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Hydrotropic Root Behavior in Water-saving Cultivation: a High-resolution Monitoring Study of Soil Water Dynamics

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Abstract

Purpose

Subsurface irrigation has been confirmed to have high water use efficiency (WUE) due to it irrigating only the crop root zone. This study investigated hydrotropic root behavior when a wet zone was produced around the roots by subsurface irrigation to clarify the dynamics of soil water content in the wet zone caused by water absorption of the growing plant.

Results

We conducted a feasibility study of a high-resolution soil moisture sensing prototype and gathered data to analyze hydrotropism and plant water absorption activity. We applied signal processing, high pass filtering, and Fast Fourier Transform (FFT) to the acquired high-resolution soil moisture data. The results showed distinct fluctuation of moisture at the boundary area, which indicated plant's biological rhythm of photosynthetic activities. We also quantified root distribution inside and outside the wet zone and observed the shape of the root system from the cross-section of the wet zone. The results show that hydrotropism restricted most of the roots to the inside of the wet zone. Furthermore, root hydrotropic response is nonuniform for all roots of an individual plant.

Conclusions

The results suggest a new method to study hydrotropic root behavior and plant photosynthetic activities. We assumed a mechanical, push-and-pull model of water dynamics at the wetting front and the root mass accumulated by hydrotropism is an important system parameter. To further evaluate a plant's hydrotropic performance, it is necessary to use stochastic analysis and/or a non-deterministic approach.

Introduction

Agriculture represents a major consumer of freshwater, accounting for about 70% of the worldwide total water withdrawal (Davies and Bennett 2015; Frenken and Gillet 2012). In addition, climate change may result in more frequent occurrences of water shortage and increase the competition for water among urban, industrial, and agricultural demands (Comas et al. 2013; Fromm 2019). With increasing water demands from other sectors, irrigation agriculture must increase food production with limited water allocation (Davies and Bennett 2015; Du et al. 2015). Crop breeding technologies have been developed for this purpose (Pennisi 2008; Tester and Langridge 2010). A major point of crop breeding is to develop ideotypes in irrigation agriculture for more efficient acquisition of water and nutrient in the irrigated area (Fromm 2019; Schmidt and Gaudin 2017). Hydrotropism allows roots to grow actively towards water source for water acquisition (Cassab et al. 2013; Dietrich 2018; Fromm 2019). Utilizing this response in irrigation agriculture is important for improving WUE.

Water-saving irrigation technologies have also been developed to increase WUE, and one such technology is subsurface irrigation (Appels and Karimi 2021; Camp 1998; Cote et al. 2003; Ma et al. 2020; Qi et al. 2021). This technology uses emitters buried in soil to deliver irrigation water directly to the crop root zone (Cote et al. 2003; Ma et al. 2020; Qi et al. 2021). Proper management of irrigation water can prevent water logging in topsoil and reduce surface evaporation, run-off, and deep percolation, resulting in improved efficiency of irrigation water use and nutrient uptake (Cote et al. 2003; Ma et al. 2020; Qi et al. 2021). So far, this technology has shown great performance in field irrigation practice, resulting in higher crop yields and quality with less irrigation water, preventing weed growth, mitigating soil N_2O emissions, and facilitating the use of degraded-quality water (Qi et al. 2021).

When performing subsurface irrigation, a localized zone of wet soil can be produced. This phenomenon can generally be observed in an open field (Yoshida and Iwasaki 2014). Studies have shown that the geometry of the wet zone under subsurface irrigation can be influenced by irrigation rate, soil hydraulic properties, and root water uptake (Shukri et al. 2013; Shukri et al. 2014; Appels and Karimi 2021). In terms of soil physics, the wet soil particles adhere to each other and form a harder part due to the cohesive force of water molecules (Jury and Horton 2004). Previous studies showed that a stable, spherical wet zone can be formed in homogeneous dry soil from a point water source, and the size of the wet zone depends on the volume of the supplied water (Li 2018; Li et al. 2018a). Beside the cohesive force, the negative pressure generated by the plant water uptake can also consolidate the zone of water retention surrounding the rhizosphere. The formed wet zone may be smaller than what it would be without plant due to root water uptake, and the water volume of the reduced region is considered the amount of water absorbed by the plant (Li et al. 2021). In other words, the wet zone changes dynamically because of the influence of the pressure fluctuation caused by irrigation and root water uptake that change the amount of water retained in the wet zone (Li et al. 2021).

When the wet zone is deformed by root water uptake and irrigation, the wetting front repeatedly moves backward and forward from its initial point. This can be reflected in the vibrational signals of soil moisture sensors. Usui et al. (2017) reported this phenomenon in a heterogeneous soil based on high-resolution observation of soil moisture (Fig.1). In Fig.1, the moisture fluctuation caused by root water uptake was observed at the boundary area between irrigated and un-irrigated soil after each irrigation event (Fig.1 (b)). This indicates that the point of wetting front can be estimated based on an analysis of the oscillation shown in the soil moisture sensors. This study focuses on the mechanism of the fluctuation phenomenon for precise water management.

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In this case, the fluctuation is very similar to a simple harmonic motion. The wetting front moved forward and backward like a spring being pushed and pulled (Fig.2). We used this model to examine the driving force for the push and pull motion of the wetting front. As shown in Fig.2, a water globe (spherical wet zone) is formed by the balancing tension force (plant uptake and water cohesion force) and suction force (soil meniscus and gravity force) under subsurface irrigation (Fig.2 (a) (b)). These balancing forces are similar to the forces operating on a mechanical spring. The shape of the water globe changes according to the changes of the driving forces. The wetting front can be considered a set of oscillators that are mechanically pulled/pushed by the driving forces (Fig.1 (c) (d)). Water supply is determined by the root water uptake that pulls the wetting front. Therefore, the spatial and temporal variation of roots modified by hydrotropism is an important factor in this model.

Plants can adapt to and regulate water uptake capacity by changing the root system architecture according to changes in their local environment (Bontpart et al. 2020; Fromm 2019; Lind et al. 2020; Scharwies and Dinneny 2019; Schmidt and Gaudin 2017; Shibusawa 1994). Studies of the physiological characteristics of the root system can be dated back to the 19th century Darwin's study "The power of movements in plants," which stated that the root tips of plants can sense the surrounding soil moisture and modify the direction of root elongation (Baluška et al. 2009). Root hydrotropism, which allows roots to exploit and intercept localized water resources in soil, may facilitate the utilization of limited water resources (Cassab et al. 2013; Cole and Mahall 2006; Dietrich 2018; Guevara and Giordano 2015; Iwata et al. 2013; Scharwies and Dinneny 2019). In the past decades, two systems have often been used to observe this phenomenon (Dietrich 2018; Eapen et al. 2005; Li et al. 2020a; Li et al. 2020b; Takahashi et al. 2002; Takahashi and Scott 1993). In one system, air is placed in an enclosed environment with a concentrated salt solution, and seedlings are mounted on a support, often foam or agar blocks, with the very root tip suspended in air. A water potential gradient can be produced in the root tip between the wet support and the surrounding air (Takahashi et al. 2002; Takahashi and Scott 1993). Another is the agar-sorbitol system, which places root tips near the border between two growth media with a water potential gradient produced by adding sorbitol to one of the media (Eapen et al. 2005; Takahashi et al. 2002). In both cases, root bending towards higher water potential is considered a hydrotropic phenotype of the test seedling. These systems have been used to identify genes involved in hydrotropism that characterize cellular and molecular events of the response (Dietrich et al. 2017; Dietrich 2018; Eapen et al. 2005; Mizuno et al. 2002; Takahashi et al. 2009). However, a major issue with these studies is that the ways plants regulate hydrotropism in the laboratory may be different from how they operate in the field condition (Cassab et al. 2013; Cole and Mahall 2006; Guevara and Giordano 2015; Li et al. 2020a).

To test whether this response happens in natural soil, a few experimental systems have been established. Cole and Mahall (2006) tested hydrotropic responses of two coastal dune shrubs under soil conditions. They produced a water potential gradient in soil by injecting water during the seedling growth to create a moisture rich patch laterally next to the growing pot, and roots growing into the patch were considered a hydrotropic response. In the study, they found no compelling evidence for hydrotropic root behavior of the test seedlings. Iwata et al. (2013) developed an experimental system to measure hydrotropic response in soil and investigate its role in root system development and crop biomass production. They grew *Arabidopsis* seedlings in rectangular plates covered with soil. A water potential gradient was produced through natural drought by placing a wetter plastic foam on one side of the soil that was half-covered with a lid. Root architecture was scanned by a scanner to study its relationship with moisture distribution. They found that hydrotropism plays an important role in root system development and crop growth. Li et al. (2020a) developed a sand system to study hydrotropism of *Arabidopsis* and tomato plants. They created water potential gradients in both oblique and vertical directions in soils and found that gravity helped roots to search for vertically oriented water but hindered the hydrotropic response in the oblique orientation. These systems are efficient to study hydrotropism of primary roots in the early growing stages. But how lateral roots (or fine roots), which form the main root system (Comas et al. 2013; Guevara and Giordano 2015; Pierret et al. 2005), respond to water potential gradients has been little studied (Dietrich 2018).

Last, a recent study tested the synergic effect of root biomass and hydrotropism on grain yield (Eapen et al. 2017). The researchers identified hydrotropic phenotypes of maize hybrids using the conventional air system and then performed field trials using hybrids with robust and weak hydrotropic responses. They found a positive interaction between root biomass and hydrotropism in enhancing grain yield (Eapen et al. 2017). Although the study showed that roots have a positive relationship with water distribution in soil, the root hydrotropic behavior in response to the dynamics of wet zone under subsurface irrigation has not been studied.

