YIELD OF DRIP-IRRIGATED RICE (*ORYZA SATIVA* L.) RESPONSE TO WATER DEFICIENCY IN DIFFERENT GROWTH STAGES

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Abstract. Rice drip irrigation cultivation is an efficient water-saving cultivation technique. However, it is a special water environment for rice, which makes rice vulnerable to water shortage during the whole growth period or at a certain stage. In this study, five water treatments were set up: drip irrigation regimes (DI), water deficient irrigation for 15 days at panicle differentiation stage (T1), booting stage (T2), flowering stage (T3) and grain filling stage (T4). Results indicated that the T1 treatment reduced the yield most, about 30.6% lower than that in DI treatment. T1 treatment significantly decreased the number of secondary branches and grains per panicle. The T2 and T3 treatment reduced the seed-setting rate of rice and led to yield reduction. The grain weight of grains on bottom secondary branches in T4 treatment was significantly decreased. Overall, In the drip irrigation management, further water shortage at different growth stages will lead to a reduction of yield. Therefore, in production practice, it is necessary to ensure adequate irrigation (soil water content kept 90% of the field water capacity at least) from the beginning of reproductive growth, especially in panicle differentiation stage. This provides a direction for breeding and water management under drip irrigation.
Keywords: *drip irrigation, water shortage, net photosynthetic rate of flag leaves, dry matter accumulation, grain filling rate*

Introduction

Rice (*Oryza sativa* L.) irrigation accounts for more than 40% of agricultural water consumption, which is one of the most water-dependent crops globally (Humphreys et al., 2010; Lee et al., 2016). With population growth, urban and industrial development, global climate change and increased environmental pollution, freshwater resources for irrigation are becoming increasingly scarce, which is a serious threat to the development of rice production (Peng et al., 2008; Chu et al., 2018). Therefore, to save water for irrigation while increasing yield is a pressing issue in rice production. Drip irrigation rice cultivation has been gradually developed in Xinjiang, an arid and water-scarce region of China, and was considered a sound agronomic technology for solving the food crisis and saving water in arid areas. Compared with flood irrigation, drip-irrigated rice can save more than 40% water (Sharda et al., 2018). Although there are reports that the yield of drip irrigation rice under good water management is equivalent to that of flooded rice. However, some studies have shown that compared with the traditional flooding cultivation of rice, the yield of drip-irrigated rice was reduced (Zhang et al., 2019 a).

Previous studies showed that the reduction of rice yield under drip irrigation is the result of insufficient secondary branches differentiation, spikelet degeneration and 1000 grain weight reduction (He et al., 2016), which to some extent shows that drip irrigation is

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a kind of adverse stress for rice yield formation (Zhang et al., 2017). At present, there are few reports on the mechanism of rice yield or yield components change under drip irrigation, especially when water shortage occurred in different growth stages of rice. Drought in the tillering stage led to insufficient tillering of flooding rice, which eventually led to a decline in yield (Du et al., 2018). But at the same time, some studies have shown that drought at tillering stage can reduce ineffective tillers and improve seed-setting rate and yield (Wu et al., 2019). Shoot biomass accumulation in rice is closely related to grain filling. Water deficiency in early rice growth significantly reduces aboveground dry matter accumulation and the number of panicles, leading to a significant decrease in yield (Yue et al., 2006), while the contribution of nonstructural carbohydrates stored in rice stems and sheaths before flowering to panicle development around 40% (Cock et al., 1972; Pan et al., 2011). There are differences in grain filling on different panicle positions in rice, with the grains in the middle and upper part of the rice panicle preferentially filling, while the grains in the bottom part of the rice panicle fill slowly and inadequately, resulting in large differences in grain weight (Mohapatra et al., 1993; Yang et al., 2000). Few reports showed the effect of drought on grain filling on different panicle positions in rice under drip irrigation cultivation. In a whole, there is a lack of systematic studies on the causes of yield reduction in drip-irrigated rice, for example, the way of drip-irrigated rice response to water shortage in different growth stages, and there is a lack of clarity on the specific process of yield reduction in drip-irrigated rice and the synergistic changes in yield constitutive factors in rice under drip irrigation.

Rice drip irrigation maintain soil moisture at 90-100% of the field water capacity through high frequency irrigation, and the variability of soil moisture in drip-irrigated rice is relatively stable compared to upland rice or dry-wet alternative irrigation. However, from a genetic and selection point of view, rice is more a kind of aquatic plant and it is more easily subject to water shortage in the whole life-span. This study attempts to study the response of drip-irrigated rice to water shortage at different growth stages and its impact on yield, so as to provide the best strategy for water management of drip irrigation rice.

