



Root water uptake under heterogeneous soil moisture conditions: an experimental study for unraveling compensatory root water uptake and hydraulic redistribution

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Abstract

Aims Plant roots often encounter heterogeneity in soil water content and respond by compensating water uptake from wet zones to cope with the transpiration demand. Simultaneously, plants may also exhibit root-mediated hydraulic redistribution from wet to dry zones. Experiments were conducted to simultaneously monitor compensated root water uptake and hydraulic redistribution in the vadose zone.

Methods Vertical and horizontal split-root lysimeters were used to hydraulically isolate maize roots under altering soil water conditions. Compensated root water uptake and root-mediated hydraulic redistribution were monitored by continuous measurement of water content in the lysimeter compartments.

Results Soil water heterogeneity and limited soil water availability were found to accelerate the root water uptake from moist region to compensate the reduced water

availability in dry zone. However, no measurable root mediated hydraulic redistribution was observed in short term basis, despite high water potential gradient in the root zone of both lysimeters. The night-time transpiration and xylem refilling processes seem to override the hydraulic redistribution on a diurnal basis in our experiment.

Conclusions Our study shows that compensated root water uptake plays a major role in meeting the transpiration demand. In contrast, the role of root mediated hydraulic redistribution is found to be negligible in maize plant.

Keywords Compensatory root water uptake · Hydraulic redistribution · Split-root lysimeter · Night-time transpiration · Xylem refilling

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Introduction

Water uptake by plant roots is often regulated by endogenous factors such as root-shoot biomass and growth stage, as well as by external factors including soil water content, nutrient availability, and prevailing weather conditions (Albasha et al. 2015). The soil water content in the root zone is often heterogeneously distributed due to multiple factors such as soil type, irrigation/rainfall variability, non-uniform root distribution, and dynamic root water uptake patterns (Doussan et al. 2006; Yadav and Mathur 2008; Dara et al. 2015). Therefore, plants often deploy compensated root water uptake (hereafter referred to as CRWU) (Green and Clothier 1995; Yadav et al.

2009), root mediated hydraulic redistribution (HR) (Richards and Caldwell 1987; Caldwell et al. 1998; Oliveira et al. 2005), and adaptive root growth (Clausnitzer and Hopmans 1994) to cope with the soil moisture heterogeneity.

CRWU is a process in which water requirements of the plant under limiting soil moisture conditions are fulfilled by enhanced uptake from wetter root zone (Šimůnek and Hopmans 2009; Couvreur et al. 2012; Javaux et al. 2013). For example, when the water content in the upper zone with a high root density decreases, water absorption from the deeper moist layers increases for compensation (Teuling et al. 2006). Thereby, CRWU allows plants to transpire at or close to the potential demand though a part of the root system is subjected to limited soil moisture availability (Soylu et al. 2017). CRWU is a prominent root water uptake mechanism in many plants with roots in the capillary zone (Kang et al. 2002; Karimov et al. 2014; Soylu et al. 2017) or zones with heterogeneous soil structure (Kuhlmann et al. 2012). In addition, CRWU can be observed when some part of root biomass gets permanently damaged (Poni et al. 1992; Vysotskaya et al. 2004; Black et al. 2011). Alternate partial root-zone drying (Kang et al. 2003; Mingo et al. 2004), regulated deficit irrigation (Kang and Zhang 2004; Leib et al. 2006; Chai et al. 2016), localized irrigation (Green and Clothier 1995), and alternate furrow irrigation (Kang et al. 2002) are some of the irrigation practices that are supposed to use CRWU to reduce evaporation loss. Therefore, an accurate estimation of CRWU is essential for understanding plant water uptake patterns and for simulating soil water flow in the vadose zone under varying soil moisture conditions.

HR is a passive transfer of soil moisture via the root system from a region of high water potential to low water potential (Oliveira et al. 2005). Thereby, under heterogeneous soil moisture condition, the roots reallocate water from wetter soil layers to drier soil layers. The transferred water is further used for transpiration (Burgess and Bleby 2006) and to some extent, moderate the intensity of CRWU (Guswa 2012). The magnitude of HR depends on multiple factors, including water potential gradient between the soil layers, root conductivity, spatial distribution of the root system, and transpiration demand (Meinzer et al. 2004; Doussan et al. 2006). HR is typically observed in deep-rooted desert plants, shrubs, and trees, for which hydraulically redistributed water contributes towards the transpiration

demand (Hultine et al. 2003; Oliveira et al. 2005; Neumann and Cardon 2012). The ecological impacts of HR such as preventing the loss of hydraulic conductivity of roots (Bauerle et al. 2008), increasing nutrients acquisition and their mobilization (Warren et al. 2008, Armas et al. 2012; Sardans and Peñuelas 2014), have also been described previously. However, studies on HR in agriculture crops under field conditions are limited and have contradictory observations on its relevance from a hydrological perspective (Zegada-Lizarazu and Iijima 2004; Cai et al. 2018; Meunier et al. 2018).

HR is more likely to happen when the transpiration demand is low, especially during night hours (Richards and Caldwell, 1987) and after rainfall (Hultine et al. 2004). However, the active night-time transpiration has been observed in many crops due to partial closure of the stomata (Tolk et al. 2006; Caird et al., 2007a, b). Moreover, studies have shown that plants can also lose the hydraulic conductivity of xylem tissues in roots, shoots and stem during day time due to embolism/cavitation as a result of soil water stress (McCully 1999; Domec et al. 2006; Lovisolo et al. 2008; Johnson et al. 2009). Depending on multiple factors such as species, genotype, stage of development, extent and severity of water stress (Thapa et al. 2011; Knipfer et al. 2017), plants can recover from cavitation by xylem refiling (McCully et al. 1998; Yu et al. 2018) during night hours (Domec et al. 2006) or after irrigation (Brodersen et al. 2010). Therefore, night-time transpiration and xylem refilling can modulate the magnitude of HR (Howard et al. 2009; Prieto et al. 2010a, b; Yu et al. 2018).

