hair density and length and deposition of organic coatings that alter water retention. Therefore, we conclude that biologically-controlled root adaptation involves multiple strategies that compensate for nutrient acquisition under mismatched resource distributions. Based on our findings, we proposed a nature-inspired nutrient management strategy for significantly curtailing water pollution from intensive agricultural systems.

1 Introduction

Spatial and temporal mismatch of water and nutrient availability within the soil profile is a frequent occurrence that confronts plants in regions with pronounced wetting-drying cycles (Bengough et al., 2011). A review of global rooting depth observations in well-drained upland environments and drought-prone regions reveals that the primary determinant of root architecture is soil moisture distribution within the soil profile (Fan et al., 2017). Plants that grow in such areas meet the bulk of their transpiration demand with subsurface soil moisture storage because the shallow soil layers tend to dry up quickly by evaporation and drainage. In contrast, organic matter and plant-available essential macro- and micro-nutrients, including N, P, K, Zn, Mn are preferentially concentrated in the shallow soil horizons (Li et al., 2013; Jobbágy and Jackson, 2001; Franzluebbers and Hons, 1996; Apostolakis and Douka, 1970). This mismatched distribution of resources necessitates nutrient uptake from relatively dry, but nutrient-rich, soil patches (Nambiar, 1976; Rose et al., 2008; Wang et al., 2009). Moreover, the release of nutrients bound in organic matter of the shallow soil layers requires mineralization to occur under sub-optimal moisture conditions (Stanford and Epstein, 1974). Adaptation of plants to these environments suggests the existence of nutrient and water acquisition strategies that allow root architecture and functions to respond to mismatched spatial and temporal nutrient and water distributions.

There has been significant progress in our understanding of how roots respond to either water or nutrient deficiency signals (Robbins and Dinneny, 2015; Hodge, 2004; Robinson et al., 1999). In water-limited areas, root growth generally tracks water infiltration patterns (Fan et al., 2017). Locally, roots also respond by modifying the water retention capability of their rhizosphere (Carminati et al., 2010, 2011; Moradi et al., 2011; Albalasmeh and Ghezzehei, 2014; Ghezzehei and Albalasmeh, 2015). Rhizosphere modification and priming by root exudation have also been credited for increasing nutrient availability and accessibility to plants (Keiluweit et al., 2015).

Under contrasting soil moisture statuses within a soil profile, plants can respond by redistributing soil water via the root architecture – a process commonly referred to as hydraulic-lift or hydraulic-redistribution (HR) (Caldwell and Richards, 1989; Bogie et al., 2018). It has been suggested that HR may serve as a carrier for nutrients from dry soil patches (Caldwell and Richards, 1989) and there exists some empirical evidence for elevated ammonification, nitrogen (N) mineralization, and plant inflorescence N uptake during times of HR (Cardon et al., 2013).

However, important questions still remain with regards to the adaptation of plants to mismatched resource distributions. Specifically, (a) whether mismatched distribution of water and nutrients within a soil profile has an adverse effect on plant performance, (b) to what extent can plants acquire nutrients from dry soil patches provided that water is available in sufficient quantity elsewhere, and (c) what mechanisms are involved in nutrient uptake from dry patches. Here, we conducted a laboratory experiment specifically designed to address these questions. Tomato plants (*Solanum lycopersicum*) were grown in split-root pots, and the spatial and temporal distributions of water and nutrients were precisely controlled during a five-month growth cycle. The overarching goal of our study was to provide a mechanistic explanation of the biophysical factors and processes that allow plants to thrive in an environment of mismatched resource distribution. This knowledge is critical for understanding and predicting how food crops intercropped with native plants in low-input agriculture respond to environmental stresses(Bogie et al., 2018). Moreover, understanding the adaptation mechanism can play a crucial role in designing nature-inspired cropping systems with high nutrient and water use efficiencies.

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2 Methods

2.1 Split-root experiments

Our experiments were conducted using laterally split soil compartments as depicted in Figure 5a and Figure S1. Tomato seedlings were germinated in potting mix and grown until they reached 5-10 cm in height. The seedlings were then removed from the pots and the roots were thoroughly washed to remove any residual nutrient from the potting mix. The roots of individual seedlings were then physically separated into two roughly equal parts that were placed in the separate compartments of the custom-designed pots (length $= 20.3\ \mathrm{cm}$; width $= 10.2\ \mathrm{cm}$; height $= 30.5\ \mathrm{cm}$), which was split into two compartments of identical volumes. The pots were filled with $8\ \mathrm{kg}$ of silica sand, of approximate median particle size of 600 µm (Laguna Clay Co., City of Industry, CA), and packed to mean bulk density of $1.4\ \mathrm{g\,cm^{-3}}$. Dielectric water content sensors (5TE of Meter, Pullman, WA) were placed at the center of each compartment at $14\ \mathrm{cm}$ below the surface. In addition, the dry compartments of treatments **D** and **C1** were outfitted with pairs of thermocouple psychrometric water potential sensors (Psypro of Wescor Inc. Logan, UT) (Brown and Bartos, 1982; Andraski and Scanlon, 2002) to measure the water potential of the root zone. The dielectric sensors were programmed to log data every $15\ \mathrm{min}$ while the psychrometers were programmed to log data every $2\ \mathrm{h}$. Nylon tubing for water and nutrient solution injection were installed in each compartment at $14\ \mathrm{cm}$ depth. After the transplantation, the pots were irrigated with $560\ \mathrm{ml}$ of deionized water (equivalent to $0.2\ \mathrm{VWC}$). The plants were allowed to adjust to the new environment for around 2 weeks with no additional irrigation or fertilization. Subsequently, the prescribed application of water and nutrient solution (General Hydroponics, Santa Rosa, CA) commenced on day 18 after transplantation according to the schedule presented in supplmental data sets. The plants were grown indoors under artificial fluorescent light sources ($6,500\ \mathrm{K}$ spectrum and $10,000\ \mathrm{lm}$ intensity) that were programmed to be on for 12 hr and off for 12 hr.

2.2 Plant and soil characterization

The plants were harvested on days 138 to 140 after transplantation and multiple indicators of plant performance were measured. Shoot dry mass determined separately for each branch of every plant. The number of flowers, number of fruits, and fruit dry mass were determined for each plant. Greenness of each leaf was determined using a hyperspectral analyzer (ASD Spectroradiometer, Malvern Panalytical, Cambridge, UK). Shoot and fruit N content across canopy were determined using a high temperature conversion elemental analyzer (Thermo Fisher Scientific, Waltham, MA). Total plant N uptake by the aboveground biomass was calculated by integrating dry-mass weighted N content for each plant. Total N uptake was corrected by subtracting the initial plant total N mass. The NUE of the aboveground biomass was determined by calculating the ratio of total plant N uptake to total N addition during the experiment. The N content of the sand medium before and after the experiment was below the detection limit.