Materials and methods

Site description and treatment

Field experiments was conducted at the Tianye Agricultural Research Institute (86°1′12″E, 44°33′0″N, Altitude 412 m) in Shihezi, Xinjiang Uygur Autonomous Region, China, in 2021. The soil field water capacity was 26.51% (w/w), and the soil bulk density was 1.30 $g \cdot cm^{-3}$, with organic matter of 3.79%, alkali-hydrolyzable nitrogen of 102.0 $mg \cdot kg^{-1}$, available phosphorus of 41.8 $mg \cdot kg^{-1}$ and exchangeable potassium of 176.0 $mg \cdot kg^{-1}$. There precipitation was of 71.1 mm during the cultivation (data obtained from local weather station, around 1 km to the experiment site). The rice variety for testing was Liangxiang-3 (*Oryza sativa* L.).

A randomized block design with three replicates was arranged including five treatments: DI, drip irrigation during the whole growth period of rice; T1, T2, T3 and T4, drip-irrigated rice with deficit irrigation for 15 days in panicle differentiation stage (code 3 BBCH), booting stage (code 4 BBCH), flowering stage (code 6 BBCH) and grain filling stage (code 7 BBCH) respectively. In DI treatment, the soil water content was kept at 90-100% of the field capacity during the whole growth period of rice. Treatments T1, T2, T3 and T4 kept the soil water content at 80-90% of the field holding

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capacity for 15 days in the stage of panicle differentiation, early booting, flowering and grain filling of drip-irrigated rice respectively, and keep the soil water content at 90-100% of the field holding capacity for the rest of the growth period. The plot area was 30 m^2. TDR (Time Domain Reflectometer, TRIME-TDR, IMKO, Germany) was used to monitor the soil water content in this study. Soil water content was monitored at a set time (AM, 09:00) every day during the experiment and supplementary irrigation was started when the soil water content fell below the lower limit of water content for the different treatments. The changes of soil water content under different water management and the precipitation during the experiment were shown in *Figure 1* The total irrigation amount of DI, T1, T2, T3 and T4 were 10558.6 $m^3 \cdot hm^{-2}$, 9470.3 $m^3 \cdot hm^{-2}$, 9558.1 $m^3 \cdot hm^{-2}$, 9373.0 $m^3 \cdot hm^{-2}$ and 9498.1 $m^3 \cdot hm^{-2}$ respectively.

The seeds were sown on April 24, 2021, with a depth of 2-3 cm, with a plant spacing of 10 cm, and the row spacing of 0.26 m, with 6-8 seeds per hill and a density of 3.0×10^5 $hill \cdot hm^{-2}$. One drip pipe service 2 rows rice drip irrigation. Fertilizer was drip-irrigated and applied with irrigation, all treatments received identical amount (N 300 $kg \cdot hm^{-2}$, P_2O_5 110 $kg \cdot hm^{-2}$, K_2O 70 $kg \cdot hm^{-2}$) of fertilizer and fertilization patterns.

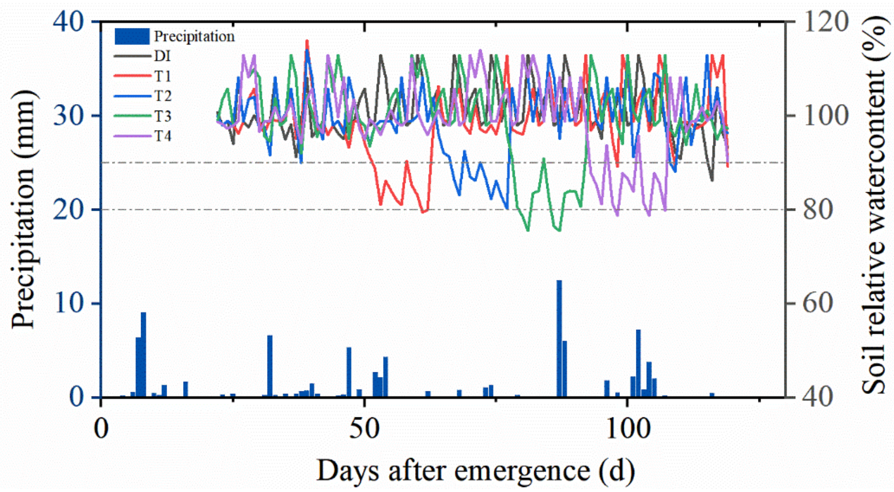

Figure 1. *Relative water content of soil under different treatments and rainfall during the study. DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed. Horizontal coordinates are time from seedling emergence to irrigation stoppage, unit: d*

Soil sampling and testing

Before sowing in 2021, five soil subsamples (0–20 cm) were randomly collected from each plot using a soil drill (5.0 cm in diameter) and mixed into one soil sample. Soil alkali-hydrolyzable nitrogen was determined from 2.0 g of air-dried soil using the alkali diffusion method. Soil available phosphorus was determined from 2.5 g of soil using the sodium bicarbonate extraction–molybdenum blue method. Soil available potassium was determined from 5.0 g of airdried soil using the ammonium acetate extraction–atomic absorption. Soil organic matter was determined from 0.1 g of air-dried soil using the potassium dichromate volumetric method.

