Low soil temperature reducing the yield of drip-irrigated rice in arid areas by influencing anther development and pollination postprint

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Abstract

Drip irrigation can produce high rice yields with significant water savings; therefore, it is widely used in arid area water-scarce northern China. However, high-frequency irrigation of drip irrigation with low temperature well water leads to low root zone temperature and significantly reduce the rice yield compared to normal temperature water irrigated rice, for example, reservoir water. The main purpose of this paper is to investigate the effects of low soil temperature on the yield reduction of drip irrigated rice in the spike differentiation stage. The experiment set the soil temperatures at 18°C, 24°C and 30°C under two irrigation methods (flood and drip irrigation), respectively. The results showed that, at the 30°C soil temperature, drip irrigation increased total root length by 53% but reduced root water conductivity by 9% compared with flood irrigation. Drip irrigation also increased leaf abscisic acid and proline concentrations by 13% and 5%, respectively. These results indicated that drip irrigated rice was under mild water stress. In the 18°C soil temperature, drip irrigation reduced hydraulic conductivity by 58%, leaf water potential by 40% and leaf net photosynthesis by 25% compared with flood irrigation. The starch concentration in male gametes was also 30% less in the drip irrigation treatment than in the flood irrigation treatment at soil temperature 18°C. Therefore, the main reason for the yield reduction of drip irrigated rice was that the low temperature aggravates the physiological drought of rice and leads to the decrease of starch content in male gametes and low pollination fertilization rate. Low temperature aggravates physiological water deficit in drip irrigated rice and leads to lower starch content in male gametes and low pollination fertilization rate, which is the main reason for the reduced yield of drip irrigated rice. Overall, the results indicated that the low soil temperatures aggravated the water stress that rice was under in the drip irrigated environment, causing declines both in the starch content of male gametes and in pollination rate. Low temperature will ultimately affect the rice yield under drip irrigation.

Full Text

Preamble

Low soil temperature reducing the yield of drip irrigated rice in arid area by influencing anther development and pollination

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Abstract: Drip irrigation can produce high rice yields with significant water savings and is therefore widely used in water-scarce northern China. However, high-frequency irrigation with low-temperature well water reduces root zone temperature and significantly decreases rice yield compared to irrigation with normal-temperature water (e.g., reservoir water). The main objective of this study was to investigate how low soil temperature reduces the yield of drip-irrigated rice during the spike differentiation stage. The experiment established soil temperatures of 18°C, 24°C, and 30°C under two irrigation methods (flood and drip irrigation). At 30°C soil temperature, drip irrigation increased total root length by 53% but reduced root water conductivity by 9% compared with flood irrigation. Drip irrigation also increased leaf abscisic acid and proline concentrations by 13% and 5%, respectively, indicating that drip-irrigated rice experienced mild water stress. At 18°C soil temperature, drip irrigation reduced hydraulic conductivity by 58%, leaf water potential by 40%, and leaf net photosynthesis by 25% compared with flood irrigation. Starch concentration in male gametes was also 30% lower in drip irrigation than in flood irrigation at 18°C soil temperature. Therefore, the primary reason for yield reduction in drip-irrigated rice is that low temperature aggravates physiological drought and leads to decreased starch content in male gametes and low pollination fertilization rates. Overall, the results demonstrate that low soil temperatures intensify water stress in drip-irrigated rice, causing declines in both the starch content of male gametes and pollination rate, ultimately affecting rice yield under drip irrigation.

Keywords: soil temperature; drip irrigation; root hydraulic conductivity; starch concentration; rice yield; arid area

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Introduction

Rice is generally grown under flooded conditions, with nearly 40% of the world' s irrigation water used for rice production—a percentage that is even higher in Asia. Fresh water is becoming increasingly scarce in many regions (Tian et al., 2017), prompting the development of water-saving technologies for rice production. Drip irrigation (DI) is a system that delivers small amounts of water near the root zone. Rice yields as high as 12,050 kg/hm² have been reported for drip-irrigated rice at the Xinjiang Tianye Agriculture Research Institute in China (Guo and Chen, 2012), with DI reducing irrigation water use by 60% compared with conventional flood irrigation (FI) (He et al., 2013). Therefore, DI offers great potential for rice producers in arid and semi-arid areas.