Due to the opaque nature of soil-grown roots and the highly varied soil water in time and space, a major difficulty in studying root hydrotropism in natural soil is observing and analyzing root growth in response to the dynamics of soil moisture distribution. Modern high-throughput phenotypic technology based on computer vision and machine learning enabled high-resolution measurement of root traits. But this technology requires extracting roots from soil to obtain the high-resolution root images (Falk et al. 2020; Mooney et al. 2012). X-ray Computed Tomography (CT) has been widely used to visualize roots in situ. This technology uses a non-destructive technique to visualize the interior of objects in 2-D and 3-D based on the attenuation of an electromagnetic wave (Mooney et al. 2012). Since the attenuation density of root and soil matrices are similar and highly dependent on soil water content, efforts to visualize root system architecture in soil have focused on the segmentation of roots from the soil pore area (Gao et al. 2019; Mooney et al. 2012; Pfeifer et al. 2015; Teramoto et al. 2020). But so far this technology has limitations in the detection of fine roots and has low contrast in heterogeneous soil and time-consuming user interaction (Gao et al. 2019).

To test the hydrotropism theory, rigorous experimental design concerning the observation and control of soil water dynamics is important. A major emphasis should be on forming a steep wetting front around the root system, while water supply inside the wet zone should sustain the crop growth. To implement such a study, high-resolution measurement of soil water dynamics around the rooting zone is prerequisite. Previous research has used high-resolution, nondestructive imaging technologies such as x-ray radiation, magnetic resonance techniques, and electrical resistance (Cassiani et al. 2016; Consoli et al. 2017; Segal et al. 2008; Shan et al. 2016; Werban et al. 2008). However, these techniques require tedious calibration of soil parameters to obtain spatial soil moisture distribution (Zhao et al. 2019), and the difficulty in accessing such devices also limits their use (Mooney et al. 2012). Moreover, most studies of the interaction between soil and root water uptake use single-point soil moisture measurement based on neutron probes or tension meters, which lacks accuracy and representativeness due to the spatially and temporally variant nature of soil-root system (Cassiani et al. 2015; Xu et al. 2018; Zhou et al. 2019). As a result, high-resolution measurement of spatiotemporal soil water dynamics has not been achieved.

This paper suggests using a high-resolution soil moisture sensor matrix to measure the micro soil water dynamics in the crop root zone. The system uses minimally sized soil moisture sensors placed in a matrix inside and outside the root zone to obtain precise, real-time signals of the temporal and spatial moisture dynamics around the growing roots. Prior to this study, the authors have used this method to confirm that a wet zone exists in water-saving cultivation of tomato plants and quantitative analysis of crop-water relation can be performed (Li et al. 2018a; Li et al. 2021). The objective of this paper is to observe and analyze hydrotropic response in the wet zone to clarify the dynamics of soil water content caused by water absorption of the growing plant. The results showed that hydrotropism restricted root growth to the inside of the wet zone, which induced distinct oscillation at the boundary area. The results demonstrate a new method for observing and analyzing hydrotropism and plant water absorption activity in subsurface irrigation.

Materials And Methods

Experimental system description

The experimental system has been described in our previous studies (Li et al. 2018a; Li et al. 2021). This study focused on producing a localized zone of water retention surrounding the growing roots that can sustain a small growth of the plant. We used high-resolution soil moisture sensors to observe micro soil water dynamics near the rooting zone. The objective of using this method is to create a stable and steep water potential gradient around the growing roots. The experimental system consisted of cultivars (two tomato samples, ANEMO, Japanese variety), environmental control components (Fig.3 parts (5)~(8)), and rooting zone moisture measurement sensors (Fig.3 part (1)). The tomatoes were grown in cylindrical pots that are 25 cm in diameter and height (Pot 1 and Pot 2 in Fig.3). An industrially regulated soil, burnt red clay, was used, which had a homogeneous composition and granularity with no organic fiber elements. The soil was dried in oven at 110°C for 24 h and then passed through a 1 mm sieve. Soil was placed into pots with a slight compaction. The packed dry bulk density was 0.75 g/cm^3. Sample tomatoes were transplanted into the pots at 30 days after sowing. Prior to transplantation, roots were carefully cleaned of the original sowing soil.

Water source was made by a round fibrous cloth (A-1, Toyobo, Tokyo, Japan), which was equipped at the tip of a plastic pipette to directly supply water into the rooting zone (Fig.3 part (3)). Infiltration of water through the fibrous cloth can produce uniform water globes by capillary water flow (Li et al. 2018a; Li et al. 2021). The size of the water globes depends on the amount of water supply and crop water absorption. The water supply was set at 10 ml per event, 4-7 events a day. A capacitance-type soil moisture sensor matrix (EC-5, Meter) was placed at the water source, 3 cm, 6 cm, 12.5 cm horizontally and 3 cm, 6 cm, 17 cm vertically from the water source (Fig. 3 part (1)). The data was automatically recorded by a data logger (EM5b, Meter) at a sampling interval of 5 min. The sensor values were calibrated against the experimental soil. Irrigation timing was manually determined to implement water-saving cultivation with minimal water for plant growth, which was based on the observation of the crop growth and soil moisture condition. Nutrients were supplied by adding liquid fertilizer of 5:5:5 (Hyponex, Osaka, Japan) to the irrigation water at a ratio of 1:500.

The experimental system was placed in a climate-controlled growth chamber (KCLP-1500LED-NCS, NK-system, Japan) 151.2 cm in height, 120 cm in width, and 80 cm in length. In the experiment, two environmental conditions were manually controlled each day. The chamber was illuminated with fluorescent lamps under condition 1 (8:00~22:00), and the lamps were turned off under condition 2 (22:00~8:00). Air temperature and maximal humidity were set at 30℃ and 60% under condition 1 and 22℃ and 60% under condition 2. The microclimate inside the growth chamber was measured using an air temperature-humidity sensor (HMP-155, Vaisala, Vantaa, Helsinki, Finland), a solar radiation sensor (LI-190, Li-Cor, Lincoln, NE, USA), and a CO_2 sensor (GMT-222, Vaisala). The experiment was conducted from September 28th, 2016 to January 23rd, 2017, which covered the period from crop transplantation to fruit bearing. The mean values of the measured environmental parameters through the experiment are shown in Table 1.

Table 1 Mean value of the experimental parameters inside the growth chamber

	Time	Temperature (℃)	Humidity (%)	Quantum （umol/m^2/s）	CO_2 (ppm)
Control condition 1 (Light on)	8:00～22:00	30	36	191	412
Control condition 2 (Light off)	22:00～8:00	22	60	0.5	416

Data processing of soil water dynamics

To analyze the dynamic changes of the wet zone, we extracted the frequency content in the soil moisture data using signal processing techniques. The moisture fluctuations at the water source are the result of infiltration, redistribution, and water absorption activities. In this study, water supply was intended to maintain a water globe (wet zone) within a small area around the crop roots. The dynamics in the water globe depended on water absorption activities. We used signal processing techniques to determine how often these activities happen. We can assume that the plant has higher frequencies in water absorption due to its biological rhythm, which interrupts the soil water dynamics (Dodd et al. 2014). Therefore, we attempted to remove the fundamental frequencies of the infiltration and redistribution corresponding to the irrigation events by applying a high-pass filter. This can also remove the DC component in the soil moisture signal. In this study, the Butterworth high-pass filter was applied to the soil moisture data. The sampling frequency of the experimental data was 0.00334 Hz. The passband cutoff frequency (Wp), stopband starting frequency (Ws), ripples in passband (Rp), and minimum actuation in stopband (Rs) of the Butterworth filter were 0.00018 Hz, 0.00015 Hz, 3 db, and 20 db, respectively. Next, to identify the natural frequencies of the AC components that were related to the water absorption activities, we applied FFT to the filtered moisture signals that included 1024 data points. We used the MATLAB R2018a^{TM} software for the filtering and FFT processing.

Root observation and analysis

To observe whether hydrotropic growth modification happen in soil, we first observed root distribution at the wet/dry soil border by carefully removing a small amount of dry soil next to the border. The moist soil particles adhere to each other and form a harder part that can be distinguished from the dry soil, which is softer. Therefore, the border can be clearly recognized and the root distribution at the border can be visually observed. Reference soil moisture was confirmed using the oven dry method by collecting three soil samples at wet, dry, and boundary areas. A photo of the observation area at the wet/dry soil border was captured. After each observation, prepared dry soil was used to recover the soil. This visual observation was conducted for Pot 1 at different growth stages as determined by numbers of branches, flowering, and fruit bearing. Pot 2 severed as a static reference for which observation was conducted only once at the end of the experiment. We also observed the growth height and daily water supply volume of both pots for growth analysis. These were non-penetrative observations.

To analyze whether hydrotropism plays a dominant role on roots' growth when a wet zone is produced around them, we quantified root distribution outside and inside the wet zone. The observation method used during and after the growing period is shown in Fig.4. When cultivation ended, we stopped water supply for 5 days to balance the water flow in the soil-root system. The soil moisture at the water source decreased to the level of the boundary area. This did not destroy the shape of the wet zone because the moisture at the boundary area changed very little compared to that at the water source. Then we carefully dug out the wet zone from the cultivated soil to analyze the root distribution on the dry and moist sides. We cut the roots that grew out of the border (approximately more than 1 cm) using a scissor along the line of the border, and then recorded the numbers (Fig.4). We then measured the length of the cut part of roots that distributed outside the wet zone. For Pot 1, the wet zone was sliced using a razor blade at the shoot base to observe the root architecture from the cross-section of the wet zone. The roots both inside and outside the wet zone were carefully sieved and washed to separate them from the soil and then dried in the oven at 80°C for 24 h to measure the dry weight. In this study, we calculated the proportion of root dry weight outside the wet zone and the root weight density inside and outside the wet zone. The root weight density inside the wet zone was calculated using the dry weight inside divided by the volume of the wet zone (which was assumed to have a spherical shape). The root weight density outside was determined using the dry weight outside divided by the volume of the dry layer where the roots exist.

