INTRODUCTION

Phosphorus (P) is an essential macronutrient for plant growth and development (Baker et al., 2015; Plaxton & Tran, 2011). Compared to nitrogen (N), P is a non-renewable resource. Despite large amounts of organic and inorganic P in natural soils, only 0.1% of the total P is available to plants because of the low solubility and rapid conversion of P compounds to unavailable or less available P after fertilizer application in the soil (Bhadouria et al., 2017; Wang...
et al., 2020). Moreover, the leaching and run-off also result in the loss of chemical P fertilizer (Carvalho, 2017; Kochian, 2012). Thus, P deficiency or low P availability is one of the limiting factors to crop production. How to alleviate or resolve P deficiency in the soil to increase crop production capacity is a major common concern. Although the application of P fertilizer alleviates the problem to some extent, it is a finite resource that is slowly depleting (Cordell et al., 2009). Therefore, enhancing the phosphorus use efficiency (PUE) in major grain crops worldwide is imperative. To date, two main pathways have been developed and utilized. Firstly, optimizing techniques for applying P fertilizer, that is, the coated P fertilizer and combined application of inorganic fertilizers and manure (Samavini et al., 2018), and secondly, breeding and screening varieties with high PUE (Zhou et al., 2016). Typically, the change in the valence of the compound (iron-, aluminum-, and calcium-inorganic phosphate) that binds to P in the soil is closely associated with the decrease in the redox potential of soil in a flooded environment, and hence, P that is fixed in the soil is released to increase P availability (Huguenin-Elie et al., 2009). From a long-term point of view, breeding and screening varieties with high PUE and enhancing biological P availability through cultivation techniques are crucial for sustainable production and food security.

Rice (Oryza sativa L.), as a staple food crop, requires huge amounts of P. Interestingly, significant genotypic variations have been observed in P acquisition and utilization, which offers the possibility for breeding and screening varieties with high PUE (Wissuwa, 2005). Ni et al. (1996) reported significant differences among five rice genotypes in shoot and root biomass and in PUE and tiller number under hydroponics and pot culture. Wissuwa and Ae (2001) investigated the P uptake of 30 rice genotypes and observed a high variation for P uptake (0.6–12.9 mg P per plant). Several recent studies in rice and other crops have reported that using genotypes with high P-uptake efficiency is the best approach for P-deficient soils, while genotypes with P efficiency produce sufficient dry matter per unit of P consumption (Bilal et al., 2018; Iqbal et al., 2019; Sandaña, 2016; Shimamura et al., 2020). Typically, low P (LP) limits the aboveground growth of rice (i.e., number of tillers, shoot biomass, leaf area index (LAI), and leaf photosynthetic rate), and varieties with strong tolerance to LP could adapt to LP environment by increasing the root growth (Deng et al., 2020). P-efficient plants are defined as those that could produce high yields per phosphorus applied or absorbed compared with other plants grown under similar agroecological conditions (Fageria et al., 2013). The mechanism underlying tolerance to LP has been investigated, such as root architecture and activity (Niu et al., 2013), genetic control of P transporters, that is, AtPT1, AtPT2 (Panigrahy et al., 2009), and rhizosphere environment (Ziegler et al., 2016). One such locus which is believed to be important is the recent identification of the PUP1 locus from rice which contains a putative kinase gene called phosphate starvation tolerance 1 (PSTOL). The gene helps rice tolerate low P conditions (Vigueira et al., 2016). However, the majority of the studies mainly focused on the seedling stage or certain growth stage, while little information was available with regard to the agronomic and physiological traits of rice varieties with differential tolerance to LP during the whole growing season.

Rice is also the largest consumer of water among all crops; it consumes approximately 80% of the total irrigated freshwater resources in Asia (Bouman, 2007). About 50% of the world’s rice production is affected by water deficit (Lal et al., 2012). A major challenge in rice production in Asia is to cope with a decline in the availability of fresh water without compromising the grain yield. In order to reduce the water input in irrigated rice, water-saving regimes can be introduced, such as alternate wetting and drying (AWD) irrigation (Belder et al., 2007; Pearson et al., 2018; Zhang et al., 2018), aerobic rice system (Lampayan et al., 2010) and non-flooded mulching cultivation (Zhang et al., 2009). Among these technologies, AWD irrigation is characterized by several repeated soil drying and re-wetting cycles. It has been reported that AWD reduces the irrigation water by 30–35% due to a decrease in the number of irrigation events and maintains or increases the grain yield and nitrogen use efficiency through reduced unproductive tillers, enhanced root growth, and increased photosynthesis and harvest index (Song et al., 2019; Sriprirom et al., 2019; Yang et al., 2007, 2017; Zhang et al., 2010). On the other hand, AWD reduces the grain yield compared to continuously submerged conditions and therefore has not been widely adopted (Belder et al., 2007; Carrijo et al., 2017). Haygarth et al. (1998) reported that AWD releases molybdate-reactive P, which is the main form of P that plants absorb from the soil. Recent studies showed that AWD increases the grain yield and also water and phosphorus use efficiency (Acosta-Motos et al., 2020; Song et al., 2021; Xu et al., 2020). Therefore, breeding and screening rice varieties with tolerance to LP and adoption of appropriate water management is one of the effective approaches to mitigate the effect of LP and limited water availability on rice production. Moreover, understanding the agronomic and physiological traits that are associated with tolerance to LP is very important in breeding varieties with high PUE and in optimizing water management strategies.

The objective of the study was to investigate whether and how an alternate wetting and drying regime could influence the tolerance to LP in rice varieties. The seasonal changes in agronomic and physiological traits of rice shoots and roots were observed; the activities of sucrose-phosphate synthase (SPS) in stems and sucrose synthase
(SuS) in grains, malondialdehyde (MDA) content, peroxidase (POD) activity, and abscisic acid (ABA) content in grains during grain filling were investigated; and the correlations of agronomic and physiological traits with grain yield and its components, non-structural carbohydrate (NSC) remobilization, PUE, and water use efficiency (WUE) were analyzed. This study would provide new insight into the mechanism underlying the tolerance to LP in rice varieties under an AWD regime, and provide valuable information for breeding varieties and high-yield cultivation of rice with high PUE.

2 | MATERIALS AND METHODS

2.1 | Plant materials and growing condition

A pot experiment was conducted outdoors in 2018 and repeated in 2019 at a research farm in Yangzhou University, Jiangsu Province, China (32°30'N, 119°25'E) during the rice-growing season (May to October). One variety with strong tolerance to LP, Yanjing 2 (YJ2, a japonica inbred), and another variety with weak tolerance to LP, Zhendao 88 (ZD88, a japonica inbred), were used. The tolerance to LP variety was evaluated and classified with reference to LP tolerance index ([grain yield of tested variety in low P× (grain yield of tested variety in LP / average grain yield of all tested varieties in LP)] / dry matter index (shoots dry weight of tested variety in LP / shoots dry weight of tested variety in control)) in our earlier work (Li et al., 2018). The two varieties have similar growth period from sowing to maturity, and seeds were obtained from Yangzhou Seed Co. (Yangzhou, Jiangsu, China). The seedlings were raised in the seedbed with sowing date on 11–12 May and transplanted to porcelain pots on 10–11 June with three hills per pot and two seedlings per hill. Plant density of the two rice varieties in production was 20–28 hills per square meter in the field-grown condition. In our study, each treatment had 50 pots as replicates, and the pots were arranged with the distance at 15 cm between two pots and 24 hills per square meter, which was similar to the plant density in the field-grown condition (Yang et al., 2004). The two rice varieties flowered at the same time in the same P level. The heading date (50% of plants) was on 14–16 August in NP and on 21–23 August in LP for both cultivars. Plants were harvested 55 days after heading. The pot was kept at 1–2 cm water level during the first 9 days after transplanting. The precipitation, solar radiation, and mean temperature during the rice-growing season across the two years measured at a weather station close to the experimental site are shown in Table S1. Weeds, insects, and diseases were controlled by either chemical or manual methods to avoid yield loss.