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Grain yield and components

At the maturity stage in 2021, the grain yield was estimated from three 1 m^2 areas of plants in the central part of each plot to avoid edge effects. Then, 5 hill rice plants from each plot were harvested to determine yield components, including panicles per hectare, grains per panicle, 1000-grain weight, primary branches and secondary branches. Divide the rice plants into root, leaves, panicle, sheath and stem, then dry to constant weight at 80 °C for 48 h at least to measure plant dry matter.

Photosynthetic

The net photosynthetic of flag leaves was measured at the end of each drought stage. Ten rice plants with identical growth were selected in each plot, and the flag leaves of each plant were labeled. The Yaxin-1102 Portable Photosynthetic Transpiration Meter (Beijing Yaxin Liyi Technology Co., Ltd.) was used to measure 10 plants at fixed points in each growth stage, 13:00-11:00 a.m., and the measuring position was the middle part of the flag leaves and avoid mid vein, new fully extend leaves were measured in T1 and T2 because the flag leaves and panicles was not shown.

Grain filling rate

The process of grain filling was measured in grain filling stage (code 7 BBCH). 150 panicles with the same panicle type and size were labeled, and mark the flowering date, in the heading and flowering stages. From 5, 9, 13, 17, 21, 25 and 32 days after flowering, take 4-5 labeled panicles from each plot to measure the grain weight on different positions of panicles (refer to the method of You et al. (2021) and slightly improve it, starting from the lower end of panicle shaft, 1-4 branches are the lower part, 5-8 branches are the middle part, and the rest are the upper part), and measure the average dry weight of each part of the grains. The processes of grain filling were fitted by Richards' growth equation (Richards., 1959) as described by Zhu et al. (1988) ($mg \cdot grain^{-1} \cdot d^{-1}$):

$$W = \frac{A}{(1 + Be^{-kt})^{(N+1)/N}} \quad \text{(Eq.1)}$$

The grain-filling rate (G) was calculated as the derivative of *Equation 1:*

$$G = \frac{AKBe^{-kt}}{(1 + Be^{-kt})^{(N+1)/N}} \quad \text{(Eq.2)}$$

where W is the grain weight, A is the maximum grain weight, t is the time after flowering (d), and B, K and N are the equation parameters.

Flag leaves area

Measurement and calculation of flag leaves area (A). The length (cm) of flag leaves was measured with a ruler, in the middle stage of grain filling. And the area (cm^2) of flag leaves was calculated according to the following formula (Yoshida et al., 1976):

$$A = \mathrm{L} \times \mathrm{W} \times \mathrm{k} \quad \text{(Eq.3)}$$

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where *A* is the area, L is the length and *W* is the width at the widest part of the flag leaves.

Irrigation water productivity (WP) and harvest index (HI)

Irrigation water productivity (*WP*) and harvest index (*HI*). *WP* was obtained as the following formula (Ghasemi-Aghbolaghi and Sepaskhah., 2018):

$$WP = \frac{\mathrm{Y}}{\mathrm{I}} \qquad \text{(Eq.4)}$$

where Y is the yield ($t \cdot hm^{-2}$) and I is the amount of irrigation ($m^{-3} \cdot hm^{-2}$).

The *HI* was calculated by the following formula:

$$HI = \frac{\mathrm{Y}}{\mathrm{M}} \qquad \text{(Eq.5)}$$

where *Y* is the yield ($t \cdot hm^{-2}$) and *M* is the biomass of rice ($t \cdot hm^{-2}$).

Data analysis

Microsoft Excel 2019 and SPSS 25.0 were used for data processing. Microsoft Excel 2019 and Origin 2021b were used to draw the figures. Duncan’s multiple range test was used to identify significant differences among the treatments ($P < 0.05$), and the data are expressed as the mean ± standard deviation ($n = 3$).

Results

Yield and yield components

Table 1 showed that T1, T2, T3 and T4 significantly reduced the yield, biomass, WP and HI compared to DI treatment. The T1 treatments reduced the yield most (30.6%), but there was no significant difference compared to T2 and T3 treatment. The biomass, WP and HI under T1, T2, T3 and T4 treatments had no significant difference. Compared with DI, water shortage in different growth period (T1, T2, T3 and T4) significantly reduced the grain yield. The irrigation water productivity (WP) was significantly reduced by water shortage, no matter it occurred in any growth stages, and harvest index was reduced with the same trend of irrigation water productivity.

There was no difference in the number of primary branches among all treatments. The T1, T2, and T3 treatment significantly reduced the percentage of productive tiller and productive panicles compared to DI and T4 treatment. T1 treatment significantly reduced the secondary branches number and grain number per panicle compared to DI treatment. T2 treatment significantly reduced the seed-setting rate compared to DI treatment. T4 treatment significantly reduced the 1000 grain weight compared to DI treatment.