Despite its water-saving advantages, most growers have observed that drip-irrigated rice produces much lower yields when irrigated with groundwater compared to surface water (e.g., reservoir water), likely due to the low temperature (12°C–15°C) of groundwater (Menberg et al., 2014). This suggests that drip-irrigated rice is more sensitive to temperature than flooded rice. Underground water often contains high concentrations of HCO . In a previous study, we demonstrated that high HCO content is not the main factor reducing rice Fe uptake and growth in drip-irrigated rice (Zhang et al., 2016), leading us to investigate whether low groundwater temperature causes the poor growth of drip-irrigated rice.

Low root zone temperatures influence both root and shoot growth. For example, Imran et al. (2013) reported that root zone temperatures below 15°C caused declines in secondary root branch development and root dry weight. Other studies indicated that root zone temperatures of 15°C led to panicle tip degeneration, delayed flowering, spikelet sterility, and non-uniform maturation (Yan et al., 2013), ultimately reducing rice yields. In drip-irrigated rice, He et al. (2013) observed mild water stress symptoms even when soil water content was maintained at 90%–95% of field capacity. In a previous study, we found that drip-irrigated rice exhibited mild water stress symptoms, with superoxide dismutase activity 5% greater, catalase activity 27% greater, and endogenous hormone concentrations 5%–11% lower compared with flood-irrigated rice. We therefore hypothesized that low soil temperature may cause more severe drought stress in drip-irrigated rice than in FI, ultimately worsening the growth of drip-irrigated rice.

The objectives of this study were to investigate the effects of DI and low soil temperatures on rice root morphology and physiology, various aspects of shoot and panicle physiology related to yield composition (including pollen viability), and to combine these parameters to reveal the mechanism by which low soil temperature severely inhibits the yield of drip-irrigated rice.

2.1 Experimental Background

The pot experimental soil was collected from the 0–20 cm depth at the Agricultural Experiment Station of Shihezi University, Shihezi, Xinjiang, China (44°18 N, 86°00 E). The soil has a sandy loam texture and is classified as a Calcareous Fluvisol according to the FAO-UNESCO classification system (FAO, 1998). Soil organic matter, alkali-hydrolyzable N, available P, and readily available K were measured using methods described by Carter and Gregorich (2007): organic matter, 15.7 g/kg; alkali-hydrolyzable N, 42.6 g/kg; available P, 12.5 g/kg; available K, 138.9 g/kg; and pH, 7.8.

Farmers generally use groundwater with temperatures ranging between 12°C–15°C to irrigate rice. We reasoned that DI with groundwater could reduce soil temperature, and if rice was already under mild water stress, the additional stress of cool soil could reduce yield even further. In an unpublished preliminary study, our research group observed that the yield of drip-irrigated rice significantly decreased when soil temperatures were maintained at 18°C for 25 consecutive days during the tillering, jointing, heading, or grain filling stages.

The local climate characteristics during temperature treatment are shown in Figure 1 [Figure 1: see original paper]. Air temperatures averaged 25.5°C, ranging from a daily minimum of 19.4°C to a daily maximum of 31.6°C, with daily radiation of 4.7 $MJ/(m^2 \cdot d)$. Afterwards, the pots were moved back to the greenhouse until maturity.

Fig. 1 Air temperature and solar radiation during panicle initiation of rice in 2017. Tmax, maximum temperature; Tmin, minimum temperature; Tmean, mean temperature.

2.2 Experimental Design

The study employed a two-factor design with two irrigation modes (DI and FI) and three soil temperature treatments (18°C, 24°C, and 30°C, referred to as T1, T2, and T3, respectively). T3 was considered optimal for rice growth, while a previous study indicated that rice under DI exhibited mild water stress and that T1 and T2 were too cool for optimal rice growth (Zhang et al., 2019). The pots were transferred to temperature-controlled tanks at the spike differentiation stage and maintained for 10 days.