2.2 | Irrigation regimes and P treatment

The experiment was a 2 × 2 × 2 (two P levels, two irrigation regimes, and two varieties) factorial design with 8-treatment combinations. Each treatment had 50 pots as replicates. Each porcelain pot (30 cm in height and 25 cm in diameter, 14.72 L in volume) was filled with 20 kg soil. The soil contained 6.8 mg/kg Olsen-P, and was taken as a low phosphorus level treatment (LP), which was mixed with sandy loam soil (Typic fluvaquents, Entisols, U.S. taxonomy) and fine sand at the ratio of 4:1. The main properties of the mixed soil were as follows: 0.91 g/kg total N, 0.152 g/kg total P, 3.17 g/kg total K, 19.3 g/kg organic matter, 79.7 mg/kg alkali-hydrolyzable N, and 51.7 mg/kg exchangeable K. The moisture capacity was 0.181 g/g, and the bulk density of the soil was 1.25 g cm⁻³. Half of the total pots were chosen as optimal phosphorus level treatment (NP) by applying P fertilizer. 1.54 g KH₄PO₄ was applied into each NP-pot at pre-transplanting, and the soil of NP contained 46.9 mg/kg Olsen-P. In order to maintain equal K supply in both LP and NP, 0.85 g KCl was applied into each LP-pot at pre-transplanting. At pre-transplanting (1 day before transplanting), 1 g N as urea was applied into the soil in each pot for both LP and NP treatments. Nitrogen as urea was also applied at the stages of early tillering (7 days after transplanting, DAT), panicle initiation (the first appearance of differentiated apex), and the initial of spikelet differentiation (the appearance of glumous flower primordia at the tips of elongating primary rachis-branches), with the N rate at 0.6, 0.6 and 0.4 g/pot, respectively. The dates of nitrogen application across the two years are shown in Table S2.

Irrigation treatments consisted of two irrigation regimes including continuous flooding (CF) and alternate wetting and moderate soil drying (AWD), and were applied from 10 days after transplanting to maturity. The CF treatment maintained a continuous flood with 1–2 cm water depth (soil water potential 0 kPa) except drainage at the mid-season until one week before the final harvest. In the AWD treatment, pots were not irrigated until soil water potential reached −15 kilopascal (kPa) at 15–20 cm depth by manually applying water. Soil water potential of −15 kPa in the AWD treatment was chosen because our earlier work (Yang et al., 2007; Zhang et al., 2009) has shown that grain yield was not significantly decreased under such a regime compared with that under the CF regime. Soil water potential in each pot under AWD was monitored at 15–20 cm soil depth with a tensionmeter consisting of a sensor of 5 cm length (Institute of Soil Sciences, Chinese Academy of Sciences, Nanjing, China), and readings were recorded at 1200 h each day. When the readings dropped to the designed values, 0.4 L of tap water was added manually to each pot for the AWD treatment. The pots were placed in a field and sheltered from rain by a removable polyethylene
southeast during rain. Soil water potential change throughout the growing season of rice was recorded in Figure S1. In high-yield paddy fields environment, water loss mainly come from evapotranspiration and percolation. Generally, there is plow layer at the bottom which could prevent percolation effectively (Tan et al., 2013). Although there was no percolation in our pot study, it took 4–6 days to reach soil water potential of −15 kPa at 15–20 cm soil depth due to less irrigation water in pots which was consistent with our previous fields studies (Yang et al., 2004, 2007; Zhang et al., 2009).

2.3 | Sampling and measurements

Plants in 10 pots for each treatment were tagged to observe the tiller number. The observation was made at mid-tillering (23–24 June), panicle initiation (9–11 July in NP, 15–17 July in LP), heading time (14–16 August in NP, 20–22 August in LP), and maturity (8–10 October in NP, 14–16 October in LP). The percentage of productive tillers was defined as the number of panicles developed from tillers and main stems at maturity as a percentage of the number of tillers and main stems at the panicle initiation. At the aforementioned growth stages, the plants of four pots from each treatment were sampled for the measurement of the shoot and root biomass, root oxidation activity (ROA), and acid phosphatase (APase, EC 3.1.3.2) activity in roots. All plant samples were separated into leaf, stems (culms +sheaths), roots, and panicles (at heading time and maturity). Then, the roots were carefully rinsed with a hydropneumatic elutriation device (Gillison’s Variety Fabrications, Benztiona, MI, USA). The sampled roots were divided into three parts: One part was used for measurements of ROA, and the other two were used for the measurement of APase activity and root biomass, respectively. The dry matter of the shoots and roots was determined after drying at 70°C to constant weight and weighed. The ROA was determined by measuring the oxidation of alpha-naphthylamine with reference to the methods of Ramasamy et al. (1997) and was expressed as μg α-NA per gram dry weight (DW) per hour (μg α-NA/g DW/h). The APase activity in the roots was analyzed using the method of Tabatabai and Bremner (1969), and was expressed as mmol/min/g FW.

The NSC content in the stems at heading time and maturity was measured according to the method described by Yoshida et al. (1976). The NSC remobilization and contribution were calculated using the formulas:

\[
\text{Remobilized NSC}(\%) = \frac{\text{NSC in the stems at heading time} - \text{NSC in the stems at maturity}}{\text{NSC in the stems at heading time}} \times 100 \tag{1}
\]

\[
\text{NSC contribution to grain}(\%) = \frac{\text{NSC in the stems at heading time} - \text{NSC in the stems at maturity}}{\text{Total grain yield}} \tag{2}
\]

Tissue P content was determined by the Inductively Coupled Plasma Emission Spectrometer (ICP) (iCAP6300, Thermo sFisher Scientific, CA, USA). The phosphorus translocation efficiency (PTE), internal phosphorus efficiency (IPE), and phosphorus harvest index (PHI) were calculated using the following formulas:

\[
\text{PTE}(\%) = \frac{P_h - P_m}{P_m} \times 100 \tag{3}
\]

\[
\text{IPE}(kg kg}^{-1}) = \frac{Y}{P_{tm}} \tag{4}
\]

\[
\text{PHI}(\%) = \frac{P_g}{P_{tm}} \times 100 \tag{5}
\]

Where \( P_h \) and \( P_m \) are the P uptake of the stem, sheath, and leaf at heading time and maturity (g per plant), respectively. \( Y \) is grain yield (g m\(^{-2}\)). \( P_g \) and \( P_{tm} \) are the P uptake of grains and plants at maturity (g per plant), respectively.

The photosynthetic rate was measured at the aforementioned growth stages using a gas exchange analyzer (Li-Cor 6400 portable photosynthesis measurement system, Li-Cor). The measurement was made from 0900 to 1100 h, when photosynthetic active radiation above the canopy was 1300 to 1500 μmol m\(^{-2}\) s\(^{-1}\). Ten leaves were used for each treatment. Leaf chlorophyll content was measured using a SPAD meter (SPAD-502, Minolta, Japan).

At the heading time, 35–40 panicles on the same day were chosen and tagged from each treatment. Ten to fifteen tagged panicles were sampled at the early-, middle-, and late-grain filling stages, namely 13, 26, and 39 days after heading time from each treatment, respectively. All grains were removed from each panicle. The sampled grains were frozen in liquid nitrogen for 3 min and then stored at −80°C for measuring the contents of MDA and ABA and the activities of POD, SuS, and SPS. The MDA content was assayed via the thiobarbituric acid (TBA) reaction (Heath & Packer, 1968). The POD activity was assayed by the method described by Cakmak and Marschner (1992). The SuS activity was determined according to the method of Yang et al. (2003). A modified method for SPS extraction was used (Yang et al., 2001), and the activity was assayed under limiting substrate conditions according to the method of Huber and Huber (1990). The enzyme activity was expressed as μmol/mg protein/h. The methods for extraction and purification of ABA were modified from those described by Bollmark et al. (1988) and He (1993). The quantification of ABA was performed using high-performance
liquid chromatography-electrospray ionization-tandem mass spectrometry (HPLC-ESI-MS/MS) system (Thermo Fisher Scientific) according to the protocol of Cao et al. (2018).

### 2.4 Final harvest

Plants of 10 pots from each treatment were harvested at maturity for the measurement of grain yield, which was then adjusted to a moisture content of 0.14 g H2O/g fresh weight. The percentage of filled grains was defined as the filled grains (specific gravity ≥1.06 g/cm³) as a percentage of total number of spikelets. The number of spikelets per panicle = grain yield per pot determined from 10 pots / (number of panicles per pot ×1000-grain weight ×percentage of filled grains). WUE was calculated using the formula: WUE = grain yield (g/pot) / the amount of irrigation water (m³).

