The effect of alternate wetting and severe drying irrigation on grain yield and water use efficiency of *Indica-japonica* hybrid rice (*Oryza sativa* L.)

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Abstract
Identification of a rice cultivar with high yield potential has been heavily sought by researchers in China, and pursuant to this goal, several *indica-japonica* hybrid rice (IJHR) cultivars have been studied for over a decade. However, in addition to high yield, it is important that the cultivar also exhibit good water use efficiency (WUE). This study compared the yield performance and WUE of the IJHR cultivars under alternate wetting and severe drying (AWSD) irrigation regimen to the *japonica* inbred rice (JIR) cultivars. Field experiments were conducted on two representative IJHR cultivars (Chunyou927 and Yongyou538) and two representative JIR cultivars (Xiushui09 and Zhejing99) in 2015 and 2016 with two different irrigation methods: continuous flooding (CF) and AWSD. Irrigation water was 275–349 mm in the AWSD irrigation regimen, which was 49.8%–56.2% of that (552–620 mm) applied to the CF irrigation regimen. Compared to CF, the AWSD irrigation method significantly decreased grain yield in both IJHR and JIR cultivars, with a more significant reduction in JIR cultivars, and WUE was improved in both the IJHR and JIR cultivars, especially in the IJHR cultivars. Compared to the JIR cultivars, the IJHR cultivars were found to have improved agronomic and physiological performances under the AWSD irrigation regimen, such as a larger sink size, higher percentage of productive tillers, higher matter production ability during reproductive and ripening periods, larger root biomass, deeper root distribution and greater nonstructural carbohydrate (NSC) accumulation in the stem at heading, larger NSC remobilization from the stem, and higher root oxidation activity and leaf photosynthetic rates during ripening period. Improved agronomic and physiological traits contributed to an increase in WUE with less yield loss for IJHR cultivars under the AWSD irrigation regimen.

Keywords
agronomic traits, alternate wetting and severe drying, grain yield, physiological traits, rice, water use efficiency
1 | INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important food crops in the world and is consumed by more than three billion people (Fageria, 2007). It has been predicted that rice yield should increase by more than 1% per year to cover the needs of a growing world population (Normile, 2008). Increasing rice productivity requires either the expansion of rice planting area or an increase in the production per unit area. Nonetheless, due to the limited availability of cultivated land and water resources, the most effective way to increase rice yield is to breed new rice cultivars with greater yield potential (Horie et al., 2005). *Indica* and *japonica*, two subspecies of Asian cultivated rice, have significant differences in their biological characteristics, ecological suitability, and stress resistance. It has long been thought that the effects of heterosis on hybrids of the two rice subspecies is a promising approach to further enhance rice yield (Kubo & Yoshimura, 2005; Xin, Wang, Yang, & Luo, 2011). However, heterosis has not always resulted in positive outcomes; for example, it resulted in a low percentage of grain filling in the *indica/japonica* F1 hybrid generation (Cheng et al., 2007). Over the past decade, great progress has been made in overcoming such issues, and many *indica-japonica* hybrid rice (IJHR) cultivars with high yield potential have been bred and are being widely cultivated in China (Yuan, 2017). In some field experiments, IJHR cultivars showed higher grain yield and nitrogen use efficiency (NUE) than the locally grown cultivars (Wei et al., 2017, 2016). However, little is known about whether IJHR cultivars have better yield performance and higher water use efficiency (WUE) under water-saving irrigation regimes.

Rice consumes a large amount of the fresh water used in agricultural production (Belder et al., 2004). Fresh water is becoming increasingly scarce due to a substantial increase in population, increasing industrial development, and the incidence of environmental pollution (Belder et al., 2004; Bouman, 2007). In order increase the rice yield to increase to feed a growing population while dealing with a limited supply of fresh water, the water management technique of alternate wetting and drying (AWD) has been developed and widely adopted in China (Belder et al., 2004; Bouman, 2007; Yang, Liu, Wang, Du, & Zhang, 2007). A wide array of studies confirm that AWD could save 15%–20% of water input when compared with the continuous flooding (CF) irrigation method, yet it remains debatable whether AWD could maintain or even increase grain yield (Carrijo, Lundy, & Linquist, 2017; Norton et al., 2017). Our previous research indicated that the alternate wetting and moderate drying (AWMD) method, in which fields were not irrigated until the soil water potential reached −15 kPa, could maintain or even increase grain yield for water-saving and drought-resistant rice (WDR) cultivars or newly bred “super” rice cultivars (Chu, Chen, Wang, Yang, & Zhang, 2014; Chu et al., 2015), and many other recent studies have produced similar results (Liang et al., 2016; Zhou et al., 2017). In general, under the AWMD irrigation regimen, the crop is irrigated 13–15 times during the total growth period. However, in some primary rice producing regions in China, such as Zhejiang Province, rice was only irrigated about 10 times during the entire growth period due to an incomplete irrigation system (investigation by our team, unpublished data). Further investigation into how IJHR cultivars perform with regard to grain yield and WUE under water-saving irrigation is merited, especially under the alternate wetting and severe drying irrigation (AWSD) method.

Understanding the agronomic and physiological traits of rice is essential to develop strategies for future breeding and crop management (Chu, Wang, Zhang, Yang, & Zhang, 2016; Xue et al., 2013). Previous studies have shown that many agronomic and physiological traits are closely associated with high grain yield of rice, such as large sink size and strong sink activity (Fu, Huang, Wang, Yang, & Zhang, 2011), large leaf area index (LAI) and leaf area duration (LAD) (Ju et al., 2015), high root and shoot biomass (Ying et al., 1998; Yoshida, Forno, & Cock, 1971), and high root oxidation activity (ROA) (Yang, Zhang, & Zhang, 2012). However, information is very limited about the agronomic and physiological traits in relation to high grain yield and WUE between IJHR cultivars and other widely cultivated rice cultivars, in particular, *japonica* inbred rice (JIR), which is typically the cultivar grown in the lower reaches of the Yangtze River in China.

The objectives of this study were to (a) investigate the yield performance and WUE of the two representative IJHR cultivars under both CF and AWSD irrigation regimens, (b) make comparisons between the agronomic traits, such as the percentage of productive tillers, LAD, crop growth rate (CGR), and root and shoot biomass, of IJHR cultivars and JIR cultivars under the AWSD regimen, and (c) understand...
the physiological basis of the yield performance for IJHR under the AWSD regimen by determining the ROA and leaf photosynthetic rate as well as the amount of nonstructural carbohydrate (NSC) in the stem at heading and its remobilization during the ripening period. Reaching these objectives will provide insight into understanding how IJHR cultivars handle the water-saving irrigation regimes and provide useful information for rice breeding and water management with the goal of achieving both high grain yield and high WUE.