The soil was air-dried after collection, passed through a 4-mm sieve, mixed with N, P, and K fertilizer, and placed in plastic pots (18 cm × 25 cm). Each pot contained 6 kg of soil. Fertilizer amounts were as follows: 0.20 g N/kg soil as urea; 0.15 g P/kg soil as triple superphosphate; and 0.2 g K/kg soil as potassium sulfate. The pots were watered to saturation and allowed to dry for 3 days before sowing rice seed.

The rice variety in this study ('T-43') has been recommended for drip-irrigated fields by the Tianye Agricultural Institute (Shihezi, China). Four hills of rice

(10 seeds per hill) were planted in each pot, and the stand was thinned to three plants per hill after emergence.

Irrigation treatments began when rice plants reached the 4–5 leaf stage. FI pots had no drainage hole, and a plastic tube was inserted into the soil for aeration: one end of the tube was above the soil surface and open to the atmosphere, while the other end was located at the bottom of the pot. The entire growth period of rice was 118 days, with total irrigation volumes of approximately 140 L/pot for FI and 50 L/pot for drip-irrigated rice. The water level in FI was maintained 4–5 cm above the soil surface by an electronic irrigation device. Soil water content in DI was controlled at >90% of field capacity using a Mariotte bottle to provide the water head (Shi et al., 2016).

Root zone soil temperature was controlled by a temperature-controlled water tank connected to a refrigeration machine (Jiale Lengnuan Technology Co., China) that could adjust water temperature between 10°C–40°C (Bai et al., 2017). A pump circulated water through plastic tubes connecting the refrigeration machines and the tanks. Water temperatures were set at 18°C, 24°C, and 30°C for the different tanks (Fig. 2 [Figure 2: see original paper]). Rice pots (both DI and FI) were initially kept in a greenhouse and then transferred into the water tanks after the temperature treatments when rice was at the differentiation stage. The temperatures of the water tanks were adjusted to 18°C, 24°C, and 30°C, respectively, before moving the pots into the tanks to avoid disturbances to soil temperature due to temperature differences between the pots and water tanks.

Fig. 2 Soil temperature control device

2.3.1 Photosynthetic Characteristics and Leaf Water Potential

Leaf photosynthetic characteristics—net photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO concentration (Ci), and transpiration rate (Tr)—were determined after temperature treatments (i.e., 65 days after emergence). The Pn, gs, Ci, and Tr of functional leaves were measured with a LI-6400XT system (LI-6400, LiCor, Inc., USA). An A6400-02B LED light source provided a photosynthetic photon flux density of 1200 mol/($m^2 \cdot s$) under the following conditions: 25°C leaf temperature, 70% relative humidity, and 380 (±10) mmol/($m^2 \cdot s$) CO . After photosynthetic measurements, leaves were immediately excised and their water potential was measured with a pressure chamber (Model 3000F01 Plant Water Status Console; Soil Moisture Equipment Corp., USA) (Scholander et al., 1965).

2.3.2 Biomass

Rice plants were collected after temperature treatments (i.e., 65 days after emergence), washed with distilled water three times, and separated into shoot and root samples. Samples were packed in kraft paper bags, fixed at 105°C for 30 minutes, dried at 80°C for 72 hours, and then weighed to determine biomass.

2.3.3 Root Morphology

Roots were excavated after temperature treatments (i.e., 65 days after emergence), gently washed with running water to remove fine soil particles, and rinsed three times with acidified deionized water. Root systems were scanned with a flatbed image scanner (Epson Expression/STD 1600 scanner, Epson, Japan), and scanned images were analyzed using WinRhizo commercial software to determine root length, surface area, and volume.

2.3.4 Root Hydraulic Conductivity, Proline, and Abscisic Acid (ABA) Concentration

Root hydraulic conductivity (Lp) was measured as described by Boursiac et al. (2005) after temperature treatments. Briefly, the root system of a freshly detopped plant was inserted into a pressure chamber filled with hydroponic solution. Pressure was slowly applied to the chamber, and the rate of sap flow (Jv) from the sectioned hypocotyl was determined with a micro flow-meter at three pressures (Pgas) between 0.01-0.04 MPa. The Lp of each root system $(\mathrm{mL}/(\mathrm{g} \cdot \mathrm{h} \cdot \mathrm{MPa}))$ was calculated from the slope of a plot (Lp = Jv/Pgas).