Panicle characteristics

The T1 treatment significantly reduced the number of grains on the top, middle and bottom secondary branches compared to DI treatment, which was the reason for the

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decrease of grain numbers per panicle of T1 treatment (*Tables 2* and *3*). The T1, T2 and T3 treatment significantly reduced the seed-setting rate of primary branches on top of the panicle compared to T4 treatment. T2 and T3 treatments decreased the seed setting rate of the top secondary branches and bottom secondary branches. Compared with DI treatment, the T4 treatment significantly reduced the grains on bottom primary and secondary branches weight, especially the grains weight on bottom secondary branches weight, which was the reason for the reduction of 1000 grain weight of T4 treatment (*Tables 2* and *3*).

Table 1. *Yield, irrigation water productivity (WP) and harvest index (HI) of rice with different irrigation regimes*

Treatment	**Yield ($t \cdot hm^{-2}$)**	**Biomass ($t \cdot hm^{-2}$)**	**Irrigation water productivity ($kg \cdot m^{-3}$)**	**Harvest index**
DI	7.70 ± 0.1 a	19.04 ± 0.5 a	0.73 ± 0.07 a	0.40 ± 0.01 a
T1	5.34 ± 0.5 c	16.32 ± 0.8 b	0.56 ± 0.05 b	0.33 ± 0.02 b
T2	5.42 ± 0.5 bc	16.72 ± 0.8 b	0.57 ± 0.05 b	0.32 ± 0.01 b
T3	5.62 ± 0.2 bc	16.52 ± 1. b	0.61 ± 0.02 b	0.34 ± 0.02 b
T4	6.12 ± 0.8 b	17.58 ± 0.3 b	0.64 ± 0.07 b	0.35 ± 0.01 b

Different letters indicate statistical significance at the P = 0.05 level within the same column (n = 3, $P < 0.05$, LSD). DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed

In general, no matter in which growth period, water shortage had a greater impact on the secondary branches of rice panicles, especially the secondary branches on the bottom part of panicles. The development of the middle part of the panicle was less affected by water shortage.

Effect of water shortage in different growth stages on photosynthetic characteristics of rice in different growth stages

In the panicle differentiation stage (code 3 BBCH), compared with DI treatment, the net photosynthetic rate (Pn) under T1 treatment decreased by 46.21%, stomatal conductance (Gs) decreased by 60.54%, and transpiration rate (Tr) decreased by 49.50%. In booting stage (code 4 BBCH), Pn, Tr and Gs of T2 treatment were 45.3%, 10.0% and 22.26% lower than those of DI respectively. In flowering stage (code 6 BBCH), Pn of T3 treatment significantly decreased by 31.0% compared to DI, T1 and T2 treatment. In the grain filling stage (code 7 BBCH), Pn and Tr of T4 treatment were significantly reduced compared to DI, T1 and T2 treatments. Meanwhile, T3 has resumed normal irrigation, and its photosynthetic characteristic values were higher than that of T4 treatment, but there was no statistical difference. The photosynthetic was restored to the level of the DI treatment 15 days after the normal drip irrigation was restored in the water shortage treatments (T1~T4) at different growth stages (*Table 4*).

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Table 2. *Yield components of rice with different irrigation regimes*

Treatment	Percentage of productive tiller (%)	Productive panicles ($\times10^6\cdot hm^{-1}$)	Seed-setting rate (%)	Primary branches per panicle	Secondary branches per panicle	Grain number per panicle	1000 grain weight
DI	83.1 a	4.11 a	74.8 a	9.3 a	13.4 a	88.6 a	28.26 ab
T1	72.4 c	3.12 c	71.2 abc	9.5 a	10.5 b	83.1 b	28.88 a
T2	71.2 c	3.14 c	68.1 c	8.7 a	11.1 ab	86.0 ab	29.50 a
T3	70.1 c	3.33 c	69.4 bc	9.4 a	11.2 ab	86.8 ab	28.02 ab
T4	76.0 b	3.67 b	72.3 ab	8.6 a	11.1 ab	85.6 ab	27.21 b

Different letters indicate statistical significance at the P = 0.05 level within the same column (n = 3, *P* < 0.05, LSD). DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed

Table 3. *Seed setting rate, grain number and average grain weight of rice on different panicle positions with different irrigation regimes*