### 2.5 Soil Olsen-P analysis

Topsoil (depth: 0–20 cm) was sampled in 5 pots from each treatment after harvest. Then, the soil samples were air-dried at room temperature and sieved to 2 mm for analysis. Subsequently, the extracts were tested using the molybdenum blue method. Olsen-P was measured using sodium bicarbonate (NaHCO₃, pH 8.5).

### 2.6 Statistical analysis

Analysis of variance (ANOVA) was performed using the SAS/STAT statistical analysis package (version 9.2, SAS Institute). The plots were generated using SigmaPlot 10.0 software. The means were tested by the least significant difference at $p = 0.05$ (LSD_{0.05}). R software (Corrplot, version 3.5.1, https://cran.r-project.org) was applied to calculate the Pearson’s correlation coefficient, redundancy analysis (RDA) and perform graphing.

ANOVA showed significant differences in the grain yield, PUE, WUE, and agronomic and physiological traits of rice shoots and roots between/among treatments (P levels and irrigation regimes), varieties, and the interaction between the treatment and the variety; however, no significant differences were detected between years and the interaction of year ×treatment, year ×variety, and year ×treatment × variety (Table S3).

### 3 RESULTS

#### 3.1 Grain yield, PUE, and WUE

Compared with NP, LP significantly reduced the grain yield by 11.0% for YJ2 with strong tolerance to LP and 24.8% for ZD88 with weak tolerance to LP, in both years and on average (Table 1). LP increased the percentage of filled grains

| Year | P level† | Irrigation regime | Variety | Panicles per pot | Spikelets per panicle | Filled grains (%) | Grain weight (mg) | Grain yield (g/pot) |
|------|----------|-------------------|---------|------------------|----------------------|------------------|------------------|-------------------|
| 2018 NP CF | ZD88 | 24.8 c d | 118.5 b | 82.2 d | 24.3 c | 58.7 b |
| | YJ2 | 28.5 a | 100.3 e | 83.6 cd | 23.5 d | 56.2 b |
| | AWD | ZD88 | 23.5 d | 125.7 a | 85.7 c | 24.6 bc | 62.3 a |
| | YJ2 | 27.0 b | 110.5 c | 88.1 b | 24.1 cd | 63.4 a |
| | LP CF | ZD88 | 20.5 e | 98.1 ef | 85.8 c | 25.6 b | 44.2 d |
| | YJ2 | 25.6 c | 90.0 g | 87.7 bc | 25.2 b | 50.9 c |
| | AWD | ZD88 | 19.3 e | 105.5 d | 88.1 b | 26.3 a | 47.2 d |
| | YJ2 | 24.3 cd | 96.5 f | 91.8 a | 25.8 ab | 55.5 b |
| 2019 NP CF | ZD88 | 24.5 bc | 120.4 b | 81.1 d | 24.1 d | 57.7 b |
| | YJ2 | 28.3 a | 102.4 de | 83.5 c | 23.2 e | 56.1 b |
| | AWD | ZD88 | 23.2 c | 128.1 a | 85.1 bc | 24.7 c | 62.5 a |
| | YJ2 | 26.8 a | 112.2 c | 88.3 b | 23.9 d | 63.5 a |
| | LP CF | ZD88 | 20.2 d | 99.2 e | 84.2 c | 25.7 b | 43.4 d |
| | YJ2 | 25.3 b | 90.1 f | 88.4 b | 25.1 c | 50.5 c |
| | AWD | ZD88 | 19.0 d | 106.1 d | 87.4 b | 26.4 a | 46.5 d |
| | YJ2 | 24.0 bc | 97.2 e | 92.7 a | 25.9 ab | 55.9 b |

†NP and LP represent optimal phosphorus level and low phosphorus level, respectively.

‡Different letters indicate statistical significance at the $p = 0.05$ level within the same column and same year.
and grain weight of the two rice varieties, and decreased the number of panicles and spikelets per panicle, relative to NP. Compared with CF, AWD significantly increased the grain yield of YJ2 and ZD88 with an average yield increase of 13.0% and 7.2% in NP, and 9.9% and 7.0% in LP, respectively (Table 1). The increase in grain yield under AWD at the two P levels was mainly due to the higher spikelet number per panicle, a greater percentage of filled grains and grain weight than those under CF (Table 1).

Compared with NP, LP significantly increased PTE, IPE, and PHI by 15.1%, 114.1%, and 28.2% for YJ2 and by 5.9%, 37.9%, and 45.0% for ZD88, respectively, on average (Table 2). In LP, PTE and IPE were higher for YJ2 than those for ZD88. Compared with CF, AWD significantly increased PTE, IPE, and PHI by 38.2%, 19.1%, and 18.3% in NP, and 10.3%, 5.8%, and 6.0% in LP, respectively, for both rice varieties in the two P levels, on average (Table 2). The concentrations of P in plant tissues at heading time and maturity are presented in Figure S2.

In comparison with NP, LP decreased the water demand (Table 3). The irrigation water input and the irrigation times in LP were reduced by 18.7% and 5 under CF, and by 11.4% and 2 under AWD, respectively. Compared with CF and on average, AWD significantly increased WUE by 50.6% for YJ2 and 46.7% for ZD88 relative to NP. Compared with CF, AWD significantly increased WUE by 10.3%, 5.8%, and 6.0% in LP, respectively, for both rice varieties in the two P levels, on average (Table 3).

The above results suggest that the variety of YJ2 with strong tolerance to LP exhibited higher grain yield than the variety of ZD88 with weak tolerance to LP. Also, AWD could mitigate the effect of low P on rice growth and increase the phosphorus and water use efficiencies, with more increase for YJ2 than for ZD88.

### 3.2 | Shoot agronomic and physiological traits

LP significantly decreased the number of tillers by 12.8% for YJ2 and 18.8% for ZD88 when compared with NP (Table 4). However, LP increased the ratio of productive tillers by 6.3% for YJ2 and 4.4% for ZD88 relative to NP. Compared with CF, AWD increased the ratio of productive tillers by 4.4% for YJ2 and 3.7% for ZD88 in NP, and 3.5% for YJ2 and 2.2% for ZD88 in LP, respectively (Table 4).

LP significantly decreased the shoot dry weight by 14.0% for YJ2 and 23.2% for ZD88 compared with NP (Figure 1a,b). Compared with CF, AWD significantly increased the shoot dry weight by 10.6% for YJ2 and 7.4% for ZD88 in NP, and 9.1% for YJ2 and 6.7% for ZD88 in LP (Figure 1a,b). Moreover, compared with NP, LP significantly decreased the NSC accumulation in the stem and sheath at heading time and maturity, and increased the NSC remobilization and contribution of NSC to grains except for ZD88 under AWD (Table 5). Compared with CF, AWD significantly increased the NSC remobilization by 52.4% for YJ2 and 46.2% for ZD88 in NP, and 17.9% for YJ2 and 16.6% for ZD88 in LP, and the contribution of NSC to grains by 56.7% for YJ2 and 56.6% for ZD88 in NP, and 25.2% for YJ2 and 21.9% for ZD88 in LP (Table 5).

| Year | P level† | Irrigation regime | Variety | PTE (%) | IPE (kg/kg) | PHI (%) |
|------|----------|-------------------|---------|---------|------------|---------|
| 2018 | NP       | CF                | ZD88    | 39.5 d‡ | 78.7 f     | 45.1 f  |
|      |          |                   | YJ2     | 40.1 d  | 75.9 f     | 45.4 f  |
|      |          | AWD               | ZD88    | 55.2 a  | 92.9 e     | 53.1 e  |
|      |          |                   | YJ2     | 55.5 a  | 89.6 e     | 53.7 e  |
|      | LP       | CF                | ZD88    | 46.5 c  | 113.3 d    | 68.5 b  |
|      |          |                   | YJ2     | 51.3 b  | 169.5 b    | 61.2 d  |
|      |          | AWD               | ZD88    | 51.4 b  | 121.6 c    | 72.8 a  |
|      |          |                   | YJ2     | 56.6 a  | 178.2 a    | 65.3 c  |
| 2019 | NP       | CF                | ZD88    | 39.2 d‡ | 79.5 f     | 45.2 f  |
|      |          |                   | YJ2     | 40.0 d  | 74.3 f     | 45.4 f  |
|      |          | AWD               | ZD88    | 54.3 a  | 94.7 e     | 53.3 e  |
|      |          |                   | YJ2     | 54.5 a  | 90.1 e     | 54.1 e  |
|      | LP       | CF                | ZD88    | 46.3 c  | 116.3 d    | 69.4 b  |
|      |          |                   | YJ2     | 51.1 b  | 173.4 b    | 61.7 d  |
|      |          | AWD               | ZD88    | 51.3 b  | 123.5 c    | 73.2 a  |
|      |          |                   | YJ2     | 56.0 a  | 181.0 a    | 65.1 c  |