Free proline concentrations in both roots and leaves were determined using a modified method described by Bates et al. (1973) after temperature treatments. Plant samples (0.2 g) were placed into 5 mL of aqueous sulfosalicylic acid (3%) and bathed in boiling water for 30 minutes. The mixture was cooled to room temperature, and a 2.0-mL aliquot of the supernatant was mixed with 2.0 mL ninhydrin and 2 mL acetic acid. The mixture was bathed for 30 minutes in boiling water, cooled on ice, and then 5 mL of toluene was added before keeping the mixture in a dark place for 5 hours. Readings of the colored product were taken at 520 nm.

ABA concentrations in leaves and roots were measured after temperature treatments. Samples were collected, frozen in liquid N, and stored at −80°C. Phytohormones were extracted and purified according to the enzyme-linked immunoassay method described by Poschenrieder et al. (1989).

2.3.5 Pollen Vigor

Pollen vigor was measured during the late booting stage. One drop of 1% iodine-potassium solution was added to the surface of a microscope slide, and pollen grains were scattered onto the slide by gently tapping open florets over the slide. Florets that had not dehisced were manually squeezed to release pollen grains (Song et al., 2015). Iodine-stained pollen grains were photographed at 10× magnification using a DP70 digital camera attached to an Axioplan 2 microscope (Carl Zeiss, Jena, Germany). Three images were taken per slide, each including approximately 40 pollen grains. Pollen grains that were stained black and had a spherical shape were considered viable, and the percentage of viable pollen grains was calculated as the ratio of viable pollen grains to total pollen grains.

2.3.6 Soluble Sugar and Starch Concentrations

Soluble sugar was measured in leaf samples one day after temperature treatments. Simultaneously, male and female gametes were collected from flowers. Equal amounts (1.5 L) of samples were added to test tubes along with 0.1% ribitol and dried using a vacuum concentrator (Labconco, Kansas City, MO). The residue was dissolved in 100 L of a mixture containing 20 mg/mL methoxyamine hydrochloride in pyridine and incubated at 30°C for 90 minutes. After incubation, 50 L of N-methyl-N-trimethylsilyltrifluoroacetamide was added and incubated at 37°C for 30 minutes. Sample solutions (10 L aliquots) were analyzed by gas chromatography/mass spectrometry (GCMS-2010 Plus; Shimadzu, Japan) under the following conditions: column, Agilent CP-Sil 8CB-MS; carrier gas, helium; injection temperature, 230°C; oven temperature, 80°C for 2 minutes followed by an increase of 15°C/min to 330°C (Matsuda et al., 2011).

2.3.7 Yield and Yield Components

Four main tillers were harvested at maturity from each replicate. Grain was threshed by hand, dried at 80°C, and weighed to determine grain yield (g per panicle) and grain weight (mg per grain). The percentage of filled grains was calculated as the number of filled grains divided by the total number of grains per panicle. Spikelet fertility (%) was calculated as the number of filled and partially filled grains divided by the total number of grains per panicle.

2.4 Statistical Analysis

Statistical analysis was performed with SPSS 17.0 analytical software, and differences between means were compared using Duncan' s multiple range tests at the 5% probability level.

3.1 Root Morphology and Hydraulic Conductivity

Root length, surface area, and volume were significantly lower in DI than in FI at T3 (Table 1). Under DI, T1 significantly increased root length but reduced root volume compared with T3. Under FI, T1 significantly reduced all three variables. At T1, root length was 54% greater, while surface area and root volume were 54% and 11% less, respectively, in DI than in FI. Irrigation and temperature treatments had no significant effect on root diameter.