2 MATERIALS AND METHODS

2.1 Experimental location and weather conditions

A 2-year field experiment was conducted in 2015–2016 at the experimental farm of the China Rice Research Institute (CNRRI), Hangzhou, Zhejiang Province, China (30.30°N, 120.2°E, with an altitude of 11 m above sea level). A rice-rape (Brassica campestris L.) cropping rotation system is the typical practice in this area. The experimental farm had been cultivated with rice-rape rotation for more than one decade. The paddy soil of the experimental field is classified as Fec-Stagnic Anthrosols that had been derived from river alluvium deposits. The composition of the topsoil was: organic matter, (0–20 cm) 38.7 g/kg; total N content, 2.02 g/kg; available N, 324.6 mg/kg; available P, 18.5 mg/kg; available K, 72.1 mg/kg; pH, 5.79. The gravimetric soil moisture content at field capacity was 0.187 kg/kg, and the bulk density of the soil was 1.12 g/cm³. The data for soil properties are means across the 2 years before transplanting. The average air temperature, precipitation, and sunshine hours during the rice growing season for 2015 and 2016 were measured at a weather station close to the experimental site and are shown in Figure 1.

2.2 Rice cultivars and cultivation management

Two representative IJHR cultivars and two representative JIR cultivars were used in the experiment. The two IJHR cultivars were Chunyou-927 (CY-927, a three-line hybrid indica-japonica rice type, Chunjiang-16A × C-927) and Yongyou-538 (YY-538, a three-line hybrid indica-japonica rice type, Yongjing-3 A × F 7538); the two JIR cultivars were Xiushui-09 (XS-09, a inbred japonica rice type, Xiushui110/Jiajing-2717) and Zhejing-99 (ZJ-99, a inbred japonica rice type, Zhejing-88/Yongjing-06-02). All the cultivars have been widely grown in this area because their pest resistance, high-yielding potential and/or better quality is better than other cultivars (Chu et al., 2018; Wei et al., 2017, 2016). The four cultivars have a similar growth period ranging from 155 to 158 days from sowing to grain maturity. The cultivar seeds were obtained from Guodao High-tech Seed Co. Ltd. (Hangzhou, Zhejiang, China). The seedlings were raised in a seedbed with a sowing date of 20 May and transplanted on 15 June at a hill spacing of 25 × 16 cm with two seedlings per hill in both study years. Weeds, insects, and diseases were controlled as required to prevent yield loss. Nitrogen fertilizer application was mainly based on the practices of the local farmers, wherein urea was applied at pretransplanting, early tillering (7 days after transplanting [DAT]), and jointing (the first appearance of differentiated apex); the proportion of N split was 60%, 10%, and 30% respectively. Similar amounts of P (60 kg/ha as a single superphosphate) and K (60 kg/ha as KCl) were applied at pretransplanting in each treatment. All cultivars (50% of plants) headed from 4 to 6 September and were harvested from 20 to 21 October.

2.3 Treatment

The experiment was laid out in a completely randomized block design with three replicates. The plots were 6 × 5 m (width, length). Plots were separated by cement walls (0.5 m in width and 1.0 m in depth) coated with an impermeable film to prevent lateral percolation between neighboring plots. Two irrigation treatments, CF and AWSD were conducted from 7 DAT, at which seedlings were recovered from transplanting injury, to maturity. In AWSD, plants were not rewatered until the soil water potential reached −30 kPa (soil moisture content...
0.152 g·g⁻¹) at a depth range of 15–20 cm. With the exception of drainage at the midseason, the CF regimen was continuously flooding with 2–3 cm of water in the plot until 1 week before harvest. Our prepared experiments found that crops are irrigated <10 times under this soil water potential during the entire growth period, which in good agreement with irrigation habit in many parts in the lower area of the Yangtze River. This soil water potential reduced yield by about 25%–30% when compared to the CF regime for some cultivated rice cultivars typically cultivated in this area. Soil water potential in the AWSD plot was monitored at a soil depth ranging from 15 to 20 cm with a tensiometer consisting of a sensor 5 cm in length. Four tensiometers were installed in each plot, and readings were recorded at 1200 hr each day. When the reading reached the threshold, the plots were flooded with water at a depth of 2–3 cm. The amount of water used for irrigation was monitored with a flow meter (model LXSGE-BMYC-15, Hangzhou Water Meter Manufacturing Factory, Hangzhou, China), which was installed in the irrigation pipelines.

### 2.4 Sampling and measurements

The leaf water potential of the upmost fully expanded leaves on stems were measured at clear midday (11:30 a.m.) at 53 (D1) and 114 (D2) DAT in 2015 and at 49 (D1) and 109 (D2) DAT in 2016 when soil water potentials were approximately −30 kPa in the AWSD regimen and at 54 (W1) and 115 (W2) DAT in 2015 and at 50 (W1) and 110 (W2) DAT in 2016 when plants were rewatered. Three pressure chambers (Model 3000, Soil Moisture Equipment Corp., Santa Barbara, CA, USA) were used for the measurement of leaf water potential; six leaves were used for each treatment.

The photosynthetic rate of the upmost fully expanded leaves on stems were measured on the aforementioned dates. Four gas exchange analyzers (Li-Cor 6400 portable photosynthesis measurement system, Li-Cor, Lincoln, NE, USA) were used to measure the leaf photosynthetic rate. The measurement was made between the hours of 9:00 a.m. and 11:00 a.m. when photosynthetic active radiation above the canopy was 1300–1500 μmol m⁻² s⁻¹; six leaves were measured for each treatment.

Twenty plants in each plot were tagged for observation of tiller number. The observation was made at 5-days intervals from transplanting to heading and at physiological maturity. The percentage of productive tillers was defined as the number of panicles that developed from tillers in relation to the number of tillers at the jointing stage.

Leaf area index (LAI) and shoot biomasses were determined at the stages of jointing, heading, and maturity. Plants from 12 hills were sampled from each treatment for each measurement. To maintain canopy conditions, the vacant spaces left after sampling were immediately replaced with hills taken from the borders, and these replanted hills were no longer subjected to sampling. All plant samples were separated into green leaf blades, stems (culms + sheaths), and panicles (at heading time and maturity). The dry matter of each component was determined after drying at 70°C to a constant weight and then weighed. The measurement of NSC in the stem at heading and physiological maturity was according to the method described by Yoshida et al. (1971).

After the leaves were removed from the stem, the leaf area was immediately measured with an area meter (LI-3000C, Li-Cor). Leaf area duration (LAD) and crop growth rate (CGR) were calculated using the following formulas:

\[
LAD (m^2/m^2 d) = \frac{1}{2} (L_1 + L_2) \times (t_2 - t_1),
\]

\[
CGR (g m^{-2} d^{-1}) = (W_2 - W_1) \times (t_2 - t_1),
\]

where \(L_1\) and \(L_2\) are the first and second LAI measurements \((m^2/m^2)\), and \(W_1\) and \(W_2\) are the first and second shoot biomass measurements \((g/m^2)\), respectively, and \(t_1\) and \(t_2\), respectively, represent the first and second \((d)\) measurements.

The amount of nonstructural carbohydrate (NSC) in the stem (culm + sheath) was determined at both heading time and maturity according to the method described by Yoshida et al. (1971).