†NP and LP represent optimal phosphorus level and low phosphorus level, respectively.
‡Different letters indicate statistical significance at the $p = 0.05$ level within the same column and same year.
Compared with NP, the reduction of leaf photosynthetic rate in LP was 12.4–13.3% for YJ2, which was less than that (18.9–21.2%) for ZD88 (Figure 2). Compared with CF, AWD mitigated the decline in the leaf photosynthetic rate in LP (Figure 2). A similar change value was also observed in leaf SPAD (Figure S3). Moreover, compared with NP, LP

| Year | P level† | Irrigation regime | Variety | Grain yield (g/pot) | Irrigation water input (×10⁻³ m³) | Number of irrigation | WUE (kg grain m⁻³) |
|------|----------|-------------------|---------|---------------------|------------------------------------|----------------------|-------------------|
| 2018 NP | CF       | ZD88              | 58.7 b† | 64.0 a              | 26 a                               | 0.92 cd              |
|       |          | YJ2               | 56.2 b  | 63.2 a              | 25 a                               | 0.89 cd              |
|       | AWD      | ZD88              | 62.3 a  | 46.6 c              | 19 c                               | 1.34 a               |
|       |          | YJ2               | 63.4 a  | 47.3 c              | 19 c                               | 1.34 a               |
|       | CF       | ZD88              | 44.2 d  | 52.5 b              | 21 b                               | 0.84 d               |
|       |          | YJ2               | 50.9 c  | 52.0 b              | 21 b                               | 0.98 c               |
|       | AWD      | ZD88              | 47.2 d  | 41.9 d              | 17 d                               | 1.13 b               |
|       |          | YJ2               | 55.5 b  | 41.3 d              | 17 d                               | 1.34 a               |
| 2019 NP | CF       | ZD88              | 57.7 b  | 63.8 a              | 26 a                               | 0.90 cd              |
|       |          | YJ2               | 56.1 b  | 62.9 a              | 25 a                               | 0.89 cd              |
|       | AWD      | ZD88              | 62.5 a  | 46.9 c              | 19 c                               | 1.33 a               |
|       |          | YJ2               | 63.5 a  | 47.4 c              | 19 c                               | 1.34 a               |
|       | CF       | ZD88              | 43.4 d  | 51.0 b              | 20 b                               | 0.85 d               |
|       |          | YJ2               | 50.5 c  | 50.8 b              | 20 b                               | 0.99 c               |
|       | AWD      | ZD88              | 46.5 d  | 41.7 d              | 17 d                               | 1.11 b               |
|       |          | YJ2               | 55.9 b  | 41.9 d              | 17 d                               | 1.34 a               |

†NP and LP represent optimal phosphorus level and low phosphorus level, respectively.

Different letters indicate statistical significance at the \( p = 0.05 \) level within the same column and same year.

| Year | P level† | Irrigation regime | Variety | Number of tillers and main stems per pot | Mid-tillering | Panicle initiation | Heading time | Maturity | Productive tillers (%) |
|------|----------|-------------------|---------|-----------------------------------------|---------------|-------------------|--------------|----------|------------------------|
| 2018 NP | CF       | ZD88              | 16.1 c† | 30.5 bc                                 | 26.9 b        | 24.8 cd           | 81.3 d       |
|       |          | YJ2               | 22.9 a  | 35.3 a                                  | 30.8 a        | 28.5 a            | 80.7 d       |
|       | AWD      | ZD88              | 15.0 c  | 27.9 d                                  | 25.5 c        | 23.5 d            | 84.3 c       |
|       |          | YJ2               | 21.8 a  | 32.1 b                                  | 29.4 a        | 27.0 b            | 84.1 c       |
|       | CF       | ZD88              | 13.3 d  | 23.9 e                                  | 22.0 d        | 20.5 e            | 85.7 bc      |
|       |          | YJ2               | 20.2 b  | 29.7 c                                  | 27.4 b        | 25.6 c            | 86.1 b       |
|       | AWD      | ZD88              | 12.2 d  | 22.0 e                                  | 20.8 d        | 19.3 e            | 87.7 a       |
|       |          | YJ2               | 19.1 b  | 27.2 d                                  | 25.8 bc       | 24.3 cd           | 89.2 a       |
| 2019 NP | CF       | ZD88              | 15.7 c  | 30.1 c                                  | 26.3 bc       | 24.5 bc           | 81.4 d       |
|       |          | YJ2               | 22.6 a  | 35.1 a                                  | 30.4 a        | 28.3 a            | 80.6 d       |
|       | AWD      | ZD88              | 14.9 c  | 27.5 d                                  | 25.3 c        | 23.2 c            | 84.4 c       |
|       |          | YJ2               | 21.7 a  | 31.8 b                                  | 29.7 a        | 26.8 a            | 84.3 c       |
|       | CF       | ZD88              | 13.2 d  | 23.7 e                                  | 21.4 d        | 20.2 d            | 85.3 bc      |
|       |          | YJ2               | 20.0 b  | 29.3 c                                  | 27.0 b        | 25.3 b            | 86.1 b       |
|       | AWD      | ZD88              | 12.0 d  | 21.8 f                                  | 20.5 d        | 19.0 d            | 87.1 b       |
|       |          | YJ2               | 18.9 b  | 26.9 d                                  | 24.7 c        | 24.0 bc           | 89.0 a       |

†NP and LP represent optimal phosphorus level and low phosphorus level, respectively.

Different letters indicate statistical significance at the \( p = 0.05 \) level within the same column and same year.
significantly decreased the SPS and SuS activities of the two rice varieties during grain filling (Figure 3). The decrease in the activities was smaller for YJ2 than that for ZD88 in LP. AWD increased the SPS activity by 20.7% for YJ2 and 18.1% for ZD88 in NP, and 15.4% for YJ2 and 14.4% for ZD88 in LP, in comparison with CF. The trends of SuS activity in grains were similar to those of SPS activity in stems (Figure 3).
### TABLE 5
Effect of irrigation regimes on non-structural carbohydrate (NSC) in stems and sheaths, and NSC remobilization of rice varieties under two soil P levels

| Year | P level† | Irrigation regime | Variety | NSC at heading time (g/pot) | NSC at maturity (g/pot) | Remobilized NSC reserve (%) | NSC contribution to grain (%) |
|------|----------|-------------------|---------|-----------------------------|-------------------------|-----------------------------|------------------------------|
| 2018 | NP       | CF                | ZD88    | 12.71 bc<sup>1</sup>        | 7.96 a                  | 37.36 e                     | 8.09 d                       |
|      |          |                   | YJ2     | 12.92 b                     | 8.34 a                  | 35.43 e                     | 8.15 d                       |
|      |          | AWD               | ZD88    | 14.97 a                     | 7.05 b                  | 52.87 b                     | 12.71 b                      |
|      |          |                   | YJ2     | 15.03 a                     | 6.89 b                  | 54.16 b                     | 12.85 b                      |
|      | LP       | CF                | ZD88    | 10.93 d                     | 6.31 c                  | 42.31 d                     | 10.47 c                      |
|      |          |                   | YJ2     | 12.43 bc                    | 6.13 c                  | 50.71 c                     | 12.38 b                      |
|      |          | AWD               | ZD88    | 12.25 c                     | 6.27 c                  | 48.80 c                     | 12.67 b                      |
|      |          |                   | YJ2     | 14.77 a                     | 6.14 c                  | 58.40 a                     | 15.53 a                      |
| 2019 | NP       | CF                | ZD88    | 13.53 b                     | 8.85 a                  | 34.61 e                     | 8.12 d                       |
|      |          |                   | YJ2     | 12.99 c                     | 8.43 a                  | 35.12 e                     | 8.23 d                       |
|      |          | AWD               | ZD88    | 15.16 a                     | 7.25 b                  | 52.21 b                     | 12.67 b                      |
|      |          |                   | YJ2     | 15.06 a                     | 7.03 b                  | 53.32 b                     | 12.81 b                      |
|      | LP       | CF                | ZD88    | 11.15 e                     | 6.58 bc                 | 41.00 d                     | 10.52 c                      |
|      |          |                   | YJ2     | 13.12 bc                    | 6.90 b                  | 47.41 c                     | 12.46 b                      |
|      |          | AWD               | ZD88    | 12.45 d                     | 6.44 c                  | 48.32 c                     | 12.92 b                      |
|      |          |                   | YJ2     | 15.06 a                     | 6.45 c                  | 57.20 a                     | 15.58 a                      |

†NP and LP represent optimal phosphorus level and low phosphorus level, respectively.