Root hydraulic conductivities were lower in DI than in FI at T1 and T2 soil temperatures (Fig. 3 [Figure 3: see original paper]). Cool soil temperature significantly reduced root Lp in both DI and FI. Under DI, T1 and T2 reduced Lp by 31%-74% compared with T3. Under FI, T1 reduced Lp by 44%; however, differences between T2 and T3 were not significant. Root hydraulic conductivity at T1 was 58% less in DI than in FI.

3.2 Proline and ABA Concentrations

Proline concentrations in both leaves and roots were greater in DI than in FI at the same soil temperature (Fig. 4 [Figure 4: see original paper]). Proline concentrations increased as soil temperatures decreased, especially in roots. Root proline concentrations under DI were 1020% greater in T1 and 147% greater in T2 compared with T3. Under FI, root proline concentrations were 552% greater in T1 and 43% greater in T2 compared with T3, though differences between T2 and T3 were not significant in FI. The effects of irrigation and soil temperature on leaf proline concentrations were similar to those on root proline concentrations, though temperature had relatively less effect on leaf proline than on root proline.

Leaf and root ABA concentrations were lower in DI than in FI at the same soil temperature (Fig. 5 [Figure 5: see original paper]). Cool soil temperature significantly increased ABA concentrations in both roots and shoots. Root ABA concentrations under DI were 75% greater in T1 than in T3. Under FI, root ABA concentrations were 35% greater in T1 than in T3. Root ABA concentrations in T1 were 51% greater in DI than in FI. ABA concentrations were greater in leaves and changed in roots, though trends were generally the same as those described for root data.

3.3 Leaf Water Potential

Leaf water potential was greater in FI than in DI at the same soil temperature (Fig. 6 [Figure 6: see original paper]). Cool soil temperature significantly reduced leaf water potential in both irrigation treatments, with larger declines in DI than in FI. T1 and T2 under DI reduced leaf water potential by 102% and 60%, respectively, compared with T3. Under FI, T1 and T2 reduced leaf water potential by 89% and 31%, respectively. Leaf water potential in T1 was 40% less in DI than in FI.

3.4 Photosynthetic Characteristics of Leaves

Photosynthetic characteristics (Pn, gs, Ci, and Tr) were greater under FI than under DI at the same soil temperature (Table 2). Cool soil temperatures significantly reduced Pn, gs, and Tr but had no effect on Ci. Leaf Pn, gs, and Tr under DI were 35%, 24%, and 31% less, respectively, in T1 than in T3. Under FI, T1 reduced Pn, gs, and Tr by 16%, 15%, and 11%, respectively. In T1, Pn, gs, and Tr were 25%, 24%, and 16% greater, respectively, in FI than in DI.

3.5 Starch Concentrations in Leaves

Leaf starch concentrations in DI were lower than those in the corresponding FI treatment. Starch concentrations generally declined as soil temperatures decreased (Fig. 7 [Figure 7: see original paper]). Under DI, starch concentrations were 40% less in T1 than in T3, though differences between T1 and T2 were not significant. Under FI, starch concentrations were 21% less in T1 than in T3, with no significant differences between T2 and T3. At soil temperature T1, starch concentrations were 50% greater in FI than in DI.

3.6 Starch Concentrations in Male and Female Gametes

Starch concentrations in male gametes of floral organs were significantly affected by low soil temperature, but starch concentration in female gametes did not show obvious changes with temperature decrease (Fig. 8 [Figure 8: see original paper]). Starch concentration in gametes generally declined as soil temperature decreased. T1 and T2 under DI reduced starch concentrations by 39% and 22%, respectively, compared with T3. T1 and T2 under FI reduced starch concentrations by 32% and 10%, respectively, compared with T3. At soil temperature T1, starch concentrations were 30% less in DI than in FI.

3.7 Pollen Viability

Pollen viability was lower in DI than in FI. T3 under DI reduced pollen viability by 7% compared with FI. Pollen viability generally declined as soil temperature decreased (Fig. 9 [Figure 9: see original paper]), with larger declines in DI than in FI. Under DI, pollen viability in T1 and T2 was reduced by 18% and 8%, respectively, compared with T3. Under FI, pollen viability was 10% less in T1 than in T3, though differences between T2 and T3 were not significant.

