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Study on Root Hydraulic Lift of Drought-Tolerant and Drought-Sensitive Potato Cultivars (*Solanum tuberosum* L.)

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Abstract: In order to investigate the relationship between hydraulic lift and drought tolerance in potato, four cultivars differing in drought susceptibilities were selected, and a pot experiment with three different irrigation conditions was carried out in a randomized complete block design. Under irrigation conditions (WW), hydraulic lift of soil water was not observed in the upper pots. Under half-irrigation (DW) and drought (DD) conditions, the water content increased in the upper pots, along with a change in root-related traits, higher biomass, and lower proline (Pro) and malondialdehyde (MDA) concentrations observed in the drought-tolerant cultivars (Longshu NO.3 and Xindaping), whereas the drought-sensitive cultivars (Favorita and Atlantic) had contrary results. As the degree of drought stress increased, the phenomenon of hydraulic lift was inhibited completely, along with a reduction in soil water content and biomass and an increase in Pro and MDA accumulation. Genotypes of Longshu NO.3 and Xindaping exhibited higher tolerance to drought stress than Favorita and Atlantic under drought conditions. In addition, similar results were also obtained for the determination of plant height, leaf water content, root activity, and root–shoot ratio. This study revealed that there was a phenomenon of hydraulic redistribution among different potato cultivars, along with hydraulic lift strongly associated with the root growth, biomass allocation, and other physiological traits that potentially confer drought resistance.

Keywords: potato; drought; hydraulic redistribution; irrigation; half-irrigation

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1. Introduction

Hydraulic lift is the process by which the plants' deep roots uptake water from the underlying soil and exude the water through the shallow roots to the upper and drier soil layer [1,2]. Although this concept was first defined in 1989 [3], conjecture about this phenomenon was proposed very early [4]. The process is considered to be largely passive, requiring a gradient in soil water potential, a higher water potential of the root xylem than the surrounding dry soil layers, and a relatively low resistance to root back-flow [5,6]. Due to the bidirectional and passive nature of this process, a more comprehensive concept of hydraulic redistribution, including hydraulic lift and the reverse of the hydraulic lift behavior, has been proposed [7]. Hydraulic lift typically occurs at night, which is beneficial for the water transportation of plants, and it may represent an important water source for neighboring plants [8]. Many techniques have been used to measure hydraulic lift under laboratory or field conditions [9].

Hydraulic redistribution has been reported to be a common phenomenon in numerous plant species including trees, shrubs, and grasses growing in various environments, from deserts to tropical forests [10,11]. Moreover, previous reports also showed that when part of the root zone was dry, grapes experienced hydraulic redistribution, an irrigation strategy in which half of the plant roots were irrigated and the other half were subjected to drought stress [12,13].

Potato is the fourth most important staple crop after wheat, rice, and maize [14]. Abiotic stresses such as drought and salinity pose a serious threat to global potato production [15]. The shortage of groundwater resources and an unfavorable rainy season are the main restricting factors affecting the yield and quality of potato tubers in semi-arid areas [16]. Potato is assumed to be susceptible to water stress, and even a very short period of water stress can cause a significant reduction in the tuber yield [17]. One hypothesis is that the root system of drought-tolerant potato should have a strong ability to extract water from deep soil [18]. It has also been reported that the properties of roots are related to the drought tolerance of potato [19]. Therefore, improving the root system is considered to be an effective way to enhance the drought tolerance of potato.

Researchers have explored the effect of different irrigation regimes on potato gas exchange, leaf water potential, leaf xylem ABA concentration, and shoot biomass under partial rootzone drying [20]. Deuterium-labeled water was applied to monitor the soil water redistribution within the potato root zone after irrigation and to quantify shallow ground water contribution to the water use of potato. These results show that the contribution of shallow water can reduce the net depth of irrigation water and save water and energy needed for pumping. The hydraulic redistribution mechanism and its importance in potato using the stable isotope of hydrogen was also studied [21].

In order to study the relationship between drought tolerance and hydraulic redistribution of potato, four potato cultivars with drought tolerance, medium drought tolerance, and drought sensitivity were selected. Then, we evaluated the root development, biomass, plant height, root activity, root–shoot ratio, and Pro and MDA contents of these four potato cultivars under different irrigation treatments to determine whether hydraulic lift played a role in drought tolerance of potatoes. This study has important reference significance for screening drought-resistance genes of potato and for breeding drought resistant potatoes.

2. Materials and Methods

2.1. Plant Materials

The four potato cultivars, Favorita (F, drought-sensitive), Atlantic (A, drought-sensitive), Longshu-3 (L-3, drought-tolerant), and Xindaping (X, medium drought-tolerant), used in this experiment were provided by the Gansu key lab of crop improvement and germplasm enhancement.

2.2. Experimental Design

The experiment was carried out in a greenhouse. The mini-tubers were grown in 5.024 L pots (20 cm in diameter, 16 cm high) filled with soil mixtures sieved in advance with a 5 mm mesh. The soil mixture was composed of 60% potting soil, 20% vermiculite, and 20% cow dung. Each treatment device was composed of two identical pots stacked up and down, both of which were filled with the same amount of soil samples. We drilled 20 holes with a diameter of 10 mm at the bottom of each upper pot so that the roots of the potato seedlings could grow into the lower pot. In addition, we drilled a 2 mm sized hole in the side of the lower pot to insert the moisture meter probe and seal it with foil when not in use to prevent moisture evaporation. In order to restrain the influence of soil capillary water, some small stones were placed between the upper and lower pots (Figure 1).