<sup>1</sup>Different letters indicate statistical significance at the $p = 0.05$ level within the same column and same year.
Compared with NP, LP significantly increased the MDA content and POD activity in grains of both rice varieties during grain filling (Figure 4). The MDA content was increased by 9.1–12.1% for YJ2 and 16.7–18.9% for ZD88 in LP. The POD activity was increased by 15.7–16.3% for YJ2 and 9.9–11.3% for ZD88 in LP. Under LP, AWD increased the MDA content and POD activity compared with CF. Under LP, the MDA content was lower for YJ2 than that for ZD88, whereas the POD activity performed the opposite (Figure 4). In addition, LP significantly decreased the ABA content in grains of both varieties during grain filling, relative to NP (Figure 5). Compared with NP, LP significantly increased the MDA content and POD activity in grains of both rice varieties during grain filling (Figure 4). The MDA content was increased by 9.1–12.1% for YJ2 and 16.7–18.9% for ZD88 in LP. The POD activity was increased by 15.7–16.3% for YJ2 and 9.9–11.3% for ZD88 in LP. Under LP, AWD increased the MDA content and POD activity compared with CF. Under LP, the MDA content was lower for YJ2 than that for ZD88, whereas the POD activity performed the opposite (Figure 4). In addition, LP significantly decreased the ABA content in grains of both varieties during grain filling, relative to NP (Figure 5). The reduction in ABA content was smaller for YJ2 (3.8–5.6%) than that for ZD88 (8.1–10.6%) in LP. Compared with CF, AWD significantly increased the ABA content in grains by 9.6% for YJ2 and 9.5% for ZD88 in NP, and 7.5% for YJ2 and 6.6% for ZD88 in LP (Figure 5). The above findings suggest that the strong tolerance to LP for YJ2 mainly was attributed to increased shoot dry weight and leaf photosynthetic rate during the main growth stages, remobilization of NSC from the stem to the grain, the activities of SPS in stems, activities of SuS and POD and ABA content in grains in the LP environment. In general, AWD reinforces the responses seen in LP.

3.3 Root morphological and physiological traits

During the whole growth period, compared with NP, LP increased root dry weight by 18.7% for YJ2 and 4.8% for ZD88, and increased the ratio of root to shoot by 27.6% for YJ2 and 28.2% for ZD88, on average (Figure 1c–f). Compared with CF, AWD significantly increased the root dry weight by 21.0% for YJ2 and 17.8% for ZD88 in NP, and 18.1% for YJ2 and 16.0% for ZD88 in LP, and increased the ratio of root to shoot by 7.1% for YJ2 and 7.1% for ZD88 in NP, and 5.1% for YJ2 and 5.5% for ZD88 in LP, on average (Figure 1c–f).

In comparison with that in NP, the ROA in LP was decreased by 9.2% and 13.2 for ZD88 under CF and AWD, respectively, and increased by 2.3% under CF and decreased by 2.3% under AWD for YJ2 (Figure 6). Compared with CF, AWD significantly increased the ROA by 10.0% for YJ2 and 9.8% for ZD88 in NP, and 5.0% for YJ2 and 5.0% for ZD88 in LP (Figure 6). Furthermore, compared with NP, LP significantly increased the APase activity in roots by 22.7–24.5% for YJ2 and 16.7–17.5% for ZD88, respectively (Figure 7). At the same P level and under AWD, the APase activity in the roots was higher for YJ2 than for ZD88 (Figure 7).

Soil Olsen-P concentration at maturity is presented in Figure S4. Whether NP or LP, AWD significantly increased the soil Olsen-P concentration compared with CF. No differences were observed in soil Olsen-P concentration between the two varieties in NP and LP under the irrigation regime (Figure S4).

The above results suggest that the strong tolerance to LP for YJ2 also contributed to improving root growth including increased root dry weight, the ratio of root to shoot, root oxidation activity and APase activity in the roots in LP environment. AWD also helped to improve root growth.

3.4 Correlations of agronomic and physiological traits with grain yield, PUE, and WUE

The correlation analysis showed that the grain yield was positively and very significantly correlated with shoot dry weight, leaf photosynthetic rate, and root oxidation activity at the main growth stages, and SPS activity in stems, SuS
activity in grains and ABA content in grains during the grain filling period, while the grain yield was negatively and significantly or very significantly correlated with the ratio of root to shoot at the main growth stages and the MDA content in grains during grain filling (Figure S5). The remobilized NSC reserve and NSC contribution to grain were positively and significantly or very significantly correlated with productive tillers, root dry weight, and Apase activity in roots at the main growth stages, and the MDA content and POD activity in grains during grain filling. PUE (PTE, IPE, and PHI) was positively and significantly or very significantly correlated with productive tillers, root dry weight, ratio of root to shoot and Apase activity in roots at the main growth stages, and MDA content and POD activity in grains during grain filling stage. WUE was positively and significantly or very significantly correlated with shoot dry weight, root dry weight, leaf photosynthetic rate, and root oxidation activity at the main growth stages, and SPS activity in stems, and SuS activity and ABA concentration in grains during grain filling (Figure S5). The redundancy analysis (RDA) shows the contribution of each agronomical and physiological parameters to the total variance among the distribution of low-phosphorous-tolerant traits and the relationships among the agronomical and physiological parameters. The eigenvalues of axis RDA1 and axis RDA2 in the RDA biplot were 56.5% and 27.5%, respectively, which jointly explained 84.0% of the total variation in the distribution of aggregates of yield and its components and PUE. Moreover, the ratio of root to shoot, productive tillers, Apase activity in root, MDA content in grains, and POD activity in grains were positively correlated with PUE. In contrast, the shoot dry weight, leaf photosynthetic rate, SPS activity in stems, and SuS activity in grains were negative correlated with PUE (Figure S6). The above correlation analysis suggests that the strong tolerance
to LP was related to the agronomic and physiological traits of the shoot and root.

4 | DISCUSSION

4.1 | Grain yield, PUE, and WUE of rice under LP and AWD

P deficiency influences the plant biological processes including nucleic acid, membrane lipid, protein synthesis, and energy metabolism, eventually causing yield reduction (Baker et al., 2015; Plaxton & Lambers, 2015). However, limited information is available in previous studies describing the differences in grain yield, water, and PUE between the rice varieties with differential tolerance to LP under various irrigation regimes and P levels. Herein, we observed that the decrease in grain yield under LP varied with rice varieties and irrigation regimes (Table 1). The grain yield with strong tolerance to LP (YJ2) was higher than that of a variety with weak tolerance to LP (ZD88). The AWD regime significantly increased grain yield for both varieties compared with CF. A higher grain yield for YJ2 than for ZD88 and under AWD than under CF was mainly attributed to a larger sink size (the number of panicles × spikelets per panicle) (Table 1). The results suggest that an AWD regime could alleviate the grain yield loss in LP environment by regulating the sink size.

