Seed priming with selenium: Effects on germination, seedling growth, biochemical attributes, and grain yield in rice growing under flooding conditions

Feng-qin Hu | Shuo-chen Jiang | Zhun Wang | Kang Hu | Yi-mei Xie | Ling Zhou | Jian-qiang Zhu | Dan-ying Xing | Bin Du

1College of Agriculture, Yangtze University, Jingzhou, China
2Shoufu Engineering Design Company Hubei Branch, Wuhan, China
3National Quality Supervision and Inspection Center of Selenium Rich Products, Enshi, China

Correspondence
Bin Du and Dan-ying Xing, College of Agriculture, Yangtze University, Jingzhou 434025, China.
Email: xiaobin@stu.scau.edu.cn; xingdy_2006@126.com

Funding information
National Natural Science Foundation of China, Grant/Award Number: U21A2039; National Public Welfare Industry Project, Grant/Award Number: 201303106

Abstract
Prevalent irregular rainfall, flooding for weed control, and unleveled fields in the middle and lower reaches of the Yangtze River all contribute to flooding stress on germination and growth of direct-seeded rice (Oryza sativa L.). Herein, some experiments were conducted so as to assess the effects of seed priming with selenium (Se) on the germination and growth of rice under hypoxia. The experiment was arranged in a completely randomized factorial design with two factors and five replicates. Factors included Se concentration (0, 30, and 60 μmol/L) and duration of flooding stress (0, 2, 4, and 8 days). The experimental results showed that Se accelerated seed germination and increased emergence index and final emergence percentage. Additionally, Se increased shoot and root lengths and dry weights, but high Se concentration (60 μmol/L) reduced 18-day-old seedling dry weight under long-term flooding (8 days). Furthermore, Se reduced malondialdehyde content and increased starch hydrolysis efficiency in seeds, superoxide dismutase, peroxidase, catalase, and glutathione peroxidase activities and seedling soluble protein and total chlorophyll contents. Se improved seedling total Se and organic Se contents while increasing total dry weight and yield. Notably, the highest yield was obtained after a 4-day flooding period. Although Se priming favored rice seedling emergence and growth under flooding conditions, Se concentrations equal or above 60 μmol/L increased the risk of seedling death during long-term flooding (≥8 days).

KEYWORDS
anaerobic sprouting, direct-seeded rice, flooding stress, selenium seed priming, starch hydrolysis efficiency
1 | INTRODUCTION

Rice (Oryza sativa L.) is one of the most important staple cereal crops in the world, and more than half of the population in China depends on rice for food (Kennedy, 2002). With the acceleration of industrialization and urbanization, the labor force engaged in agricultural production in China is rapidly shifting to secondary and tertiary industries, leading to a rapid rise in the costs of agricultural labor (Lu et al., 2019). The traditional system of rice production in China, which involves the transplanting of seedlings from a nursery into a paddy field, faces unprecedented challenges because the production pattern is labor, water, and energy intensive, making the overall process less profitable (Ge et al., 2018). As an alternative, and owing to its low-cost and labor-saving features, direct seeding is currently receiving much attention worldwide and is being widely promoted, especially in China. Direct seeding contributes less greenhouse gas emissions than rice transplanting, thereby contributing to environmental protection efforts and sustainable agricultural development (Tao et al., 2016).

However, when direct seeding is subjected to heavy precipitation or unleveled fields during seed germination and seedling growth, rice seeds become susceptible to flooding (Lal et al., 2018). Moreover, weeds are more competitive than rice seeds and may severely inhibit the growth of directly seeded rice seedlings (Chamara et al., 2018). Fortunately, soil flooding after direct seeding is an effective, environmentally friendly, and low-cost weed control method (Chamara et al., 2018). Nevertheless, irregular rainstorms, unleveled fields, or flooding for weed prevention may cause hypoxia (low O₂ availability) or anoxia (no O₂) stress in rice seedlings. Although rice is the only cereal crop that can germinate and extend its coleoptile under oxygen-limited conditions (Ismail et al., 2009), an insufficient oxygen supply will inhibit the aerobic respiration of rice, causing carbohydrates stored in the endosperm to provide only a small amount of energy through oxidation pathways to support the elongation of the coleoptile. Consequently, rice seedlings may fail to develop roots and leaves (Ismail et al., 2009). Limiting oxygen may induce restricted seedling growth or death, the formation of uneven and insufficient production groups, and, eventually, reduced grain yields (Lal et al., 2018). Rice seedlings resist flooding mainly through two mechanisms: (1) the low-oxygen quiescence syndrome, whereby the rice shoot does not elongate upon submergence but regrows after de-submergence, or (2) low-oxygen escape syndrome, whereby the shoot extends rapidly under flood waters to reach the water surface (Ma et al., 2020).