Though the mechanisms of root water uptake, including CRWU and HR, were studied under varying soil moisture conditions (Drew 1975; Koebernick et al. 2015; Dara et al. 2015), the cause and impact on each other require further investigations. As both mechanisms can be triggered under heterogeneous soil moisture conditions, we studied the co-occurrence and magnitude of these mechanisms in maize plant. This can be achieved by generating a water potential gradient between root zones followed by measuring the change in soil water content as a proxy for water uptake/release by plant roots. However, an accurate estimation of root water uptake is often limited by the soil water flux due to the water potential gradient between the root zone (Musters and Bouten 2000). Therefore, we

performed a series of split-root lysimeter experiments, wherein the plant roots are compartmentalized into hydrologically isolated regions aligned vertically or horizontally. Further, the role of nighttime transpiration and xylem refilling were also investigated in association with HR. Therefore, the current study aimed at improving the understanding of root water uptake by maize under heterogeneous soil moisture conditions while simultaneously considering CRWU and HR.

Materials and methods

Experimental rationale and setup

The design of the vertical and horizontal split-root lysimeters and the location of sensors is shown in Fig. 1. The design and experimental strategies of the column lysimeter are described in the supporting information (S1). The vertical split-root lysimeter is constructed by assembling two chambers made of acrylic glass with an internal measurement of $12 \times 22 \times 43$ cm (L \times W \times H). The horizontal split-root lysimeter is made of a cylindrical PVC column with an internal diameter of 12.7 cm and a height of 55 cm, divided into two compartments using beeswax

of 1 cm thickness. The consistency of the wax was reduced by adding vegetable oil to avoid crack during root growth and diurnal temperature variations. A provision for drainage was also made at the bottom of all lysimeter compartments, along with the option for irrigating them separately. The soil substratum made of silt, clay, and organic matter in the proportion of 16:4:1 (bulk density 1.36 g/cm^3) was used as the growing medium in the experimental setup. Germinated seedlings of maize were planted in the lysimeters.

In the vertical split-root lysimeter, the root cap with apical meristem (1 cm from the tip) of the seedlings was excised and transplanted to the seedling chamber that placed directly in the middle of the lysimeter (Fig. 1a). This was to enhance the primary lateral root growth (Brouder and Cassman, 1994; Fernández et al. 2011), which leads to equal distribution of roots between the compartments while interconnected only via the plant biomass. One week after transplantation, the lysimeters were thinned to two seedlings per setup. All lysimeters were kept outdoors during the growing stage and irrigated daily and weekly with the NPK (16–16–16) solution till their reproductive stage. To minimize the impact of radiation-induced heating of the root zone on root growth, lysimeters were wrapped with jute and kept moist during the growth period (Poni et al. 1992).

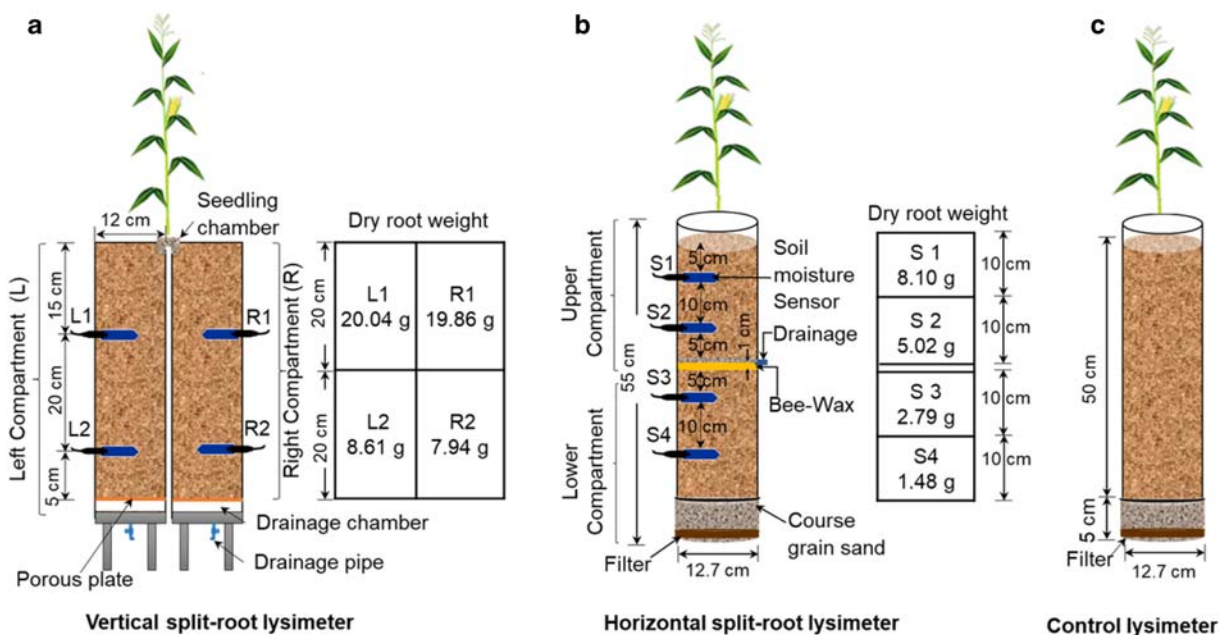


Fig. 1 Schematic representation of the split-root lysimeter experiment setups. **(a)** The vertical split-root lysimeter with soil moisture sensor locations. The root distribution is represented in the right panel in terms

of its dry weight (in grams). **(b)** The horizontal split-root lysimeter. **(c)** The control lysimeter with dimensions