Results

Soil moisture responses

The soil moisture analysis was based on the same method used in previous works (Li et al. 2018a; Li et al. 2021). Figure 5 shows the response of soil moisture at each location in a time series from 88 days after transplanting. The values represent soil moisture at positions close to the root zone and those away from the root zone, which respond to water supply through capillary flow from the point water source. The blue curve at the top is the air temperature inside the growth chamber. The next red line is the volumetric water content (VWC) at the position of the water source where the plant was grown. The VWC curve shows two periodical responses. One is the longer period that synchronized with the growth chamber's daily setting; the other was caused by water supply events during the lighting period each day. Each peak represents a single water supply event. VWC values at the water source varied around 15% to 20% during the growing period (Li et al., 2021). The waveform of soil moisture at this point was a result of water infiltration, redistribution, and plant absorption activities. Therefore, it is possible to use FFT to show the natural frequencies of these components. The curves H1, H2, V1, and V2 are, respectively, soil moisture at positions 3 cm and 6 cm horizontally from the water source (H1, H2) and vertically (V1, V2). These values indicated moisture at the boundary area between wet and dry soil. The curves H3 and V3 show measurements of, respectively, dry soil 12 cm horizontally from the water source and 17 cm vertically from the water source. These values confirmed that the water supply did not cause excessive water flow into the dry soil. As a result, moisture distribution was in the rooting zone, in the cm order resolution.

Figure 6 (a) shows the filtered waveform of soil water dynamics in time domain at the water source by the high-pass filter. The filter removed fundamental fluctuations caused by infiltration and redistribution responses corresponding to irrigation events that included 16 harmonics of the fundamental frequency. It should be noted that short-period fluctuations can be seen within each lighting period. The higher frequencies in the waveform contain information of plant physiological activities. This indicates that the temporal fluctuation of the plant photosynthetic activities hidden in the moisture signal can be extracted using signal processing.

Figure 6 (b) shows the amplitude frequency after FFT of the filtered data. The data shows intrinsic responses of a cyclic system with harmonic waves that are integer multiples of the fundamental frequency. The fluctuation attenuated after 40 cycles/24h. The amplitude indicates the contribution of the harmonic to the moisture fluctuation, which depended on the irrigation events and root water uptake. Three peaks near 20 cycles/24h can be identified. The lower peaks on both sides (18 and 20 cycles/24h) are the harmonics caused by irrigation events during the lighting period (Supplementary Fig.1). The highest peak at 19 cycles/24h (76 min in period) is considered to be caused by root water uptake. This reflects the periodic activities of plant photosynthesis.

Figure 7 shows the frequency spectrum after FFT of the moisture data at other sensor locations without filtering. The H1, H2, V1 and V2 are locations near the boundary between wet/dry soil, and H3 and V3 are locations in the dry soil. The peak at 1 cycle/24h is the fundamental frequency accompanied by irrigation events. Even in the dry soil, the moisture fluctuation existed as shown in Fig.7. Generally, the amplitudes of the fundamental frequency at these positions were much lower than that at the water source and decreased with increased distance from the water source. This indicates the attenuation of moisture fluctuation and reduced effect of irrigation. Distinct peaks were identified at V2 at 10 cycles/24h. This is the harmonic of the irrigation events during the lighting period. The water uptake peak at 19 cycles/24h mentioned above can also be seen. Because a higher amplitude means a larger contribution to the moisture fluctuation, this indicates that the tension force by root water uptake in the vertical direction affected the fluctuation and plant water absorption significantly affected moisture fluctuation at the boundary area. Taken together, the results support a new method for observing and analyzing plant photosynthetic activities.

Metric potential gradient

The soil moisture values were transferred to water potential through a water retention curve of the experimental soil (Fig.8). The water potential value at the water source varied from -0.22 MPa (15%) to -0.1 MPa (20%). In this experiment, accumulated soil water content in the wet zone fluctuated around -0.22 MPa (pF 3.4), which was the wilting point and can be treated as a threshold for water supply. The plant recovered from wilting by absorbing water after each water supply event when water potential peaked around –0.1 MPa. The plant cannot absorb water from the dry soil where the water potential is much lower than the wilting point. Therefore, the wet soil area for plant growth and the dry soil area below the wilting point were clearly separated in the same soil. As shown in Fig.8, the results indicate that a stable soil water potential gradient close to 0.02 MPa/mm was produced near the boundary area.

Root distribution at the wet/dry soil boundary during crop growth

To observe root growth in response to soil water dynamics in the wet zone, we disturbed Pot 1 several times during the experiment and examined root distribution at the wet/dry boundary (Fig. 9). In this study, Pot 2 severed as a static reference for which observation was conducted only once at the end of the experiment. Changes in growing stages of shooting, flowering, and fruit maturing of both Pot 1 and Pot 2 were observed, which represent changes in plant physiological status that may affect the structure of the root system. As shown in Fig. 9, we observed many root tips distributed at the boundary, but not obviously penetrating into the dry soil.

The gravimetric water content on the wet and dry sides and at the boundary area was determined using the conventional oven dry method. The moisture level of the dry soil was maintained around 10% during the growing period. The fluctuation of soil moisture in the wet soil may be caused by water supply and plant root water uptake. An average of 12% moisture difference can be seen between the dry and wet soil.

The relationship between plant height and water supply for Pot 1 is shown in Fig.10. During the experiment, the plant increased its height in response to the volume of water supply in the wet zone. A linear relationship between the plant height and the cumulative water supply can be observed. The plant absorbed water from the wet zone where the roots mostly distributed. Because no water loss from the root zone was observed, it can be assumed that almost all water supplied to the wet zone were absorbed by the plant.

Observation of root distribution at the end of the experiment

The hydrotropism theory assumes that all roots will grow towards the point water source. In addition, since the wet zone was controlled by the water-saving cultivation method, it can be assumed that the root zone will be inside the wet zone. To confirm these two assumptions, the wet zone was taken out from the cultivated soil at the end of the experiment for observation and analysis of root distribution. Figure 11 shows the roots distribution in the wet zone. Some roots grew out of the wet/dry soil border into the dry soil for several centimeters (Supplementary Fig.2). Also, we observed several roots left at the bottom when we removed the wet zone. This may be caused by the gravitropic effect being stronger than the hydrotropic response.

We then cut the roots that grew out of the border along the edge of the border (approximately more than 1 cm) and recorded the numbers of the roots. We also measured root length in the dry soil and obtained the dry weight of roots inside and outside the wet soil. Table 2 shows these and other results including root dry biomass and root weight density inside and outside the wet zone, root number and root length outside the wet zone, the total dry mater, yield, and WUE (Table 2). The proportion of root dry weight outside the wet soil were 2.63% and 5.61%, the total root numbers outside the wet zone were 82 and 138, and the WUE were 6.96 g/L and 5.30 g/L for Pot 1 and Pot 2, respectively. The mean root length outside the wet zone were 2.1 cm for both plants. As these results showed, root distribution characteristics at the dry/wet soil border and their relationships with yield and WUE can be precisely measured and analyzed, and most roots distributed inside the wet zone (Fig.11, Supplementary Fig.3).

Table 2 Root distribution inside and outside the wet zone, plant yield, and WUE.

	Pot 1	Pot 2
Root dry biomass inside (g)	1.48	1.01
Root dry biomass outside (g)	0.04	0.06
Total root dry biomass (g)	1.52	1.07
Proportion of root outside (%)	2.63	5.61
Root weight density inside (g/L)	3.72	1.93
Root weight density outside (g/L)	0.05	0.07
Ratio of density outside to inside (%)	1.34	3.63
Total root number outside	82	138
Total root length outside (cm)	172.2	290.4
Mean root length outside (cm)	2.1	2.1
Total dry mater (g)	6.12	4.71
Number of fruits	2	1
Yield (g)	36.06	32.14
WUE (g/L)	6.96	5.30

Root skeleton from the cross-section of the wet zone

The soil moisture dynamics show that the plant absorbed water mainly from the region close to the water source. To observe the root architecture inside the wet zone, we sliced the wet zone with a razor blade to observe the root skeleton from the cross-section as shown in Fig.11. The hole at the center of the soil shows where the water supply tube had been placed. It can be found that some of the roots orientated towards the inside of the wet zone, while outwards elongation of roots was also observed. The wet zone limited the root architecture to a spiral shape at the cross-section (Supplementary Fig.3). It appears that the roots grew downward and around obstacles (the water supply tube) and then bent back towards the inside of the wet zone (Li et al. 2018b). Although some roots overcame the effect of gravity and grew towards water, the hydrotropic response was not a universal response for all the roots observed in this study. This result also suggests that it is possible to control the root area by controlling the wet zone and thus establish new cultivation techniques for crop growth control and/or increased planting density.

Discussion

Moisture fluctuation in the wet zone

To observe and analyze hydrotropic root behavior in soil under water-saving condition, this study produced a controlled wet zone during plant growth from where the plants can absorb water. In the wet zone, moisture fluctuation mainly depended on infiltration from water source and root water uptake. After each water supply event, the moisture near the water source peaked and redistributed to the surrounding soil by water potential gradient (Jury and Horton 2004). This matrix potential gradient may result in a larger wet zone if the cumulative flux of water into the wet zone increases. In this study, the total size of the wet zone did not much change and the accumulated water content was maintained at a constant level in the wet zone. This was because the water consumed by root water uptake (output) balanced the inflow of water (input). In this study, the water supply was designed to meet the minimal need of plant growth with the focus on controlling the wet zone at a constant size. Therefore, the water supply into the soil-plant system mainly depended on soil water capacity and root water uptake. The water status in the wet zone was determined based on the change of soil moisture storage. The fluctuation of moisture in the wet zone indicates that root water uptake and water inflow from irrigation compensated water consumption by roots. We applied FFT to the high-resolution soil moisture data to show the fluctuation activities. In this study, the moisture fluctuations were the most sensitive at positions close to the water source, which was caused by irrigation events. The moisture fluctuations at other locations were much smaller, indicating smaller effect from the irrigation.