After harvest, the soil compartments were allowed to air-dry until the water content reached 3.5% to 4% by volume. A uniform soil drying condition was established by subjecting the pots to constant airflow inside a fume hood. Then the soil from one replicate of each treatment was carefully scooped out at $2\ \mathrm{cm}$ depth intervals. The coarse root pieces in each interval were removed by gently sieved through size $0.4\ \mathrm{mm}$ sieve and manually picked out for further gravimetric measurement.

Rhizosheath, i.e. the combination of root tissues and sand-covered on the root surfaces, from another replicate of each treatment was preserved with minimum agitation, for microscopic analysis. Confocal images were obtained using a Zess LSM 880 Airyscan confocal microscope and EC Plan-Neofluar 10x/0.30NA objective lens (Carl Zeiss Microscopy LLC, White Plains, NY). $405\ \mathrm{nm}$ and $488\ \mathrm{nm}$ lasers were used to excite and acquire autofluorescent compounds from the roots. T-PMT detector was used to acquire transmitted light images. SEM images were taken at $3\ \mathrm{kV}$ after coating with gold (E5000 Sputter Coater, Quorum Technologies Ltd, East Sussex, UK) using ZEISS GeminiSEM 500 scanning electron microscope (Carl Zeiss Microscopy LLC, White Plains, NY). Image analysis and processing was done using ImageJ (Schneider et al., 2012).

2.3 Statistical and data analysis

Plant physiological indicators were compared across treatments using a Welch's analysis of variance (ANOVA) (Welch, 1947) and posthoc Games-Howell test for multiple comparison from R (Games and Howell, 1976).

For the dry compartment of treatment **D**, rhizosphere water content (θ) was estimated from water potential (ψ) measurement using water retention curves fitted with Brooks Corey model: $\theta/\theta_S = (\psi/\psi_o)^{\lambda}$ (Brooks and Corey, 1966, 1964) (Figure S4). The water retention curve of silica sand mixed with nutrient solution ($520\ \mathrm{mgN/L}$, a concentration that is consistent with the pore water in the dry compartment of treatment **D**) was determined by water potentiometer (WP4C of Meter, Pullman, WA). Rhizosphere wetting was calculated by subtracting minimum daily rhizosphere water content from the subsequent daily maximum values. More detail of the calculation is provided in supplemental information.

3 Results

3.1 Plant physiological characteristics

In the primary treatment of our experiment (labeled **D**) $\approx 90\%$ of the irrigation water was applied to one compartment of the pot, while the other received 100% of the nutrient supply delivered along with the remaining 10% water. In a control experiment (labeled **C1**), we added 100% of the nutrients to the wet compartment of the split-root pots, while the dry compartment received the remaining 10% of the water without nutrients. In a second control experiment (labeled **C2**), both compartments received equal amounts of water and nutrients (See Figure S1). We used nutrient-free sand as a growing medium in order to fully constrain nutrient availability to the targeted region.

We measured a series of indicators to assess whether mismatched resource distributions influenced plant performance. Critical indicators of above-ground plant performance, including total above-ground biomass, fruit mass, number of flowers, N uptake by total biomass and fruits, and N use efficiency (NUE) are reported in Figure 1. Additional measures of plant performance, including N distribution and leaf greenness within individual plant canopy are reported in Figure S2. The latter was evaluated in terms of normalized difference vegetation index (NDVI) captured by hyperspectral analyses of leaf samples. Considerable variability in N concentration and NDVI was observed within each plant, with younger leaves at the top of the canopy having higher N and NDVI than the oldest leaves at the base of the canopy (Figure S2). However, there were no signif-

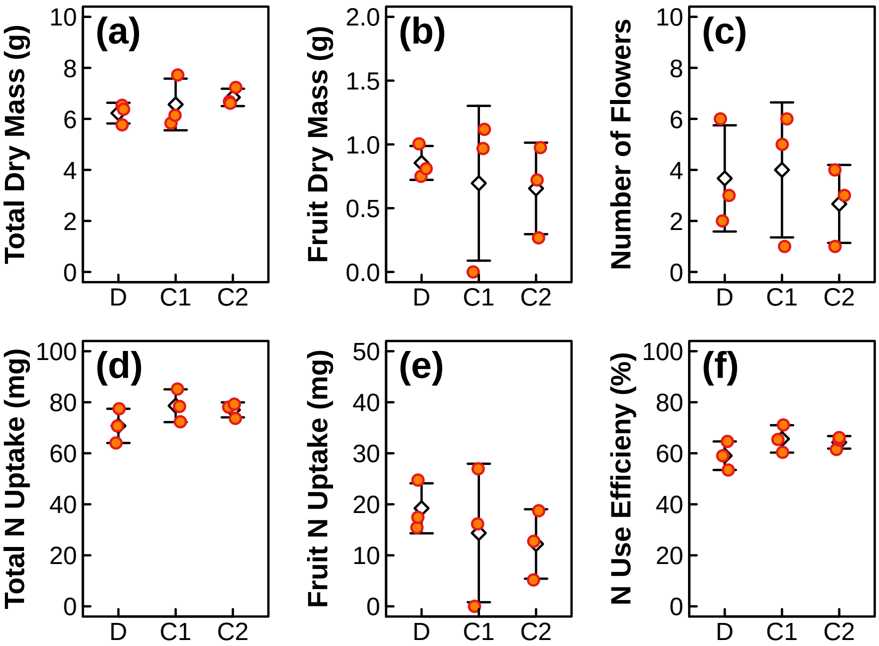

Figure 1. Comparison of plant physiological indicators in treatment **D**, **C1** and **C2**. Note: no statistically significant difference in those indicators was observed across treatments ($p > 0.05$).

icant differences at the whole-plant scale in all the indicators we measured ($p > 0.05$; Table A1). These findings unequivocally demonstrated that mismatch of spatial distributions of water and nutrients does not have a measurable effect on the above ground measures of performance, provided that both resources are available in equal amounts.