For continuous measurement of soil water content, four soil moisture sensors (WaterScout SM 100, sensing area is 6 cm × 2 cm) were installed in each zone of the lysimeter as shown in Fig. 1. In the vertical split-root lysimeter, two sensors were installed per compartment, one at a distance of 15 cm below the root-shoot junction (L1/R1) and the other 5 cm above the bottom drainage (L2/R2). In horizontal split-root lysimeter, the sensors were installed at the locations of 10 cm (S1), 20 cm (S2), 33 cm (S3), and 43 cm (S4) from the top. The reading from each sensor was considered as the average soil water content of the corresponding zone. The entire experimental setup was mounted over a weighing machine (Wensar counter scale 30 kg, accuracy 0.1 g) for the mass balance analysis. Control lysimeters were built in parallel to corresponding split-root lysimeters for measuring potential transpiration (Fig. S1A and Fig. S2A, respectively).

Vertical split-root lysimeter

The vertical lysimeter was left unirrigated to bring the soil water content in both compartments to wilting point by allowing the plants to transpire over multiple days (phase I) (Fig. 2a I). Phase II was initiated by irrigating the right compartment to field capacity, while the left compartment remained under water stress (Fig. 2a II). When the soil water content in the right compartment reached the wilting point, phase III was initiated by switching irrigation to the left compartment (Fig. 2a III). Phase IV began by irrigating both compartments to field capacity when the left compartment reached the wilting point (Fig. 2a IV). At the end of phase IV, the shoot biomass of the plant was excised from its root, the stem-root interface was sealed with parafilm to prevent sap flow, and the right compartment was then irrigated to field capacity (Fig. 2a V, S1B). At the end of phase V, each compartment was segmented into two sections of 20 cm each (Fig. S1C, D), the roots were separated from the soil by washing, and the dry weight of the roots from each section was measured (Fig. 1a).

Horizontal split-root lysimeter

Phase I of the horizontal split-root experiment was initiated by irrigating both compartments to field capacity (Fig. 2b I). The lysimeter was then left unirrigated for one week, while the soil water content was recorded continuously. Phase II started from the wilting point of

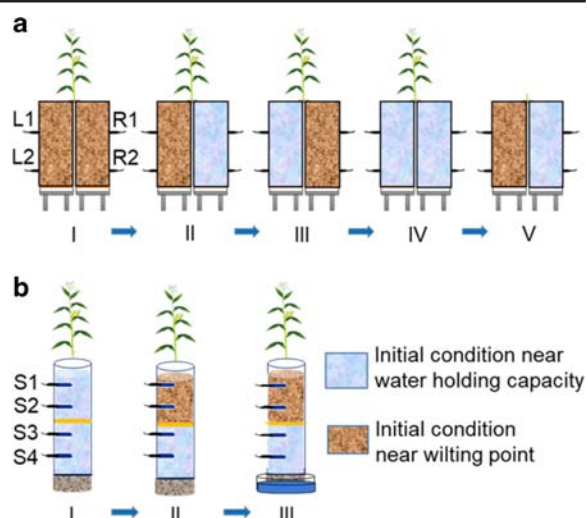


Fig. 2 Schematic representation of irrigation during different phases of vertical and horizontal split-root lysimeter experiments. The initial soil water content of blue coloured compartments was near to field capacity, while the sand filling represents the compartments with soil water content near the wilting point. **(a)** Irrigation scenarios in the vertical split-root lysimeter: (I) Both left and right compartments are under water stressed conditions; (II) The right compartment is irrigated while the left compartment is under water stress; (III) The left compartment is irrigated and the right compartment is under water stress; (IV) Both compartments are irrigated; (V) Zero transpiration conditions with the irrigated right compartment after shoot removal. **(b)** Irrigation scenarios in the horizontal split-root experiment: (I) Both left and right compartments irrigated to field capacity; (II) The lower compartment irrigated while the upper compartment is under water stress; (III) The water table as a bottom boundary condition

phase I, by irrigating only the lower compartment (Fig. 2b II). When the soil water content in the lower compartment declined to 3% due to continuous transpiration, the water table treatment (phase III) was performed for three days (Fig. 2b III). For this, the whole lysimeter setup was kept partially immersed in a water reservoir under a constant level of water and the surface evaporation was prevented. In the end, the lysimeter was segmented into four sections of 10 cm each, such that the sensor location was in the middle of each section. The roots were then collected, washed (Fig. S1B), and the dry root biomass was determined (Fig. 1b).

Estimation of actual and potential transpiration

Potential transpiration from all lysimeters was estimated from its corresponding control lysimeter. For that, a control lysimeter was maintained along with each split-root lysimeter setup under the same environmental

conditions. Before each experiment, a correlation function (K) for transpiration was obtained for each split-root lysimeter with its corresponding control (Table S1). For that, the soil water content in the main lysimeter and its control were maintained in the optimal range, and the transpiration flux was measured at multiple time intervals. From this data, a correlation coefficient (K) (Ray and Sinclair 1997; Vamerali et al. 2003) was obtained by assuming a linear relationship between the transpiration rate from the main experiment and its control. Here we assumed that the change in plant biomass during the yield formation stage of the maize plant is in the same proportion (Koca and Ereku 2016). Therefore, the potential transpiration from the main lysimeter (T_p) can be estimated from the transpiration rate of the control (T_{pc}) using the correlation coefficient, K ($T_p = T_{pc} * K$).