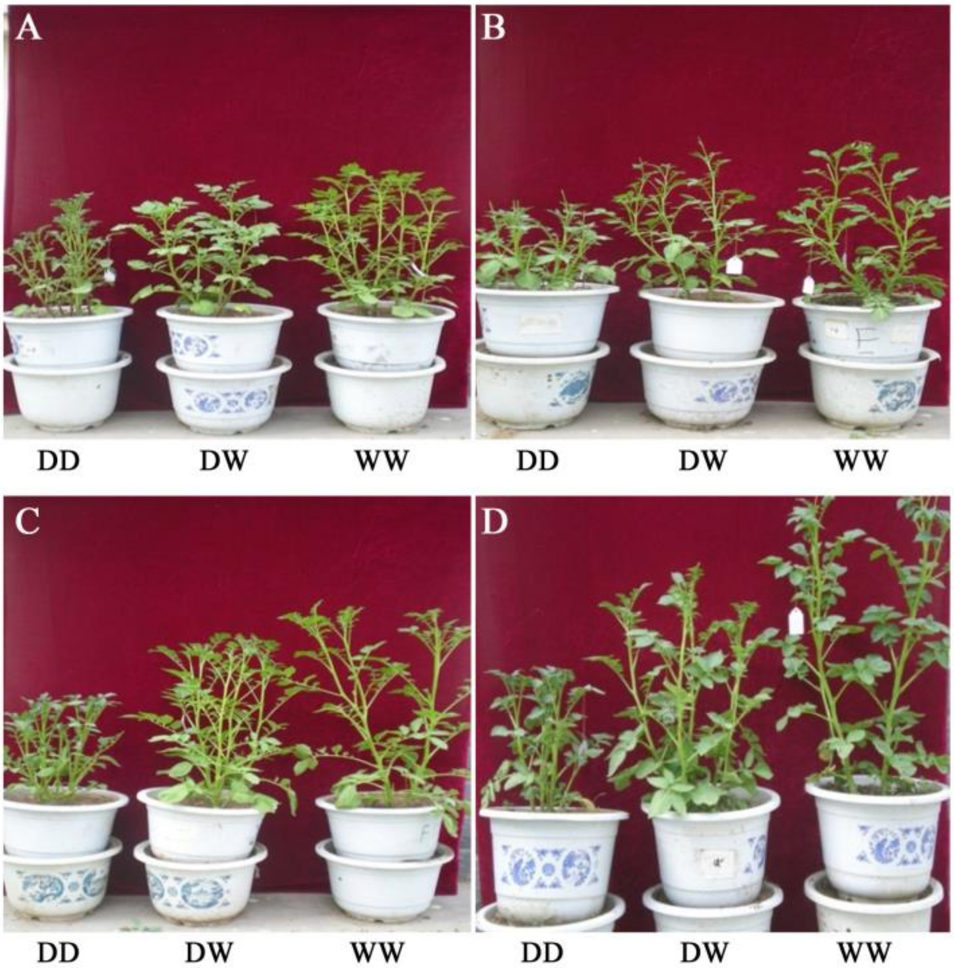

Figure 1. Phenotypes of four varieties under different irrigation conditions. (**A**): Favorita, (**B**): Atlantic, (**C**): Longshu No.3, (**D**): Xindaping. DD (drought): After the beginning of treatment, we stopped watering the top and bottom pots, subjecting them to drought stress under natural conditions. DW (half-irrigation): After the beginning of treatment, the top pots were not watered and the bottom pots were watered normally, which stimulates the phenomenon of hydraulic lift. WW (irrigation): After the beginning of treatment, the top and bottom pots were watered normally as controls.

2.3. Drought Treatments

The pot's surface was covered with polyvinyl beads to minimize evaporation from the soil. Three different treatments were conducted: WW (watering both pots), DW (only watering bottom pot), and DD (drought stress on both pots). There were four watering points in the whole drought treatment process, as follows: 3 July 19:00, 4 July 19:00, 5 July 19:00, 8 July 19:00. For the DW condition, irrigation of the top pot was stopped at the potato squaring stage to generate a water deficit, but the bottom pot continued to receive irrigation. Thus, a gradient in soil water potential between the top and bottom pots was generated, which is the driving force for hydraulic lift. For the WW condition, the top and bottom pots were watered at the same time according to the watering method in the DW treatment. For the DD condition, the upper and lower pots stopped receiving water when the stress experiment began. The soil water content was measured at three time points each day (00:00, 6:00, and 18:00). The soil water content of each pot was detected using a time-domain reflectometer (TDR). In the assay, 40-day-old potato seedlings under normal conditions were used for drought stress, and all data were measured after 8 days of treatment.

2.4. Sampling and Measuring

The whole plants and roots were separated from the potting soil and dried in an oven at 80 °C (24 h); then, the dry weight was recorded. The root systems of each plant were also collected and washed carefully with tap water. The total volume, length, and number of root tips of the top root and bottom root were determined using a root scanner (WinRHIZO, Regent, Canada). In addition, the root–shoot ratio was calculated for the dry weight of the aboveground and underground parts with the following formula: root–shoot ratio = dry weight of root/dry weight of shoot.

Root activity was measured with the tribenzyl tetrazole chloride (TTC) method [22,23], as follows: First, make a TTC standard curve. Take 0.2 mL of 0.4% TTC solution and put it into a 10 mL flask, add $Na_2S_2O_4$ powder and shake, and then dilute it with ethyl acetate to scale. Putting 0.25 mL, 0.50 mL, 1.00 mL, 1.50 mL, and 2.00 mL of this solution into respective 10 mL flasks, use ethyl acetate to fix it according to the scale to obtain the standard colorimetric series containing 25 µg, 50 µg, 100 µg, 150 µg, and 200 µg of formazan. Taking the blank as the reference, measure the absorbance at 485 nm and obtain the standard curve. Next, put 0.5 g of the root tip into a 10 mL beaker, add 10 mL of an equal mixture of 0.4% TTC solution and phosphoric acid buffer solution, fully immerse the root in the solution, keep it in the dark for 1–3 h at 37 °C, and then add 2 mL of 1 mol/L sulfuric acid to stop the reaction. Finally, take out the root, absorb the water, grind it in a mortar with 3–4 mL of ethyl acetate and a small amount of quartz sand to extract the formazan, transfer the red extract into the tube, add ethyl acetate to 10 mL, perform colorimetry with a spectrophotometer at 485 nm, measure the absorbance with a blank test as a reference, and check the standard curve to calculate the reduction amount of tetrazolium. The root activity is calculated with the following formula: root activity = tetrazolium reduction amount/root weight × time.

Samples for proline quantification consisted of 30 leaves of 10 plants. The material was shock frozen in liquid nitrogen and stored at −80 °C. The proline content was measured using the triketohydrindene hydrate method. A total of 0.5 g of fresh leaf tissue was homogenized in a boiling tube in the presence of 3% sulfosalicylic acid. The homogenate was centrifuged at 3000× *g* for 20 min after 10 min of boiling. The supernatant was mixed with 2 mL acetic acid and 3 mL acid ninhydrin. The mixture was boiled for another 1 h and the absorbance of the clean supernatant at 520 nm was determined using a UV-visible spectrophotometer (UV-1200, Meipuda instrument Co., LTD, Shanghai, China). The content of proline (µg/g, FW) = (the concentration of proline × the volume of extracting solution/the volume of extracting sample solution)/(fresh weight).

Malondialdehyde (MDA) was measured using the barbituric acid method. A total of 0.5 g of fresh leaves was ground in the presence of 2 mL of 10% trichloroacetic acid (TCA). The homogenate was centrifuged at 3500× *g* for 10 min. An amount of 2 mL of the supernatant was mixed with an equal amount of 0.6% thiobarbituric acid (TBA). The mixture was then incubated in a boiling water bath for 30 min, chilled in an ice bath, and then left at room temperature. The absorptions of the supernatant at 532 nm, 600 nm, and 450 nm were used to determine the MDA content as µmol/L: C (MDA content) = 6.45 × (A532 − A600) − 0.56 × A450. The final MDA content of the samples was calculated and expressed as µM MDA per gram of fresh weight: MDA (µM/g, FW) = MDA (µmol/L) × extracting solution volume (mL)/fresh weight (g).

2.5. Data Analysis

The mean value of each trait was taken from the measurement of at least three replicates, and the standard error of the means was calculated. Duncan's multiple range tests were used to compare the two population variances. The statistical analyses were organized and analyzed with Excel and SPSS, and the figures were generated with GraphPad Prism.

3. Results

3.1. Changes in Soil Moisture under Different Treatments

Under the WW condition, an increase in soil water content was observed in all pots at AM 0:00 due to watering, but it did not increase further at AM 6:00 after every watering point (Figure 2). Under the DW condition, for the drought-tolerant cultivar Longshu No.3 (L-3), a dramatic increase in water in the upper pots was observed at AM 6:00 5-July (Figure 3). The same phenomenon was also observed at AM 6:00 on 7-July and AM 6:00 on 8-July, and even more strongly at AM 6:00 on 9-July. The other three cultivars, Favorita (F), Atlantic (A), and Xindaping (X), also had similar trend changes in soil water content, but not as obvious as Longshu No.3. Among them, the drought-tolerant variety Xindaping increased more significantly than the two drought-sensitive cultivars Favorita and Atlantic at 6:00 on July 9. Under the DD condition, there was no significant change in the soil water content of all four cultivars (Figure 4). These results suggest that hydraulic lift truly occurs in potato only when water potential difference exists. In addition, the hydraulic lift capacity of drought-tolerant cultivars Longshu No.3 and Xindaping was stronger than that of the other two relatively drought-sensitive cultivars.