3.2 Plant root distribution and rhizosphere characteristics

The pattern of root proliferation is often associated with localized root feedbacks to the spatial distributions of water or nutrients within soil profile (Robbins and Dinneny, 2018; Fan et al., 2017; Boyer et al., 2010; Orosa-Puente et al., 2018). However, how and to what extent mismatched water and nutrient distributions affect root architecture is mostly unknown. In Figure 2 (a), we provide a visual demonstration of the root proliferation during a growth period when 100% of the nutrients are isolated from 90% of the irrigation water (treatment **D**). It is remarkable that the density of the roots in the wet and dry compartments are indistinguishable, despite the vast disparity in water availability. The soil that surrounded the roots was carefully extracted using a pipette tip connected to a vacuum. Therefore, the three-dimensional root architecture is not apparent in Figure 2 (a)

Quantitative comparison of the root mass distribution between the two compartments and among the treatments is provided in Figure 2 (f-h) and Table A2. The soil in both compartments of selected replicates was excavated at depth intervals of 2 cm, and all roots within each soil volume were extracted. The roots in the nutrient-free wet compartment of treatment **D** were mostly uniformly distributed throughout the depth profile, with a slight increase near the bottom, suggesting slight accumulation of

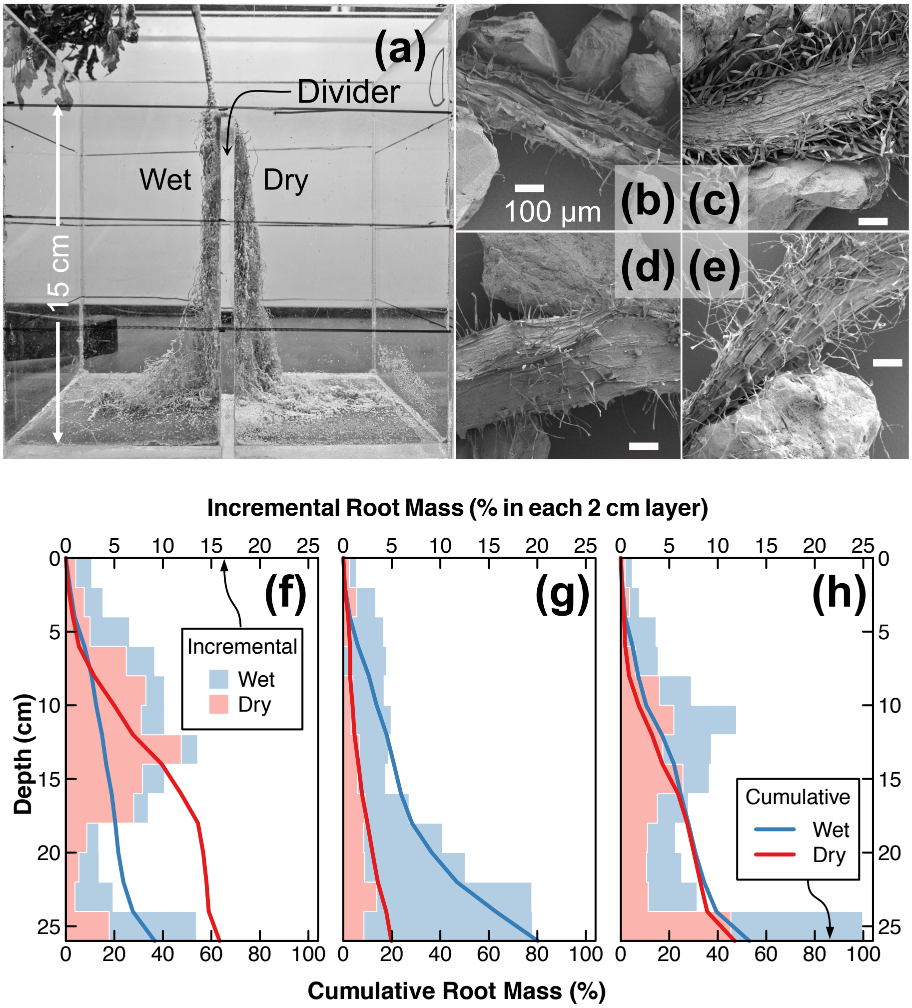

Figure 2. Root architecture of one tomato plant treated with mismatched distribution of water and nutrients (treatment **D**) at the end of the experiments (a); SEM images of representative rhizosheath collected from the "Wet" and "Dry" compartments of treatment **D** (b, c) and **C1** (d, e); Incremental and cumulative root mass distribution along the soil profile in treatment **D**, **C1** and **C2** (f, g, h). Note: A separate sample in a shorter compartment with scaled water and nutrient application was selected to demonstrate the non-destructive root image (a); the apparent root distribution in (a) does not represent the incremental root mass distribution in (f).

drained moisture at the base of the compartment. In contrast, the roots grown in the nutrient-rich dry compartment were concentrated in the mid-section, coinciding with the depth at which nutrient solution was supplied using a subsurface injector. Overall, the nutrient-rich dry compartment accounted for 60% of the total root biomass.

The root density in the nutrient-rich wet compartment of the first control treatment **C1** increased with depth, with a notable accumulation of root biomass at the base. This accumulation suggests that in addition to the accumulation of drained water,

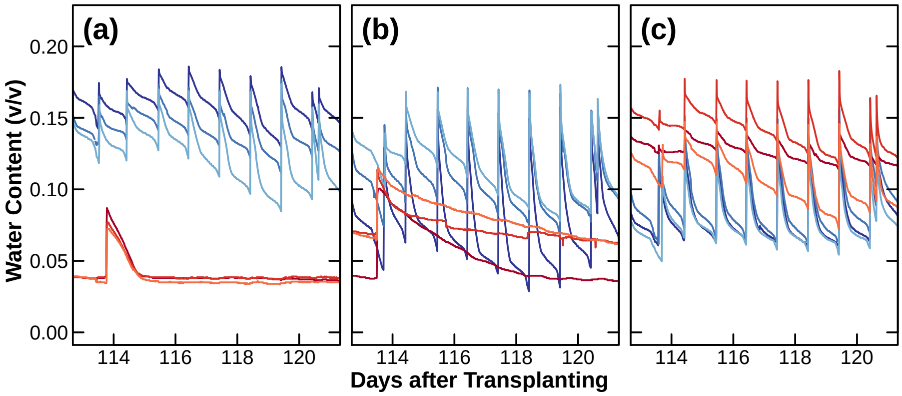

Figure 3. Changes in soil volumetric water content (v/v) over time in "Wet" and "Dry" compartments of treatment **D**, **C1** and **C2** (a, b, c). Replicates are shown in different colors.

leaching must also have resulted in a substantial accumulation of plant-available nutrients at the base of the compartment. It is important to recall that had this been an open profile, a portion of the nutrient supply could have leached below the rooting depth. The root growth in the nutrient-free dry compartment was stunted and accounted for only 20% of the total root biomass. There was no difference in root density and distribution between the two compartments of the second control treatment **C2**, where water and nutrient were supplied equally to both compartments.

The roots in all the treatments exhibited the formation of rhizosheath, which is often associated with soil binding by either root exudates or root-hairs and is credited for the facilitation of water and nutrient extraction (Pang et al., 2017; Watt et al., 1994; Albalasmeh and Ghezzehei, 2014). There were no visual differences in the appearance and abundance between the rhizosheaths formed in the wet and dry compartments or among treatments. However, closer inspection under Scanning Electron Microscope (SEM) revealed significantly denser root hairs in the dry compartment of treatment **D**. This observation is consistent with the emerging consensus on the importance of nutrients in regulating the growth and development of root hairs (Zhang et al., 2018).