Although moisture reduction in the wet zone was mostly affected by root water uptake in this study, the diffusion of water from the water source to the surrounding soil was also detected by the moisture sensors because of their pinpoint measurement characteristic. Therefore, the reductions of moisture values shown by the sensors were also affected by redistribution of water. To analyze the moisture fluctuation of the wet zone caused by root water take, we applied a high-pass filter to remove the moisture fluctuation caused by water infiltration and redistribution corresponding to the irrigation events. Root water uptake depends on soil water status and potential transpiration. It decreases when soil moisture is limited and fluctuates due to the rhythmic activities of the plant (Dodd et al. 2014). The changes in root water uptake can induce moisture oscillation around the roots. The oscillation of photosynthetic activities has been demonstrated in previous studies, which is regulated by stomata and depends on environmental and soil water conditions (Dodd et al. 2014; Hirose et al. 1991). In this study, the exact frequencies of water absorption activity were identified.

Furthermore, the FFT results showed distinct peaks at the boundary area (Fig.7(V2)). This indicates that root water uptake caused the distinct moisture fluctuations. This phenomenon has been observed in previous studies based on high-resolution observation of soil water dynamics (Fig.1) (Usui et al., 2017). In terms of soil physics, the movement of the wetting front is driven by the matric potential gradient. The change of soil water with matric water potential is determined by soil water capacity (Jury and Horton 2004). We can assume that changes in water potential caused by root water uptake induced the moisture fluctuation at the boundary area. In this study, such fluctuations were identified based on the FFT analysis. This suggests a new method to analyze plant biological rhythms using frequency data of soil water dynamics.

Hydrotropic root behavior in the wet zone

To further investigate the driving force of the oscillation phenomenon at the boundary area caused by root water uptake, we observed the hydrotropic root behavior. In this study, the water potential gradient produced by the water supply was about 0.02 MPa/mm at the front of the irrigation water. This gradient is sufficient to induce hydrotropic response (Tsuda et al. 2003). According to hydrotropism, roots modify their growth direction towards higher moisture. In this study, roots stopped growth in the dry soil and most root biomass was distributed inside the wet zone (Table 2). On the other hand, some roots grew out of the wet/dry soil border for several centimeters (2 cm in average), which suggests a weaker hydrotropic response of these roots. Gravitropism, which induces roots to grow to deeper soil, also plays an important role in root formation as described in previous studies (Dietrich 2018; Fromm 2019; Li et al. 2020a). Accordingly, in this study, roots growing in dry soil at the bottom of the wet zone were observed. In plant physiology, elongation of roots is caused by turgor pressure in the growing tissue, and growing tissues show lower turgor when grown in a medium with low water potential. Therefore, the limited supply of water in the dry soil and turgor pressure in the root-tip cells may be insufficient to drive cell elongation (Fromm 2019; Scharwies and Dinneny 2019), which explains why the roots stopped growing when they penetrated into the dry soil.

To analyze the restriction of the wet zone on proportion of hydrotropic root growth, we quantified the roots inside and outside the wet zone. In this study, we cut the roots along the edge of the wet/dry border of the wet zone to measure dry biomass distribution outside the wet zone. Because this part of the roots did not grow towards higher water content, it can be considered that these roots grew against the hydrotropic response. In this study, the root dry biomass in the dry soil were 2.63% and 5.61%, respectively, for the two plant samples. According to hydrotropism, each root serves as a water sensor that can perceive water potential gradients and modify their growth direction towards higher moisture (Eapen et al. 2005). It can be assumed that plants with fewer roots distributed in the dry soil can perceive wet zones more precisely, which is preferable in subsurface irrigation to make more efficient use of the irrigation water in the wet zone (Schmidt and Gaudin 2017; Shukri et al. 2013; Shukri et al. 2014). Our study provides a method to quantify root distribution that is against hydrotropic responses. Our data are based on limited samples. To provide more robust evidence on the effect of hydrotropism, more observation samples and stochastic analyses or non-deterministic principles are needed (Shibusawa 1994).

In our study, the plant absorbed water only from the wet zone produced by the subsurface irrigation method. According to the soil moisture dynamics measured by the high-resolution moisture sensor matrix, the plant absorbed water mainly from the region close to the water source. We observed that the root skeleton showed a spiral shape with some roots bent back towards the water source for water acquisition (Supplementary Fig.3). It can be considered that the wet zone restricted the roots growth by hydrotropic behavior. This result supports that the architecture of the root system adapts to the position of the water sources, which has been demonstrated in previous study (Lind et al. 2020). On the other hand, since some roots grew out of the wet zone, it can be assumed that the hydrotropic response is not uniform among roots within an individual crop. To evaluate the plant hydrotropic ability, more samples are needed to perform stochastic analyses (Shibusawa 1994). Hydrotropism has been confirmed in laboratory germination experiments (Dietrich 2018). In this study, it was confirmed in actual crop cultivation. Our observation confirmed that the root system was in a limited zone caused by hydrotropism.

Mechanical model of moisture vibration in wet zone

When a wet zone is formed in the soil, a threshold of penetration pressure exists at the border between wet and dry soil. Water will not flow into the surrounding dry soil when the penetration pressure is lower than the threshold (Jury and Horton 2004). As water supply continues, the wet zone can be enlarged due to the meniscus phenomenon. If the volume of available water is controlled through irrigation to balance the moisture flow between the plant and the surrounding soil, the penetration pressure may not exceed the threshold and the wet zone can be maintained at a constant volume. Increasing water supply may increase the soil suction force, resulting in the expansion of the wet front. But since the root zone can be modified by hydrotropism and the corresponding increase in water uptake, plant water uptake can be considered to dynamically equilibrate with the penetration pressure generated by capillary forces to stabilize the wet zone. In this case, the wetting front moves backward and forward from the initially observed point when the pressure head of water supply is adjusted. Because this phenomenon is similar to a simple harmonic motion, we used a mechanical pull-and-push spring model to describe the dynamics of the wetting front (Fig.2). In this model, the pressure head of water supply is controlled to maintain the water potential in the wet zone at a dynamic equilibrium under the vector sum of tension force (root water uptake and cohesion force) and suction force (soil meniscus and gravity force). The magnitude of the vector sum applied on the wetting front is proportional to the size of the wet zone. Because the root mass modified by hydrotropic behavior is a major factor that influences the tension force, water supply can be modified to maintain the balance for precise irrigation. Therefore, the system parameter is determined by the root mass that is accumulated by hydrotropic behavior during the crop growth. This mechanical model may function when the vector sum applied on the wetting front does not disturb the balance state, which simulates the elastic deformation of a spring.

Method for observing hydrotropism in water-saving cultivation

Because the water potential gradient in soil varies considerably, observing hydrotropism of the whole root system throughout plant reproductive stages is difficult. This study used a soil moisture sensor matrix method to measure the soil water dynamics in crop rooting zone. The characteristics of soil water content can be obtained inside and outside the wet zone. The use of in-situ measurement for soil moisture profiling along soil depth has been reported before, but the resolution used in previous studies is insufficient when studying plant physiological activities because bulky sensors used in multi-points measurement may disturb soil structure and result in measurement errors (Xu et al. 2018; Zhou et al. 2019). In this study, we increased the observation resolution to the centimeter order using small soil moisture sensors, and a sharp water potential gradient was maintained at the wet/dry boundary throughout the growing period. As a result, the response of plant physiological activities to soil water content can be precisely observed and analyzed.

The high-resolution measurement system developed in this study requires considerable time and labor for system installation and data collection, which restricts its use to obtain replicable data. Also, offline measurement using a data logger may risk inadequacy or missing data due to the possibility of disconnection of cables during data collection. Moreover, to perform more detailed analyses of roots' directional growth, non-destructive methods such as X-ray Computed Tomography (CT) will be necessary to capture continuous images of the roots' growth. Automated experimental cultivation systems and robotic manipulations coupled with multidimensional information processing techniques will be necessary for obtaining continuous and reproducible observation of hydrotropism in water-saving cultivation.

Conclusion

We conducted a feasibility study of a high-resolution soil moisture sensing prototype and gathered data to analyze hydrotropism and plant water absorption activity. We investigated hydrotropic root behavior when a wet zone around crop roots was produced using subsurface irrigation. The dynamics of soil water content in the wet zone was observed by the high-resolution soil moisture sensor matrix. To identify the frequency components of the fluctuation, we applied a high-pass filter and FFT to the acquired high-resolution soil water dynamics data. The results indicate that root water uptake caused the distinct oscillation at the boundary area, which suggests a new method for observing the rhythm of photosynthetic activities. We also observed root growth in response to the dynamics of soil water content in the wet zone. We quantified the proportion of root mass inside and outside the wet zone and observed the shape of the root system from the cross-section of the wet zone. The results show that hydrotropism restricted the root system within a limited zone. Furthermore, the results indicate root hydrotropic response is not uniform for all roots of an individual plant, which suggests stochastic approach to evaluate its performance. We assumed a mechanical, push-and-pull model of water dynamics at the wetting front and the root mass accumulated by hydrotropism is an important system parameter. This study provided a new concept for precise water management under subsurface irrigation utilizing the plant hydrotropic response to soil water dynamics. This concept was experimentally verified based on high-resolution observation of soil water dynamics. Future studies may explore an automated experimental system and robotic manipulations for continuous and reproducible observation of hydrotropism in water-saving cultivation.

Abbreviations

DC: Direct current; AC: Alternating current; FFT: Fast Fourier Transform; WUE: Water use efficiency; VWC: Volumetric water content.