Panicle position	Treatment	Seed-setting rate (%)		Grain numbers		Average grain weight (mg)	
		Primary branches	Secondary branches	Primary branches	Secondary branches	Primary branches	Secondary branches
Top	DI	76.2±5.5 ab	73.7±2.2 a	17.2±0.7 a	10.7±0.5 a	31.8±0.2 a	29.3±0.3 a
	T1	72.4±3.3 b	67.1±4.2 a	17.3±2.5 a	6.5±1.1 c	31.9±1.3 ab	29±0.4 a
	T2	73.7±1.3 b	50.5±2.7 b	16.9±1 a	8.8±1.7 ab	31.4±1.3 b	27.9±0.3 a
	T3	70.5±0.6 b	57.6±5.3 b	16.9±0.9 a	8.5±0.1 b	31.3±0.5 b	28.9±2.1 a
	T4	80.6±3.3 a	73±5.7 a	18.9±3.1 a	9.7±1.7 ab	31.6±1.7 b	27.9±1.2 a
Middle	DI	75.6±1.4 a	66.7±4.9 a	19.1±1.3 a	20.7±2 a	31.4±1.0 a	27.8±0.1 a
	T1	75.2±6.3 a	62.1±13.7 a	18.9±0.1 a	14.7±3.7 b	31.4±1.0 a	28.7±0.8 a
	T2	71±2 a	61.4±7.3 a	19.7±1.5 a	17.9±1.4 ab	31.8±0.3 a	25.9±1.7 a
	T3	68.6±5.8 a	58.9±6.1 a	18.9±1.6 a	16.5±3.2 ab	31.1±0.2 a	27.2±0.7 a
	T4	75.3±4 a	68.3±6.6 a	18.9±1.8 a	16.8±1.5 ab	31.3±0.8 a	26.2±3.0 a
Bottom	DI	62.2±10.7 a	54.2±8.9 ab	16.9±1.9 a	8.1±3.6 a	30.4±0.5 a	26.3±1 a
	T1	68.1±5.2 a	60.5±2.5 a	16.9±0.8 a	4.6±1.1 b	29.2±0.2 b	26.4±0.6 a
	T2	60.1±6.4 a	48.8±6 b	15.3±1 a	8.2±1.1 a	28.4±0.3 bc	26.7±0.3 a
	T3	69.9±8 a	46.4±6.3 b	17±0.7 a	8.5±1.9 a	28.4±0.2 bc	26.9±1.2 a
	T4	69.3±8.5 a	53.2±3.1 ab	15.5±1.2 a	8.1±3.1 a	28.1±0.8 c	24.4±0.4 b

Different letters indicate statistical significance at the P = 0.05 level within the same panicle position of the column (n = 3, P < 0.05, LSD). DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed

Dry matter accumulation and flag leaves area

The T1, T2, T3 and T4 treatments were significantly reduced the dry matter mass of rice plants compared to DI treatments (*Fig. 2a*). The proportion of rice panicles to total plant dry matter mass was the largest in the DI treatment at 49.17%. The percentage of panicles dry matter mass to total plants dry matter mass under T1, T2, T3 and T4 treatments was less than that under the DI treatment.

From the perspective of flag leaves growth (*Fig. 2b*), the T1 treatments significantly reduced flag leaves area compared to DI, T3 and T4. The flag leaves area of T2 treatment was smaller than that of DI, T3 and T4 treatments, but the difference was not statistically significant.

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Table 4. *Photosynthetic characteristics of rice in different growth period with different irrigation regimes*

Period	Treatment	Pn (mmol CO_2 m^{-2} s^{-1})	Tr (mmol H_2Om^{-2} s^{-1})	Gs (mmol·m^{-2} s^{-1})	Ci (μmolCO_2 mol^{-1})
Panicle differentiation	DI	16.73 ± 1.36 a	7.03 ± 0.81 a	275.50 ± 29.52 a	220.92 ± 13.78 a
	T1	9.06 ± 1.32 b	3.55 ± 0.4 b	109.07 ± 11.47 b	188.14 ± 9.66 b
Booting	DI	11.56 ± 1.70 a	5.61 ± 0.43 ab	172.58 ± 18.64 a	143.10 ± 2.31 c
	T1	11.53 ± 2.14 a	6.17 ± 0.45 ab	169.67 ± 25.12 a	168.35 ± 12.26 b
	T2	8.67 ± 0.71 b	5.03 ± 0.35 b	134.16 ± 14.69 b	184.77 ± 4.69 a
Flowering	DI	5.70 ± 0.49 a	4.04 ± 0.21 a	87.32 ± 6.08 a	191.63 ± 14.95 a
	T1	5.64 ± 1.16 a	4.02 ± 0.61 a	87.23 ± 15.07 a	191.38 ± 16.63 a
	T2	5.90 ± 1.23 a	3.79 ± 0.53 ab	77.73 ± 12.4 a	180.43 ± 10.80 a
	T3	3.90 ± 1.29 b	3.21 ± 0.46 b	77.45 ± 12.31 a	189.73 ± 5.45 a
Grain filling	DI	8.12 + 0.93 a	5.15 + 0.59a	116.38 + 16.08 a	206.07 + 6.83 a
	T1	8.26 ± 1.48 a	4.99 ± 0.64 ab	135.74 ± 19.27 a	217.70 ± 2.62 a
	T2	8.64 ± 1.11 a	4.97 ± 0.89 ab	135.85 ± 32.65a	227.23 ± 27.77 a
	T3	7.24 ± 0.77 b	4.48 ± 0.35 bc	100.92 ± 9.48 b	211.53 ± 18.65 a
	T4	5.45 ± 0.68 c	3.90 ± 0.29 c	89.83 ± 7.47 c	214.13 ± 7.59 a