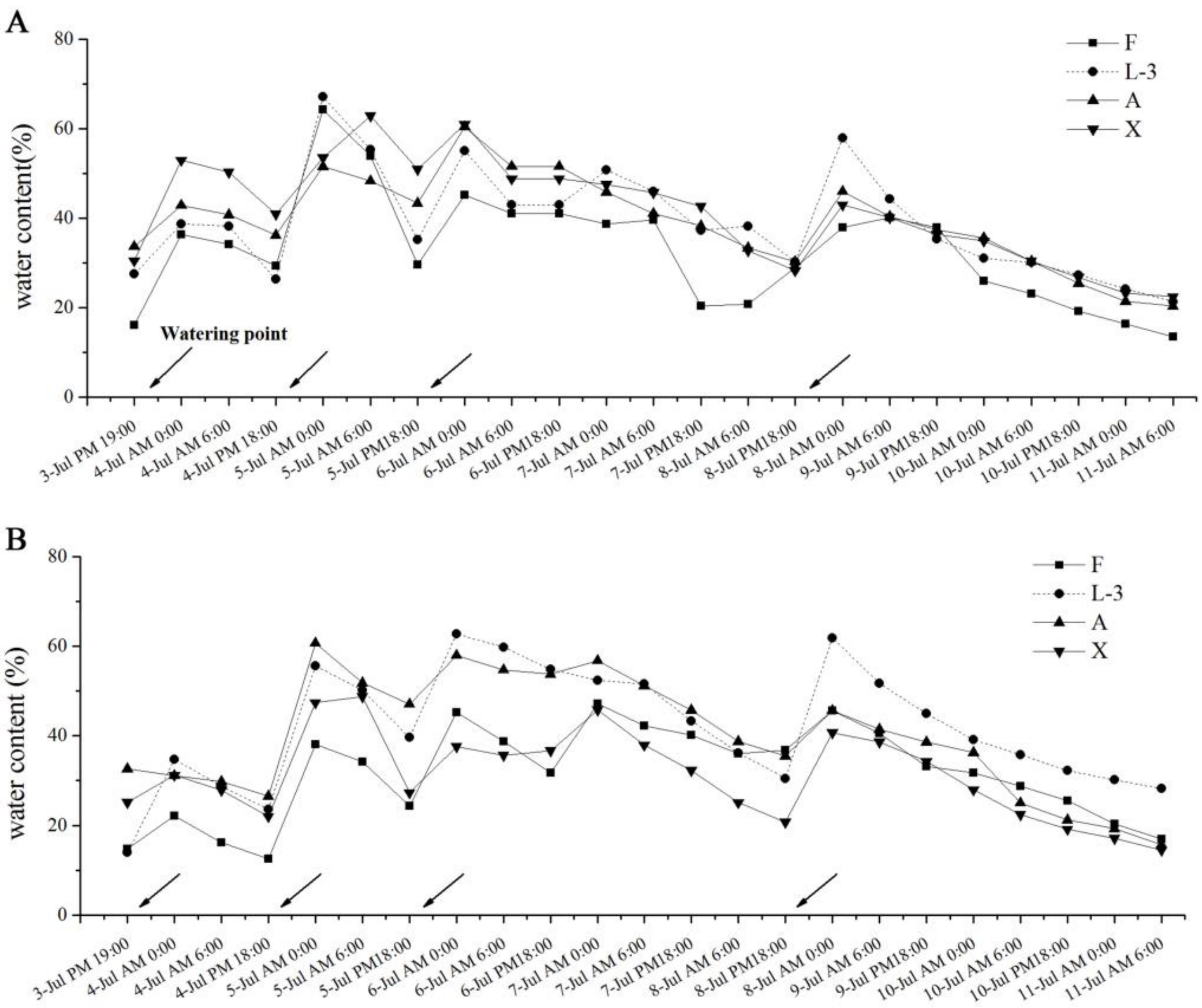

Figure 2. Soil water content under WW (irrigation) conditions. (**A**), top pots. (**B**), bottom pots. The arrows indicate the time points of watering. F, L-3, A, and X indicate different potato cultivars. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar.

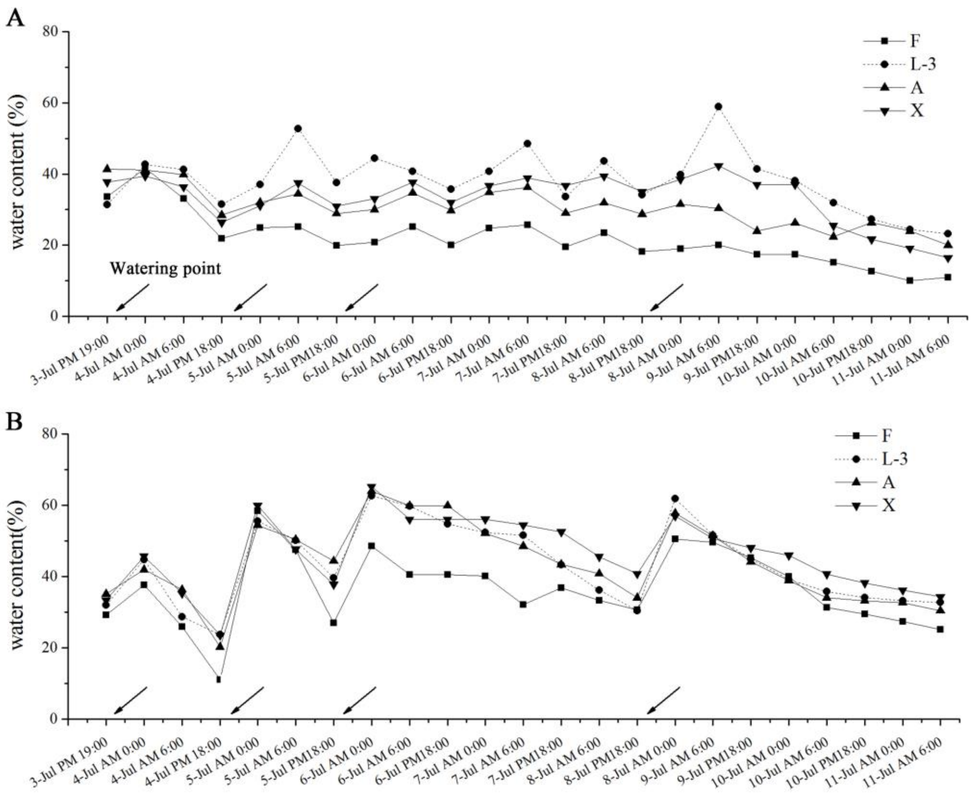

Figure 3. Soil water content under DW (half-irrigation) conditions. (**A**), top pots. (**B**), bottom pots. The arrows indicate the time points of watering. F, L-3, A, and X indicate different potato cultivars. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar.

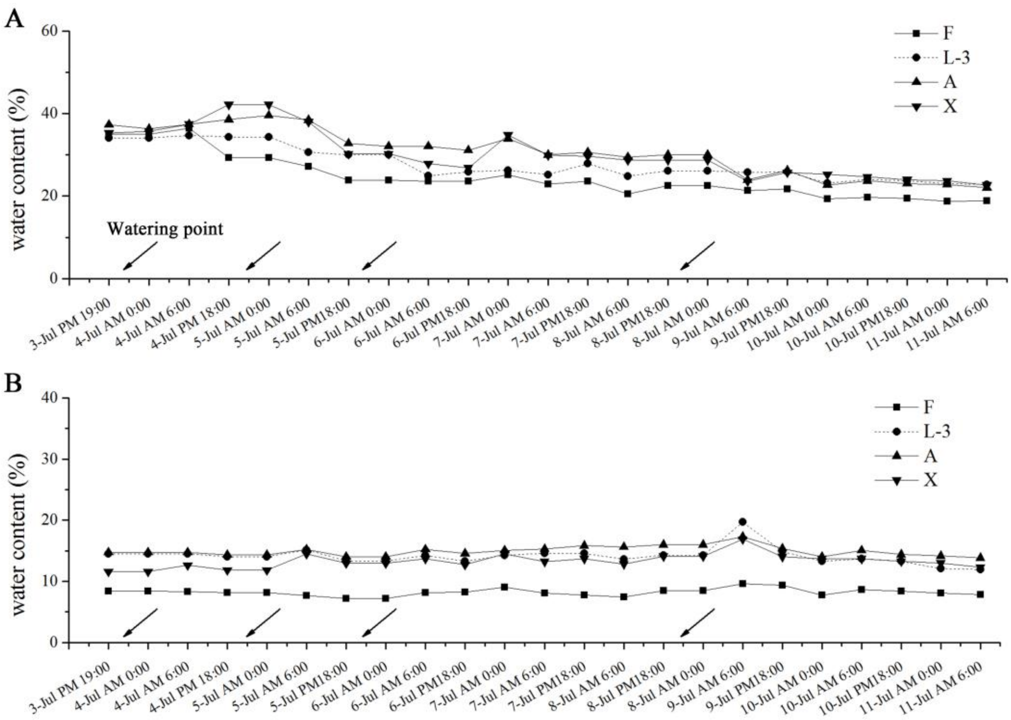

Figure 4. Soil water content under DD (drought) conditions. (**A**), top pots. (**B**), bottom pots. The arrows indicate the time points of watering. F, L-3, A, and X indicate different potato cultivars. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar.