Declarations

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Conflicts of interest/Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Author contributions

All authors contributed to the study concept and design. Material prepared, data collection and analysis were performed by [Qichen Li] and [Toshiaki Sugihara]. The project was supervised by [Sakae Shibusawa] and [Minzan Li]. The first draft of the manuscript was written by [Qichen Li], and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Figures

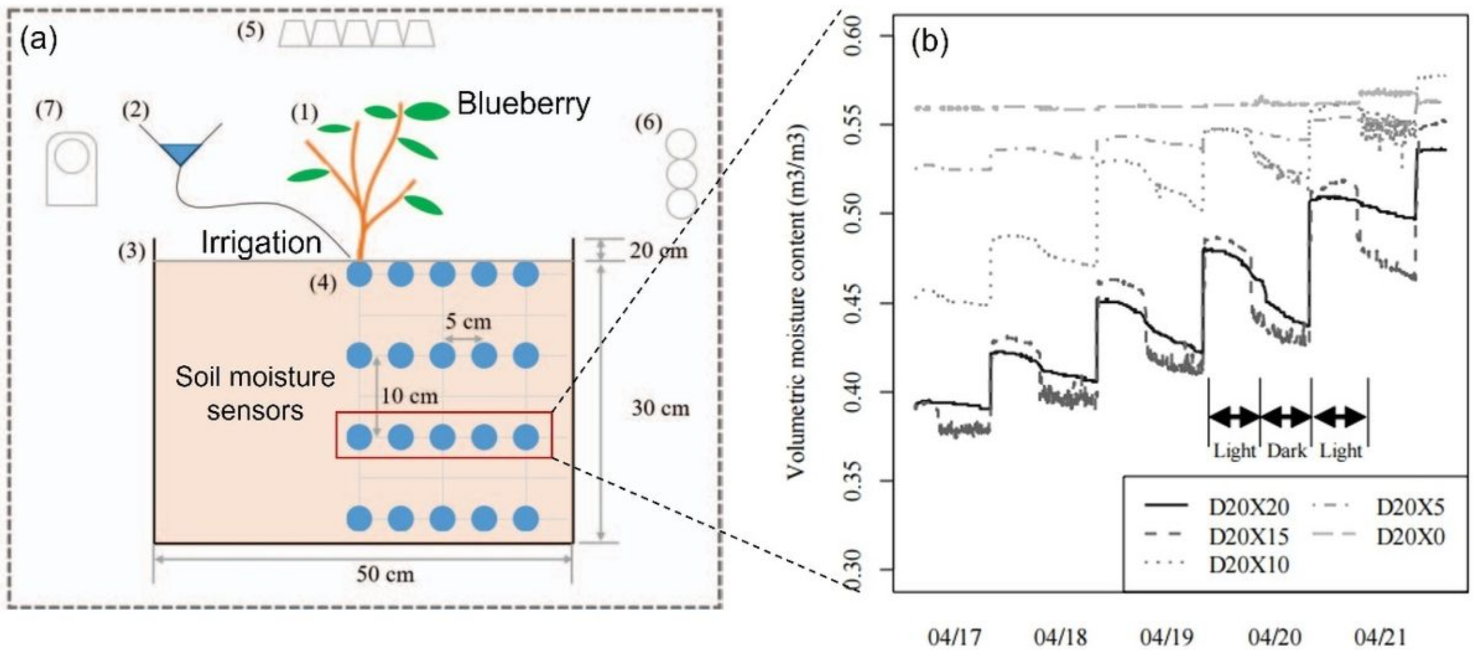

Figure 1

Oscillation of soil moisture at the boundary area observed using high-resolution soil moisture sensors. (a) The plant (blueberry) is cultivated in a climate-controlled growth chamber. (b) Moisture values at 20 cm depth. The sensor positions are denoted by depth and horizontal distance from the cultivar (e.g., D20X15 indicates 20 cm in depth and 15 cm in horizontal distance from the plant) (Usui et al. 2017).

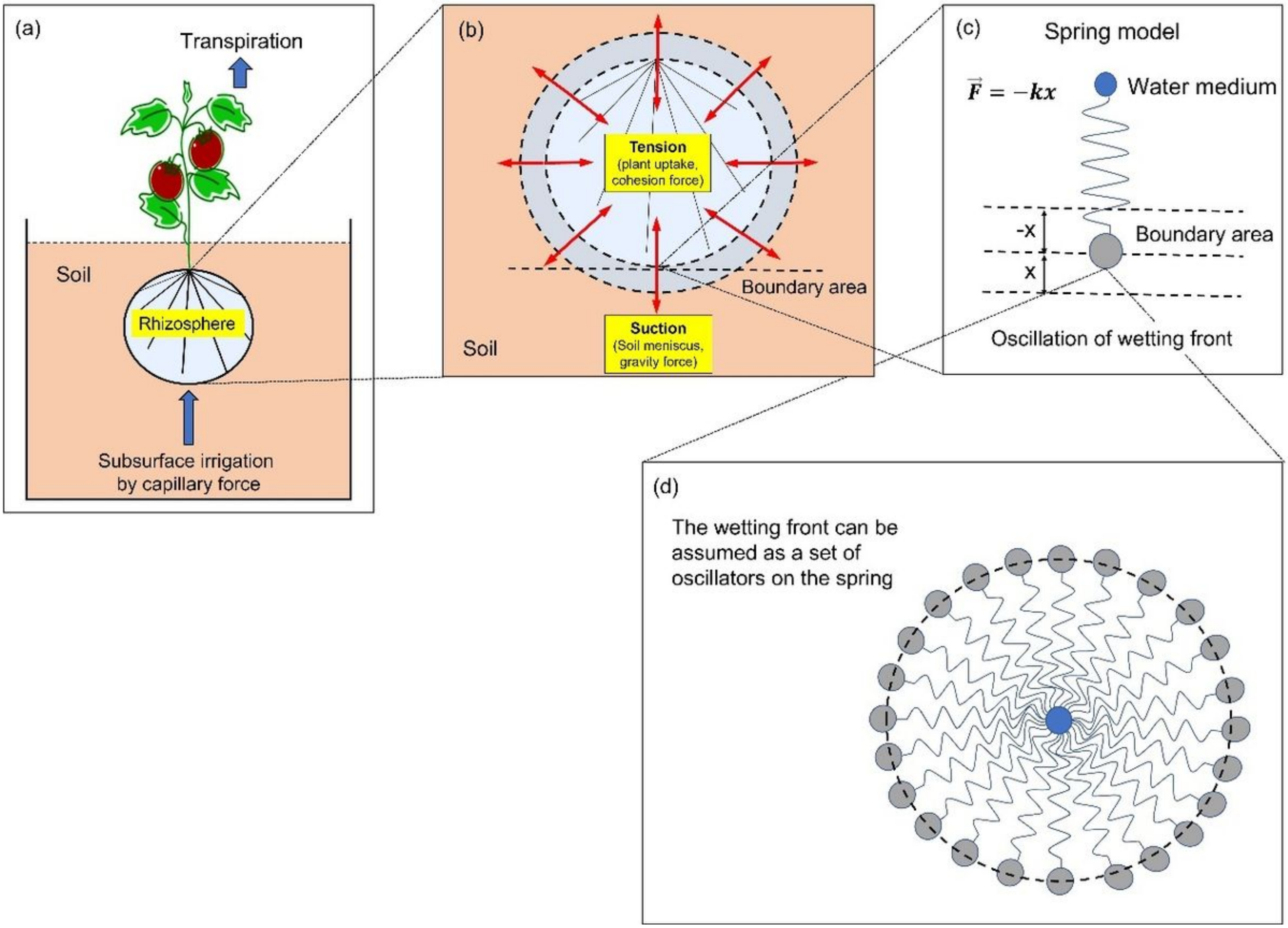

Figure 2

Schematics of the oscillation of the wetting front based on a mechanical model. (a) A wet zone is formed through subsurface irrigation with water supplied by capillary force. (b) Dynamics of the wetting front according to the vector sum of tension (plant uptake and cohesion force) and suction (soil meniscus and gravity force). (c) A spring model is assumed to describe the vibration of the point at the wetting front based on Hooke's law. F is the vector sum of tension and suction, k is the proportional coefficient determined by hydrotropic root behavior, and x is the displacement from the initially observed point. (d) The wetting front can be assumed as accumulation of oscillators on the spring.