NSC remobilization (%) = \(\frac{\text{NSC in the stem at anthesis} - \text{NSC in the stem at maturity}}{\text{NSC in the stem at anthesis}} \times 100\)

Root dry weight was determined at heading time. For each root sampling, a block of soil \((25 \times 16 \times 20\) cm) around each individual hill was removed by using a sampling core. This root sample contains approximately 95% of the total root biomass (Yang et al., 2008). Plants from three hills each plot on were pooled for each measurement. Each root sample of soil was cut into two parts, each with a depth of 10 cm. The root samples of soil were carefully rinsed by a hydropneumatic elutriation device (Gillison’s Variety Fabrication Inc., Benzonia, MI, USA). After combining roots of three hills and recording their fresh weight, portions of each root sample were used for measurements of root length. The rest of the roots were dried in an oven at 70°C to a constant weight and were weighed. Root oxidation activity (ROA) was measured on the same dates as the leaf photosynthetic rate measurements. ROA was determined by measuring the oxidation of alpha-naphthylamine (α-NA) according to the method of Chu et al. (2014).

The measurement of grain yield and yield components was performed as described by Yoshida et al. (1971). Plants in the two rows on each side of the plot were discarded to avoid border effects. Grain yield was determined from a harvest area of 6.0 m² in each plot and adjusted to 14% moisture. The aboveground biomass and yield components, i.e., the number of panicles per square meter, number of spikelets per
panicle, percentage of filled grains, and grain weight, were determined in plants from a 1.0-m² random area (excluding the border ones) for each plot. The percentage of filled grains was defined as the number of filled grains (specific gravity ≥ 1.06 g/cm³) in relation to the total number of spikelets. Harvest index (HI) and WUE were calculated using the following formulas:

\[
HI = \frac{\text{total grain weight}}{\text{total above ground biomass}}
\]

\[
\text{WUE}(\text{kg/m}^3) = \frac{\text{grain yield}}{\text{the amount of water from irrigation and precipitation during the growing season}}
\] (5)

2.5 | Statistical analysis

Analysis of variance was performed using a SAS/STAT statistical analysis package (version 6.12, SAS Institute, Cary, NC, USA). The statistical model used included sources of variation due to replication, year, cultivar, irrigation

**FIGURE 2** Soil water potential of different rice cultivars under various irrigation treatments in 2015 and 2016. CF and AWSD represent continuously flooding and alternate wetting and severe drying irrigation respectively. Vertical bars represent ± SEM where it exceeds the size of the symbol.
treatment, and the interaction of year × cultivar, year × treatment and cultivar × treatment. Data from each sampling date were analyzed separately. Means were tested by the least significant difference at $p = 0.05$ (LSD 0.05).

3 | RESULTS

3.1 | Soil water potential and leaf water potential

Although the total rainfall from transplanting to maturity was greater in 2015 (668 mm) than in 2016 (498 mm), the difference in the rainfall during the mid and late growing season (from August to October) was rather small between 2015 and 2016 (299 mm in 2015, 278 mm in 2016) (Figure 1). Changes in soil water potential were similar in both years (Figure 2). If there was no rain, it took 8–10 days to reach a soil water potential of −30 kPa in the AWSD regimen depending on the plant growth stage (Figure 2). The CF regimen received 24–26 instances of irrigation, whereas in the AWSD regimen, the plants were irrigated 9–11 times from transplanting to maturity. Irrigation occurred 1–2 times less in 2015 than in 2016 due to more rainfall during the growing season in 2015 than in 2016. The differences in soil water potential were not significant between different rice cultivars when the irrigation regimen was the same (Figure 2).
Figure 3 shows the changes in the mid-day (11:30 a.m.) leaf water potential under both the CF and AWSD irrigation regimens and when soil water potentials were approximately −30 kPa in the AWSD plot. During the soil drying period, leaf water potentials were −0.56 to −0.65 MPa at D1, −0.90 to −1.23 MPa at D2 in the AWSD regimens, and significantly lower (−0.39 to −0.63 MPa) than those in the CF regimen (Figure 3). When plants were rewatered (W1 and W2), leaf water potentials showed no significant difference among different cultivars (Figure 3). The IJHR cultivars showed higher leaf water potential at D1 under the AWSD regimen, but the difference was not significant. Leaf water potential was significantly higher for the IJHR cultivars than the JIR cultivars at D2 (Figure 3), indicating that the IJHR cultivars could maintain a higher plant water content than the JIR cultivars during the growth period, especially during the ripening period.

3.2 | Agronomic traits

3.2.1 | Tiller number and percentage of productive tillers

The number of tillers varied with cultivar, irrigation treatment, and measurement period (Table 1). The JIR cultivars had more tillers than the IJHR cultivars at different measurement periods under both the CF and AWSD irrigation methods. The AWSD method significantly decreased tillers for both the JIR cultivars and the IJHR cultivars. Due to there being more rainfall in 2015 (369 mm) than in 2016...
(220 mm) during the vegetative period, tillers at jointing were higher in 2015 than those in 2016 for all of the cultivars under the AWSD regimen, especially JIR cultivars (Figure 1; Table 1). The percentage of productive tillers in the IJHR cultivars was higher than in the JIR cultivars under both the CF and AWSD irrigation methods, but more so under AWSD (Table 1). Compared to CF, the AWSD irrigation method resulted in an increase in the percentage of productive tillers for both the JIR cultivars and the IJHR cultivars, implying that AWSD could control the production of noneffective tillers for both the JIR and IJHR cultivars (Table 1).

### 3.2.2 Leaf area index and leaf area duration

Similar to its effect on the number of tillers, the AWSD irrigation regimen reduced LAI at different measurement periods as well as LAD during the total growth period (Table 2, Figure 4). The JIR cultivars have a larger LAI at the jointing stage and a greater LAD during the vegetative growth period, i.e., from transplanting to jointing, than the IJHR cultivars under the CF irrigation regimen, and no significant difference was found between the JIR cultivars and the IJHR cultivars under the AWSD irrigation regimen (Table 2, Figure 4). The

| Year and cultivar<sup>a</sup> | Irrigation regimen<sup>b</sup> | Jointing stage | Total | Effective leaf area<sup>c</sup> | Maturity |
|-------------------------------|-------------------------------|----------------|-------|-------------------------------|----------|
|                               |                               |                |       | (LAI) (%)                     |          |
| 2015                          |                               |                |       |                               |          |
| XS-09                         | CF                            | 5.51 a<sup>d</sup> | 7.02 b | 5.86 c 83.5 c 1.78 d         |          |
|                               | AWSD                          | 4.67 d         | 5.72 c | 5.06 d 88.5 b 1.35 e         |          |
| ZJ-99                         | CF                            | 5.48 a         | 7.14 b | 5.91 c 82.8 c 1.85 cd        |          |
|                               | AWSD                          | 4.71 cd        | 5.85 c | 5.13 d 87.7 b 1.29 e         |          |
| CY-927                        | CF                            | 5.04 b         | 8.12 a | 7.08 a 87.2 b 2.42 a         |          |
|                               | AWSD                          | 4.73 cd        | 7.08 b | 6.55 b 92.5 a 2.05 bc        |          |
| YY-538                        | CF                            | 5.12 b         | 7.92 a | 6.87 a 86.8 b 2.19 b         |          |
|                               | AWSD                          | 4.82 c         | 6.89 b | 6.33 b 91.8 a 1.89 c         |          |