Selenium (Se) is an essential trace element for maintaining the normal functioning of many physiological processes (Kieliszek & Błażejak, 2016; Pappas et al., 2019). All forms of life, from primitive cells to complex organisms, require certain amounts of Se to be incorporated to special enzymes and cellular components for their metabolic functions (Oraby et al., 2015; Rayman, 2012). Studies have shown that low concentration of Se is beneficial for plant growth and development (Feng et al., 2013; Kaur et al., 2014). A small amount of Se can not only improve the quality and yield of plants but also modulate multiple stress-responsive genes (Gupta & Gupta, 2017; Moulick et al., 2016; Wang et al., 2017). Khaliq et al. (2015) found that when soaking rice seeds with pure Se content between 15 and 60 μmol/L, the germination potential and germination rate of seeds were improved, as well as the activities of various enzymes. In vivo, antioxidative effect is one of the most important physiological functions of Se (Misra et al., 2015). Se can effectively improve the activity of antioxidant enzymes, reduce oxidative damage, and promote plant growth (Filek et al., 2008; Pedrero et al., 2008). Further, Se favors rice seedling emergence and seedling quality ( Lidon et al., 2018).

Although studies on the effects of flood conditions or selenium on rice performance have been widely reported, still rarely study has been accomplished about the effects of Se on seed germination and seedling growth under flooding conditions. Herein, we hypothesized that seed priming with Se ensures the uniformity of germination and enhances seedling growth under limited-oxygen conditions. Therefore, our objective was to investigate the effectiveness of Se application as a seed germination initiator under flooding conditions.

2 | MATERIALS AND METHODS

The experiment was laid out in a split-plot design with flooding duration (FD) as the main plot and Se concentration as the subplot. FD at four levels and Se at three levels were tested with five replicates, and 60 subplots were established in pots (Experiment 1) and in the field (Experiment 2). The FD levels comprised flooding with 10 cm (Ella et al., 2011; Sarkar, 2012) of water for 0 (FD₀), 2 (FD₂), 4 (FD₄), or 8 d (FD₈) after rice sowing. Se levels comprised dry rice seeds primed by immersion in a sodium selenite (Na₂O₃Se) solution at Se 0 (Se₀), 30 (Se₃₀), or 60 μmol/L (Se₆₀).

In each treatment, after the rice seeds were disinfected with 15% NaClO for 15 min and rinsed with distilled water for 20 min, 25 g of seeds was placed in a 200-ml conical flask containing a 125 ml initiator solution. The flask was placed in an incubator in darkness, at 25 ± 1°C and 80% relative humidity. After 24 h, the seeds were filtered through gauze, placed in distilled water for 20 min, rinsed five times with ultra-pure water, and set aside. Autoclavable glass Petri dishes lined with double layers of filter paper were placed on a laboratory bench and left to air-dry for 24 h.

The soil used in Experiment 1 was a silty clay loam with 24% sand (2.00–0.02 mm), 40% silt (0.02–0.002 mm), and 36% clay (<0.002 mm), collected from the plow layer (0–20 cm) of an arable field in Yangtze University, Hubei Province, Southern China. Each kilogram of soil at pH 5.94 contained 34.52 g of organic matter, 224.19 mg of available N, 1.37 mg of available P, 127.24 mg of available K, and 0.29 mg of total Se. The soil was air-dried, sieved to <5 mm, and homogenous. Basal fertilizers (120 mg N/kg soil as NH₄NO₃, 30 mg P/kg soil, 75.5 mg K/kg soil as K₂HPO₄) were added to the soil and mixed thoroughly. The mixed soil (5 kg) was packed into plastic pot with a diameter of 25 cm in diameter and a height of 30 cm. One hundred seeds were evenly sprinkled on the soil surface in each treatment, then immediately irrigated water by 10 cm, and maintained at a constant water level during inundation. After flooding duration ended, all
treatments maintained a 1 cm water level until harvest (18 days). The FD were randomly arranged on a frame inside a glasshouse at 28/25°C day/night and a 16 h/day photoperiod with natural sunlight supplemented with sodium vapor lamps to maintain a light intensity > 350 μmol m⁻² s⁻¹.

Experiment 2 was conducted in 2018–2019 at the Yangtze University farm in Jingzhou County, Hubei Province, China (112°04'–112°05'N, 30°32'–30°33'E). The soil was the same as that used in Experiment 1. After land preparation, seeds treated in the same manner as those in Experiment 1 were sown directly in the field at a rate of 60 kg ha⁻¹, followed immediately by 10-cm-high flooding. After flooding duration ended, the guidelines for the local high-yield field water management mode were utilized. Each plot was fertilized as follows: N 150 kg ha⁻¹, P₂O₅ 59 kg ha⁻¹, and K₂O 120 kg ha⁻¹ applied in the form of CO(NH₂)₂, (NH₄)₂HPO₄, and KCl, respectively. Specifically, 60% of N was applied as a basal fertilizer and the remaining 40% as a tillering fertilizer, whereas 100% of P₂O₅ and K₂O were applied as base fertilizers. Treatments were arranged in a randomized complete block design with five replications and a plot area of 24.0 m² (6 × 2 m). Manual weeding was performed in the early tiller, late tiller, and heading stages. Pest and disease incidence were intensively controlled.