Different letters indicate statistical significance at the P = 0.05 level within the same growth stage of the column. DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed

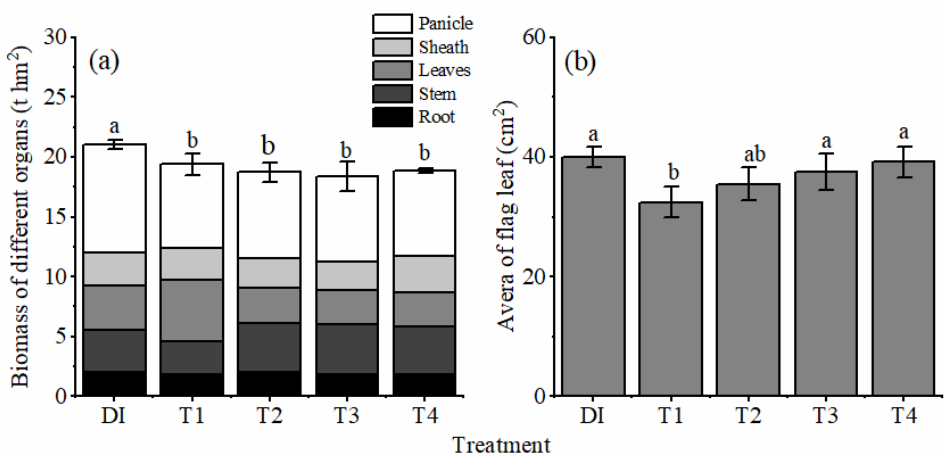

Figure 2. *Dry matter accumulation and flag leaves area in grain filling stage (code 7 BBCH) under different irrigation regimes. (a), Different letters indicate statistical significance at the P = 0.05 level within the same column (n = 3, P < 0.05, LSD); (b), Different letters on each column indicate significant differences in flag leaves area among treatments (n = 3, P < 0.05, LSD). DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed*

Grain filling rate on different panicle positions

The T1, T2, T3 and T4 treatment reduced the grain filling strength of grains on different panicle positions compared to DI treatment (*Fig. 3*). The maximum grain filling rate (G_{max}) of the median primary branches on the panicle under T3 treatment

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was higher than that of T1, T2 and T4 treatment, but the initial grain filling rate was reduced, the duration of grain filling was shortened and the time to reach the G_{max} (T_{max}) was delayed (7 days) compared to T1, T2 and T4 treatments, therefore, its grain weight is not greatly impacted (*Table 5*).

Table 5. *Parameters of Richards' growth equation for fitting filling rate of grains on different panicle position of rice*

Panicle position	Treatment	G_{max} (mg grain^{-1} d^{-1})		G_{mean} (mg grain^{-1} d^{-1})		T_{max} (d)	
		Primary branches	Secondary branches	Primary branches	Secondary branches	Primary branches	Secondary branches
Top	DI	1.94 a	2.21 a	0.72 a	0.63 a	15.0 a	20.1 b
	T1	1.80 a	2.14 ab	0.71 ab	0.64 a	14.1 a	21.2 a
	T2	1.72 a	2.05 ab	0.67 c	0.63 a	15.2 a	20.3 b
	T3	1.75 a	1.81 c	0.68 bc	0.65 a	16.3 a	19.2 c
	T4	1.80 a	1.94 bc	0.71 a	0.65 a	15.1 a	17.2 d
Middle	DI	2.0 ab	2.04 a	0.80 a	0.73 a	14.1 b	23.2 a
	T1	2.01 ab	1.82 b	0.73 ab	0.65 ab	16.3 b	22.3 a
	T2	1.67 c	1.53 bc	0.72 ab	0.61 b	16.2 b	22.2 a
	T3	2.10 a	1.50 bc	0.64 b	0.62 b	23.3 a	21.16 b
	T4	1.80 bc	1.73 b	0.73 ab	0.59 b	13.1 c	21.32 b
Bottom	DI	1.99 ab	2.00 a	0.79 a	0.68 a	20.0 a	21.11 c
	T1	1.98 b	1.83 ab	0.65 b	0.60 a	19.3 a	24.1 b
	T2	2.06 ab	1.85 ab	0.61 b	0.63 a	20.2 a	23.2 b
	T3	2.18 a	1.99 a	0.64 b	0.64 a	19.2 a	23.9 b
	T4	1.92 b	1.76 b	0.63 b	0.59 a	19.2 a	25.3 a

Different letters indicate statistical significance at the P = 0.05 level within the same panicle position of the column. G_{max} indicates the maximum grain filling rate, G_{mean} indicates the average grain filling rate, T_{max} indicates the time to reach the maximum grain filling rate. DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed

The maximum and average grain filling rates on the bottom primary and secondary branches of T4 treatment were the lowest, and the bottom secondary branches of T4 treatment reached the maximum grain filling rate (T_{max}) at the latest, which was the reason why the grain weight of the bottom primary and secondary branches of T4 treatment decreased (*Table 5*).