3.2. Changes in Biomass under Different Treatments

In order to determine the effect of hydraulic lift on potato growth, the dry matter of shoots and roots under different treatments was also measured (Figure 5). The results showed that, compared with other cultivars, Longshu No.3 had the smallest decrease in biomass under the DD condition. The biomass of Longshu No.3 under the DW condition did not decrease significantly compared with that under the WW condition. However, the biomass of Atlantic, which had the biggest reduction, was reduced by 53% and 77% under the DW and DD conditions, respectively. In addition, the determination of root dry weight in the upper pot showed that the water-saving measures inhibited the accumulation of root dry matter in the four potato plants. Longshu No.3 performed better, and its dry matter accumulation was the highest under the three conditions, which was significantly higher than the other three varieties. The measured results of root dry weight in the lower pot also showed the same trend as that in the upper pot (Figure 6). These results suggest that hydraulic lift plays an important role in potato growth, especially under semi-drought conditions.

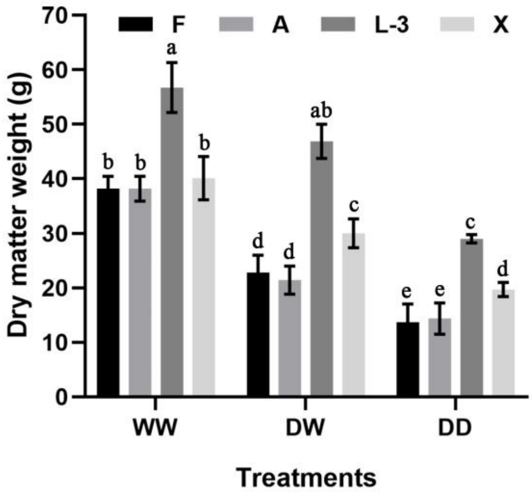

Figure 5. Dry matter weight of above-ground parts of four potato cultivars under different conditions. WW, irrigation condition. DW, half-irrigation condition. DD, drought condition. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar. Each value is the average of three replicates, and error bars represent ± SD. Different letters (a–e) represent significant differences at $p < 0.05$ level.

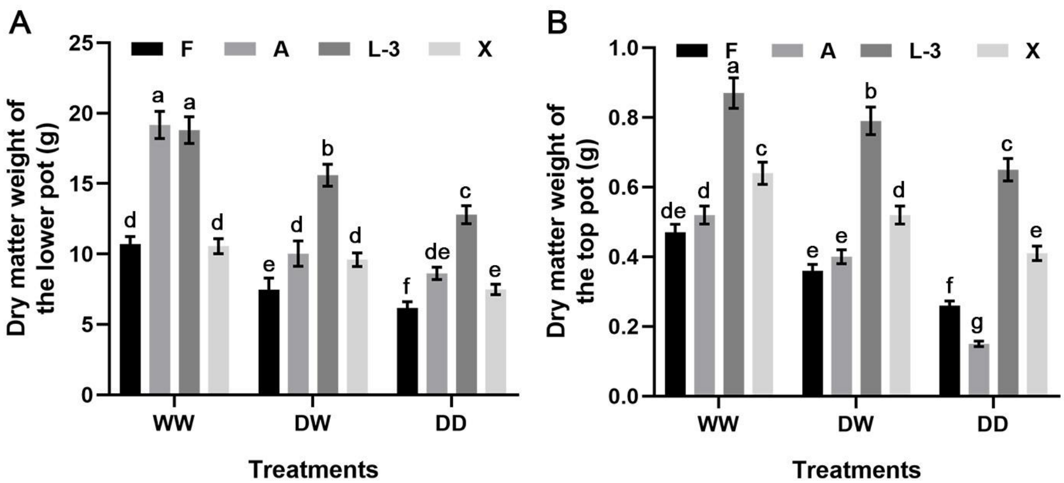

Figure 6. Dry matter weight of four potato cultivars' roots under different conditions. (**A**), dry matter weight of the lower pot. (**B**), dry matter weight of the top pot. WW, irrigation condition. DW,

half-irrigation condition. DD, drought condition. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar. Each value is the average of three replicates, and error bars represent ± SD. Different letters (a–g) represent significant differences at $p < 0.05$ level.

3.3. Changes in the Root Architecture under Different Treatments

Under stress conditions, the size of roots usually relates to the biomass of the whole plant. In addition, roots in the bottom pot play an important role in the capacity of hydraulic lift. Therefore, we measured the root length and root tip numbers of the bottom pots under different treatments. Under the DW condition, the root tip number (Figure 7a,b) and root total length (Figure 7c,d) increased in Longshu No.3 by 15% and 15% compared to WW treatment, respectively. Meanwhile, under the DW and DD conditions, there was no significant difference between Xindaping and the control in these two root characteristics. However, the root length and root tips of Favorita and Atlantic exhibited a significant reduction under DW or DD treatment.