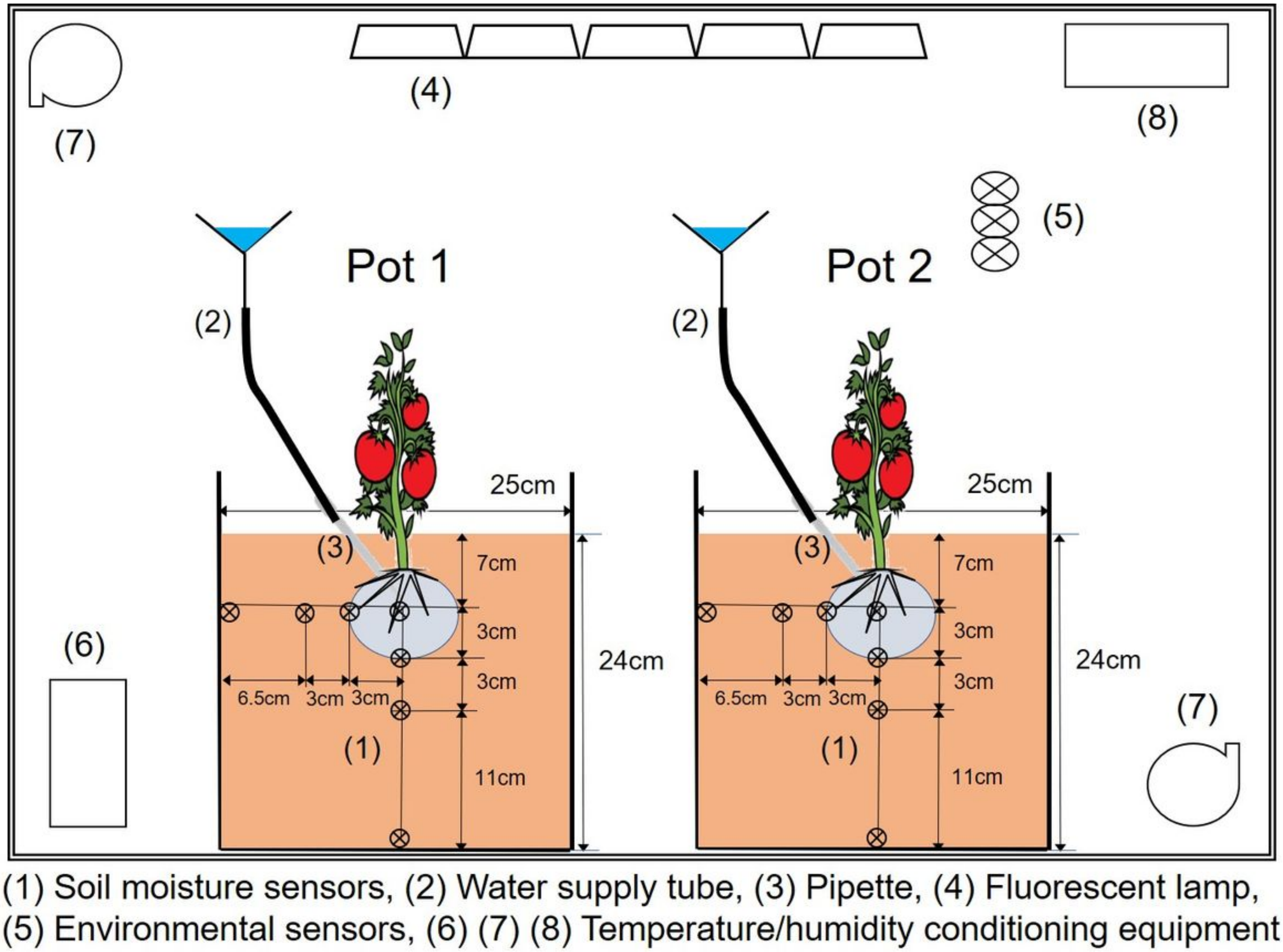

Figure 3

Experimental system

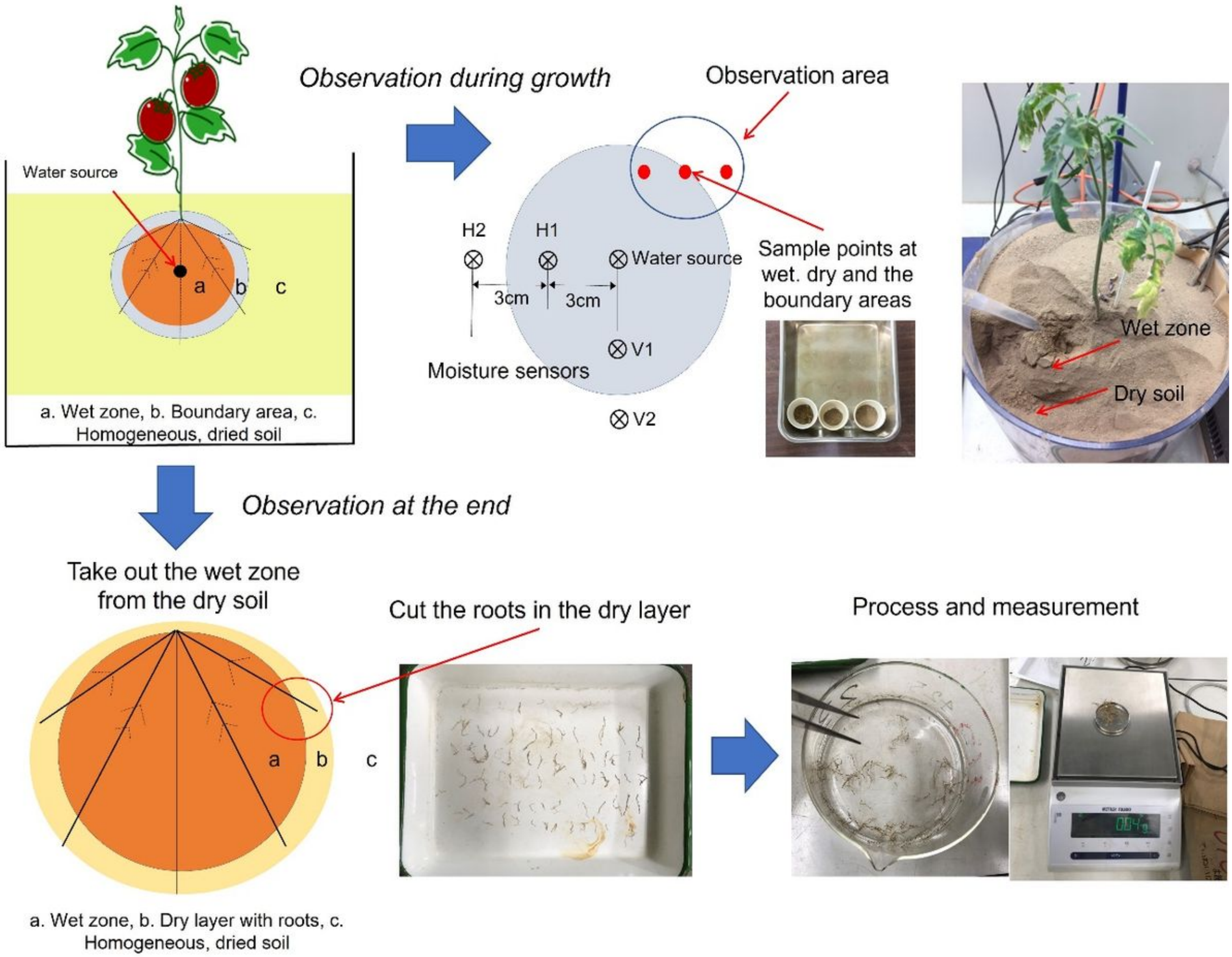

Figure 4

The process to observe and analyze hydrotropic root behavior during and after plant cultivation