3.3 Plant water and nutrient uptake dynamics

The above observations show that the adaptation of the root characteristics (Figure 2) explains how plants respond to mismatched water and nutrient distributions without incurring performance loss (Figure 1). However, understanding the mechanism of nutrient uptake from dry soil patches requires a closer look at the dynamics of soil water content and water potential in the wet and dry compartments. In Figure 3, a snapshot of typical soil water content dynamics over one week is shown (see Figure S3 for complete dataset). The wet compartments of treatments **D** and **C1**, as well as both compartments of treatment **C2** remained comparably wet because of the frequent irrigation. However, there was a considerable difference in water content dynamics between the dry compartments of treatments **D** and **C1**. Specifically, in the presence of nutrients, the water content in the dry compartment of treatment **D** was depleted within one day after each application of nutrient solution (weekly to bi-weekly interval). Whereas the water content of the nutrient-free dry compartment of treatment **C1** declined slowly over a

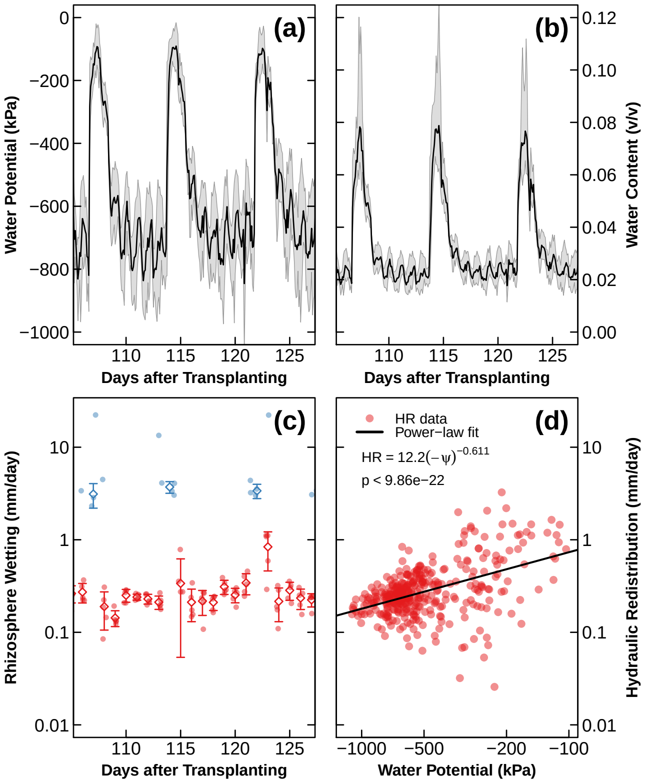

Figure 4. Changes in soil water potential (a), water content (b), and rhizosphere wetting (c) from HR and injection as a function of time in "Dry" compartment of treatment **D**; HR outflow magnitude as a function of water potential (ψ): HR described by a power-law model is shown in solid line (d).

week. This difference in water uptake rate is consistent with the root density differences between the dry compartments shown in Figure 2 (f) and 2 (g).

The soil water potential data (Figure 4 (a)) was converted to rhizosphere water content dynamics (Figure 4 (b); see Figure S5 for complete dataset) using a soil water retention curve (Figure S4 and Table S1). The effects on soil water potential from increasing nutrient concentrations were considered by using pore water with appropriate nutrient concentrations. Close inspection of the HR water content dynamics reveals that HR does not significantly contribute to transpiration at the whole-plant scale, given that the small volume of water is reversibly taken up the roots. However, it can be essential in enhancing root survival and growth (Boyer et al., 2010; Bauerle et al., 2008), as well as serving as a critical carrier for nutrient acquisition from dry soil patches. Furthermore, the preferential proliferation of root hairs in the nutrient-rich dry compartment suggests that HR was an essential factor in creating a habitable environment.

The water content dynamics data can be utilized to infer the quantity of water that is released during each episode of HR. In Figure 4 (c) we show the increase soil moisture across all five working sensors (reported as an equivalent soil moisture

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depth in the 50 mm soil intervals where maximum root density was observed). The magnitude of HR remained consistent for the most part of the study, with slight increases observed in the first few days after each injection of nutrient solution. These data can also be used to analyze the role of rhizosphere water status on the magnitude of HR (Meinzer et al., 2004; Prieto et al., 2010; Scholz et al., 2008). We observed that the magnitude of HR outflows to be inversely correlated with rhizosphere water potential ($p < 0.05$ in Figure 4 (d)). This demonstrates that the rhizosphere soil under drier conditions exerts the larger resistance to flow. Previous evidence suggests that emerging root hairs, exudates, and mucilage in the rhizosphere soils modify pore size distribution (Koebernick et al., 2019) and elevate rhizosphere water retention and hydraulic conductivity (Carminati et al., 2010; Moradi et al., 2011; Albalasmeh and Ghezzehei, 2014). Besides, root exudation could have changed the soil water potential directly due to the release of hydrated metabolites from root tips (McCully and Boyer, 1997). Fluorescence images of the sand grains in the rhizosphere revealed extensive organic coating with root hairs and amorphous fluorescent compounds (Figure S6), suggesting a modification of biophysical soil properties by root-soil interactions (Keyes et al., 2017). Therefore, it appears that the elevated HR dynamics we observed were actively facilitated by root activities.

4 Discussion

Plant responses to water and nutrient stresses have been the subject of extensive research in ecological and agricultural settings (Robinson, 1994; Jackson et al., 1990). Typically, these stresses are considered individually or as compounded factors. However, how plants cope with mismatched distribution of water and nutrients in the soil profile is rarely examined. We did not observe a measurable difference in reproductive success (number of flowers and fruits) and nutrient acquisition between unstressed plants and plants that experienced severe partial-root nutrient and water stresses. While rapid nutrient capture from brief pulses, i.e. intermittent wetting, could have been essential in plant performance, it is important to note that the plants subjected to mismatched resource allocation derived all their nutrient uptake from a soil patch that persistently remained dry at -900 to $-500\,\mathrm{kPa}$ (85% of growing time), which corresponds to residual moisture status for the coarse sandy soil used in this experiment. Thus, we can confidently conclude that plant performance is less sensitive to localized water and nutrient stresses provided that both resources are available in sufficient quantities within the rooting zone.

Therefore, we can safely assert that plants subjected to mismatched resource distribution employed strategies that are distinct from plants grown under uniform resource availability. Specifically, we suggest a three-part mechanism that appears to be at play, which are schematically illustrated in Figure 5.

First, roots proliferated in dry soil patches provided that the available nutrients are constrained in the dry patches and water is available in sufficient quantity elsewhere (Figure 2 (f)). The root proliferation is the prerequisite for the rapid nutrient capture in such a short time window, i.e. 15% of the growing period. Moreover, multi-scale signaling and feedbacks appear to be involved. The marked differences in root allocations between the two compartments of the three treatments, despite having received equal amounts of water and nutrients, points towards a complex whole-plant scale regulation of root growth. The accumulation of roots in the mid-section of the dry compartment of treatment **D** supports strong signaling by localized nutrient concentration.