Throughout the experiment, the soil water content in the control lysimeter was maintained in the optimal range by replenishing water lost by transpiration. Surface evaporation from the main split-root lysimeters and their corresponding controls was prevented by a layer of sand and aluminium foil (Faria et al. 2010; Moradi et al. 2011). As the exposure of the soil surface to the atmosphere was restricted, it was assumed that the evaporation loss during the experiment was negligible. This suggests that the weight loss from any lysimeter between two time points was exclusively due to the transpiration flux. To measure the actual and potential transpiration rates, the weight of the lysimeter setups and their corresponding controls were recorded every day at 7 am, 10 am, 1 pm, 4 pm, and 7 pm throughout the experiment. Actual transpiration during any time interval was then obtained by mass balance. Corresponding potential transpiration was estimated by multiplying the transpiration flux from the control lysimeter with its correlation coefficient (K).

Results

CRWU under varying soil moisture conditions in maize

Vertical split-root lysimeter

During the early days of phase II and III (days 2, 3, 6, 7), the transpiration demand of the plant was

fulfilled from the irrigated compartment, while the soil water content in the other compartment was near the wilting point (Fig. 3a, c, d). Also, a sharp decline in the soil water content in the irrigated compartments was observed during these days, as compared to phase IV. These observations confirm the occurrence of CRWU by enhanced water uptake from the irrigated compartments that compensated the water uptake reduction from the dry compartments (Šimůnek and Hopmans 2009; Yadav et al. 2009). Also, after irrigating the dry compartment during the phase change, the transpiration rate was fully recovered, indicating that the roots in dry compartments remained viable despite temporary water stress.

The relative soil water depletion from zones R1 and R2 of the wet compartment on day 2 (phase II) was 81.5% and 18.5%, respectively, while the depletion from zones L1 and L2 of the dry compartment remained negligible (Fig. 3b). Similarly, on day 6 of the experiment (phase III), the relative soil water depletion was nearly 76.7% and 23.3% from zones L1 and L2, respectively, while it remained insignificant from zones R1 and R2. During days 10 and 11 (phase IV), the relative soil moisture depletion from zones L1, L2, R1, and R2 was 37.8%, 11.45%, 39.7%, and 11%, respectively. Comparable root distribution and soil moisture depletion on days 10 and 11 with optimal soil water content suggest a linear correlation between water uptake and root density (Fig. 3b). As the soil water content was gradually depleted from the high root density regions (below 15%, phase II, III, and IV), a shift in the location of water extraction to low root density zones and an increased absorption rate from these zones were observed. For example, on day 4 (phase II), the relative water depletion from location R1 decreased to 25.7% and from R2 increased to 74.3%, while it remained unchanged in the dry compartment. Similarly, on day 10, the relative water depletion from L1 and R1 was 41.6%, and 39.4%, whereas it was 11.5%, and 7.5% from L2 and R2 respectively. On day 14, the relative water depletion from locations L1 and R1 decreased to 13.8% and 12.3%, respectively (Fig. 3b). In comparison, it increased from L2 and R2 to 37.7% and 36.2%, respectively, indicating that compensatory water uptake from zones L2 and R2, and thus the potential transpiration rate was maintained (Fig. 3d). It was further

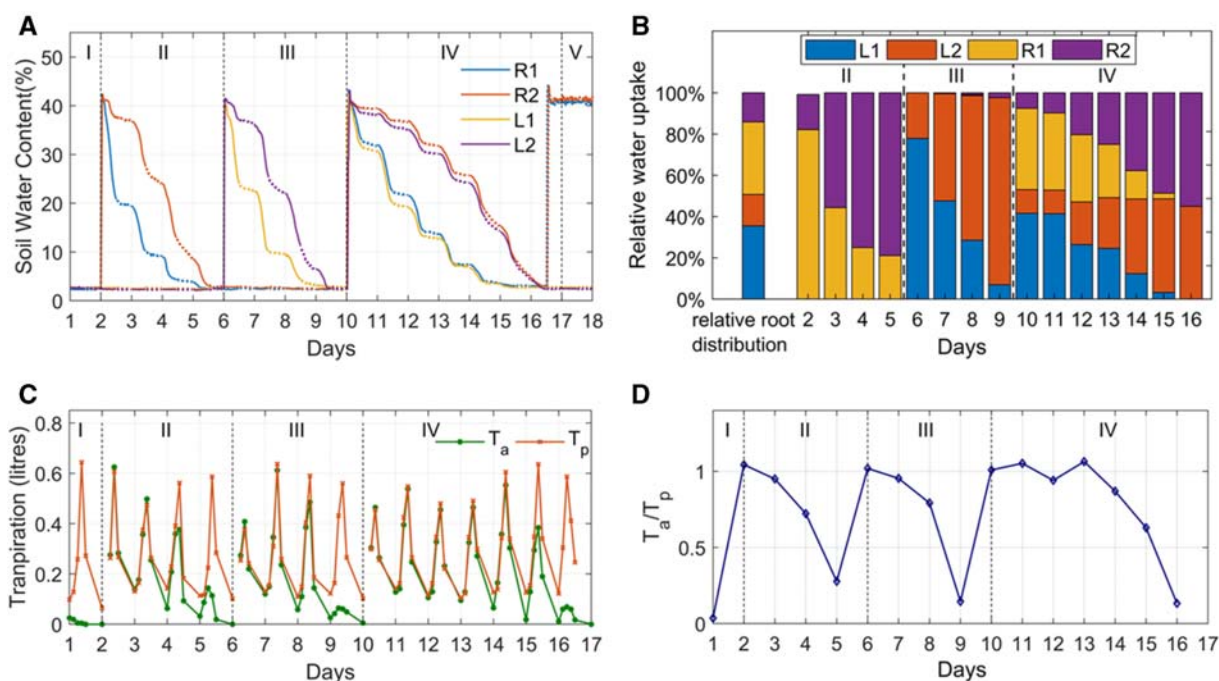


Fig. 3 The vertical split-root lysimeter with a fully grown maize plant under varying soil moisture conditions. **(a)** Soil water content recorded by soil moisture sensors from four different locations under different irrigation scenarios. Solid lines indicate the soil water content variation during day time and dotted lines indicate the soil water content during