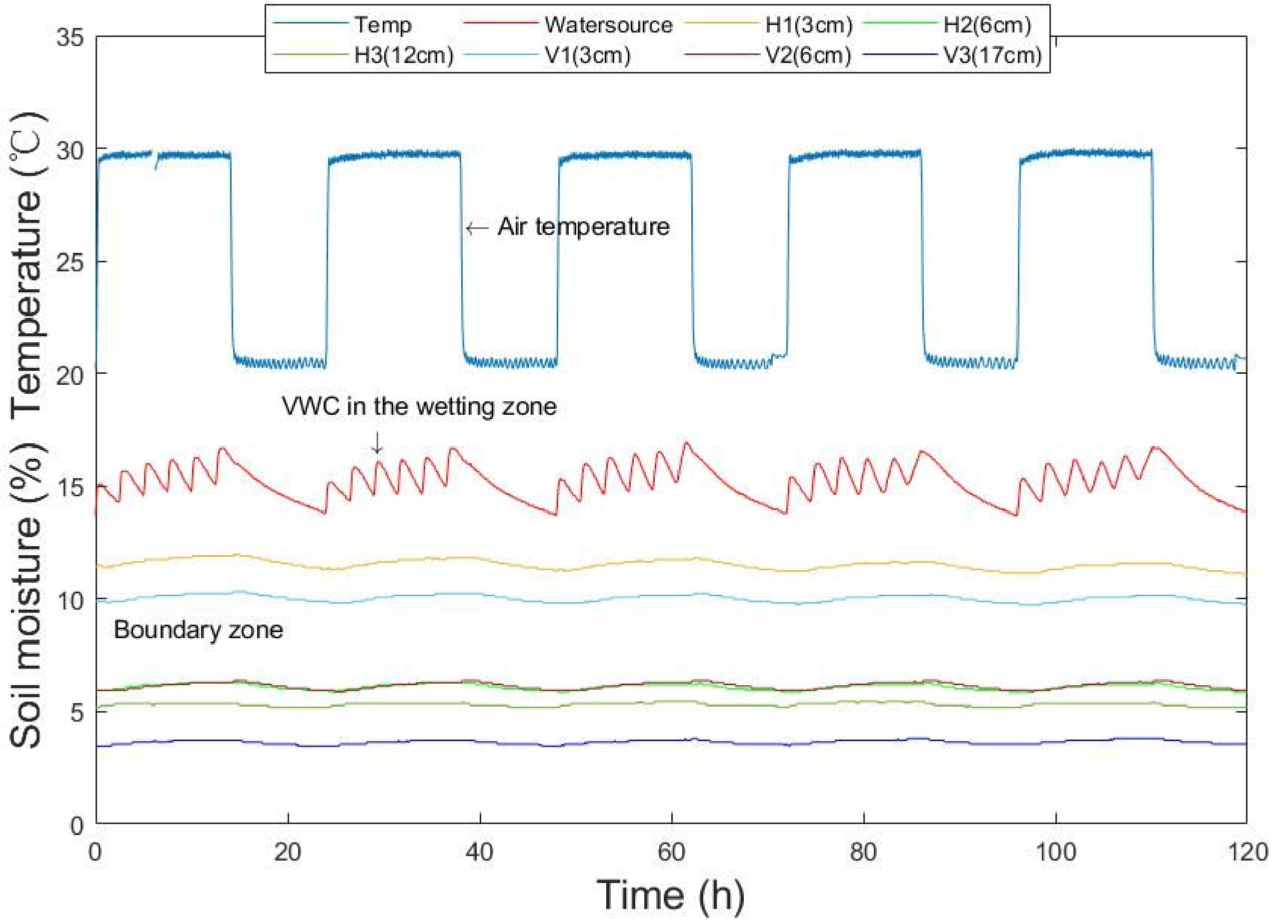

Figure 5

Soil moisture responses at each location in time series

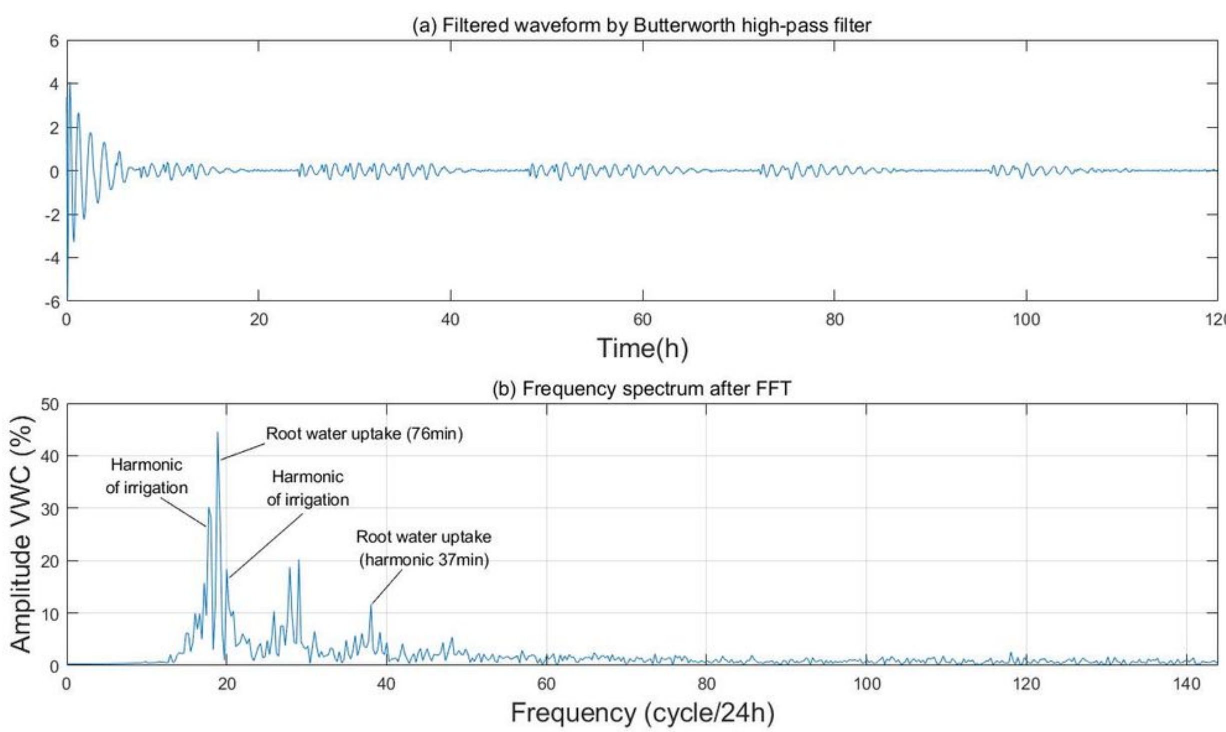

Figure 6

Frequency analysis of soil moisture dynamics at the water source. (a) Filtered waveform by the Butterworth high-pass filter. (b) Frequency spectrum after FFT of the filtered moisture data