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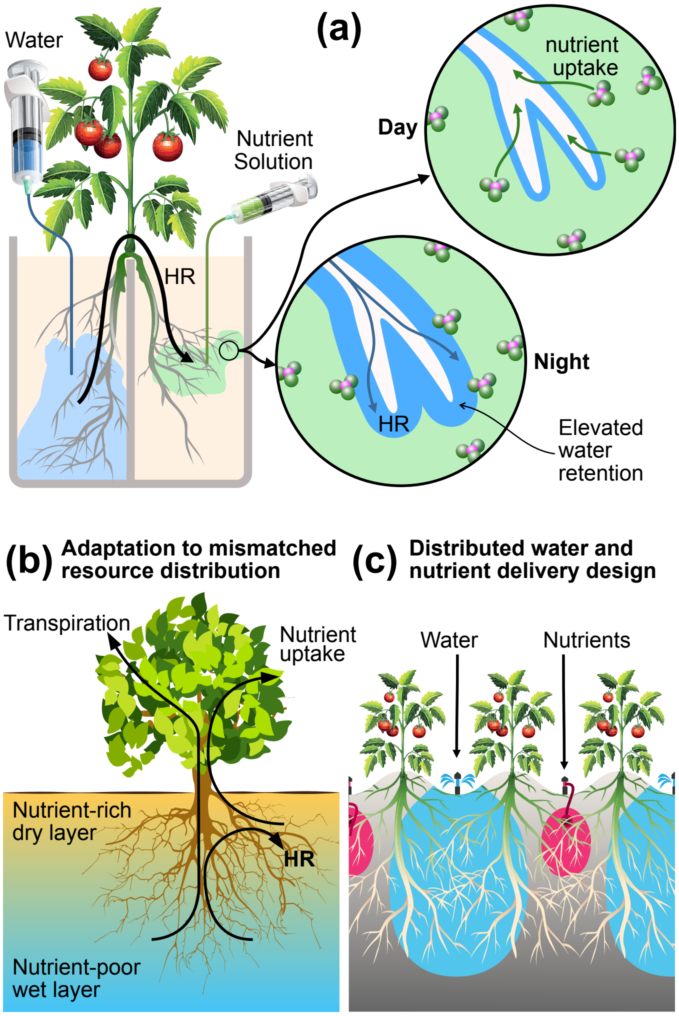

Figure 5. Experimental demonstration of three-part mechanisms of plant root feedbacks in response to mismatched distribution of water and nutrient – root proliferation, HR-supported water retention elevation and active, thriving root biomass for nutrient uptake in nutrient-rich dry soil patches (a); in natural environments, plants experience mismatched distribution of water and nutrient along the vertical gradients in soil profile and develop root proliferation, HR-facilitated transpiration and nutrient uptake to support their growth and survival (b); a nature-inspired engineering approach that capitalizes on the roots' ability to acquire water and nutrients from spatially isolated regions through applying irrigation water and fertilizers to alternating rows (c).

Second, roots appear to rely on hydraulic redistribution (HR) to maintain substantial root biomass in dry soil patches (Boyer et al., 2010) as well as to facilitate transport and uptake of nutrients (Figure 4 (a-c)). The roots grown in dry nutrient-rich patches also appear to be more vigorous than roots grown in nutrient-free dry patches as evidenced by the marked difference in drying after intermittent wetting events (compare Figure 3 (a) and 3 (b), respectively). However, despite the fast initial decline in water content, HR prevented the water potential from ever approaching permanent wilting point ($-1500\,\mathrm{kPa}$) as shown in

Figure 4 (a). This suggests that HR helps maintain and rejuvenate root activities until conditions of nutrient uptake become favorable (Bauerle et al., 2008).

Third, HR appears to be induced or accelerated by the action of roots. Absence of HR in treatment **C1** given identical partitioning of water between the two compartments supports the suggestion that HR is not as previously suggested a “sweet accident” passively regulated by physical conditions of the environments, but a biologically-mediated feedback process triggered by mismatched distribution of water and nutrients (Matimati et al., 2014). Primarily, drying of the rhizosphere soil in the dry compartment by root uptake provides the necessary water potential gradient to pull water from the wet compartment. However, drying also counters HR by dropping hydraulic conductivity (van Genuchten, 1980), which restricts the ability of HR to be transported away from root surfaces. Therefore, rhizosphere hydraulic conductivity plays the dominant role in controlling HR, as evidenced by the positive correlation between water potential and HR shown in Figure 4 (d) (Meinzer et al., 2004; Prieto et al., 2010; Scholz et al., 2008).

In this study, two possible pathways allow roots to modify rhizosphere hydraulic properties. One is through emerging root hairs that alters the soil porosity and connectivity at the root-soil interfaces. The other is through localized elevation of water retention around active roots by root-secreted organic materials (Carminati et al., 2010; Moradi et al., 2011; Albalasmeh and Ghezzehei, 2014). Therefore, we suggest that root morphological adaptation and exudation in nutrient-rich dry patches may play an integral part in HR-assisted sustenance of roots and nutrient acquisition. Fluorescence images of sand particles from the nutrient-rich dry compartments exhibited evidence of organic coatings that support this hypothesis (Figure S6).

It should be noted that the current study considered an ideal condition with a single plant species grown in the homogenous texture of sandy soils. Such conditions nearly never occur in natural systems due to the complexity of environmental factors and response variation between different plant species. Therefore, extensive studies beyond the controlled system involving different plant species and soil types are required for further mechanistic understanding.

5 Conclusions

Our findings demonstrated that plants could utilize heterogeneously distributed resources without adverse impact on their performance, provided that these resources are present in sufficient quantities. Specifically, we showed the ability of plants to acquire 100% of their nutrient needs under the extreme mismatch of water and nutrient distributions. We provided multiple lines of evidence that suggest a successful adaptation to such an environment involves coordination between components of the root system that inhabit environments with contrasting resource availability. Critical to this mechanism is a reliance on multiple strategies, including extensive root proliferation that allows rapid nutrient capture from immediate widows of availability under favorable moisture conditions, and sustained HR to support an active root system and facilitate nutrient transport under unfavorable or drought stress conditions. It appears that HR is biologically regulated when its occurrence supports the acquisition of nutrients. Regulating mechanisms include the enhancement of rhizosphere water retention but root exudation and development of dense and thick roothairs.

The findings of this study, which was carried out under a highly controlled laboratory environment, sheds light on how plants thrive in regions where surface soil drying is typical, and water and nutrient availabilities are often spatially mismatched. As illustrated in Figure 5 (b), actively controlled HR employed by plant roots can support active, thriving root biomass in the shallow nutrient-rich soils. Furthermore, HR induced wetting can support microbial communities that sustain vigorous nutrient cycling in the otherwise dry soil layers. Facilitation mechanisms could include regulation of root exudation on microbial activities (Williams and de Vries, 2020). This hypothesis is consistent with the frequent occurrence of HR in deep-rooted shrubs of arid and semi-arid regions (Kizito et al., 2007; Bogie et al., 2018). The fact that we observed HR in a shallow-rooted herbaceous plant (tomato) suggests that the mismatch of resources rather than climate and plant types are the primary drivers of HR.