night. **(b)** Relative soil moisture depletion (root water uptake) from sensor zones L1, L2, R1, and R2 in the vertical split-root lysimeter and the corresponding relative root distribution. **(c)** Actual transpiration (T_a) and potential transpiration (T_p) measured in litres at a regular time interval. **(d)** Daily relative transpiration

confirmed from the control setup that the potential transpiration rate was maintained despite the prevailing soil water stress in some regions during phase II, III, and IV (Fig. 3c, days 2–3, 6–8, and 13–14).

When the soil water content in both compartments of the vertical split-root lysimeter was near field capacity (days 10 and 11), water uptake from zones L2 and R2 was nearly 11.5% and 9% of the total diurnal water uptake rate, respectively (Fig. 3b). During phase II and III, when CRWU occurred under heterogeneous water distribution, the water uptake from zones L2 and R2 was as high as 70% (day 4) and 75% (day 8), respectively, of the corresponding total diurnal water uptake quantity. This suggests that when compensation occurs, a fraction of roots in the wet soil exhibits a high water absorption rate per unit of its dry weight as compared to the roots present in the dry zone. Thus, under localized water stress condition, the roots that are “active” in supplying water to plants can be defined as the portion of roots that are exposed to soil with favorable water content.

Horizontal split-root lysimeter

On days 1 and 2 of phase I in horizontal split-root lysimeter experiment, relative soil moisture depletion from zones S1, S2, S3, and S4 was 46%, 25%, 19%, and 10%, respectively, and the corresponding root distribution was 47%, 29%, 16%, and 8% (Fig. 4b). This indicates that the water extraction rate from the soil is linearly correlated with the root density distribution under optimal soil moisture condition, as reported previously by Yu et al. (2007) and Yadav et al. (2009). After that, when the soil water content of a region was reduced below 15%, the root water extraction rate from that zone decreased substantially (Fig. 4a, b). Also, the zone of maximum root water uptake shifted downwards into deeper soil layers with a lower root density. Water absorption from these deeper soil layers increased to cope with the transpiration demand. The highest rate of water uptake from zone S4 with the lowest root density was observed during the final days of phase I and II when the average soil water content in the lysimeter fell below 10%. This indicates that reduced root water uptake from the dry zone was

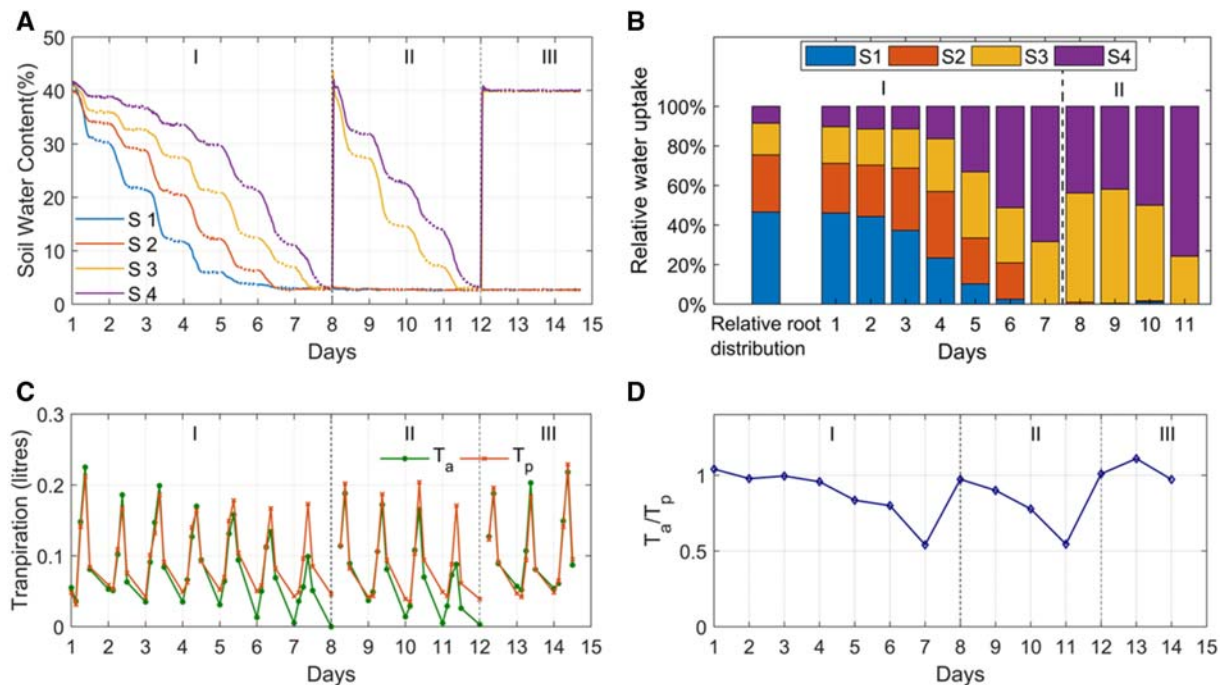


Fig. 4 The horizontal split-root lysimeter with a fully grown maize plant under different soil moisture conditions. **(a)** Soil water content variations recorded using soil moisture sensors under different irrigation scenarios. Day time soil water content is represented by solid lines and dotted lines represent the night time soil water content. **(b)** Relative soil

moisture depletion (root water uptake) from sensor zones S1, S2, S3, and S4 in the horizontal split-root lysimeter and the corresponding root distribution in the zones. **(c)** Actual transpiration (T_a) and potential transpiration (T_p) measured at a regular time interval. **(d)** Daily relative transpiration

fully or partially compensated by enhanced water uptake from the wetter zone (Fig. 4b).