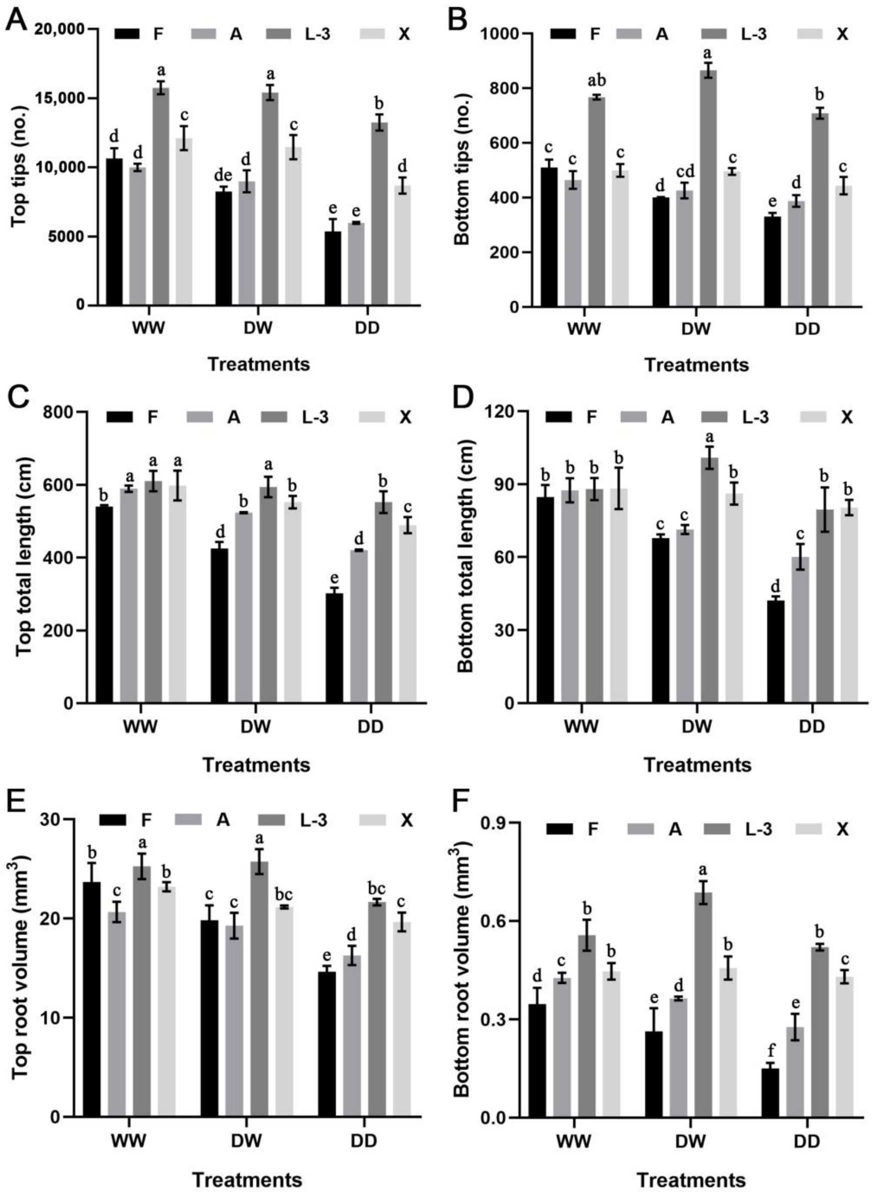

Figure 7. Phenotypic indexes of roots of four potato cultivars under different conditions. (**A**), the number of roots in top pots. (**B**), the number of roots in bottom pots. (**C**), the total length of roots

in top pots. (**D**), the total length of roots in bottom pots. (**E**), the volume of roots in top pots. (**F**), the volume of roots in bottom pots. WW, irrigation condition. DW, half-irrigation condition. DD, drought condition. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar. Each value is the average of three replicates, and error bars represent ± SD. Different letters (a–f) represent significant differences at $p < 0.05$ level.

Moreover, DW treatments also decreased the bottom root total volume by 18% in Favorita and by 22% in Atlantic, with a non-significant difference in Xindaping, but the volume increased by about 28% in Longshu No.3 (Figure 7e,f). Under the DD condition, all four potato cultivars showed significant decreases in the bottom roots' total length, roots tip number, and root total volume after 9 d of treatment. Overall, these results exhibited that root growth of the drought-tolerant cultivar Longshu No.3 could be induced by drought stress, which makes it more likely to experience hydraulic lift and more adaptable in semi-arid environments.

3.4. Changes in the Plant Height and LWC under Different Treatments

The height of the potato plants was significantly different under stress treatments (Figure 8a). Compared with the control, the plant height of Favorita and Atlantic decreased by 39% and 38%, respectively. The height of Longshu No.3 decreased by 16% compared with the control, which was significantly different. Under DW conditions, the cultivars with strong drought resistance maintained normal growth due to the water absorption and extraction of roots, while the cultivars with weak drought resistance were obviously affected by drought stress. The height of Favorita and Atlantic decreased by 31% and 22%, respectively, under DW conditions, which was significantly different from that of the control. The height of Longshu No.3 and Xindaping with strong drought resistance decreased by 4% and 7%, respectively, which was not significantly different from that of the control, indicating that drought-resistant potato cultivars could maintain normal plant growth by extracting water from roots.

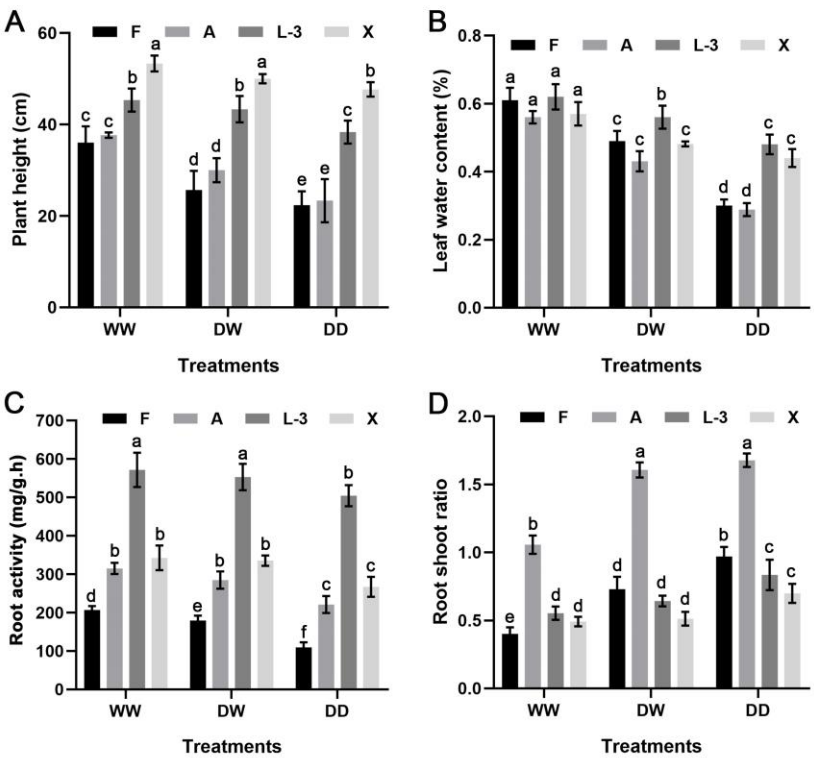

Figure 8. Determination of stress-related growth indexes under different conditions. (**A**), the plant height. (**B**), the leaf water content. (**C**), the root activity. (**D**), the root shoot ration. WW, irrigation

condition. DW, half-irrigation condition. DD, drought condition. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar. Each value is the average of three replicates, and error bars represent ± SD. Different letters (a–e) represent significant differences at $p < 0.05$ level.

The leaf water content was affected by different water-stress conditions (Figure 8b). Under the DD condition, the leaf water content of Favorita and Atlantic decreased by 51% and 46%, respectively. Longshu No.3 and Xindaping were less affected by drought stress, but both decreased by about 22%. Under the DW condition, the leaf water content of Favorita and Atlantic decreased by 20% and 30%, respectively, while Longshu No.3 and Xindaping decreased by 10% and 16%, respectively. The results showed that the leaf water content of Favorita and Atlantic decreased more greatly under the same drought-stress conditions.

3.5. Changes in the Root Activity and Root–Shoot Ratio under Different Treatments

Root activity is one of the most important indicators for measuring the status of plant roots, which directly affects plant water absorption, respiration, photosynthesis, etc. Therefore, the root activity can directly reflect the root growth state of plants. In this study, drought stress decreased the reducing ability of potato roots, which directly affected the root activity of drought-sensitive cultivars (Figure 8c). There were some differences in root activity among different potato cultivars under different treatments. Under DD conditions, the root activity levels of Favorita and Atlantic were 108.23 and 221.02, respectively, which decreased significantly by 47% and 30% compared with the control. However, there were no significant differences in Longshu No.3 or Xindaping after stress. Under the DW condition, only Favorita's root activity decreased significantly, and there were no significant changes in the other three cultivars.

Under drought stress, the water absorbed by plant roots could not fully meet the needs of photosynthesis and transpiration, which inhibited photosynthesis and reduced the number of assimilation products, resulting in a decrease in the aboveground biomass and an increase in the root–shoot ratio. In this study, the root–shoot ratios of Favorita, Atlantic, Longshu No.3, and Xindaping under the DD condition increased by 142%, 56%, 51%, and 56%, respectively, which were significantly different from those of the control. Under the DW condition, the root–shoot ratios of Favorita and Atlantic increased by 82% and 52% compared with the control group, respectively. However, there were no significant differences in Longshu No.3 and Xindaping (Figure 8d). In conclusion, Longshu No.3 had a stronger capacity for hydraulic lift.