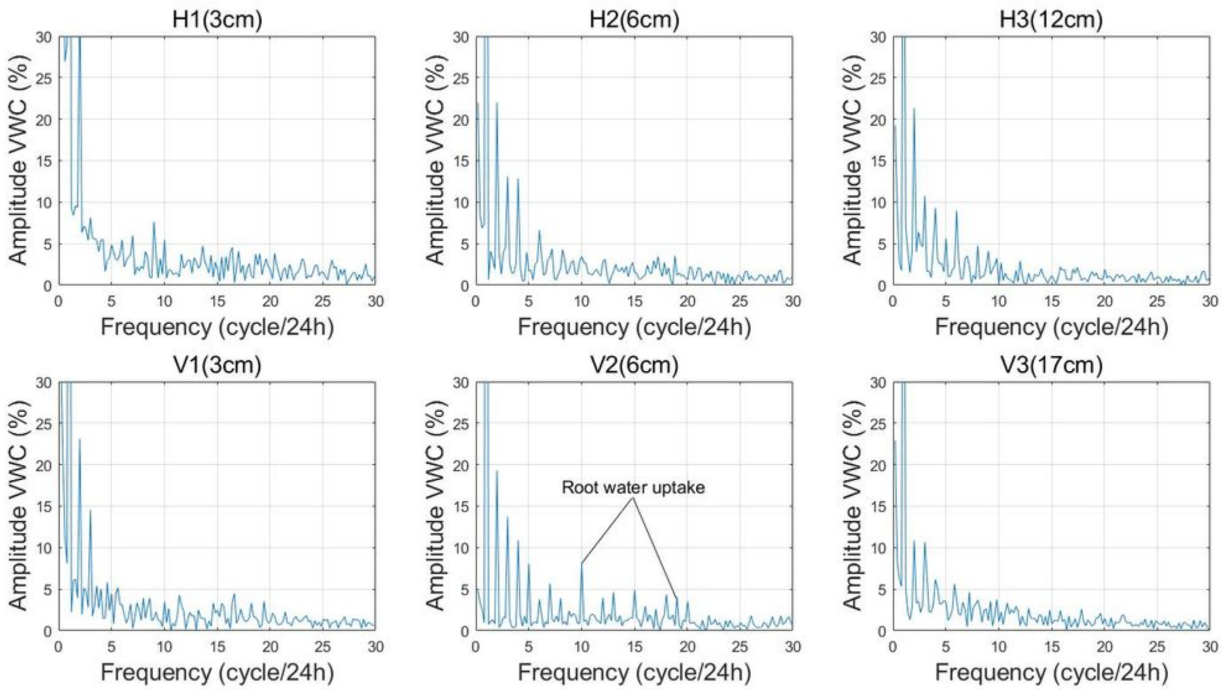

Figure 7

Frequency analysis of soil moisture dynamics at each sensor location

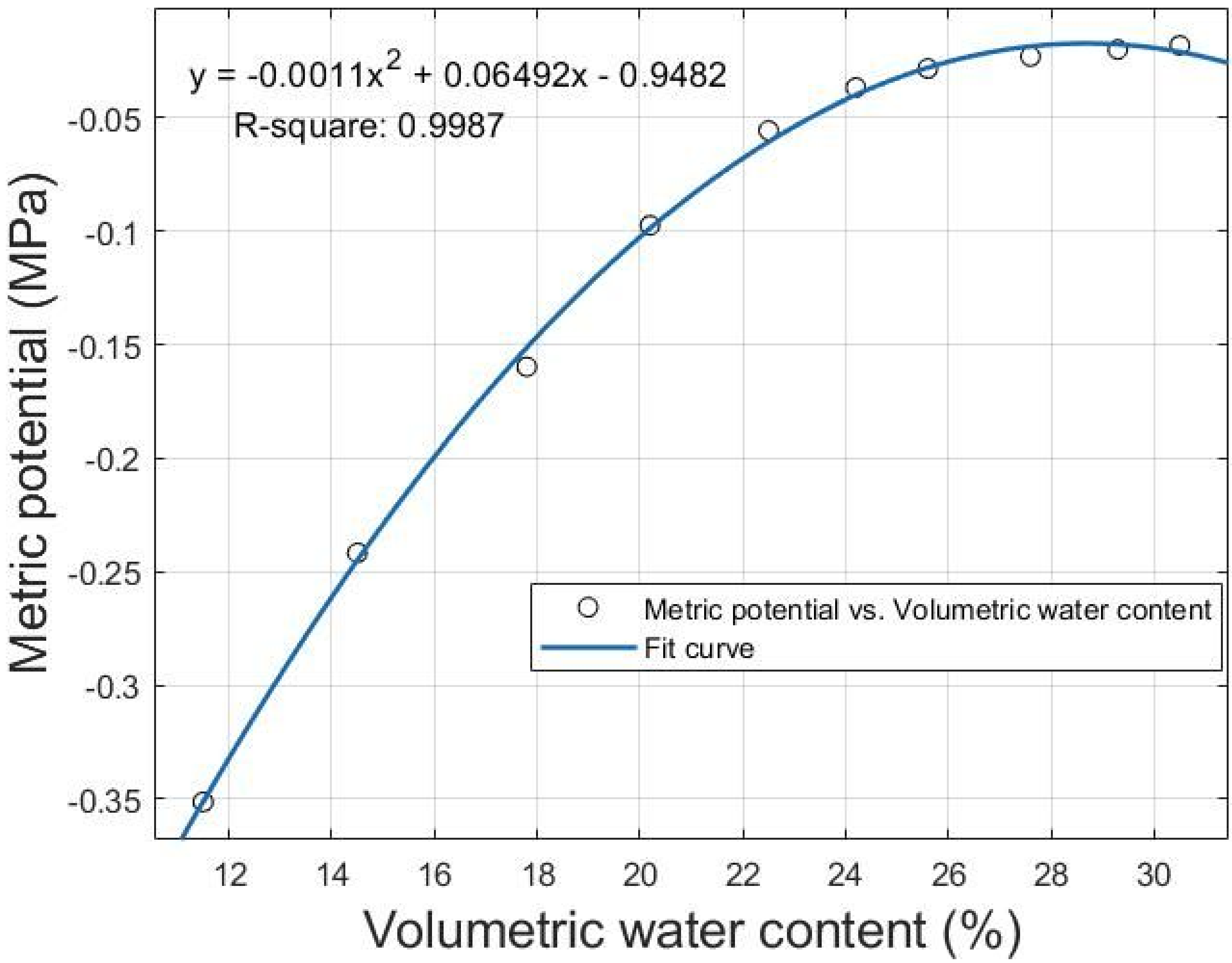

Figure 8

Relationship between VWC and water potential gradient of the experimental soil

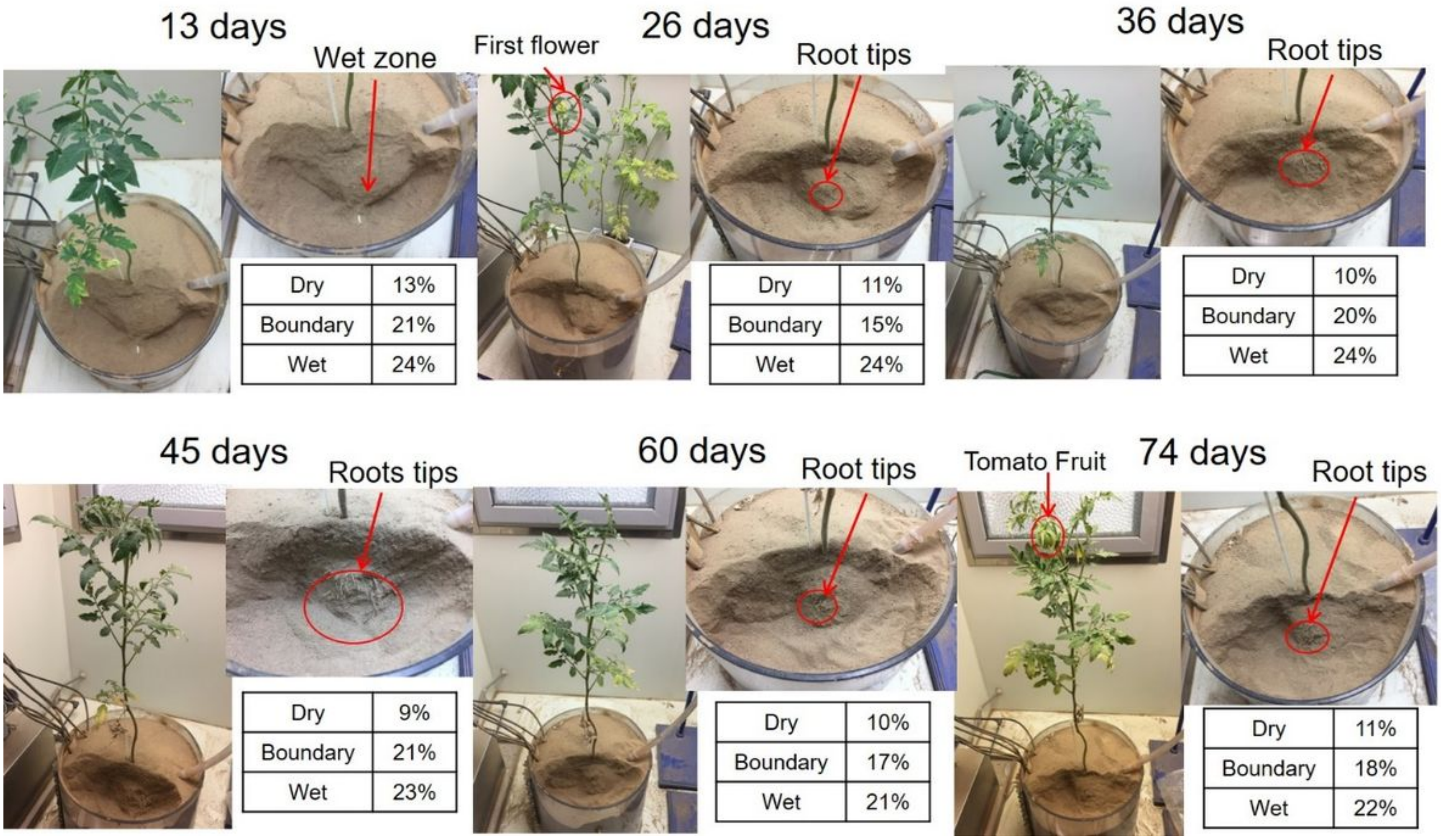

Figure 9

Root behavior at the wet/dry soil boundary for Pot 1 on various days after transplanting.

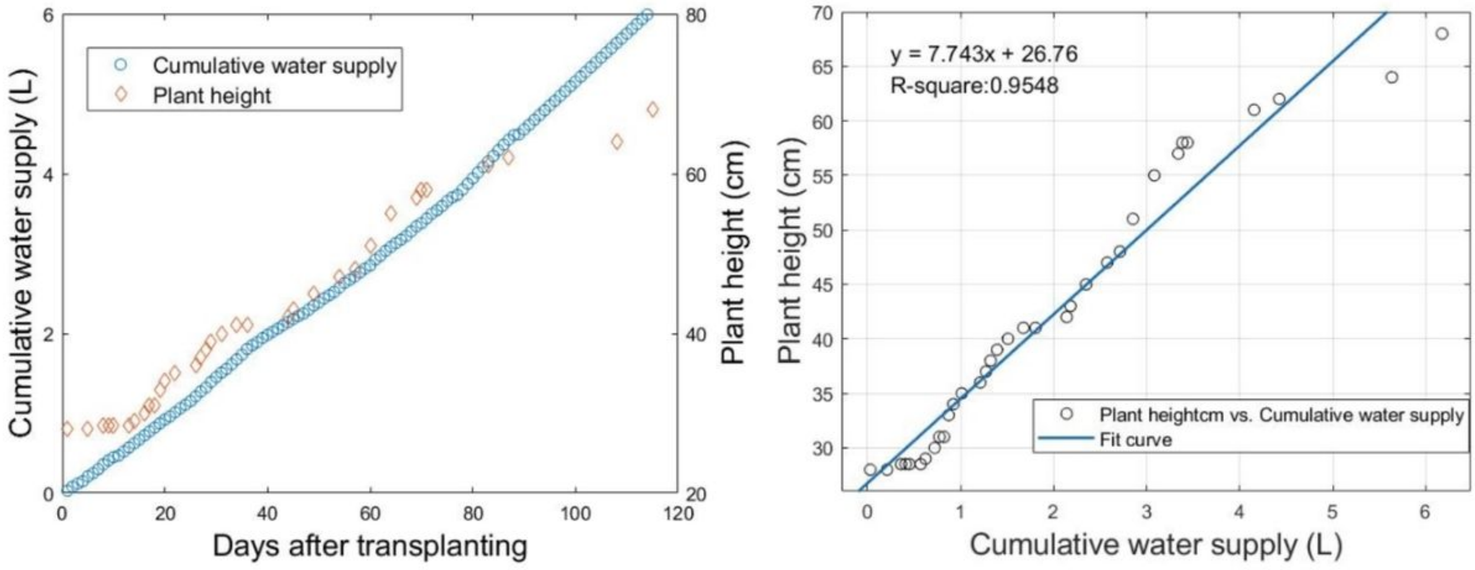

Figure 10

Relationship between crop growth and water supply

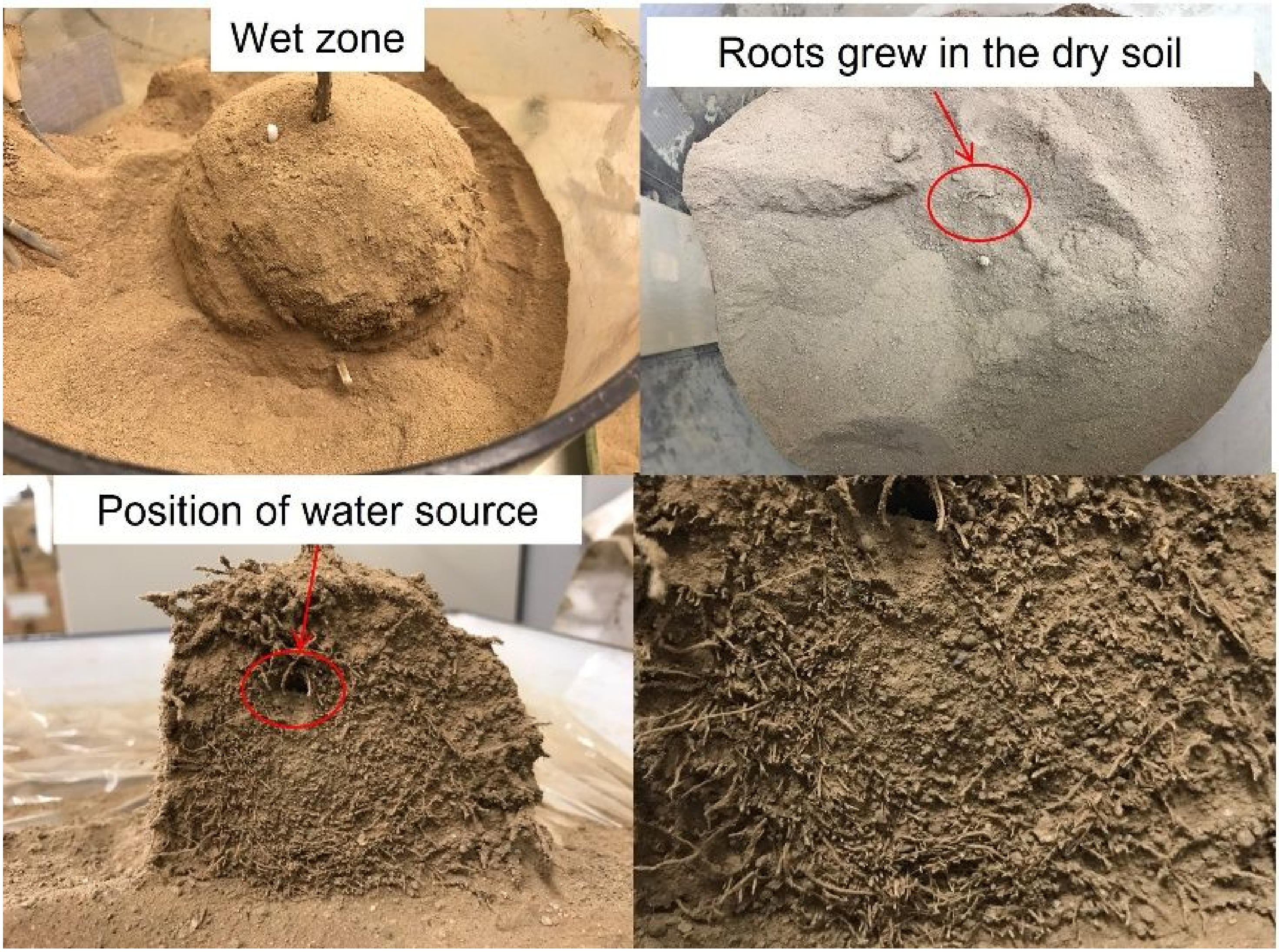

Figure 11

Observation of root distribution by taking out the wet zone from the soil at the end of the experiment

Supplementary Files

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- Supplementaryfigures.docx