Discussion

From the perspective of plant physiology, earlier studies suggested changes in physiological factors such as superoxide dismutase and catalase activities in drip-irrigated rice plants only through evidence from hydroponic experiments, indicating that the water status of drip irrigation is a light water shortage on rice (Zhang et al., 2019 a), but this does not represent the real drip irrigation environment. We also observed that the HI of normal drip-irrigated rice was higher than that of different growth stages water

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shortage treatments (T1~T4) (*Table 1*), which indicating that in drip irrigation on rice produced water shortage is already the maximum upper limit, further water shortage will be detrimental to the physiological metabolism of drip-irrigated rice and significantly inhibit carbohydrate mass transport, leading to a substantial decrease in yield, but the effect of water shortage on yield factors differed among growth stages.

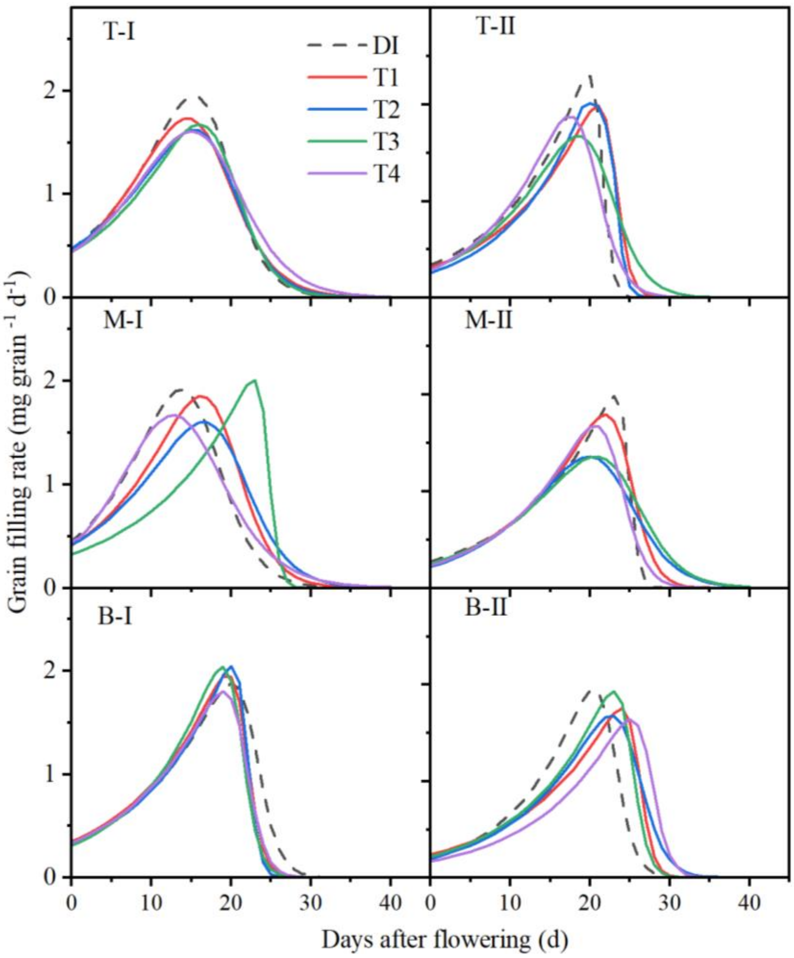

Figure 3. *Grain filling rate on different panicle positions under different irrigation regimes. DI: normal drip irrigation, T1: water shortage in panicle differentiation (code 3 BBCH) for15 d, T2: water shortage in booting (code 4 BBCH) for 15 d, T3: water shortage in flowering (code 6 BBCH) for15 d, T4: water shortage in grain filling (code 7 BBCH) for 15 d, relative soil moisture content of all water shortage treatments maintained 80-100%, soil moisture content kept 90-100% when irrigation resumed. T, M and B represent the top, middle and bottom of the panicle respectively, and the Roman numerals I and II represent the primary and secondary branches respectively*

Water shortage in any growth period will reduce the biological yield of drip irrigation rice (*Table 1*). In addition, the photosynthesis intensity of water shortage treatment in each period also decrease greatly (*Table 4*). We have reason to believe that 90% - 100% relatively soil water content is the lower limit of water demand for rice, further water deficit will hamper the growth of rice. The HI under different growth stages water shortage treatments (T1~T4) were significantly decreased by 19.01%,

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19.77%, 15.70%, 13.97% respectively compared to DI treatment. This showed that water shortage severely interferes with the reproductive growth of rice and the allocation of carbohydrate allocation in rice, however, the underline reason is not clear.