The identification of economic and sustainable approaches to improve PUE is a high priority in rice production (Huguenin-Elie et al., 2009; Zhou et al., 2016). In recent years, improving the PUE through fulfilling the potential of P efficient rice varieties has gained increasing attention (Cordell et al., 2009; Liang et al., 2014; Ren et al., 2018). Hammond et al. (2009) proposed that PUE consists of two parts: IPE and P dry matter production efficiency (DPE), and that using IPE to characterize PUE is reliable for food crops.
On the other hand, PTE is considered a critical index of PUE (Goldstein et al., 1988). In this study, we used three indexes, PTE, IPE, and PHI, to characterize PUE. The results showed that PUE (PTE, IPE, and PHI) was significantly higher in LP than in NP for both varieties, especially for YJ2 (Table 2), suggesting that rice plants could adapt to LP environment, and using a rice variety with strong tolerance to LP could achieve a dual goal of high grain yield and PUE. Several studies have shown that AWD increased the grain yield compared to either continuous floods or farmer practices (Sriphirom et al., 2019; Yang et al., 2017; Zhang et al., 2010). However, in some studies, AWD neither altered nor decreased the yield (Belder et al., 2007; Carrijo et al., 2017; Shaibu et al., 2015; Yao et al., 2012). The discrepancies among the studies could be attributed to the variations in the hydrological conditions of soil and the timing of the irrigation method applied. In our AWD study, the soil water potential was set to −15 kPa as the threshold for irrigation, this value was mild and safe under temperate conditions in eastern China. Our results indicate that AWD is effective in compensating the grain yield loss due to LP (Tables 2 and 3).

### 4.2 Agronomic and physiological performances of rice under LP and AWD

The studies describing the effect of the AWD regime in LP on agronomic and physiological performance in rice varieties with differential in the tolerance to LP during the whole growing season are scarce, although there are some reports on rice seedlings (Ai et al., 2009; Gamuyao et al., 2012). Then, how could the AWD regime enhance the tolerance to LP in rice? There are several explanations based on our observations. Firstly, the AWD regime increased the dry matter accumulation during the main growth stages compared with CF, especially for the strong tolerance to low-P variety YJ2, despite restricted shoot growth in LP environment (Figure 1). The improved canopy structure in
the AWD regime was mainly attributed to a larger percentage of productive tillers, which in turn avoided redundant vegetative growth (Table 4, Figure 1a,b). The improved canopy structure was closely correlated to the appropriate decrease in water and fertilizer consumption during the production of unproductive tillers (Li et al., 2014; Wang et al., 2016). Secondly, the AWD regime improved the leaf photosynthesis throughout the growth period in LP, with more improvement for YJ2 than ZD88 (Figure 2). In our study, we observed that AWD increased the leaf photosynthetic rate compared with CF in LP which might be attributed to the increased leaf P concentration during the grain filling stage and leaf chlorophyll content throughout the growing period (Figures S2 and S3). The increases in leaf photosynthesis contribute to a large shoot biomass, and consequently mitigating the decline in the grain yield caused by LP stress. Thirdly, the AWD regime promoted both NSC accumulation at heading time and pre-stored carbon remobilization from stems to grains during the maturity period (Table 5), which increases harvest index and resource use efficiencies (Yang & Zhang, 2010). We also observed that SPS activity was higher for YJ2 than for ZD88 in LP, and the activity was enhanced by the AWD (Figure 3). SPS is one of the rate-limiting key enzymes in sucrose synthesis that plays a critical role in regulating the sucrose content of plant cells (Yang & Zhang, 2006; Yang et al., 2003). These results indicate that the AWD regime promotes the starch hydrolysis in the stem and the remobilization of carbohydrates to the grains, thereby increasing the harvest index and resource use efficiency (Yang & Zhang, 2006, 2010).

It is generally believed that plant roots play vital roles in regulating shoot growth and nutrient absorption and utilization (Zhang et al., 2009, 2018). The enhancement in LP tolerance under the AWD regime could account for several aspects root morphology and physiology. Firstly, compared with CF, the AWD regime increased the root biomass and the ratio of root to shoot in LP, with more increase for YJ2 than ZD88 (Figure 1c–f). A larger root system under the AWD enhances P acquisition in LP availability (Dissanayaka et al., 2018). Secondly, the AWD regime improved the ROA in both NP and LP with improved strong tolerance to LP variety YJ2 (Figure 6). The high root activity secures a high photosynthetic rate by supplying a sufficient amount of nutrients, water, and hormones to the shoot (Zhang et al., 2018). Thirdly, the APase activity in the roots was increased under the AWD regime (Figure 7). The increase in the APase activity in plant roots improved the PUE (Liang et al., 2010). In our study, we observed that LP increased the APase activity in roots for two varieties compared with NP, with more increase for YJ2 than for ZD88 (Figure 7). Zhou et al. (2016) reported that higher APase activity in roots was observed in the P-efficient soybean genotypes under low P conditions compared with P-inefficient. Thus, we speculated that the APase in roots plays a key role in adaptability to LP environments.

We also observed that dry matter accumulation, leaf photosynthetic rate, SPS activity in the stem, root biomass, ROA, and APase activity in the roots were very significantly and positively correlated with the grain yield and PUE (Figure S5). Together, these results demonstrate that the AWD regime enhances the rice tolerance to LP by improving the biological process in both shoots and roots achieves a high grain yield and PUE in the LP environment.

**4.3 Sink activity during grain filling of rice under LP and AWD**

Grain filling is the critical stage of yield formation in rice when fertilized ovaries develop into caryopses. It has been reported that grain filling in rice is closely related to sink activity, which consist of multiple factors and key enzymes involved in carbohydrate utilization and storage (Yang & Zhang, 2010). Among these enzymes, SuS is predominant
in the sink accumulating carbohydrate reserves and catalyzes the first step in the conversion of sucrose to starch; these activities are regarded as biochemical markers of sink activity (Zhang et al., 2015). The present results showed that LP decreased the SuS activity in grains of the two rice varieties during the grain filling period, and the SuS reduction of YJ2 was smaller than that of ZD88, but the AWD regime increased the SuS activity in grains (Figure 3). Thus, we argue that an accelerated grain weight by the AWD regime in LP is attributed to an increased sink activity via enhanced SuS activity in the grain. In addition, the LP increased the MDA content in grains during grain filling (Figure 4). The AWD regime reduced the MDA content and increased the POD activity in grains, with more decrease or increase for YJ2 than for ZD 88 (Figure 4), implying that a AWD regime would modulate the harsh environment of LP by elevating the antioxidant capacity in rice.

ABA, one of the most important phytohormones, has been demonstrated to be involved in abiotic stress responses, such as drought and heat stress in plants (Yang & Zhang, 2006; Zhu et al., 2018). ABA is a sensitive signal that is increased during the soil drying period (Xiong & Zhu, 2002; Yang et al., 2017). In our study, we also observed that AWD significantly increased grain ABA during grain filling compared with CF (Figure 5) which matches previous reports (Norton et al., 2017). Although studies on ABA response to drought in rice have been frequently reported, whether ABA is involved in P deficiency is not yet clarified. The current results showed that the AWD regime increased ABA content in rice grains during grain filling in LP compared with CF (Figure 5). Correlation analysis showed that the ABA content in grains was positively and significantly correlated with remobilized NSC reserve, grain yield, and WUE (Figure S5). Zhang et al. (2015) pointed out that ABA in the grains in the moderate soil-drying regime enhanced the activities of antioxidative enzymes and reduced the free radicals in grains, and accelerated the grain filling rate of rice. Therefore, we speculate that an increase in ABA under the AWD regime might play a critical role in alleviating low P stress by regulating the antioxidative systems in grains, and consequently, enhance the grain filling and increase grain yield and PUE of rice.

5 | CONCLUSION

LP decreased the grain yield, which varied according to the rice varieties. Under LP, the variety of YJ2 with strong tolerance to LP exhibited higher grain yield than ZD88 with weak tolerance to LP. An AWD regime increased the grain yield, PUE, and WUE, with a higher increase for YJ2 than for ZD88. The superiority in LP for YJ2 was attributed to productive tillers, increased root dry weight, the ratio of root to shoot, the remobilization of NSC from stems to grains, and enhanced APase activity in roots and the POD activity in the grain. Therefore, improved agronomic and physiological performances of roots and shoots via regulation of appropriate cultivation techniques would enhance the tolerance of rice to LP environment.

6 | CONFLICT INTEREST

The authors declare that they have no competing interests.

ACKNOWLEDGMENTS

This work was supported by the National Key Research and Development Program (2016YFD0300206-4, 2018YFD0300801, 2017YFD0301206), the National Natural Science Foundation of China (31871559, 32071943, 32071944), the Project Funded by the Priority Academic Program Development of Jiangsu Higher Education Institutions, Six talent peaks project in Jiangsu Province (SWYY-151), Jiangsu Agriculture Science and Technology Innovation Fund (CX(18)3007) and the Top Talent Support Plan of Yangzhou University (2015-01).