The lessons gleaned from the above effective resource utilization strategies can serve as templates for highly efficient, nature-inspired agricultural systems. The use of synthetic fertilizers, particularly N, played a significant role in boosting crop production (Tilman et al., 2002). While the NUE in many industrialized countries has been increasing at a modest rate, the yield gains achieved in most developing countries over the past half-century came at a significant decline in NUE (Zhang et al., 2015) and environmental and ecological degradations, including air and water pollution and the accumulation of potent greenhouse gases (Bowles et al., 2018). To meet the 2050 global food demand while safeguarding environmental quality would require harvested N to increase by 45% while NUE to increase from 40% to 70% (Zhang et al., 2015). Therefore, economically affordable approaches to reducing N loss from agriculture are critical to achieving this goal. Our findings suggest that the colocation of nutrients and water, which is the main driver for N loss by leaching and volatilization, is not necessary to maintain productivity. Thus, spatially isolating the bulk of irrigation water from the applied N can be effective in drastically cutting N losses. We suggest one such approach, illustrated in Figure 5 (c), that uses existing technologies and minimal investment. This approach involves applying irrigation water and fertilizers to alternating rows and capitalizing on the roots' ability to acquire both resources effectively.

Code and data availability. The data sets and R code were uploaded in Dryad with a doi:10.6071/M39M2T. The unpublished dataset and code for review was shared using this temporary link: click for data sets and code for review.

Appendix A: Comparison of root distribution

The distribution of root mass within the top, middle, and bottom (0-8, 8-18, 18-26 cm) depth intervals were compared using a two-way ANOVA test and Games-Howell posthoc test for multiple comparisons (Games and Howell, 1976). The results of mean ± standard deviation along with significant letters were shown in Table A2.

Table A1. Welch's anova test of physiological indicators across treatments

Physiological characteristics	p-value
1. Total dry mass (g)	0.30
2. Shoot dry mass (g)	0.28
3. Initial dry mass (g)	0.16
4. Flower no.	0.73
5. Fruit no.	0.95
6. Fruit dry mass (g)	0.70
7. Fruit nitrogen content (%)	0.28
8. Fruit nitrogen uptake (mgN)	0.48
9. Shoot nitrogen content (%)	0.24
10. Shoot nitrogen uptake (mgN)	0.28
11. Total nitrogen uptake (mgN)	0.43
12. Nitrogen usage efficiency (%)	0.43
13. Leaf NDVI	0.10

Table A2. Games-Howell's comparison of root mass distribution (%) along soil depths. Values with different letters indicate significant difference ($p < 0.05$)

Depth (cm)	D		C1		C2	
	Wet	Dry	Wet	Dry	Wet	Dry
0-8	2.7 ± 1.1 ac	2.9 ± 2.3 abc	2.6 ± 1.6 ac	0.7 ± 0.6 c	1.8 ± 1.1 ac	0.9 ± 0.5 c
8-18	2.0 ± 0.4 ac	8.6 ± 1.9 b	3.6 ± 0.7 ab	1.4 ± 0.6 c	4.1 ± 1.6 abc	4.8 ± 1.1 ab
18-26	4.1 ± 3.5 abc	2.2 ± 1.6 ac	13.0 ± 4.4 abc	2.5 ± 0.7 ac	6.3 ± 0.2 abc	4.9 ± 0.4 abc

Author contributions. J.Y., T.A.G. designed and performed the research; J.Y., N.A.B, and T.A.G. analyzed the results and wrote the paper.

270 *Competing interests.* The authors declare no conflict of interest.

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References

Albalasmeh, A. A. and Ghezzehei, T. A.: Interplay between soil drying and root exudation in rhizosheath development, Plant and Soil, 374, 739–751, https://doi.org/10.1007/s11104-013-1910-y, http://link.springer.com/10.1007/s11104-013-1910-y, 2014.

Andraski, B. J. and Scanlon, B. R.: Thermocouple psychrometry, in: Methods of Soil Analysis: Part 4 Physical Methods, edited by Jacob H. Dane, G. Clarke Topp, and Soil Science Society of America, pp. 609–642, Soil Science Society of America, Madison, WI, https://doi.org/10.2136/sssabookser5.4.c22, http://pubs.er.usgs.gov/publication/70194882, 2002.

Apostolakis, C. G. and Douka, C. E.: Distribution of Macro- and Micronutrients in Soil Profiles Developed on Lithosequences and under Biosequences in Northern Greece1, Soil Science Society of America Journal, 34, 290–296, https://doi.org/10.2136/sssaj1970.03615995003400020031x, http://dx.doi.org/10.2136/sssaj1970.03615995003400020031x, 1970.

Bauerle, T. L., Richards, J. H., Smart, D. R., and Eissenstat, D. M.: Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil, Plant, Cell & Environment, 31, 177–186, https://doi.org/10.1111/j.1365-3040.2007.01749.x, 2008.

Bengough, A. G., McKenzie, B. M., Hallett, P. D., and Valentine, T. A.: Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits, Journal of Experimental Botany, 62, 59–68, https://doi.org/10.1093/jxb/erq350, https://doi.org/10.1093/jxb/erq350, citation Key Alias: bengoughRootElongationWater2011a, 2011.

Bogie, N. A., Bayala, R., Diedhiou, I., Conklin, M. H., Fogel, M. L., Dick, R. P., and Ghezzehei, T. A.: Hydraulic redistribution by native sahelian shrubs: bioirrigation to resist in-season drought, Frontiers in Environmental Science, 6, 98, https://doi.org/10.3389/fenvs.2018.00098, https://www.frontiersin.org/article/10.3389/fenvs.2018.00098, bogie2018, 2018.

Bowles, T. M., Atallah, S. S., Campbell, E. E., Gaudin, A. C. M., Wieder, W. R., and Grandy, A. S.: Addressing agricultural nitrogen losses in a changing climate, Nature Sustainability, 1, 399–408, https://doi.org/10.1038/s41893-018-0106-0, http://www.nature.com/articles/s41893-018-0106-0, 2018.

Boyer, J. S., Silk, W. K., and Watt, M.: Path of water for root growth, Functional Plant Biology, 37, 1105–1116, https://doi.org/10.1071/FP10108, http://www.publish.csiro.au/FP/FP10108, 2010.

Brooks, R. H. and Corey, A. T.: Hydraulic properties of porous media, no. 3 in Hydrology papers, Colorado State University, [Hydrology and Water Resources Program], Fort Collins, 1964.