2016

| Year and cultivar<sup>a</sup> | Irrigation regimen<sup>b</sup> | Jointing stage | Total | Effective leaf area<sup>c</sup> | Maturity |
|-------------------------------|-------------------------------|----------------|-------|-------------------------------|----------|
|                               |                               |                |       | (LAI) (%)                     |          |
| XS-09                         | CF                            | 5.42 a         | 6.85 c | 5.66 d 82.6 e 1.65 c         |          |
|                               | AWSD                          | 4.28 cd        | 5.62 d | 4.92 c 87.5 bc 1.21 d        |          |
| ZJ-99                         | CF                            | 5.31 a         | 7.03 bc| 5.87 d 83.5 de 1.76 c        |          |
|                               | AWSD                          | 4.23 cd        | 5.49 d | 4.84 e 88.1 b 1.18 d         |          |
| CY-927                        | CF                            | 5.05 b         | 7.85 a | 6.82 a 86.9 c 2.35 a         |          |
|                               | AWD                           | 4.35 c         | 6.97 c | 6.39 c 91.7 a 2.11 b         |          |
| YY-538                        | CF                            | 5.11 b         | 8.03 a | 6.90 a 85.9 cd 2.45 a         |          |
|                               | AWSD                          | 4.17 d         | 7.15 b | 6.61 b 92.5 a 2.04 b         |          |

### Analysis of variance

| Year (Y) | Cultivar (C) | Irrigation regimen (I) | Y × C | Y × I | C × I | Y × C × I |
|----------|--------------|------------------------|-------|-------|-------|-----------|
| **       | **           | **                     | **    | **    | **    | **        |
| *        | NS           | NS                     | NS    | NS    | NS    | NS        |

<sup>a</sup>XS-09 and ZJ-99 are japonica inbred cultivars; CY-927 and YY-538 are indica-japonica hybrid rice cultivars. <sup>b</sup>CF and AWSD represent continuously flooding and alternate wetting and severe drying irrigation respectively. <sup>c</sup>Effective leaf area is defined as the leaf area of the productive tillers and main stems, and the percentage of effective LAI is defined as the effective LAI as a percentage of total LAI. <sup>d</sup>Different letters indicate statistical significance at the p = 0.05 level within the same column and same year.

*, **F values significant at the P = 0.05 and P = 0.01 levels, respectively. NS means non-significant at the P = 0.05 level.
effective LAI at heading (the LAI of productive tillers + main stems), LAI at the heading and maturity stages, and LAD during the reproductive and ripening phases (from jointing to heading and from heading to maturity) were significantly higher for the IJHR cultivars than for the JIR cultivars under both CF and AWSD irrigation regimes, more so under the AWSD regimen (Table 2, Figure 4). Furthermore, the IJHR cultivars have a higher ratio of the effective LAI to the total LAI compared to the JIR cultivars under both CF and AWSD irrigation regimes (Table 2).

### 3.2.3 Shoot and root biomass

The shoot biomass at different growth stages and crop growth duration (CGR) is presented in Figures 5 and 6, respectively, for the different growth stages. Similar to tillers, shoot dry weight at the jointing stage and CGR during the vegetative period were higher in 2015 than in 2016 under the AWSD irrigation regimen due to more rainfall in 2015 (Figures 1, 5 and 6). The JIR cultivars had greater shoot biomass at jointing and stronger ability of matter production during the vegetative period under the CF irrigation method, while no significant difference was found between the JIR and the IJHR cultivars under the AWSD irrigation method (Figures 5 and 6). The IJHR cultivars showed greater shoot dry weight and CGR during the reproductive and ripening periods under both the CF and AWSD irrigation methods than the JIR cultivars at heading and maturity (Figures 5 and 6).

Root biomass under the AWSD irrigation regimen was markedly decreased for the JIR cultivars by 11.4%–17.7% when compared with those under the CF regimen, whereas it showed no significant difference between the CF and AWSD regimens for the IJHR cultivars (Table 3). The IJHR cultivars have a larger biomass than the JIR cultivars under both the CF and AWSD irrigation regimens (Table 3). When compared with the CF method, the AWSD method significantly increased the root-shoot ratio for both the IJHR cultivars and the JIR cultivars at heading, indicating that the AWSD irrigation method could promote root growth. Further observation showed that, when total root weight was divided into two parts, i.e., the 0–10 cm soil layer and the 10–20 cm soil layer, the IJHR cultivars had larger root biomass in both the 0–10 cm soil layer and the 10–20 cm soil layer than the JIR cultivars under both the CF and AWSD regimens (Table 3). We also found that IJHR cultivars had a higher deep root proportion (the proportion of root weight in the 10–20 cm soil layer) than the JIR cultivars under both irrigation methods.
soil layer to total root weight) than the JIR cultivars under both the CF and AWSD irrigation regimens, more so under AWSD, indicating a deeper root distribution in soil for the IJHR cultivars than for the JIR cultivars (Table 3).

### 3.3 Physiological traits

#### 3.3.1 ROA and leaf photosynthetic rate

Although the IJHR cultivars had higher ROA than the JIR cultivars during the early growth stage (D1 and W1) under the CF irrigation method, the difference was not significant (Table 4). However, we found that the IJHR cultivars have significantly higher ROA during the late growth stage (D2 and W2) under the CF irrigation method, indicating that the IJHR cultivars could maintain a high root activity during the ripening period (Table 4). When compared with those under the CF irrigation method, ROA was decreased during the soil-drying period (D1 and D2) for both the IJHR and the JIR cultivars, and with more reduction for the JIR cultivars (Table 4). When plants were rewatered during the early growth period (W1), ROA was pronouncedly increased for the IJHR cultivars, and there was no significant differences in the JIR cultivars between the CF and AWSD irrigation regimens (Table 4). However, when plants were rewatered during the late growth period (W2), there was also no significant difference between CF and AWSD for IJHR cultivars, but ROA was significantly lower for JIR cultivars under the AWSD irrigation regimen than those under the CF irrigation regimen (Table 4). A similar observation was made regarding the photosynthetic rate of the upmost fully expanded leaves.