ORCID

Yaping Deng https://orcid.org/0000-0002-3027-9992
Junfei Gu https://orcid.org/0000-0003-0002-0725
Jianchang Yang https://orcid.org/0000-0003-4222-2376

REFERENCES

Acosta-Motos, J. R., Rothwell, S. A., Massam, M. J., Albacete, A., Zhang, H., & Dodd, I. C. (2020). Alternate wetting and drying irrigation increases water and phosphorus use efficiency independent of substrate phosphorus status of vegetative rice plants. Plant Physiology and Biochemistry, 155, 914–926. https://doi.org/10.1016/j.plaphy.2020.06.017.
Ai, P., Sun, S., Zhao, J., Fan, X., Xin, W., Guo, Q., Yu, L., Shen, Q., Wu, P., Miller, A. J., & Xu, G. (2009). Two rice phosphate transporters, OsPht1:2 and OsPht1:6, have different functions and kinetic properties in uptake and translocation. Plant Journal, 57, 798–809. https://doi.org/10.1111/j.1365-313X.2008.03726.x.
Baker, A., Ceasar, S. A., Palmer, A. J., Paterson, J. B., Qi, W., Muench, S. P., & Baldwin, S. A. (2015). Replace, reuse, recycle: improving the sustainable use of phosphorus by plants. Journal of Experimental Botany, 66, 3523–3540. https://doi.org/10.1093/jxb/erv210.
Belder, P., Bouman, B. A. M., & Spiertz, J. H. J. (2007). Exploring options for water saving in lowland rice using a modeling approach. Agricultural Systems, 92, 91–114. https://doi.org/10.1016/j.agsy.2006.03.001.
Bhadouria, J., Singh, A. P., Mehra, P., Verma, L., Srivastawa, R., Parida, S. K., & Giri, J. (2017). Identification of purple acid phosphatases in Chickpea and potential roles of CaPAP7 in seed phytate accumulation. Scientific Reports, 7, 11012. https://doi.org/10.1038/s41598-017-11490-9.
Bilal, H. M., Aziz, T., Magsood, M. A., Farooq, M., & Yan, G. (2018). Categorization of wheat genotypes for phosphorus efficiency. *PLoS One, 13*, e0205471. https://doi.org/10.1371/journal.pone.0205471.

Bollmark, M., Kubat, B., & Eliasson, L. (1988). Variations in endogenous cytokinin content during adventitious root formation in pea cuttings. *Journal of Plant Physiology, 132*, 262–265. https://doi.org/10.1016/S0176-1671(88)80102-0.

Bouman, B. A. M. (2007). A conceptual framework for the improvement of crop water productivity at different spatial scales. *Agricultural Systems, 93*, 43–60. https://doi.org/10.1016/j.agsy.2006.04.004.

Cakmak, I., & Marschner, H. (1992). Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase in bean leaves. *Plant Physiology, 98*, 1222–1227. https://doi.org/10.1104/pp.98.4.1222.

Cao, X., Zhu, C., Zhang, C., Hussain, S., Zhu, L., Zhang, J., & Jin, Q. (2018). Mixed-nitrogen nutrition-enhanced mediation of drought tolerance of rice seedlings associated with photosynthesis, hormone balance and carbohydrate partitioning. *Plant Growth Regulation, 84*, 451–465. https://doi.org/10.1007/s10725-017-0352-6.

Carrijo, D. R., Lundy, M. E., & Linquist, B. A. (2017). Rice yields and water use under alternate wetting and drying irrigation: A meta-analysis. *Field Crops Research*, 203, 173–180. https://doi.org/10.1016/j.fcr.2016.12.002.

Carvalho, F. P. (2017). Mining industry and sustainable development: time for change. *Food and Energy Security, 6*, 61–77. https://doi.org/10.1002/fees.109.

Cordell, D., Drangert, J. O., & White, S. (2009). The story of phosphate starvation inducible metabolism in *Lycopersicon esculentum*. *Plant Physiology, 87*, 711–715. https://doi.org/10.1104/pp.107.118153.

Goldstein, A. H., Baertlein, D. A., & McDaniel, R. G. (1988). Phosphate starvation inducible metabolism in *Lycopersicon esculentum*. *Plant Physiology, 87*, 711–715. https://doi.org/10.1104/pp.87.3.711.

Hammond, J. P., Broadley, M. R., White, P. J., King, G. J., Bowen, H. C., Hayden, R., Meacham, M. C., Mead, A., Overs, T., Spracklen, W. P., & Greenwood, D. J. (2009). Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. *Journal of Experimental Botany, 60*, 1953–1968. https://doi.org/10.1093/jxb/erp083.

Haygarth, P., Hepworth, L., & Jarvis, S. (1998). Forms of phosphorus transfer in hydrological pathways from soil under grazed grassland. *European Journal of Soil Science, 49*, 65–72. https://doi.org/10.1046/j.1365-2389.1998.00131.x.

He, Z. (1993). Enzyme linked immunosorbent assay for endogenous plant hormones. In Z. He (Ed.), *Guidance to experiment on chemical control in crop plants* (pp. 60–68). Agricultural University Publishers. (In Chinese).

Heath, R. L., & Packer, L. (1968). Photoperoxidation in isolated chloroplasts I. Kinetics and stoichiometry of fatty acid peroxidation. *Archives of Biochemistry and Biophysics, 125*, 189–198. https://doi.org/10.1016/0003-9861(68)90654-1.

Huber, S. C., & Huber, J. L. (1990). Activation of sucrose phosphate synthase from darkened spinach leaves by an endogenous protein phosphatase. *Archives of Biochemistry and Biophysics, 282*, 421–426. https://doi.org/10.1016/0003-9861(90)90138-O.

Huguenin-Elie, O., Kirk, G. J. D., & Frossard, E. (2009). The effects of water regime on phosphorus responses of rainfed lowland rice cultivars. *Annals of Botany, 103*, 211–220. https://doi.org/10.1093/aob/mcn199.

Iqbal, A., Gui, H., Zhang, H., Wang, X., Pang, N., Dong, Q., & Song, M. (2019). Genotypic variation in cotton genotypes for phosphorus-use efficiency. *Agronomy-Base 1*, 6, 689. https://doi.org/10.3390/agronomy9110689.

Kochian, L. V. (2012). Rooting for more phosphorus. *Nature, 488*, 466–467. https://doi.org/10.1038/488466a.

Lal, R., Delgado, J. A., Gulliford, J., Nielsen, D., Rice, C. W., & Van Pelt, R. S. (2012). Adapting agriculture to drought and extreme events. *Journal of Soil and Water Conservation, 67*, 162A–166A. https://doi.org/10.2489/jswc.67.6.162a.

Lampayan, R. M., Bouman, B., de Dios, J. L., Espiritu, A. J., Soriano, J. B., Lactaoen, A. T., Faronilo, J. E., & Thant, K. M. (2010). Yield of aerobic rice in rainfed lowlands of the Philippines as affected by nitrogen management and row spacing. *Field Crops Research, 116*, 165–174. https://doi.org/10.1016/j.fcr.2009.12.007.

Li, Y. Y., Xu, G. W., Li, J. F., Guo, J. R., Wang, Z. Q., & Yang, J. C. (2018). Tolerance to low phosphorus and its agronomic and physiological characteristics of rice cultivars. *Chinese Journal of Rice Science, 32*, 51–66 (in Chinese with English abstract) http://doi.org/10.16819/j.1001-7216.2018.7047. http://doi.org/10.16819/j.1001-7216.2018.7047.

Li, Y., Xue, L. H., Fan, F. Y., & Yang, L. Z. (2014). Effects of interaction of N and P on rice canopy spectral reflectance and its PNN identification. *Scientia Agricultura Sinica, 47*, 2742–2750.

Liang, C., Tian, J., Lam, H. M., Lim, B. L., Yan, X., & Liao, H. (2010). Biochemical and molecular characterization of PvPAP3, a novel purple acid phosphatase isolated from common bean enhancing extracellular ATP utilization. *Plant Physiology, 152*, 854–865. https://doi.org/10.1104/pp.109.147918.

Liang, C., Wang, J., Zhao, J., Tian, J., & Liao, H. (2014). Control of phosphate homeostasis through gene regulation in crops. *Current Opinion in Plant Biology, 21*, 59–66. https://doi.org/10.1016/j.pbi.2014.06.009.