Brooks, R. H. and Corey, A. T.: Properties of porous media affecting fluid flow, Journal of the irrigation and drainage division, 92, 61–90, 1966.

Brown, R. and Bartos, D.: A Calibration Model for Screen-caged Peltier Thermocouple Psychrometers, no. 293 in Research Paper, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, https://books.google.com/books?id=BGnpPYgkC6AC, 1982.

Caldwell, M. M. and Richards, J. H.: Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots, Oecologia, 79, 1–5, https://doi.org/10.1007/BF00378231, http://link.springer.com/10.1007/BF00378231, 1989.

Cardon, Z. G., Stark, J. M., Herron, P. M., and Rasmussen, J. A.: Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences, Proceedings of the National Academy of Sciences, 110, 18 988–18 993, https://doi.org/10.1073/pnas.1311314110, http://www.pnas.org/cgi/doi/10.1073/pnas.1311314110, 2013.

Carminati, A., Moradi, A. B., Vetterlein, D., Vontobel, P., Lehmann, E., Weller, U., Vogel, H.-J., and Oswald, S. E.: Dynamics of soil water content in the rhizosphere, Plant and Soil, 332, 163–176, https://doi.org/10.1007/s11104-010-0283-8, https://doi.org/10.1007/s11104-010-0283-8, 2010.

Carminati, A., Schneider, C. L., Moradi, A. B., Zarebanadkouki, M., Vetterlein, D., Vogel, H.-J., Hildebrandt, A., Weller, U., Schüler, L., and Oswald, S. E.: How the Rhizosphere May Favor Water Availability to Roots, Vadose Zone Journal, 10, 988–998, https://doi.org/10.2136/vzj2010.0113, http://dx.doi.org/10.2136/vzj2010.0113, 2011.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., and Otero-Casal, C.: Hydrologic regulation of plant rooting depth, Proceedings of the National Academy of Sciences, 114, 10 572–10 577, https://doi.org/10.1073/pnas.1712381114, http://www.pnas.org/lookup/doi/10.1073/pnas.1712381114, 2017.

Franzluebbers, A. and Hons, F.: Soil-profile distribution of primary and secondary plant-available nutrients under conventional and no tillage, Soil and Tillage Research, 39, 229–239, https://doi.org/10.1016/S0167-1987(96)01056-2, http://www.sciencedirect.com/science/article/pii/S0167198796010562, 1996.

Games, P. A. and Howell, J. F.: Pairwise Multiple Comparison Procedures with Unequal N's and/or Variances: A Monte Carlo Study, Journal of Educational Statistics, 1, 113–125, https://doi.org/10.3102/10769986001002113, https://doi.org/10.3102/10769986001002113, 1976.

Ghezzehei, T. A. and Albalasmeh, A. A.: Spatial distribution of rhizodeposits provides built-in water potential gradient in the rhizosphere, Ecological Modelling, 298, 53–63, https://doi.org/10.1016/j.ecolmodel.2014.10.028, https://linkinghub.elsevier.com/retrieve/pii/S0304380014005262, 2015.

Hodge, A.: The plastic plant: root responses to heterogeneous supplies of nutrients, New Phytologist, 162, 9–24, https://doi.org/10.1111/j.1469-8137.2004.01015.x, http://doi.wiley.com/10.1111/j.1469-8137.2004.01015.x, 2004.

Jackson, R. B., Manwaring, J. H., and Caldwell, M. M.: Rapid physiological adjustment of roots to localized soil enrichment, Nature, 344, 58–60, https://doi.org/10.1038/344058a0, http://www.nature.com/articles/344058a0, 1990.

Jobbágy, E. G. and Jackson, R. B.: The distribution of soil nutrients with depth: Global patterns and the imprint of plants, Biogeochemistry, 53, 51–77, https://doi.org/10.1023/A:1010760720215, https://doi.org/10.1023/A:1010760720215, 2001.

Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., and Kleber, M.: Mineral protection of soil carbon counteracted by root exudates, Nature Climate Change, 5, 588, https://doi.org/10.1038/nclimate2580, 2015.

Keyes, S. D., Zygalakis, K. C., and Roose, T.: An Explicit Structural Model of Root Hair and Soil Interactions Parameterised by Synchrotron X-ray Computed Tomography, Bulletin of Mathematical Biology, 79, 2785–2813, https://doi.org/10.1007/s11538-017-0350-x, https://doi.org/10.1007/s11538-017-0350-x, 2017.

Kizito, F., Sène, M., Dragila, M., Lufafa, A., Diedhiou, I., Dossa, E., Cuenca, R., Selker, J., and Dick, R.: Soil water balance of annual crop–native shrub systems in Senegal's Peanut Basin: The missing link, Agricultural Water Management, 90, 137–148, https://doi.org/10.1016/j.agwat.2007.02.015, http://www.sciencedirect.com/science/article/pii/S0378377407000522, 2007.

Koebernick, N., Daly, K. R., Keyes, S. D., Bengough, A. G., Brown, L. K., Cooper, L. J., George, T. S., Hallett, P. D., Naveed, M., Raffan, A., and Roose, T.: Imaging microstructure of the barley rhizosphere: particle packing and root hair influences, New Phytologist, 221, 1878–1889, https://doi.org/10.1111/nph.15516, https://onlinelibrary.wiley.com/doi/abs/10.1111/nph.15516, 2019.

Li, F., Liu, M., Li, Z., Jiang, C., Han, F., and Che, Y.: Changes in soil microbial biomass and functional diversity with a nitrogen gradient in soil columns, Applied Soil Ecology, 64, 1 – 6, https://doi.org/https://doi.org/10.1016/j.apsoil.2012.10.006, http://www.sciencedirect.com/science/article/pii/S0929139312002454, 2013.

Matimati, I., Anthony Verboom, G., and Cramer, M. D.: Do hydraulic redistribution and nocturnal transpiration facilitate nutrient acquisition in Aspalathus linearis?, Oecologia, 175, 1129–1142, https://doi.org/10.1007/s00442-014-2987-6, http://link.springer.com/10.1007/s00442-014-2987-6, 2014.

McCully, M. E. and Boyer, J. S.: The expansion of maize root-cap mucilage during hydration. 3. Changes in water potential and water content, Physiologia Plantarum, 99, 169–177, https://doi.org/10.1111/j.1399-3054.1997.tb03445.x, https://doi.org/10.1111/j.1399-3054.1997.tb03445.x, publisher: John Wiley & Sons, Ltd, 1997.

Meinzer, F. C., Brooks, J. R., Bucci, S., Goldstein, G., Scholz, F. G., and Warren, J. M.: Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types, Tree Physiology, 24, 919–928, https://doi.org/10.1093/treephys/24.8.919, 2004.

Moradi, A. B., Carminati, A., Vetterlein, D., Vontobel, P., Lehmann, E., Weller, U., Hopmans, J. W., Vogel, H.-J., and Oswald, S. E.: Three-dimensional visualization and quantification of water content in the rhizosphere, New Phytologist, 192, 653–663, https://doi.org/10.1111/j.1469-8137.2011.03826.x, https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.2011.03826.x, 2011.