The comparable actual and potential transpiration rates estimated from the control lysimeter further confirmed the existence of CRWU (Fig. 4c, days 4–6, 8–9, and 12–14). On day 8 (phase II), when only the lower compartment was irrigated while the upper compartment was near the wilting point, a reduction in root water uptake from the upper compartment was fully compensated by increased water uptake from the lower compartment. Likewise, during the water table boundary treatment (phase III), when the roots in the lower compartment received ample water, a reduction in root water uptake from the upper compartment was almost fully compensated by an increased uptake from the lower compartment supplied with water by a capillary rise, and thereby the transpiration demand was fulfilled (Fig. 4d). Moreover, during the water table treatment, around 24% of fine roots in the lower compartment that had access to the capillary water mostly contributed towards the transpiration demand. In comparison, water uptake from the remaining 76% of fine roots was negligible. Thus, a fraction of the root biomass present in

the moist layer meets the plants' transpiration demand through the CRWU.

Root mediated HR under heterogeneous soil moisture conditions

Vertical split-root lysimeter

Previous studies (Ryel et al. 2002; Mendel et al. 2002; Amenu and Kumar 2008; Couvreur et al. 2014) revealed that the high water potential gradient in the root zone along with the reduced transpiration demand can result in the redistribution of soil moisture through root-shoot biomass. Phase II and III of the vertical split-root lysimeter experiment were performed with an objective to create a high water potential gradient between the two compartments. In the split-root lysimeter experiments, HR can be analyzed by observing an increase in the soil water content in the dry compartment during low transpiration periods. A high water potential gradient between the hydraulically isolated compartments was generated during phase II (Fig. 2a II, Fig. 3a II). A reciprocal water potential gradient was also generated in phase

III between the compartments to make sure that both compartments possess active roots despite being temporarily subject to water-stress (Fig. 2a III, Fig. 3a III). Since the maize plant was in yield-forming stage and retained comparable root biomass in both compartments (Fig. S1D), redistribution of water between the wet to dry compartments was expected. Although the night hours in early days of phase II and III supported favorable conditions for HR, no considerable increase in the soil water content was observed in the dry compartments (Fig. 3a II zone L1 and L2, Fig. 3a III zone R1 and R2), indicating the absence of HR.

To assess any possible existence of passive HR between the compartments in the absence of transpiration, the shoot biomass was removed, the right compartment was irrigated, and the soil moisture distribution was monitored over a period of 24 h (phase V) (Fig. 2aA V, Fig. S1B). It was hypothesized that HR through the roots should occur under a high water potential gradient as long as roots are intact and hydrated even in the absence of shoot biomass (Leffler et al. 2005). The existence of a strong soil moisture gradient between the two compartments interconnected via the shared root system and the absence of any measurable change in water content in the two compartments suggested the lack of measurable passive redistribution of soil moisture by roots (Fig. 3a V). A high water potential gradient created after the removal of the plant shoot biomass did not result in a redistribution of soil water to the dry zone, even in the absence of transpiration.

Horizontal split-root lysimeter

During the early days of phase II and III of the horizontal split-root lysimeter experiment, a strong water potential gradient and hydraulic isolation existed between the upper and lower compartments (Fig. 4a). In the groundwater table treatment, during the transition from phase II to III, soil water content in the sensor regions S3 and S4 were increased to the optimal soil moisture range, while the upper compartment remained unaffected. The night hours of phase III (days 12, 13, and 14) were found to be favorable for HR. However, a visible increase in the soil water content was not observed in the dry compartment (Fig. 4a III). Phase III was further extended for three more days and two nights, but no measurable HR was observed by the sensors.

Night-time transpiration and xylem refilling under different soil moisture conditions

Vertical split-root lysimeter

Under optimal soil moisture conditions, the night-time transpiration was up to 12% of the total transpiration. This suggests its significant contribution towards the daily transpiration flux (Fig. 5a). In contrast, a reduction in the night-time transpiration on days 4, 8, and 13–14, compared with the control suggests that night-time transpiration can also be affected by soil water stress. When the daily transpiration rate dropped below 70% of the potential transpiration demand, the observed night-time transpiration was negligible (on days 5, 9, 15, and 16). Moreover, during days 4, 8, 14, and 15, a high water uptake rate by plant roots was observed during night (e.g., Fig. 3a: zones R2 and L2, days 14–15, dotted lines, Fig. S3B), while night-time transpiration was nearly zero (Fig. 3c). Although the plant showed temporary wilting during these days, the recovery during night hours suggested the existence of xylem refilling.

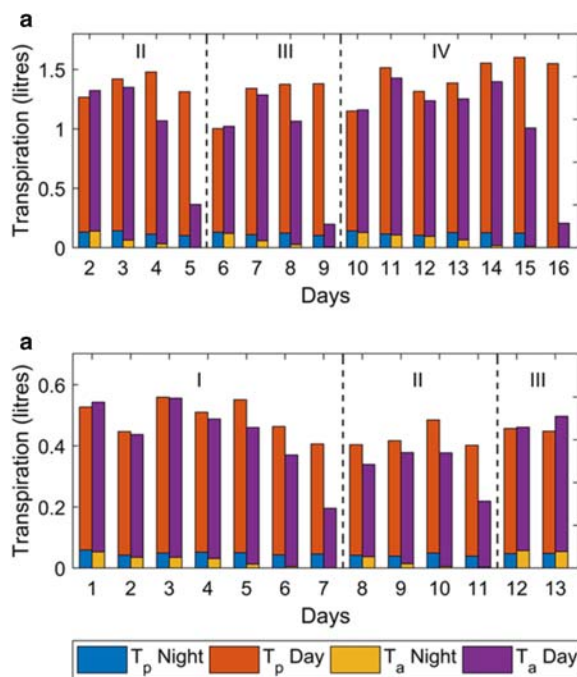


Fig. 5 Actual (t_a) and potential (T_p) transpiration fluxes measured during day and night from the (a) vertical split-root lysimeter and (b) horizontal split-root lysimeter