3.8 Dry Matter Quantity

Root, shoot, and total dry weights under DI were lower than those under FI. Starch concentrations generally declined with decreasing soil temperature (Table 3). Cool soil temperature significantly reduced shoot dry weight in both DI and FI, with larger declines in DI than in FI. In DI, root, shoot, and total dry weights in T1 were 55%, 34%, and 47% lower than in T3, respectively. In FI, shoot and total dry weights decreased but not significantly, while root and total dry weights were significantly lower (22% and 18%, respectively) in T1 than in T3.

3.9 Yield and Yield Components

Yield and yield components under DI were lower than those under FI. Starch concentrations generally declined as soil temperatures decreased (Table 4). In DI, filled grain number, total grain number, and yield were 66%, 37%, and 65% less, respectively, in T1 than in T3. Under FI, filled grain number, total grain number, and yield were 49%, 25%, and 49% less, respectively, in T1 than in T3.

Discussion

Roots are important because they not only absorb water and nutrients but also synthesize bioactive compounds that are transported to other plant organs (Daryanto et al., 2017). In a previous study, we observed that drip-irrigated rice exhibited mild water stress symptoms even when soil water content was maintained at 90%–95% of field capacity (He et al., 2013). Drought-stressed plants expend more energy to extract water and nutrients from deeper soil, ultimately resulting in greater root length (Pucholt et al., 2015). This experiment showed that the root:shoot ratio of rice in T3 (optimal soil temperature) was 11% greater in DI than in FI (Table 3), suggesting that longer roots in the DI treatment also indicate moisture stress.

The physiological function of the root system is affected by many factors, including temperature. Some studies suggest that plants are more sensitive to low soil temperature than to low air temperature (Hatfield and Prueger, 2014). Root ABA concentration is believed to be the most likely signal reflecting physiological stress (Pinto and Reynolds, 2015). Low temperatures cause significant increases in root ABA concentrations, which directly or indirectly affect physiological processes in the shoot. Additionally, photosynthetic product transport in plants is blocked and ABA content accumulates in leaves under low temperature (Theocharis et al., 2012). The results of this study showed that T1 increased ABA and proline concentrations in rice roots compared with T3 (Figs. 4 and 5), and these increases were greater in DI than in FI. Saab et al. (1990) reported that low root zone temperature causes an imbalance in physiological metabolism by reducing root water content and increasing ABA concentrations. Our results indicate that low soil temperature aggravated the effects of mild drought stress that rice was already experiencing in DI.

The root system is one of the major regulatory sites for water movement through whole plants. Therefore, a decrease in Lp affects plant water status, stomatal conductance, photosynthesis, growth, and productivity. Lp values were always lower in DI than in FI (Fig. 3), though differences between treatments became larger as root zone temperature decreased. At soil temperature T1, Lp was 58% less in DI than in FI. Overall, the results indicate that DI reduced the capacity of the root system to supply water to other parts of the plant compared to FI, and this problem was exacerbated when root zone temperatures were low.

Most water absorbed by roots is used for plant transpiration. Rice leaves roll or dry out when root-zone temperatures are low even when soil water content is high (Murai-Hatano et al., 2008). The results of this study agree with Malcolm et al. (2014), who reported that low temperature stress to rice roots can indirectly influence leaf photosynthesis and biomass accumulation. In this study, at T1, leaf Pn was significantly (25%) less and leaf proline and ABA concentrations were significantly (40% and 26%) greater in DI than in FI (Table 2). Dry matter accumulation and yield at T1 were 50% and 49% less in DI than in FI (Tables 3 and 4). Soil temperatures were the same in DI and FI, with the only difference being soil moisture content. Therefore, the results indicate that low temperatures aggravated drought stress in DI, leading to greater yield loss in DI than in FI.