#### 3.3.2 Preanthesis NSC accumulation in stems and NSC remobilization

As shown in Figure 7, for the same rice cultivar, the AWSD irrigation regimen induced a significant reduction in NSC accumulation in the stems at the heading time compared to that under the CF irrigation regimen. Also, a decrease was seen in NSC accumulation in the stems of 27.8%–31.8% for the JIR cultivars and 16.1%–19.2% for the IJHR cultivars at the heading. The AWSD irrigation regimen significantly increased the remobilization of NSC from stems for the four rice cultivars, with an increase in 9.2%–12.5% for the JIR cultivars and 14.9%–17.1% for the IJHR cultivars.
3.4 | Grain yield and WUE

When compared with that under the CF irrigation regimen, grain yield under the AWSD regimen was significantly lower for both IJHR cultivars and JIR cultivars. A decrease in yield of 23.5%–28.1% was seen under the AWSD regimen for the JIR cultivars and 14.8%–16.6% for the IJHR cultivars. Comparing the two cultivars, the IJHR cultivars showed significantly higher grain yield than the JIR cultivars under the CF and AWSD irrigation regimens (Table 5). When compared with the JIR cultivars, the IJHR cultivars showed an increase in the yield of 24.9%–25.3% under the CF irrigation regimen, and 37.8%–46.1% under the AWSD irrigation regimen. For the JIR cultivars, a lower grain yield under the AWSD irrigation regimen was mainly attributed to a reduction in number of panicles, spikelets per panicle, and percentage of filled grains. However, only the number of panicles was significantly reduced under the AWSD irrigation regimen for the IJHR cultivars. Although spikelets per panicle and percentage of filled grains were reduced under the AWSD irrigation regimen for the IJHR cultivars, the difference was not significant (Table 5).

The level of water due to irrigation throughout the growing season was 275–349 mm in the AWSD regimen, which was 49.8%–56.2% of that (552–620 mm) applied to the CF regimen (Figure 8). Compared with that under the CF irrigation regimen, WUE (grain yield over the amount of water from irrigation and precipitation) for IJHR under AWSD increased by 6.7%–9.7% and 15.1%–17.4% in 2015 and 2016 respectively. The WUE showed no significant difference between the CF and AWSD irrigation regimens for the JIR cultivars in 2015 and 2016 (Figure 8).

4 | DISCUSSION

4.1 | Agronomic and physiological traits for indica-japonica hybrid rice under alternate wetting and severe drying irrigation

Some researchers have reported that IJHR cultivars have strong biomass production and greater yield potential than JIR cultivars or indica hybrid rice cultivars (Wei et al., 2017, 2016; Yuan, 2017), and our results have confirmed the findings of earlier reports (Table 5). The present study determined that, compared to CF, the AWSD irrigation...
TABLE 3 Root biomass and root-shoot ratio of rice under different irrigation regimens

| Year and Cultivar<sup>a</sup> | Irrigation regimen<sup>b</sup> | Total root DW (g/m<sup>2</sup>)<sup>c</sup> | Ratio of root to shoot | Root DW in 0–10 cm soil layer (g/m<sup>2</sup>) | Root DW in 10–20 cm soil layer (g/m<sup>2</sup>) | Percentage of root DW in 10–20 cm to total root DW |
|-------------------------------|-------------------------------|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| 2015                          |                               |                                 |                 |                 |                 |                 |
| XS-09 CF                      | CF                            | 137.7 c<sup>d</sup>             | 0.135 c         | 87.0 b          | 50.7 c          | 36.8 c          |
| AWSD                          | 122.1 d                       | 0.143 ab                        | 71.8 d          | 50.3 c          | 41.2 b          |
| ZJ-99 CF                      | CF                            | 136.2 c                         | 0.132 c         | 88.0 b          | 48.2 cd         | 35.4 c          |
| AWSD                          | 114.1 d                       | 0.141 b                         | 68.8 d          | 45.3 d          | 39.7 b          |
| CY-927 CF                     | CF                            | 158.9 a                         | 0.133 c         | 94.1 a          | 64.8 ab         | 40.8 b          |
| AWSD                          | 155.4 ab                      | 0.148 a                         | 84.5 bc         | 70.9 a          | 45.6 a          |
| YY-538 CF                     | CF                            | 153.1 ab                        | 0.132 c         | 92.3 a          | 60.8 b          | 39.7 b          |
| AWSD                          | 148.9 b                       | 0.146 a                         | 82.9 c          | 66.0 ab         | 44.3 a          |
| 2016                          |                               |                                 |                 |                 |                 |                 |
| XS-09 CF                      | CF                            | 147.8 c                         | 0.132 d         | 96.2 ab         | 51.6 c          | 34.9 c          |
| AWSD                          | 125.9 d                       | 0.147 b                         | 77.8 d          | 48.1 cd         | 38.2 b          |
| ZJ-99 CF                      | CF                            | 141.6 c                         | 0.138 c         | 94.0 b          | 47.6 d          | 33.6 c          |
| AWSD                          | 116.6 e                       | 0.144 b                         | 74.4 d          | 42.2 e          | 36.2 b          |
| CY-927 CF                     | CF                            | 165.1 a                         | 0.135 cd        | 104.2 a         | 60.9 b          | 36.9 b          |
| AWSD                          | 160.5 ab                      | 0.153 a                         | 91.7 bc         | 68.9 a          | 42.9 a          |
| YY-538 CF                     | CF                            | 161.7 ab                        | 0.131 d         | 100.4 a         | 61.3 b          | 37.9 b          |
| AWSD                          | 158.2 b                       | 0.155 a                         | 87.8 c          | 70.4 a          | 44.5 a          |

Analysis of variance

| Source                        | Year (Y) | Cultivar (C) | Irrigation regimen (I) | Y × C | Y × I | C × I | Y × C × I |
|-------------------------------|-----------|--------------|------------------------|-------|-------|-------|-----------|
| Year (Y)                     | NS        | NS           | NS                     | NS    | NS    | NS    | NS        |
| Cultivar (C)                 | **        | **           | **                     | **    | **    | **    | **        |
| Irrigation regimen (I)       | **        | **           | **                     | **    | **    | **    | **        |
| Y × C                         | NS        | NS           | NS                     | NS    | NS    | NS    | NS        |
| Y × I                         | NS        | NS           | NS                     | NS    | NS    | NS    | NS        |
| C × I                         | **        | **           | **                     | **    | **    | **    | **        |
| Y × C × I                     | NS        | NS           | NS                     | NS    | NS    | NS    | NS        |

<sup>a</sup>XS-09 and ZJ-99 are japonica inbred cultivars; CY-927 and YY-538 are indica-japonica hybrid rice cultivars. <sup>b</sup>CF and AWSD represent continuously flooding and alternate wetting and severe drying irrigation respectively. <sup>c</sup>DW means dry weight. <sup>d</sup>Different letters indicate statistical significance at the $p = 0.05$ level within the same column and same year. *F* values significant at the $P = 0.05$ and $P = 0.01$ levels, respectively. NS means non-significant at the $P = 0.05$ level.
CHU et al. regimen reduced the irrigation input and induced a reduction in grain yield of 23.5%–28.1% in the JIR cultivars; however, the reduction was only 14.8%–16.6% in the IJHR cultivars (Table 5), and the WUE was not significantly different between the CF and AWSD irrigation regimens for the JIR cultivars. Nonetheless, the AWSD irrigation regimen significantly increased the WUE in the IJHR cultivars by 6.7%–9.7% and 15.1%–17.4% in 2015 and 2016 respectively. (Figure 8). These findings suggest that for the IJHR cultivars, the AWSD irrigation method could achieve the dual goal of sharply reducing water consumption with minimal yield penalty.