Horizontal split-root lysimeter

Similarly, in the horizontal split-root lysimeter, when the soil water content was not limiting on days 1, 2, 3, and 8, the night-time transpiration rate was comparable to the control experiment (Fig. 4c, Fig. 5b). During these days, night-time transpiration accounted for 8–12% of the total daily transpiration loss. On days 6 and 7, when the day-time transpiration reduced, the night-time transpiration flux was insignificant compared to the control. Since the control and horizontal split-root lysimeter experiments were carried out under the same environmental conditions, the soil moisture availability was the single most important factor that controlled night-time transpiration. Under water stress, the transpiration flux overrides the water absorption rate during day time. While the night-time transpiration flux was negligible, the overall root water uptake during this period was higher than the normal rate, as shown by the dotted portion of the S3 and S4 lines on days 5, 6, and 11 in Fig. 4a and Fig. S4B. Also, the plant showed signs of temporary wilting in the evening of these days along with overnight recovery apparently through xylem refilling.

Discussion

In the current study, the quantitative and qualitative implications of the CRWU and HR mechanisms were investigated by alleviating the transpiration due to soil moisture heterogeneity. Fully grown maize plants of yield formation stage were used in all experiments due to their extensive root system that helped in the effective compartmentalization of roots. This further ensured minimal impact of biomass change on transpiration measurements (Koca and Erekul 2016). Also, a comparable soil water content recorded by all four sensors after irrigation indicated that the soil was homogeneously packed.

Compensated root water uptake

In agreement with the previous studies (e.g., Šimůnek and Hopmans 2009; Yadav et al. 2009; Faria et al. 2010), the split-root experiments suggested that CRWU plays a critical role in the survival of plants under heterogeneous soil moisture conditions. In this study, when one half of the root system in the vertical split-root

lysimeter was under severe water-stressed condition, almost 100% compensation was observed due to an increase in water uptake from the other half of the lysimeter. Similarly, in the horizontal split-root lysimeter, the water absorption capacity of the roots in the lower compartment, increased upto four times. Our results suggest that compensation occurs when a fraction of the root biomass present in the wet zone becomes extremely effective in absorbing water from the moist soil compared to the roots present in the dry soil. Due to this compensatory root water uptake, total water extraction was not substantially reduced, which is in agreement with previous reports (e.g., Cabelguenne and Debaeke 1998; Dara et al. 2015). However, when the average soil water content in the lysimeter dropped below a certain threshold, the roots were unable to fully compensate. Therefore, the transpiration rate was not maintained at its optimal level. In agreement with our findings, Tan and Buttery (1982) reported that root water uptake from the half root zone of peach seedlings was sufficient for meeting the transpiration demand while the other part of the root zone was dry. Similar findings were made in plants like potato (Stalham and Allen 2004; Liu et al. 2008), kiwifruit vines (Green and Clothier 1995), sorghum (Faria et al. 2010), tomato (Mingo et al. 2004), and bell pepper (Yao et al. 2001).

The groundwater table treatment in the horizontal split-root and column lysimeter experiments (Supporting Information S1) confirmed that even a small portion of roots that can grow into the deep moist soil layer might be of considerable advantage to plants through CRWU (Šimůnek and Hopmans 2009; Jarvis 2011). Furthermore, when compensation occurs, the relative root distribution and water uptake profiles become dissimilar. Consequently, the root distribution becomes a poor indicator of the root water uptake distribution (Šimůnek and Hopmans 2009; Javaux et al. 2013). When the soil water content is above 15% in all regions, the root water uptake was relatively proportional to the root density distribution. When the soil water content in the high root density region dropped below 15%, the water uptake from this region decreased, and root water uptake shifted to next highest root density region.

During phase II and III in the vertical split-root lysimeter, when irrigation was switched from one compartment to another, the plant shifted their source of water uptake from the dry zone to the wet zone and

initiated CRWU without much delay. This also shows that even when roots' permeability was reduced due to soil drying (North and Nobel 1991), it rapidly recovered upon rewetting (Kang and Zhang, 2004; Liu et al. 2008). This suggests that the alternate partial root-zone drying method can be practiced effectively in maize. Furthermore, the same experimental strategy can be used for studying compensatory nutrient uptake for effective fertigation.

Root mediated hydraulic redistribution

Although there are several studies on HR, its implication on the root water uptake is still unclear in maize and other crops (Wan et al. 2000; Zegada-Lizarazu and Iijima 2004). Thus, we investigated the existence of HR in maize under our experimental conditions. No measurable HR was observed in any of our experiments, even under a strong water potential gradient. Previous studies have considered HR as a passive process that occurs due to the difference in the soil water potential between root zones (Mendel et al. 2002; Amenu and Kumar 2008). Being a passive phenomenon, it was reasonable to expect HR between the hydraulically isolated compartments, yet connected through the root-shoot junction. Previous studies by Faria et al. (2010) and Meunier et al. (2018) observed the root mediated water redistribution from a high soil water content zone (25%–35%) to medium dry zone (10%). In our experiments, there were multiple events in both vertical and horizontal split-root lysimeter experiments where a part of the root system was exposed to medium dry conditions. However, no measurable HR was observed in both cases.