3.6. Changes in the Proline Content under Different Treatments

The accumulation of proline is one of the adaptive responses that is frequently observed in plants to limit the effects of drought stress. Proline can protect cells by balancing the osmotic intensity of the cytoplasm, vacuoles, and external environment. Under the DW condition, the content of proline in Favorita and Atlantic increased, while that in Longshu No.3 and Xindaping did not change significantly (Figure 9a). According to the above results, there are differences in the hydraulic lifting capacity of different cultivars of potato, and this ability of Longshu No.3 and Xindaping is stronger than that of the other two cultivars. The non-significant increase in proline in Longshu No.3 and Xindaping may be because they had strong hydraulic lift capacity, redistributed water, and reduced the drought degree of the upper pot. Under the DD condition, hydraulic lift barely occurred, and the content of proline in the leaves of Longshu No.3 increased by 69% compared with that under WW treatment, which was the largest among the four cultivars. The increases in Xindaping, Atlantic, and Favorita were lower, but only by 47%, 26%, and 19%, respectively. These results demonstrate that Favorita and Atlantic are truly less drought-tolerant than Longshu No.3 and Xindaping under drought stress.

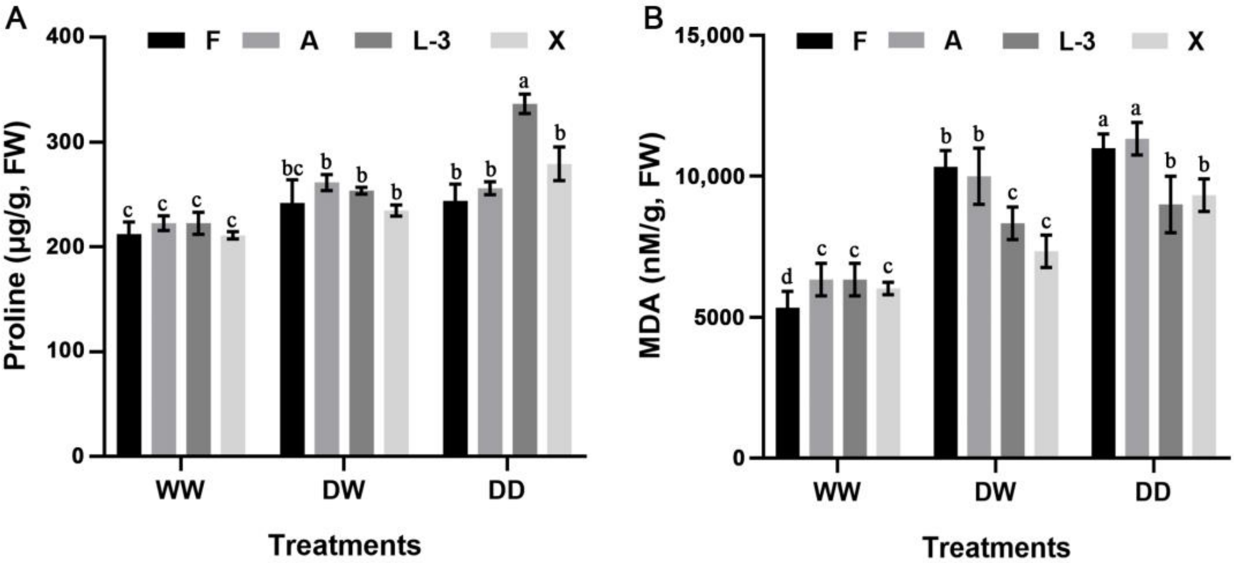

Figure 9. Determination of physiological indexes related to stress under different conditions. (**A**), proline content. (**B**), MDA content. WW, irrigation condition. DW, half-irrigation condition. DD, drought condition. F, Favorita cultivar. L-3, Longshu No.3 cultivar. A, Atlantic cultivar. X, Xindaping cultivar. Each value is the average of three replicates, and error bars represent ± SD. Different letters (a–d) represent significant differences at $p < 0.05$ level.

3.7. Changes in the MDA Content under Different Treatments

Under stress conditions, plant organs can produce lipid free radicals through lipid peroxidation, resulting in denaturation of cell membranes and cell damage. MDA is one of the final products of lipid peroxidation damage, and it is an important indicator for reflecting the degree of plant damage caused by stress. Under the DW condition, the MDA content of Favorita and Atlantic increased by 107% and 58%, respectively, while that of Longshu No.3 and Xindaping increased by only 16% and 14%, respectively (Figure 9b). Under DD treatment, the difference was even bigger: MDA content increased in Favorita and Atlantic by 188% and 129%, respectively, while it increased in Longshu No.3 and Xindaping by 37% and 54%, respectively. These results showed that the MDA accumulation of the drought-tolerant cultivars Longshu No.3 and Xindaping was lower than that of the two drought-sensitive cultivars under osmotic stress. The slight change in MDA content in Longshu 3 and Xindaping under DW conditions indicates that hydraulic lift may offer better protection from oxidative damage.

To better understand the association of hydraulic lift with other drought-response traits, a correlation analysis was conducted for all traits (Table 1). Among hydraulic lift, root total length, root tip number, root total volume, and dry matter weight, a positive significant correlation was detected between any two of them. Interestingly, a strong positive correlation was observed between hydraulic lift and root total volume. In addition, there was a significant negative correlation between hydraulic lift and MDA, while the correlation between hydraulic lift and proline was not significant.

Table 1. The correlation analysis of physiological traits and hydraulic lift.

	RL	RT	RV	DM	Pro	MDA	HL
RL	1.000	0.787 **	0.908 **	0.826 **	−0.181	−0.862 **	0.597 *
RT	0.787 **	1.000	0.948 **	0.823 **	0.087	−0.541	0.355 *
RV	0.908 **	0.948 **	1.000	0.829 **	0.052	−0.657 *	0.501 **

Table 1. *Cont.*

	RL	RT	RV	DM	Pro	MDA	HL
DM	0.826 **	0.823 **	0.829 **	1.000	−0.395	−0.817 **	0.600 *
Pro	−0.181	0.087	0.052	−0.395	1.000	0.540	−0.441
MDA	−0.862 **	−0.541	−0.657 *	−0.817 **	0.540	1.000	−0.683 **
HL	0.597 *	0.355 *	0.501 **	0.600 *	−0.441	−0.683**	1.000

RL: root total length; RT: root tip number; RV: root total volume; DM: dry matter weight (above-ground); Pro: proline; MDA: malondialdehyde; HL: hydraulic lift. * represents significance at $p \leq 0.05$; ** represents significance at $p \leq 0.01$.

4. Discussion

As the soil dries in the upper soil layers, root–soil contact and soil hydraulic conductance decrease rapidly due to root shrinkage, and rehydration leads to complete reversal of the shrinkage and increased soil hydraulic conductance [24]. The soil water depletion in the upper soil steepens the water potential gradient between the upper and lower soil layers, which then drives subsequent night-time recharge [25]. This cycle can go on and on, which redistributes water from the sparsely rooted deep soil to the densely rooted upper soil, resulting in a greater water-use rate and higher dry-matter production [26]. This kind of root hydraulic lifting has been studied more in forests, but the research in potato is still insufficient.

Root hydraulic lift occurs between the roots and the soil, but it often happens under low transpiration conditions, and there should be a certain water potential difference in the soil around the root zone [27]. Therefore, we watered the lower pot and did not water the upper pot to produce hydraulic lift and measured the soil moisture before and after irrigation every day during the experimental cycle. Under the DW condition, higher and faster increases in water content were observed in the upper pots of the two drought-resistant cultivars, Longshu No.3 and Xindaping, compared to the two drought-sensitive cultivars, Favorita and Atlantic, after being left overnight. However, there was no hydraulic lift in the upper pots under the DD and WW conditions. According to these results, we can see that different types of drought-resistant potato cultivars have different hydraulic lift capacities. In this study, the capacity of hydraulic lift at the flowering stage was tested, which will play an important role in the irrigation system of potato agricultural applications.