Prior to this study, little information was available about the agronomic and physiological traits associated with both high grain yield and high WUE for IJHR cultivars under an AWSD irrigation regimen. When compared with those in JIR cultivars under the AWSD irrigation regimen, the main agronomic and physiological traits that are associated with higher grain yield and WUE in the IJHR cultivars were found to be: (a) larger sink size as a result of larger spikelets per panicle (Table 5); (b) less redundant vegetative growth and higher matter production ability during reproductive and ripening periods (Figures 5 and 6); (c) larger root biomass and deeper root distribution at heading (Table 3), (d) more NSC

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### TABLE 4 Root oxidation activity and photosynthetic rate of leaves under different irrigation regimens

| Year and cultivar | Irrigation regimen | Root oxidation activity (μg α-naphthylamine g⁻¹ DW h⁻¹) | Leaf photosynthetic rate (μmol m⁻² s⁻¹) |
|------------------|-------------------|-----------------------------------------------------------|----------------------------------------|
|                  |                   | D1 | W1 | D2 | W2 | D1 | W1 | D2 | W2 |
| 2015             |                   |    |    |    |    |    |    |    |    |
| XS-09            | CF                | 484 ab | 476 bc | 282 c | 287 b | 24.4 a | 24.3 b | 18.5 d | 18.6 c |
|                  | AWSD              | 376 d | 470 c | 236 e | 267 c | 18.3 c | 23.9 b | 14.5 f | 16.7 d |
| ZJ-99            | CF                | 490 ab | 462 cd | 297 b | 296 b | 24.3 a | 24.5 ab | 19.8 c | 20.2 ab |
|                  | AWSD              | 388 d | 454 d | 230 e | 254 c | 18.6 c | 24.2 b | 14.1 f | 18.2 c |
| CY-927           | CF                | 508 a | 470 c | 317 a | 312 a | 24.6 a | 24.5 ab | 20.5 b | 20.3 ab |
|                  | AWSD              | 454 b | 518 a | 248 d | 305 ab | 20.1 b | 24.9 a | 15.9 e | 19.8 b |
| YY-538           | CF                | 498 a | 486 b | 305 ab | 296 b | 24.8 a | 24.3 a | 21.5 a | 20.9 a |
|                  | AWSD              | 442 b | 522 a | 254 d | 303 ab | 20.5 b | 24.7 a | 16.4 e | 20.5 ab |
| 2016             |                   |    |    |    |    |    |    |    |    |
| XS-09            | CF                | 488 b | 482 c | 297 b | 303 b | 24.2 ab | 23.8 bc | 18.8 c | 19.1 c |
|                  | AWSD              | 350 d | 475 c | 185 e | 243 d | 18.8 e | 23.5 bc | 15.7 e | 17.8 d |
| ZJ-99            | CF                | 497 ab | 467 cd | 280 b | 279 c | 23.8 ab | 23.1 c | 19.8 b | 19.7 b |
|                  | AWSD              | 366 d | 455 d | 210 d | 251 d | 19.4 d | 22.7 c | 15.3 e | 16.9 e |
| CY-927           | CF                | 515 a | 510 b | 323 a | 314 ab | 23.9 ab | 23.5 bc | 21.1 a | 20.8 a |
|                  | AWSD              | 435 c | 581 a | 246 c | 308 ab | 22.7 c | 25.9 a | 16.5 d | 20.3 ab |
| YY-538           | CF                | 521 a | 514 b | 308 ab | 310 ab | 24.9 a | 24.3 b | 20.3 b | 19.7 b |
|                  | AWSD              | 423 c | 555 a | 239 c | 327 a | 23.7 b | 26.1 a | 16.9 d | 20.2 ab |

Analysis of variance

| Year (Y) | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Cultivar (C) | ** | * | ** | * | ** | * | ** | * | ** |
| Irrigation regimen (I) | ** | * | ** | * | * | * | * | * | * |
| Y × C | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Y × I | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| C × I | NS | NS | NS | NS | NS | NS | NS | NS | NS |

*XS-09 and ZJ-99 are japonica inbred cultivars; CY-927 and YY-538 are indica-japonica hybrid rice cultivars. °CF and AWSD represent continuously flooding and alternate wetting and drying irrigation respectively. ‘D1 and D2 indicate 53 and 114 days after transplanting (DAT) in 2015 and 49 and 109 DAT in 2016, respectively, when soil water potential was approximately −30 kPa in the AWSD regimen. W1 and W2 denote 54 and 115 DAT in 2015 and 50 and 110 DAT in 2016, respectively, when plants were rewatered in the AWSD regimen. °Different letters indicate statistical significance at the p = 0.05 level within the same column and same year.

**, ***F values significant at the p = 0.05 and p = 0.01 levels respectively. NS means nonsignificant at the p = 0.05 level.
accumulation in the stem before heading, more NSC remobilization from the stem to the grain during grain filling, and a higher harvest index (Figure 8, Table 5); (e) higher plant activity as shown by a higher ROA and leaf photosynthetic rate during soil-drying and more recovery during rewatering during the ripening period (Table 4). We speculate that improved agronomic and physiological traits would contribute to a higher grain yield and WUE in the IJHR cultivars under the AWSD irrigation regimen.