Spike differentiation is an important stage of yield formation and is also when rice is most sensitive to temperature stress (Glaubitz et al., 2015). The optimum temperature during panicle differentiation is 26°C–30°C (Gunawardena et al., 2003). Starch plays a significant role in pollen maturity as it accumulates specifically in pollen to provide energy for pollination (Datta et al., 2002). In this study, irrigation method and soil temperature significantly affected starch concentrations in male but not female gametes. Starch concentrations in male gametes were 32%–39% less in T1 than in T3. Furthermore, at T1, starch concentrations in male gametes were 30% less in DI than in FI (Fig. 8), indicating that male gamete development was affected by low soil temperature during panicle differentiation. One reason is that leaf Pn was lower in DI than in FI, resulting in decreased starch production (Fig. 7) and causing pollen viability to decline (Fig. 9). This inhibited pollination, resulting in a significant increase in the void rate and a reduction in yield (Table 4). Correlation analyses conducted for rice yield with root water conductivity, ABA concentration, proline concentration, and starch concentration showed significant positive correlations between rice yield and starch concentration ($R^2 = 0.964$, $P < 0.01$) and root water conductance ($R^2 = 0.895$, $P < 0.01$) in male gametes. Significant negative correlations were found between rice yield and ABA concentration in roots ($R^2 = 0.915$, $P < 0.01$) and leaves ($R^2 = 0.949$, $P < 0.01$). These results further explain that the main factors affecting rice yield are starch concentration in male gametes and root system water conductance (Datta et al., 2002). Researchers have reported that pollen development is terminated when starch levels fall below a certain threshold and that pollen sterility is associated with inefficiency in starch accumulation (Datta et al., 2002). Pollen starch accumulation can also be severely affected by brief water stress during meiosis.

We conclude that low root zone temperature leads to pollen abortion in drip-irrigated rice primarily because starch synthesis is blocked. The additional stress of low soil temperature makes drip-irrigated rice even more sensitive during the spike differentiation period.

Conclusions

Low root zone temperatures reduce water absorption by rice roots. As a result, leaf water potential declines, stomata close, and both carbon assimilation and starch production are reduced. The negative effects of low root zone temperature are more serious under drip-irrigated rice than under flood-irrigated rice. Therefore, we conclude that low soil temperature at the panicle stage aggravates physiological water deficit under drip irrigation, leading to reduced starch content in male gametes, low fertilization rates, and reduced yield.

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References

Bai R X, Chen L, Zhang X J, et al. 2017. Effect of salinity and soil temperature on the growth and physiology of drip-irrigated rice seedlings. Archives of Agronomy and Soil Science, 63(4): 513–524.

Bates L S, Waldren R P, Teare I D. 1973. Rapid determination of free proline for water-stress studies. Plant and Soil, 39(1): 205–207.

Boursiac Y, Chen S, Luu D T, et al. 2005. Early effects of salinity on water transport in Arabidopsis roots. Molecular and cellular features of aquaporin expression. Plant Physiology, 139(2): 790–805.

Carter M R, Gregorich E G. 2007. Soil Sampling and Methods of Analysis. Boca Raton: CRC Press, 350–375.

Daryanto S, Wang L, Jacinthe P A. 2017. Global synthesis of drought effects on cereal, legume, tuber and root crops production: A review. Agricultural Water Management, 179: 18–33.

Datta R, Chamusco K C, Chourey P S. 2002. Starch biosynthesis during pollen maturation is associated with altered patterns of gene expression in maize. Plant Physiology, 130(4): 1645–1656.

FAO (Food and Agriculture Organization of the United Nations). 1998. World Reference Base for Soil Resources. In: FAO. World Soil Resource Reports. Rome, ISSS (International Society of Soil Science), ISRIC (International Soil Reference and Information Centre).

Glaubitz U, Erban A, Kopka J, et al. 2015. High night temperature strongly impacts TCA cycle, amino acid and polyamine biosynthetic pathways in rice in a sensitivity-dependent manner. Journal of Experimental Botany, 66(20): 6385-6397.

Gunawardena T A, Fukai S, Blamey F P, et al. 2003. Low temperature induced spikelet sterility in rice. I. Nitrogen fertilisation and sensitive reproductive period. Crop & Pasture Science, 54(10): 937–946.