As water was redistributed to the drier upper soil through hydraulic lift, the root–soil interface resistance was decreased by increasing the accessibility of water to the majority of the root system [28]. In Longshu No.3, water redistribution through hydraulic lift increased moisture availability in the rooted zone, which resulted in little reduction in biomass under a semi-drought environment, while other potato cultivars had a much larger reduction. We also noticed that the root total volume, length, and tip number of Longshu No.3 in the bottom pot were much higher than those of the other cultivars [29]. This may be the reason why the root system of Longshu No.3 had a stronger hydraulic lifting capacity. Of course, water redistribution will further promote root growth and development under stress environments.

It has been argued that genotype differences in root proliferation are positively correlated with root vigor in some crops, such as wheat, which could facilitate phenotype screening to select for drought-tolerant cultivars [30]. In our study, the increase in total root length and volume of Longshu No.3 under semi-irrigation conditions was higher than that under drought treatment. These results are consistent with those of pea, where water stress resulted in a significant reduction in stem weight and an increase in root length [31]. The increased root biomass of water-stressed genotypes may be due to their ability to transfer assimilates to promote root growth and thus utilize deeper soil moisture. Compared with full irrigation, the drought-tolerant cultivars Longshu No.3 and Xindaping showed significant differences in root traits under half-irrigation conditions, while the drought-sensitive cultivars Favorita and Atlantic showed no significant differences. The total root length, root tip number, and root volume of the drought-tolerant cultivars at the bottom increased in varying degrees, while these values in drought-sensitive cultivars decreased obviously. Similar results have been reported in *Faidherbia albida*, which improves drought resistance mainly by producing longer taproots. *Acacia nilotica* enhances drought resistance by producing larger roots and increasing its contact surface with the soil. In addition, increased root growth due to water stress was reported in sunflower [32]. Seiler and Gazell [33] concluded that extreme soil drying ultimately reduced root growth.

The accumulation of proline has been advocated as a parameter of selection for stress tolerance [34,35]. Water-deficit stress increases the levels of proline. High proline synthesis in stressed plants under field conditions could favor better recovery of the plants [36]. In the present study, the proline content in leaves of four potato genotypes was significantly affected by drought stress and increased to a larger extent for the drought-tolerant cultivars Longshu No.3 and Xindaping than the drought-sensitive cultivars Favorita and Atlantic. Among them, Favorita had the smallest increase. The proline content in Favorita and Atlantic increased under half irrigation compared with full irrigation, while the content in Longshu No.3 and Xindaping did not change much. The insensitivity of Longshu No.3 and Xindaping to semi-arid treatment may be due to their higher hydraulic lifting capacity, which can redistribute water to the upper pot and reduce the degree of drought stress.

MDA is an end product of membrane lipid peroxidation [37,38]. The high accumulation of MDA is often concomitant with water-deficit-stress sensitivity [39]. Drought-tolerant *Malus prunifolia* showed better chloroplast structure under drought stress, and the accumulation of H_2O_2 and MDA was lower than that of drought-sensitive *Malus hupehensis* [40,41]. In our study, MDA content increased gradually with the increase in drought stress degree, inducing degradation of the membrane system. This result is consistent with the observation results on the wheat [42] salt-tolerance genotype and sesame [43] drought-tolerant variety under water stress. In addition, the negative correlation between HL and MDA under half-irrigation conditions reached a very significant level (Table 1). Compared with the drought-tolerant cultivars Longshu No.3 and Xindaping, the drought-sensitive cultivars Favorita and Atlantic had significantly increased MDA content, which suggests that hydraulic lift may provide better protection from oxidative damage.

Although hydraulic lift has been observed in a few plants, genetic variation and the links between hydraulic lift and drought tolerance have not been reported in potato. In this study, we have found significant variation in hydraulic lift among drought-sensitive and drought-tolerant potato cultivars. More importantly, we showed the strong link of hydraulic lift with drought-tolerance characteristics, and the degree of hydraulic lift is consistent with drought tolerance. The drought-tolerant cultivars had a stronger ability for extracting water from the bottom soil than drought-sensitive cultivars.

5. Conclusions

Overall, our research results show that the existence of a certain water potential difference between the upper and lower soil layers is the basic prerequisite for root water extraction. Under dry or wet conditions, there was almost no water extraction for potato roots, while an obvious root water extraction effect could be observed under the upper dry and lower wet conditions. Under semi-arid conditions, potato varieties with weak drought resistance showed great differences in physiological and biochemical aspects, such as increased proline content and decreased root activity. Potato varieties with strong drought resistance, such as Longshu No.3, were less affected, and could promote potato root growth and utilize deep water more efficiently without affecting the normal growth of crops.

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References

1. Alagele, S.M.; Jose, S.; Anderson, S.H.; Udawatta, R.P. Hydraulic lift: Processes, methods, and practical implications for society. *Agrofor. Syst.* **2021**, *95*, 641–657. [CrossRef]
2. Zhang, W.Q.; Zwiazek, J.J. Hydraulic redistribution in slender wheatgrass (*Elymus trachycaulus* Link Malte) and yellow sweet clover (*Melilotus officinalis* L.): Potential benefits for land reclamation. *Agronomy* **2018**, *8*, 308. [CrossRef]
3. Caldwell, M.; Richards, J. Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **1989**, *79*, 1–5. [CrossRef]
4. Caldwell, M.M.; Dawson, T.E.; Richards, J.H. Hydraulic lift: Consequences of water efflux from the roots of plants. *Oecologia* **1998**, *113*, 151–161. [CrossRef]
5. Domec, J.; Warren, J.; Meinzer, F.; Brooks, J.; Coulombe, R. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: Mitigation by hydraulic redistribution. *Oecologia* **2004**, *141*, 7–16. [CrossRef]
6. Xu, W.; Niu, F.; Kang, F.; Xu, B.; Deng, X.; Palta, J.A.; Chen, Y. Biomass allocation and competitive ability of a semiarid perennial grass and a legume in Mixtures under periodical soil water decreasing conditions. *Agronomy* **2022**, *12*, 2256. [CrossRef]
7. Oliveira, R.S.; Dawson, T.E.; Burgess, S.S.; Nepstad, D.C. Hydraulic redistribution in three Amazonian trees. *Oecologia* **2005**, *145*, 354–363. [CrossRef]
8. Mohammadi, A.S.; Zahra, N.; Hajiaghaei, K.M.; Asgari, L.B.; Nobaharan, K.; Astatkie, T.; Siddique, K.H.; Farooq, M. Role of root hydraulics in plant drought tolerance. *J. Plant Growth Regul.* **2022**, *17*, 1–16. [CrossRef]
9. Zapater, M.; Hossann, C.; Bréda, N.; Bréchet, C.; Bonal, D.; Granier, A. Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees* **2011**, *25*, 885–894. [CrossRef]
10. Wang, Y.; Jia, B.; Xie, Z. Impacts of hydraulic redistribution on eco-hydrological cycles: A case study over the Amazon basin. *Sci. China Earth Sci.* **2018**, *61*, 1330–1340. [CrossRef]
11. Neumann, R.B.; Cardon, Z.G. The magnitude of hydraulic redistribution by plant roots: A review and synthesis of empirical and modeling studies. *New Phytol.* **2012**, *194*, 337–352. [CrossRef] [PubMed]
12. Bauerle, T.; Richards, J.; Smart, D.; Eissenstat, D. Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant Cell Environ.* **2008**, *31*, 177–186. [CrossRef] [PubMed]
13. Smart, D.; Carlisle, E.; Goebel, M.; Nuñez, B.A. Transverse hydraulic redistribution by a grapevine. *Plant Cell Environ.* **2005**, *28*, 157–166. [CrossRef]
14. Ruan, S.; Wang, L.; Li, Y.; Li, P.; Ren, Y.; Gao, R.; Ma, H. Staple food and health: A comparative study of physiology and gut microbiota of mice fed with potato and traditional staple foods (corn, wheat and rice). *Food Funct.* **2021**, *12*, 1232–1240. [CrossRef]
15. Dahal, K.; Li, X.-Q.; Tai, H.; Creelman, A.; Bizimungu, B. Improving potato stress tolerance and tuber yield under a climate change scenario—A current overview. *Front. Plant Sci.* **2019**, *10*, 563. [CrossRef]
16. Ji, A.; It, B.; Id, A. Influence of water-based and contact heating preparation methods on potato mechanical properties, mastication, and sensory perception. *Int. J. Gastron. Food Sci.* **2021**, *25*, 100401.
17. Nasir, M.W.; Toth, Z. Effect of drought stress on potato production: A review. *Agronomy* **2022**, *12*, 635. [CrossRef]
18. Boguszewska-Mańkowska, D.; Zarzyńska, K.; Nosalewicz, A. Drought differentially affects root system size and architecture of potato cultivars with differing drought tolerance. *Am. J. Potato Res.* **2020**, *97*, 54–62. [CrossRef]
19. Hill, D.; Nelson, D.; Hammond, J.; Bell, L. Morphophysiology of potato (*Solanum tuberosum*) in response to drought stress: Paving the way forward. *Front. Plant Sci.* **2021**, *11*, 597554. [CrossRef]
20. Liu, F.; Shahnazari, A.; Andersen, M.N.; Jacobsen, S.E.; Jensen, C.R. Physiological responses of potato (*Solanum tuberosum* L.) to partial root-zone drying: ABA signalling, leaf gas exchange, and water use efficiency. *J. Exp. Bot.* **2006**, *57*, 3727–3735. [CrossRef]
21. Satchithanantham, S.; Krahn, V.; Sri Ranjan, R.; Sager, S. Shallow groundwater uptake and irrigation water redistribution within the potato root zone. *Agric. Water Manag.* **2014**, *132*, 101–110. [CrossRef]
22. Aschmedes, G.; Hlmer. A new thiobarbituric acid (TBA) method for determining free malondialdehyde (MDA) and hydroperoxides selectively as a measure of lipid peroxidation. *J. Am. Oil Chem. Soc.* **1989**, *66*, 813–817. [CrossRef]
23. Whalley, W.R.; Binley, A.; Watts, C.; Shanahan, P.; Dodd, I.C.; Ober, E.; Ashton, R.; Webster, C.; White, R.; Hawkesford, M.J. Methods to estimate changes in soil water for phenotyping root activity in the field. *Plant Soil* **2017**, *415*, 407–422. [CrossRef]
24. Yang, Y.; Reddy, K.R.; Du, Y.; Fan, R. Short-term hydraulic conductivity and consolidation properties of soil-bentonite backfills exposed to CCR-impacted groundwater. *J. Geotech. Geoenviron.* **2018**, *144*, 04018025. [CrossRef]
25. Müllers, Y.; Postma, J.A.; Poorter, H.; van Dusschoten, D. Stomatal conductance tracks soil-to-leaf hydraulic conductance in faba bean and maize during soil drying. *Plant Physiol.* **2022**, *1*, 2279–2294. [CrossRef] [PubMed]
26. Scoffoni, C.; Sack, L.; Ort, D. The causes and consequences of leaf hydraulic decline with dehydration. *J. Exp. Bot.* **2017**, *68*, 4479–4496. [CrossRef]