Nambiar, E. K. S.: Uptake of Zn65 from dry soil by plants, Plant and Soil, 44, 267–271, https://doi.org/10.1007/BF00016978, https://doi.org/10.1007/BF00016978, 1976.

Orosa-Puente, B., Leftley, N., von Wangenheim, D., Banda, J., Srivastava, A. K., Hill, K., Truskina, J., Bhosale, R., Morris, E., Srivastava, M., Kümpers, B., Goh, T., Fukaki, H., Vermeer, J. E. M., Vernoux, T., Dinneny, J. R., French, A. P., Bishopp, A., Sadanandom, A., and Bennett, M. J.: Root branching toward water involves posttranslational modification of transcription factor ARF7, Science, 362, 1407–1410, https://doi.org/10.1126/science.aau3956, http://www.sciencemag.org/lookup/doi/10.1126/science.aau3956, 2018.

Pang, J., Ryan, M. H., Siddique, K. H. M., and Simpson, R. J.: Unwrapping the rhizosheath, Plant and Soil, 418, 129–139, https://doi.org/10.1007/s11104-017-3358-y, http://link.springer.com/10.1007/s11104-017-3358-y, 2017.

Prieto, I., Kikvidze, Z., and Pugnaire, F. I.: Hydraulic lift: soil processes and transpiration in the Mediterranean leguminous shrub Retama sphaerocarpa (L.) Boiss, Plant and Soil, 329, 447–456, https://doi.org/10.1007/s11104-009-0170-3, https://doi.org/10.1007/s11104-009-0170-3, 2010.

Robbins, N. E. and Dinneny, J. R.: The divining root: moisture-driven responses of roots at the micro- and macro-scale, Journal of Experimental Botany, 66, 2145–2154, https://doi.org/10.1093/jxb/eru496, https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4817643/, 2015.

Robbins, N. E. and Dinneny, J. R.: Growth is required for perception of water availability to pattern root branches in plants, Proceedings of the National Academy of Sciences, 115, E822–E831, https://doi.org/10.1073/pnas.1710709115, http://www.pnas.org/lookup/doi/10.1073/pnas.1710709115, 2018.

Robinson, D.: The responses of plants to non-uniform supplies of nutrients, New Phytologist, 127, 635–674, https://doi.org/10.1111/j.1469-8137.1994.tb02969.x, https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.1994.tb02969.x, 1994.

Robinson, D., Hodge, A., Griffiths, B. S., and Fitter, A. H.: Plant root proliferation in nitrogen–rich patches confers competitive advantage, Proceedings of the Royal Society of London. Series B: Biological Sciences, 266, 431–435, https://doi.org/10.1098/rspb.1999.0656, https://royalsocietypublishing.org/doi/abs/10.1098/rspb.1999.0656, tex.eprint: https://royalsocietypublishing.org/doi/pdf/10.1098/rspb.1999.0656, 1999.

Rose, T. J., Rengel, Z., Ma, Q., and Bowden, J. W.: Hydraulic lift by canola plants aids P and K uptake from dry topsoil, Australian Journal of Agricultural Research, 59, 38, https://doi.org/10.1071/AR07146, http://www.publish.csiro.au/?paper=AR07146, 2008.

Schneider, C. A., Rasband, W. S., and Eliceiri, K. W.: NIH Image to ImageJ: 25 years of image analysis, Nature Methods, 9, 671–675, https://doi.org/10.1038/nmeth.2089, https://doi.org/10.1038/nmeth.2089, 2012.

Scholz, F. G., Bucci, S. J., Goldstein, G., Moreira, M. Z., Meinzer, F. C., Domec, J.-C., Villalobos-Vega, R., Franco, A. C., and Miralles-Wilhelm, F.: Biophysical and life-history determinants of hydraulic lift in Neotropical savanna trees, Functional Ecology DOI: 10.1111/j.1365-2435.2008.01452.x, 22, 773–786, https://www.fs.usda.gov/treesearch/pubs/34589, 2008.

Stanford, G. and Epstein, E.: Nitrogen Mineralization-Water Relations in Soils1, Soil Science Society of America Journal, 38, 103–107, https://doi.org/10.2136/sssaj1974.03615995003800010032x, http://dx.doi.org/10.2136/sssaj1974.03615995003800010032x, 1974.

Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R., and Polasky, S.: Agricultural sustainability and intensive production practices, Nature, 418, 671–677, https://doi.org/10.1038/nature01014, https://doi.org/10.1038/nature01014, 2002.

van Genuchten, M. T.: A Closed-form Equation for Predicting the Hydraulic Conductivity of Unsaturated Soils1, Soil Science Society of America Journal, 44, 892, https://doi.org/10.2136/sssaj1980.03615995004400050002x, https://www.soils.org/publications/sssaj/abstracts/44/5/SS0440050892, 1980.

Wang, X., Tang, C., Guppy, C. N., and Sale, P. W. G.: The role of hydraulic lift and subsoil P placement in P uptake of cotton (Gossypium hirsutum L.), Plant and Soil, 325, 263–275, https://doi.org/10.1007/s11104-009-9977-1, http://link.springer.com/10.1007/s11104-009-9977-1, 2009.

Watt, M., McCully, M. E., and Canny, M. J.: Formation and Stabilization of Rhizosheaths of Zea mays L. (Effect of Soil Water Content), Plant Physiology, 106, 179–186, https://doi.org/10.1104/pp.106.1.179, http://www.plantphysiol.org/content/106/1/179, 1994.

Welch, B. L.: The Generalization of ‘Student’s’ Problem when Several Different Population Variances are Involved, Biometrika, 34, 28–35, https://doi.org/10.2307/2332510, http://www.jstor.org/stable/2332510, 1947.

Williams, A. and de Vries, F. T.: Plant root exudation under drought: implications for ecosystem functioning, New Phytologist, 225, 1899–1905, https://doi.org/10.1111/nph.16223, https://doi.org/10.1111/nph.16223, publisher: John Wiley & Sons, Ltd, 2020.

Zhang, D.-J., Yang, Y.-J., Liu, C.-Y., Zhang, F., and Wu, Q.-S.: Root Hair Growth and Development in Response to Nutrients and Phytohormones, in: Root Biology, edited by Giri, B., Prasad, R., and Varma, A., pp. 65–84, Springer International Publishing, Cham, https://doi.org/10.1007/978-3-319-75910-4_3, https://doi.org/10.1007/978-3-319-75910-4_3, 2018.

Zhang, X., Davidson, E. A., Mauzerall, D. L., Searchinger, T. D., Dumas, P., and Shen, Y.: Managing nitrogen for sustainable development, Nature, 528, 51, https://doi.org/10.1038/nature15743, 2015.