Various studies have shown that night-time transpiration can be significant (e.g., Caird et al., 2007b; Gleason et al. 2017; Claverie et al. 2018). In agreement with this, it was observed that night-time transpiration accounted for 8–12% of total daily transpiration under optimal soil water supply. Water loss measured during the night from all lysimeters was comparable to their corresponding controls. When the maize plant was subjected to limited water availability, the night-time transpiration was reduced significantly, which is in agreement with Ludwig et al. (2006) and Howard and Donovan (2007).

An unexpected soil moisture depletion was noticed during night hours while the plant was experiencing water stress, which is in contrary to

the observed night-time transpiration. During this period, the actual transpiration was below its potential rate, and plant showed signs of temporary wilting during day time and recovered during night. The xylem refilling process seemed to be triggered during night hours. As a result, water uptake was higher than the transpiration rate, as also reported by Gleason et al. (2017). The night-time transpiration and xylem refilling processes might thus override the HR on a diurnal basis in our experiment. Various other studies have found a substantial decrease in the magnitude of hydraulically redistributed water when the night-time transpiration increased due to the vapor pressure deficit (Howard et al. 2009; Prieto et al. 2012). Likewise, the xylem refilling or rehydration of plant tissues during the night time may also reduce HR significantly (Prieto et al. 2012; Neumann et al. 2014; Yu et al. 2018).

There is some consensus that when the soil water content in the root zone reaches near the wilting point, the change in rhizosphere properties such as root and soil shrinking (North and Nobel 1991; Hu et al. 2011; Zarebanadkouki and Carminati 2014), mucilage shrinking and biodegradation (Zarebanadkouki and Carminati 2014) may occur. These physico-chemical changes may lead to the formation of air-filled gaps between the soil and the roots (Sharp and Davies, 1985; Carminati, et al. 2013) or even to water repellence by roots due to drying of mucilage around the roots (Moradi et al. 2012). This may lead to substantial localized hydraulic resistance in the soil at the root vicinity that may lead to inadequate contact between the soil and root surfaces. Thus, the hydraulic conductance at the soil-root interface could decrease, or even result in rupture of the hydraulic continuum, which may limit the HR in extremely dry soil (Carminati and Vetterlein 2013; Couvreur et al. 2020). Also, the low soil hydraulic conductivity may reduce the diffusion of exuded water from the roots, which may limit the measurement of HR with soil moisture sensors. Thus, a strong water potential gradient may not necessarily favor the occurrence of HR (Carminati and Vetterlein 2013; Couvreur et al. 2020). Another reason for not observing the HR is the prompt triggering of the CRWU on the next day before moisture can diffuse from the root-soil interface into the soil due to the low soil hydraulic conductivity. Moreover, the root development stage at which HR was determined would also

affect the HR magnitude (Zegada-Lizarazu and Iijima, 2004; Shen et al. 2011).

Although evidence indicates that HR is a common phenomenon in crops, its magnitude may vary among the plants under different experiment conditions. For instance, in a split-root study, Wan et al. (2000) observed HR in the drought-tolerant strains of maize but not in the drought-susceptible one. Also, HR was not observed in maize using isotope analysis in a split-root study by Zegada-Lizarazu and Iijima (2004). Likewise, Corak et al. (1987) detected HR in alfalfa plants, whereas Dirksen and Raats (1985) could not observe. Similarly, HR was detected in pearl millet (Vetterlein and Marschner 1993), pigeon pea (Sekiya and Yano 2004), and oat (McCully 1995). However, Zegada-Lizarazu and Iijima (2004) could not detect HR in any of these species using the stable hydrogen isotope in a split-root setup. Further, Shen et al. (2011) found that the contribution of HR water towards transpiration in wheat was negligible, while Valizadeh et al. (2003) found that HR helped in the acquisition of nutrient from dry soil patch in wheat. In a split-root experimental study with isotopes to investigate the existence of HR in sixteen agricultural crops by Zegada-Lizarazu and Iijima (2004), nine species did not show the evidence for HR. Although there is limited evidence for HR in agriculture crops (e.g., Zegada-Lizarazu and Iijima 2004; Sekiya and Yano 2004), its magnitude is often very low, which raises a question about the relevance of HR in supporting the root water uptake demand under field conditions, particularly on a diurnal scale. For example, Cai et al. (2018) reported that hydraulically redistributed water in wheat was too low to be detected by soil moisture sensors. The contradictory observations in terms of HR suggest the need to use multiple techniques for the precise estimation of HR in crops under field conditions (Rothfuss and Javaux 2016). The current method, which is based on soil water content variations, is effective in providing the quantitative analysis of hydraulically redistributed water. However, the measurement of soil water content is often limited to the vicinity of the sensor. In our experiments, despite using multiple methods under varying soil moisture conditions, no measurable HR was observed at the point of measurement. Further investigations are needed to verify if the HR can be significant during a period of long-term reduced transpiration conditions.

Conclusions

The contribution of CRWU and HR towards transpiration in plants under limiting soil moisture conditions remain elusive. We used multiple methods in parallel to verify the presence of CRWU and HR under varying soil moisture conditions. Our results suggest that the majority of the transpiration demand is aided by CRWU and not by HR. Though the possible existence of HR under given experimental conditions cannot be excluded, HR is unlikely to have a direct hydrological impact. Therefore, our research suggests that the role of HR in meeting the transpiration demand can be neglected when modeling the transpiration in maize. The current research also suggests the use of maize plant as a model system for studying alternate partial root-zone drying.

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Author's contributions AT and BKY designed the experiments. AT performed the experiments. BKY, AT, and JS analyzed the data. AT, BKY, and JS wrote the manuscript.

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