27. Ishikawa, C.M.; Bledsoe, C. Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: Evidence for hydraulic lift. *Oecologia* **2000**, *125*, 459–465. [CrossRef]
28. Colombi, T.; Torres, L.C.; Walter, A.; Keller, T. Feedbacks between soil penetration resistance, root architecture and water uptake limit water accessibility and crop growth–A vicious circle. *Sci. Total Environ.* **2018**, *626*, 1026–1035. [CrossRef]
29. Xu, H.; He, H.; Yang, K.; Ren, H.; Zhu, T.; Ke, J.; You, C.; Guo, S.; Wu, L. Application of the nitrogen nutrition index to estimate the yield of indica hybrid rice grown from machine-transplanted bowl seedlings. *Agronomy* **2022**, *12*, 742. [CrossRef]
30. Palta, J.A.; Chen, X.; Milroy, S.P.; Rebetzke, G.J.; Dreccer, M.F.; Watt, M. Large root systems: Are they useful in adapting wheat to dry environments? *Funct. Plant Biol.* **2011**, *38*, 347–354. [CrossRef]
31. Chen, L.; Wang, C.; Yang, S.; Guan, X.; Zhang, Q.; Shi, M.; Yang, S.T.; Chen, C.; Chang, X.L. Chemical reduction of graphene enhances in vivo translocation and photosynthetic inhibition in pea plants. *Environ. Sci. Nano* **2019**, *6*, 1077–1088. [CrossRef]
32. Tahir, M.H.N.; Imran, M.; Hussain, M.K. Evaluation of sunflower (*Helianthus annuus* L.) inbred lines for drought tolerance. *Int. J. Agric. Biol.* **2002**, *3*, 398–400.
33. Seiler, J.; Cazell, B. Influence of water stress on the physiology and growth of red spruce seedlings. *Tree Physiol.* **1990**, *6*, 69–77. [CrossRef]
34. Yancey, P.H.; Clark, M.E.; Hand, S.C.; Bowlus, R.D.; Somero, G.N. Living with water stress: Evolution of osmolyte systems. *Science* **1982**, *217*, 1214–1222. [CrossRef] [PubMed]
35. Lin, C.C.; Kao, C.H. Proline accumulation is associated with inhibition of rice seedling root growth caused by NaCl. *Plant Sci.* **1996**, *114*, 121–128. [CrossRef]
36. Esfandiari, E.; Shakiba, M.; Mahboob, S.; Alyari, H.; Shahabivand, S. The effect of water stress on the antioxidant content, protective enzyme activities, proline content and lipid peroxidation in wheat seedling. *Pak. J. Biol. Sci.* **2008**, *11*, 1916–1922. [CrossRef]
37. Tsikas, D. Assessment of lipid peroxidation by measuring malondialdehyde (MDA) and relatives in biological samples: Analytical and biological challenges. *Anal. Biochem.* **2017**, *524*, 13–30. [CrossRef]
38. Rems, L.; Viano, M.; Kasimova, M.A.; Miklavčič, D.; Tarek, M. The contribution of lipid peroxidation to membrane permeability in electropermeabilization: A molecular dynamics study. *Bioelectrochemistry* **2019**, *125*, 46–57. [CrossRef]
39. Slama, I.; Tayachi, S.; Jdey, A.; Rouached, A.; Abdelly, C. Differential response to water deficit stress in alfalfa (*Medicago sativa*) cultivars: Growth, water relations, osmolyte accumulation and lipid peroxidation. *Afr. J. Biotechnol.* **2011**, *10*, 16250–16259.
40. Wang, S.; Liang, D.; Li, C.; Hao, Y.; Ma, F.; Shu, H. Influence of drought stress on the cellular ultrastructure and antioxidant system in leaves of drought-tolerant and drought-sensitive apple rootstocks. *Plant Physiol. Biochem.* **2012**, *51*, 81–89. [CrossRef]
41. Jangid, K.K.; Dwivedi, P. Physiological and biochemical changes by nitric oxide and brassinosteroid in tomato (*Lycopersicon esculentum* Mill.) under drought stress. *Acta Physiol. Plant.* **2017**, *39*, 73. [CrossRef]
42. Sairam, R.; Srivastava, G.; Agarwal, S.; Meena, R. Differences in antioxidant activity in response to salinity stress in tolerant and susceptible wheat genotypes. *Biol. Plant.* **2005**, *49*, 85–91. [CrossRef]
43. Fazeli, F.; Ghorbanli, M.; Niknam, V. Effect of drought on biomass, protein content, lipid peroxidation and antioxidant enzymes in two sesame cultivars. *Biol. Plant.* **2007**, *51*, 98–103. [CrossRef]