4.2 The contribution of agronomic traits to grain yield and water use efficiency

The agronomic traits underlying the observed better yield performance and higher WUE in IJHR cultivars under the AWSD irrigation regimen is not fully understood. The present study showed that, compared to the JIR cultivars, the IJHR cultivars exhibited less redundant vegetative growth, as shown by an increase in the percentage of productive tillers as well as the ratio of the effective LAI to the total LAI at heading (Tables 1 and 2). Less redundant vegetative growth could improve canopy quality, which in turn reduces water and nitrogen utilization in unproductive tillers and increases radiation use efficiency (Yang & Zhang, 2010a), thereby leading to higher yield and WUE. We also found that the IJHR cultivars had a stronger ability to produce matter during the reproductive and ripening periods (Figures 5 and 6). The aboveground dry weight at heading time and maturity as well as CGR and LAD during the reproductive and ripening period were significantly greater for the IJHR cultivars than the JIR cultivars, especially under the AWSD irrigation regimen (Figures 4, 5, and 6). Some previous studies indicated that a greater CGR during the reproductive period could increase the sink capacity by promoting spikelet differentiation and reducing spikelet degeneration as well as increasing endosperm cell proliferation at the early seed development stage (Fageria, 2007; Horie et al., 2005). In the present study, we found that under the AWSD irrigation regimen the spikelets per panicle were reduced in the JIR cultivars by 12.1%–14.4%, while only a reduction in 1.8%–4.6% in the IJHR cultivars was found (Table 5). We suspect that the larger sink size in the IJHR cultivars might be attributable to greater CGR during the reproductive period and a higher percentage of productive tillers. It is also proposed that a greater CGR during the ripening period could also increase sink
| Year and cultivar<sup>a</sup> | Irrigation regimen<sup>b</sup> | Grain yield (t/ha) | Panicles per m<sup>2</sup> | Spikelets per panicle | Total spikelets (×10<sup>4</sup>/m<sup>2</sup>) | Filled grains (%) | Grain weight (mg) | Harvest index<sup>c</sup> (%) |
|----------------------------|-----------------------------|-------------------|-----------------|-------------------|---------------------|-----------------|------------------|--------------------|
| **2015**                  |                             |                   |                 |                   |                     |                 |                  |                    |
| XS-09                     | CF                          | 9.30 c<sup>d</sup> | 310 a           | 132 c             | 4.03 e              | 89.5 a           | 25.4 a           | 48.2 d            |
|                            | AWSD                        | 7.11 d            | 275 b           | 115 d             | 3.14 f              | 87.5 b           | 25.7 a           | 49.5 bc           |
| ZJ-99                     | CF                          | 9.59 bc           | 320 a           | 140 c             | 4.54 d              | 87.4 b           | 24.5 bc          | 47.9 d            |
|                            | AWSD                        | 7.34 d            | 288 b           | 123 d             | 3.51 f              | 85.3 c           | 24.3 c           | 49.6 b            |
| CY-927                    | CF                          | 12.01 a           | 175 d           | 320 a             | 5.70 b              | 87.2 b           | 24.6 b           | 49.2 c            |
|                            | AWSD                        | 10.05 b           | 155 e           | 305 b             | 4.58 d              | 86.8 b           | 24.5 bc          | 50.5 a            |
| YY-538                    | CF                          | 11.59 a           | 197 c           | 309 ab            | 6.30 a              | 85.4 c           | 22.3 d           | 48.8 c            |
|                            | AWSD                        | 9.87 b            | 176 d           | 295 b             | 5.25 c              | 84.9 c           | 22.4 d           | 50.7 a            |
| **2016**                  |                             |                   |                 |                   |                     |                 |                  |                    |
| XS-09                     | CF                          | 9.75 c            | 305 a           | 138 c             | 4.28 d              | 90.5 a           | 25.6 a           | 47.8 d            |
|                            | AWSD                        | 7.03 d            | 273 b           | 118 d             | 3.25 e              | 86.3 b           | 25.3 a           | 50.5 b            |
| ZJ-99                     | CF                          | 9.96 bc           | 324 a           | 137 c             | 4.38 d              | 91.2 a           | 24.6 b           | 48.2 d            |
|                            | AWSD                        | 7.16 d            | 285 b           | 120 d             | 3.46 e              | 86.2 b           | 24.3 b           | 50.3 b            |
| CY-927                    | CF                          | 12.06 a           | 178 d           | 325 a             | 5.69 b              | 85.8 b           | 24.3 b           | 49.5 c            |
|                            | AWSD                        | 10.19 c           | 150 e           | 319 ab            | 4.79 c              | 86.2 b           | 24.7 b           | 51.2 a            |
| YY-538                    | CF                          | 12.64 a           | 204 c           | 323 ab            | 6.36 a              | 84.9 c           | 22.6 c           | 49.3 c            |
|                            | AWSD                        | 10.55 b           | 178 d           | 312 b             | 5.32 b              | 84.4 c           | 22.5 c           | 51.5 a            |

**Analysis of variance**

|                  | Year (Y) | Cultivar (C) | Irrigation regimen (I) | Y × C | Y × I | C × I | Y × C × I |
|------------------|----------|--------------|------------------------|-------|------|------|----------|
| **Year (Y)**     | NS       | **          | NS                     |       |      |      | NS       |
| **Cultivar (C)** | NS       | NS          | NS                     |       |      |      | NS       |
| **Irrigation regimen (I)** | NS | NS | NS |       |      |      | NS | **         |
| **Y × C**        | NS       | NS          | NS                     |       |      |      | NS       |
| **Y × I**        | NS       | NS          | NS                     |       |      |      | NS       |
| **C × I**        | NS       | NS          | NS                     |       |      |      | NS       |
| **Y × C × I**    | NS       | NS          | NS                     |       |      |      | NS       |

<sup>a</sup>XS-09 and ZJ-99 are *japonica* inbred cultivars; CY-927 and YY-538 are *indica-japonica* hybrid rice cultivars. <sup>b</sup>CF and AWSD represent continuously flooding and alternate wetting and severe drying irrigation respectively. <sup>c</sup>Total grain weight (dry weight)/total aboveground biomass (dry weight). <sup>d</sup>Different letters indicate statistical significance at the $p = 0.05$ level within the same column same year. <sup>e</sup>,**F** values significant at the $p = 0.05$ and $p = 0.01$ levels respectively. NS means nonsignificant at the $p = 0.05$ level.
strength and source activity, resulting in enhanced grain filling (Zhang et al., 2013). Therefore, we propose that the ability of less redundant vegetative growth during the vegetative period and more dry matter production during the reproductive and ripening period are important agronomic traits underlying higher grain yield and WUE for the IJHR cultivars under the AWSD irrigation method.

Root biomass has been regarded as the most important root morphological trait (Palta & Yang, 2014; Zhang et al., 2017). Some previous studies indicated that a larger root biomass could absorb more nitrogen and water from soil and support a greater rate of aboveground biomass production (Yang, Yang, Yang, & Zhu, 2004; Zhang, Xue, Wang, Yang, & Zhang, 2009). In this study, we observed that the IJHR cultivars have larger root biomass than JIR cultivars at the heading stage under both the CF and AWSD irrigation regimens, particularly under the AWSD irrigation regimen (Table 3). It is believed that a large root biomass is required to support a large aboveground biomass production (Garnett, Conn, & Kaiser, 2009; Yang et al., 2012); we thus infer that improvements in root growth contribute to greater shoot biomass production, higher grain yield, and better WUE in the IJHR cultivars. Previous studies have suggested that plants with deeper root distributions in the soil maintain a high plant water status under drought conditions and absorb more water from deep soil under a water-saving irrigation regimen or soil water deficit, which consequently contributes to higher water and nitrogen utilization efficiency (Chu et al., 2015, 2018). In the present study, we detected a higher root biomass at the 10–20 cm soil depth in the IJHR cultivars than that in the JIR cultivars, particularly under the AWSD irrigation regimen (Table 3). We speculate that a deeper root distribution in the soil for IJHR cultivars contributes to more water uptake from deeper layers of soil under the AWSD irrigation regimen. Therefore, we conclude that a larger root biomass, particularly a deeper root distribution, contributes to a higher grain yield and WUE in the IJHR cultivars under the AWSD irrigation regimen.