Guo Q R, Chen L. 2012. The advantages and prospects of rice cultivation techniques under-mulch-drip irrigation. China Rice, 18(4): 36–39. (in Chinese)

Hatfield J L, Prueger J H. 2015. Temperature extremes: effect on plant growth and development. Weather and Climate Extremes, 10: 4–10.

He H, Ma F, Yang R, et al. 2013. Rice performance and water use efficiency under plastic mulching with drip irrigation. PLoS ONE, 8(12): e83103.

Imran M, Mahmood A, Römheld V, et al. 2013. Nutrient seed priming improves seedling development of maize exposed to low root zone temperatures during early growth. European Journal of Agronomy, 49: 141-148.

Malcolm P J, Holford P, Barchia I, et al. 2014. High and low root zone temperatures at bud-break reduce growth and influence dry matter partitioning in peach rootstocks. Scientia Horticulturae, 171: 83-90.

Matsuda, F, Yamasaki M, Hasunuma T, et al. 2011. Variation in biomass properties among rice diverse cultivars. Bioscience Biotechnology and Biochemistry, 75(8): 1603-1605.

Menberg K, Blum P, Kurylyk B L, et al. 2014. Observed groundwater temperature response to recent climate change. Hydrology and Earth System Sciences, 18(11): 4453-4466.

Murai-Hatano M, Kuwagata T, Sakurai J, et al. 2008. Effect of low root temperature on hydraulic conductivity of rice plants and the possible role of aquaporins. Plant and Cell Physiology, 49(9): 1294-1305.

Pinto R S, Reynolds M P. 2015. Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. Theoretical and Applied Genetics, 128(4): 575-585.

Poschenrieder C, Gunsé B, Barceló J. 1989. Influence of cadmium on water relations, stomatal resistance, and abscisic acid content in expanding bean leaves. Plant Physiology, 90(4): 1365-1371.

Pucholt P, Sjödin P, Weih M, et al. 2015. Genome-wide transcriptional and physiological responses to drought stress in leaves and roots of two willow genotypes. BMC Plant Biology, 15(1): 244-244.

Saab I N, Sharp R E, Pritchard J, et al. 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. Plant Physiology, 93(4): 1329-1336.

Scholander P F, Bradstreet E D, Hemmingsen E A, et al. 1965. Sap pressure in vascular plants: negative hydrostatic pressure can be measured in plants. Science, 148(3668): 339-346.

Shi X, Zhou Q, Wang Y, et al. 2015. Research on soil moisture dynamic under negative pressure irrigation. In: Wang Y P, Zhao J H. Proceedings of the International Conference on Energy, Environment and Materials Science (EEMS 2015). Boca Raton: CRC Press, 25-26.

Song G, Wang M, Zeng B, et al. 2015. Anther response to high-temperature stress during development and pollen thermotolerance heterosis as revealed by pollen tube growth and in vitro pollen vigor analysis in upland cotton. Planta, 241(5): 1271-1285.

Theocharis A, Clément C, Barka E A, et al. 2012. Physiological and molecular changes in plants grown at low temperatures. Planta, 235(6): 1091-1105.

Tian F, Yang P, Hu H, et al. 2017. Energy balance and canopy conductance for a cotton field under film mulched drip irrigation in an arid region of northwestern China. Agricultural Water Management, 179: 110-121.

Yan Q, Duan Z, Mao J, et al. 2013. Low root zone temperature limits nutrient effects on cucumber seedling growth and induces adversity physiological response. Journal of Integrative Agriculture, 12(8): 1450-1460.

Zhang J, Hou J, Zhang H, et al. 2019. Low soil temperature inhibits yield of rice under drip irrigation. Journal of Soil Science and Plant Nutrition, 19(1): 228-236.

Zhang X J, Zhang S J, Zhao H, et al. 2016. Effect of HCO on rice growth and iron uptake under flood irrigation and drip irrigation with plastic film mulch. Journal of Plant Nutrition and Soil Science, 178(6): 944-952.

Note: Figure translations are in progress. See original paper for figures.

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