Ni, J. J., Wu, P., Lou, A. C., Zhang, Y. S., & Tao, Q. N. (1996). Low phosphorus effects on the metabolism on rice seedlings. *Communication in Soil Science and Plant Analysis, 27*, 3073–3084. https://doi.org/10.1080/00103629609369762.

Niu, Y. F., Chai, R. S., Jin, G. L., Wang, H., Tang, C. X., & Zhang, Y. S. (2013). Responses of root architecture development to low
phosphorus availability: a review. *Annals of Botany*, 112, 391–408. https://doi.org/10.1093/aob/mcs285.

Norton, G. J., Shafaei, M., Travis, A. J., Deacon, C. M., Danku, J., Pond, D., Cochrane, N., Lockhart, K., Salt, D., Zhang, H., Dodd, I. C., Hossain, M., Islam, M. R., & Price, A. H. (2017). Impact of alternate wetting and drying on rice physiology, grain production, and grain quality. *Field Crops Research*, 205, 1–13. https://doi.org/10.1016/j.fcr.2017.01.016.

Panigrahy, M., Rao, D. N., & Sarla, N. (2009). Molecular mechanisms in response to phosphate starvation in rice. *Biotechnology Advances*, 27, 389–397. https://doi.org/10.1016/j.biotechdev.2009.02.006.

Pearson, K. A., Millar, G. M., Norton, G. J., & Price, A. H. (2018). Phosphorus uptake and utilization efficiency in rice grown with reduced phosphorus availability: a review. *Annals of Botany*, 112, 391–408. https://doi.org/10.1093/aob/mcs285.

Plaxton, W. C., & Tran, H. T. (2011). Metabolic adaptations of plants subjected to water stress during filling. *Food and Energy Security*, 7, e00149. https://doi.org/10.1002/fes3.149.

Plaxton, W. C., & Lambers, H. (2015). Phosphorus metabolism in plants. *Annual Review of Plant Biology*, 48, 3–15. https://doi.org/10.1146/annurev-arplant-050814-010319.

Plaxton, W. C., & Tran, H. T. (2011). Metabolic adaptations of plants subjected to water stress during filling. *Plant Physiology*, 156, 1006–1015. https://doi.org/10.1104/pp.111.175281.

Ren, P., Meng, Y., Li, B., Ma, X., Si, E., Lai, Y., Wang, H. (2018). Molecular mechanisms of acclimatization to phosphate starvation and recovery underlying full-length transcriptome profiling in barley (*Hordeum vulgare* L.). *Frontiers in Plant Science*, 9, 500. https://doi.org/10.1016/j.apsb.2019.02.006.

Shimamura, E., Merckx, R., & Smolders, E. (2020). Limited effects of the soluble organic phosphorus fraction on the root phosphorus uptake efficiency of upland rice genotypes grown in acid soil. *Soil Science and Plant Nutrition*, 106, 1–10. https://doi.org/10.1080/00380768.2020.1864230.

Yang, J., Liu, K., Wang, Z., Du, Y., & Zhang, J. (2007). Water-saving and grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Plant and Soil*, 283, 101. https://doi.org/10.1007/s11104-005-1117-9.

Yang, J., & Zhang, J. (2010). Crop management techniques to enhance harvest index in rice. *Frontiers in Plant Science*, 1, 54–69. https://doi.org/10.1016/j.jclepro.2019.03.212.

Yang, J., Liu, K., Wang, Z., Du, Y., & Zhang, J. (2007). Water-saving and high-yielding irrigation for lowland rice by controlling limiting values of soil water potential. *Journal of Integrative Plant Biology*, 49, 1445–1454. https://doi.org/10.1111/j.1672-0972.2007.00555.x.

Yang, J., & Zhang, J. (2005). Combining a modelling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. *Plant and Soil*, 269, 57–68. https://doi.org/10.1007/s11104-004-0254-1.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., Liu, K., Wang, Z., Du, Y., & Zhang, J. (2007). Water-saving and high-yielding irrigation for lowland rice by controlling limiting values of soil water potential. *Journal of Integrative Plant Biology*, 49, 1445–1454. https://doi.org/10.1111/j.1672-0972.2007.00555.x.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.

Yang, J., & Zhang, J. (2006). Grain filling of cereals under low phosphorus availability: a review. *Journal of Agricultural and Food Chemistry*, 55, 131–136. https://doi.org/10.1021/jf0615544.
Yang, J., Zhang, J., Ye, Y., Wang, Z., Zhu, Q., & Liu, L. (2004). Involvement of abscisic acid and ethylene in the responses of rice grains to water stress during filling. *Plant Cell and Environment, 27*, 1055–1064. https://doi.org/10.1111/j.1365-3040.2004.01210.x.

Yang, J., Zhou, Q., & Zhang, J. (2017). Moderate wetting and drying increases rice yield and reduces water use, grain arsenic level, and methane emission. *Crop Journal*, 5, 151–153. https://doi.org/10.1016/j.cj.2016.06.002.

Yao, F. X., Huang, J. L., Cui, K. H., Nie, L. X., Xiang, J., Liu, X. J., Wu, W., Chen, M. X., & Peng, S. B. (2012). Agronomic performance of high-yielding rice variety grown under alternate wetting and drying irrigation. *Field Crops Research, 126*, 16–22. https://doi.org/10.1016/j.fcr.2011.09.018.

Yoshida, S., Forna, D., Cock, J., & Gomez, K. (1976). *Laboratory manual for physiological studies of rice* (3rd ed.). IRRI, Los Baňos, Philippines.

Zhang, H., Chen, T., Wang, Z., Yang, J., & Zhang, J. (2010). Involvement of cytokinins in the grain filling of rice under alternate wetting and drying irrigation. *Journal of Experimental Botany, 61*, 3719–3733. https://doi.org/10.1093/jxb/erq198.

Zhang, H., Liu, K., Wang, Z. Q., Liu, L. J., & Yang, J. C. (2015). Abscisic acid, ethylene and antioxidative systems in rice grains in relation with grain filling subjected to post-anthesis soil-drying. *Plant Growth Regulation, 76*, 135–146. https://doi.org/10.1007/s10725-014-9983-z.

Zhang, H., Xue, Y., Wang, Z., Yang, J., & Zhang, J. (2009). An alternate wetting and moderate soil drying regime improves root and shoot growth in rice. *Crop Science, 49*, 2246–2260. https://doi.org/10.2135/cropsci2009.02.0099.

Zhang, H., Yu, C., Kong, X., Hou, D., Gu, J., Liu, L., Wang, Z., & Yang, J. (2018). Progressive integrative crop managements increase grain yield, nitrogen use efficiency and irrigation water productivity in rice. *Field Crops Research, 215*, 1–11. https://doi.org/10.1016/j.fcr.2017.09.034.

Zhang, Z., Xue, Y., Wang, Z., Yang, J., & Zhang, J. (2009). The relationship of grain filling with abscisic acid and ethylene under non-flooded mulching cultivation. *Journal of Agricultural Science, 147*, 423–436. https://doi.org/10.1017/S0021859609008557.

Zhou, T., Du, Y. L., Ahmed, S., Liu, T., Ren, M. L., Liu, W. G., & Yang, W. Y. (2016). Genotypic differences in phosphorus efficiency and the performance of physiological characteristics in response to low phosphorus stress of soybean in southwest of China. *Frontiers in Plant Science, 7*, 1776.

Zhu, X. F., Zhao, X. S., Wu, Q., & Shen, R. F. (2018). Abscisic acid is involved in root cell wall phosphorus remobilization independent of nitric oxide and ethylene in rice (*Oryza sativa*). *Annals of Botany, 121*, 1361–1368. https://doi.org/10.1093/aob/mcy034.

Ziegler, J., Schmidt, S., Chutia, R., Müller, J., Böttcher, C., Strehmel, N., Scheel, D., & Abel, S. (2016). Non-targeted profiling of semipolar metabolites in Arabidopsis root exudates uncovers a role for coumarin secretion and lignification during the local response to phosphate limitation. *Journal of Experimental Botany, 67*, 1421–1432. https://doi.org/10.1093/jxb/erv539.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

---

**How to cite this article:** Deng Y, Qiao S, Wang W, et al. Tolerance to low phosphorus was enhanced by an alternate wetting and drying regime in rice. *Food Energy Secur*. 2021;00:e294. https://doi.org/10.1002/fes3.294