Earlier studies have shown that drip irrigation cultivation inhibits secondary branches differentiation in rice, but the exact process of yield reduction in drip-irrigated rice was not clear (He et al., 2016; Kato et al., 2008). This study showed that compared with the DI treatment, the number of secondary branches and grain numbers per panicle were significantly decreased under T1 treatment, indicating that drought during the panicle differentiation stage (code 3 BBCH) had the greatest adverse impact on the formation of secondary branches and the number of grains per panicle (*Table 1*). There was almost no impact of water shortage on the number of primary branches under all water shortage treatments. The T2 and T3 treatment significantly reduced the seed-setting rate. However, the reasons for the decrease of seed setting rate caused by T2 and T3 treatment may be different, previous study have shown that the of drip irrigation rice decreases and the pollen vigor decreases after physiological drought, so grain’s fertilization was disturbed under the T3 treatment, however, starch accumulation in the pollen was impacted under the T2 treatment (Zhang et al., 2019 b).

Amin et al. (2021) and Oliveira and Marenco (2019) believe that water shortage in milk ripening stage will lead to the reduction of photosynthetic product accumulation, insufficient grain filling, and a significant reduction in 1000 grain weight, but some studies showed that drought in milk ripening stage can improve seed-setting rate, reduce 1000 grain weight, and the yield decline was not obvious (Li et al., 2016; Wang et al., 2020). Mild dry-wet alternation can improve 1000 grain weight and seed setting rate, and promote the filling of weak grains (Gao et al., 2021). This study showed that, water shortage treatment at grain filling stage (code 7 BBCH) (T4) produced least 1000 grain weight compared to DI, T1, T2 and T3 treatment (*Table 2*) and we also found that the reason was grain weight decline on bottom primary and secondary branches of the panicle (*Table 3*).

This study also found that water shortage in the early stage also had a greater impact on the growth and development of flag leaves of rice (*Fig. 2b*), flag leaves most contribute to crop yield (Tanaka et al., 2022; Fan et al., 2015). Therefore, even if irrigation and photosynthesis were restored at the later stage of T1, T2 and T3, its grain filling density still be affected. The peak of grain filling on the middle primary branches of the panicle under water shortage at flowering stage (code 6 BBCH) was higher, but the duration of grain filling was shortened and the highest peak of grain filling was delayed around 1 week (*Fig. 3*), which may be the reason for the significant reduction of grain weight on the middle primary branches of the panicle under T3 treatment (*Table 3*). The T4 treatment also weakened photosynthesis in the flag leaves (*Table 4*), reducing the grain filling intensity of the grains on the inferior panicle position and delaying the time to peak (*Fig. 3*), ultimately leading to a greater reduction in its 1000 grain weight.

Compared with normal drip irrigation rice, the yield of water shortage rice decreased by 30.6% in panicle differentiation stage (code 3 BBCH), 29.6% in booting stage (code 4 BBCH), 27% in flowering stage (code 6 BBCH) and 20.5% at grain filling stage (code 7 BBCH), indicating that the impact of water shortage in the initial stage of drip irrigation on rice yield is greater than that in the later stage, so to meet early water demand is more important than later growth stages from view of practice. Research in upland rice found that the maximum irrigation water productivity (WP) was 0.81 $kg \cdot m^{-3}$, significantly

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higher than that of flooded rice (0.52 kg·m^{-3}) (Sharda et al., 2016). In this study, the WP of drip-irrigated rice was 0.73 kg·m^{-3}, 28% higher than that of flooded rice. It shows that drip-irrigated rice has a practical significance to areas with poor water resources. Some reports show that water shortage in tillering stage can optimize the population quality and improve the yield of rice, which they attribute to the relatively strong drought tolerance in tillering stage (Shimono and Okada, 2019). Our study found that water shortage in reproductive growth stage had a particularly serious impact on the accumulation of biomass, the development of secondary branches and the formation of seed-setting rate of drip-irrigated rice (*Tables 2* and *4*). Therefore, the amount and frequency of irrigation should be guaranteed from panicle differentiation to booting stage (code 4 BBCH) of drip-irrigated rice in order to maintain the normal growth and development of spikelet of rice. As the biomass of drip-irrigated rice was significantly reduced, increasing the sowing density of drip-irrigated rice can be used as an compensate measurement for drip-irrigated rice production to maintain a relatively high yield (Parthasarathi et al., 2018).

Conclusions

Water deficiency in drip-irrigated rice in the stage of panicle differentiation, early booting, flowering and grain filling resulted in 10% to 13% yield reduction. Water shortage in panicle differentiation stage (code 3 BBCH) mainly inhibited the formation of secondary branches of drip-irrigated rice, resulting in a decrease of the number of grains per panicle. Water shortage in early booting or flowering stage (code 4 BBCH or code 6 BBCH) affected the spikelet differentiation and pollination process of rice, reduced the seed-setting rate of rice and led to yield reduction. Water shortage in filling stage mainly led to insufficient filling of inferior grains, reduced 1000 grain weight and reduced yield due to poor photosynthesis. Thus, it is necessary to ensure adequate irrigation (the soil water content should be kept above 90% of the field capacity) from the beginning of reproductive growth, especially in panicle differentiation stage (code 3 BBCH). This provides a direction for breeding of rice varieties and irrigation strategy under drip irrigation.

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