4.3 Physiological mechanism involved in higher grain yield and higher WUE

The physiological activity of roots is an important component of the physiological characteristics of rice. Higher root
physiological activity also plays a significant role in slowing leaf senescence, prolonging the grain-filling stage, and enriching the grain (Yang et al., 2012). The ROA has been regarded as the most important root physiological trait, and a higher ROA is necessary to maintain root biomass, root and shoot growth, and ion uptake (Ramasamy, tenBerge, & Purushothaman, 1997; Yang et al., 2004). Some previous studies indicated that AWMD could enhance root activity during mid- or late-grain filling stages (Chu et al., 2016; Wang et al., 2016)). The present results indicated that the IJHR cultivars had higher ROA during the soil drying period when compared with JIR cultivars under the AWSD irrigation regimen, especially at the second soil drying time (Table 4). Furthermore, ROA had increased more for the IJHR cultivars than for the JIR cultivars during the rewatering time (Table 4). The results imply that the IJHR cultivars have a better ability to maintain their physiological functions under drought and recover their functions after the stress has passed. We argue that the ability of roots to maintain their activity during soil drying and recover their function during rewatering is an important physiological trait for the IJHR cultivars to achieve the dual goal of mild production shortages in grain yield and saving water under the AWSD irrigation regimen.

Grain yield can be defined as the product of yield sink capacity and filling efficiency (Kato & Takeda, 1996). It is generally believed that the IJHR cultivars have more spikelets per panicle/square meter than the JIR cultivars. However, there is often a negative correlation between yield sink capacity and filling efficiency (Venkateswarlu & Visperas, 1987). However, in the present study, the grain filling rate showed no significant difference for the IJHR cultivars between the CF and AWSD irrigation regimens, while a significant reduction in the grain filling rate was induced by the AWSD irrigation regimen for the JIR cultivars. How could IJHR cultivars maintain a high grain filling rate under the AWSD irrigation regimen? The mechanism is unclear. Based on our observations in this study, there could be two possible explanations. First, a greater CGR and LAD during the ripening period could enhance grain filling (Figures 4 and 6). Second, an enhancement promoted prestored carbon remobilization from the stems during the ripening period could increase the grain filling rate (Figure 8). Herein we found that, when compared with the CF regimen, NSC accumulation in the stems at the heading stage was significantly reduced for both the IJHR and the JIR cultivars under the AWSD irrigation regimen, and the AWSD reduced NSC accumulation in the stems by 27.8%–31.8% for the JIR cultivars and by 16.1%–19.2% for the IJHR cultivars. We also found that the AWSD irrigation regimen intensified NSC remobilization from the stems to the grains during the ripening period in all rice cultivars, particularly in the IJHR cultivars (Figure 8). Past research has shown that increasing carbon remobilization from vegetative tissues to grains contributes to a higher rice grain yield (Yang & Zhang, 2010b). We speculate that the enhanced remobilization of accumulated NSC from the stems to the grain during the ripening period contributes to an increase in grain filling efficiency and a higher HI under the AWSD regimen, thus leading to better yield performance and higher WUE.

There is no doubt that an AWD irrigation regime could reduce irrigation water input (Carrijo et al., 2017; Norton et al., 2017; Yang et al., 2007). In the present study, the AWSD irrigation regimen significantly decreased grain yield of both the IJHR and the JIR cultivars, but it is also remains debatable whether the AWD irrigation regime could increase or maintain grain yield. A meta-analysis study analyzed 56 studies with 528 side-by-side comparisons of AWD with CF, found that AWD decreased rice grain yield by 5.4% (Carrijo et al., 2017). However, some studies come from southeast China have shown that a AWMD irrigation method could increase grain yield and water productivity (Chu et al., 2015; Yang et al., 2007; Yang, Huang, Duan, Tan, & Zhang, 2009; Zhang et al., 2009; Zhou et al., 2017); elevated hormonal levels, in particular increases in abscisic acid levels during soil drying and cytokinin levels during rewatering; and enhanced carbon remobilization from vegetative tissues to grain (Yang et al., 2017; Zhang, Chen, Wang, Yang, & Zhang, 2010; Zhang et al., 2012). Furthermore, AWMD could reduce CH₄ emissions from the paddy field, thereby decreasing global warming potential and greenhouse gas intensity (Chu et al., 2015).

In the present study, there were on any rainproof equipment in both two study years, and we suspected that the rainfall might influence irrigation water input, grain yield and WUE. The rainfall was greater in 2015 (668 mm) than in 2016 (498 mm) during the growing season, and the irrigation water input was increased by 11.8% in 2016 than in 2015. Due to more rainfall during the early growth period in 2015 (369 mm), both the IJHR cultivars and the JIR cultivar have more tillers, greater shoot dry weight and higher LAI at jointing, and greater CGR and LAD during the vegetative period than in 2016. Although rainfall could enhance rice growth during the vegetative period, grain yield and WUE almost the same between two study years under AWSD. We suspected that rainfall have a significant impact on irrigation water input and no effect on grain yield and WUE under the AWSD irrigation regimen.

Besides water, N is another factor that plays a crucial role in increasing farm yield in rice production (Kamiji,
Yoshida, Palta, Sakuratani, & Shiraiwa, 2011). However, NUE in China is considerably lower than the world average (Ju et al., 2009). How to improve NUE is another important problem in rice production. Varietal improvement and crop management are two important ways to increase NUE in rice production. Previous studies indicated that the IJHR cultivars had higher grain yield and NUE than the main locally grown cultivars (Wei et al., 2017, 2016). Whether AWD-based irrigation could increase N uptake and NUE is still debatable. Some researchers have indicated that the adoption of an AWD irrigation regime may reduce the total N uptake in plants due to increases in N losses through ammonia volatilization, nitrification, and denitrification ((Eriksen, Kjeldby, & Nilsen, 1985; Sah & Mikkelsen, 1983). However, many other researchers reported that an AWD-based water-saving irrigation regimen could increase the total cumulative plant N and NUE (Wang et al., 2016; Xue et al., 2013). Further research on the interactions between the AWD irrigation method and N management on the grain yield of IJHR cultivars, NUE, and WUE should be conducted.

5 | CONCLUSIONS

Compared with the JIR cultivars, the IJHR cultivars possess not only a greater yield potential under the CF irrigation regimen but also better yield performance and higher WUE under the AWD irrigation regimen. Larger sink size, deeper root distribution, less redundant vegetative growth, higher matter production ability during the reproductive and ripening period, higher ROA and leaf photosynthetic rates during soil-drying, more recovery during rewetting, a higher rate of NSC accumulation in the stems before heading, and larger NSC remobilization from the stem during the ripening period are important agronomic and physiological traits that are closely related to higher grain yield and WUE in the IJHR cultivars subjected to the AWD irrigation regimen.

ACKNOWLEDGMENTS

We are grateful for grants from the National Key Research and Development Program of China (Grant Nos. 2016YFD0300108 and 2016YFD0300507), the National Natural Science Foundation of China (Grant nos. 31501264, 31671638 and 31501264), the National Rice Industry Technology System (Grant No. CARS-01).

CONFLICT OF INTEREST

None declared.

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None declared.
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How to cite this article: Chu G, Chen T, Chen S, Xu C, Wang D, Zhang X. The effect of alternate wetting and severe drying irrigation on grain yield and water use efficiency of Indica-Japonica hybrid rice (*Oryza sativa* L.). *Food Energy Secur*. 2018;7:e00133. https://doi.org/10.1002/fes3.133