2.1 | Rice emergence

In Experiment 1, seedling emergence was counted daily using the method prescribed by the Association of Official Seed Analysts until the 10th day. A seedling was scored as emerged when its hypocotyl length was ≥ 2 mm. The time to start emergence (TSE) of seeds were recorded. The time taken to 50% emergence (E₁₀), mean emergence time (MET), emergence index (EI), and final emergence percentage (FEP) of seeds were calculated as follows (Khaliq et al., 2015):

\[ E_{10} = ti + \left(\frac{(nj - ni)}{nj - ni}\right)\frac{(tj - ti)}{nj - ni} \]  (1)

where \( N \) is the number of emerged seeds in 10 days and \( ni \) and \( nj \) are the cumulative numbers of emerged seeds by adjacent counts at time \( ti \) and \( tj \), respectively (\( ni < N/2 < nj \)).

\[ MET = \frac{\sum Dn}{\sum n} \]  (2)

where \( n \) is the number of seeds emerged on day \( D \) and \( D \) is the number of days counted from the beginning of emergence, \( D \leq 10 \).

\[ EI = \frac{\sum Et}{Dt} \]  (3)

where \( Et \) is the number of seeds emerged on day \( t \) and \( Dt \) is time corresponding to \( Et \), \( 1 \leq t \leq 10 \).

\[ FEP = \frac{E_{18}}{\text{Number of all seeds}} \times 100 \]  (4)

where \( E_{18} \) is the number of emerged seeds in the 18th day.

2.2 | Seedling morphology

In Experiment 1, shoot and root lengths of five randomly selected seedlings were measured both 10 and 18 days after sowing from each experimental unit in normally emerging seedlings. Five measured seedlings were oven-dried at 70°C for 72 h to get the dry biomass. Then, the dried samples were ground into powder to pass through a .15-mm sieve and sealed in ziplock bags before Se analysis.

2.3 | Biochemical analyses

In Experiment 1, lipid peroxidation in the rice seeds on the second day was determined from the malondialdehyde (MDA) content using the thiobarbituric acid method (Yang et al., 2014). The α-amylase activity in ground rice seeds on the second day was measured according to a reported technique (Mahakham et al., 2017). Total soluble sugar and starch contents in the rice seeds on the second day were quantified according to Khaliq et al. (2015). The activities of superoxide dismutase (SOD) at 560 nm, catalase (CAT) at 240 nm, peroxidase (POD) at 470 nm, and glutathione peroxidase (GPx) at 340 nm in rice seedlings in the 18th day were determined according to the methods in Du et al. (2019). Soluble protein content in rice seedlings in the 18th day was quantified according to the method of Bradford (1976).

2.4 | Yield and total dry weight

In Experiment 2, grain yields and total dry weight were measured at maturity by taking 5-m² plant samples at the center of each plot. Plant samples were separated from the filled grains and straw. Filled grains and straw were dried in an oven at 70°C to a stable weight and weighted, and grain yield was calculated at 14% moisture content. The grain was further processed into polished rice, and polished rice samples were ground into powder to pass through a .15-mm sieve and sealed in ziplock bags before Se analysis.

2.5 | Determination of Se concentrations

Contents of total Se and organic Se in the seedlings (Experiment 1) and polished rice (Experiment 2) were determined according to the method of Deng et al. (2017).

2.6 | Statistical analyses

All experimental data are expressed as means ± standard errors (SE) of five replicates. The dates were subjected to the two-way analysis (ANOVA) to determine the effects of flooding duration, Se treatments, and interaction between them, respectively. Significant differences between flooding duration and Se treatments among the
same year were tested by Duncan’s multiple range tests. The significance level was $p < .05$.

### 3 | RESULTS

#### 3.1 | Rice emergence

Flooding duration, Se treatment, and their interaction significantly affected rice emergence, although the interaction had no significant effect on TSE (Table 1). Generally, as flooding duration increased, TSE and MET increased, whereas EI decreased. Further, $E_{50}$ was highest at FD$_4$ and FEP was highest at FD$_2$. Additionally, as Se concentration increased, TSE, $E_{50}$, and MET decreased, whereas EI and FEP increased. It is worth noting that when flooding duration was less than 8 days, EI and FEP increased with the rising Se concentration, but when it extended for 8 days, EI and FEP in Se$_{60}$ were lower than those in Se$_{30}$. The results above indicate that long-term flooding limits seed germination and Se priming promoted seed germination; however, when flooding duration was 8 days, Se$_{60}$ had a negative effect on seed germination.

#### 3.2 | Seedling morphology

Flooding duration, Se treatment, and their interaction significantly affected seedling morphology, although the interaction had no significant effect on shoot length on the 18th day (Table 2). As flooding duration increased, its negative effects on the growth of shoots and roots gradually increased. Compared with FD$_0$, shoot length, root length, and dry biomass in FD$_8$ declined by 41.74%, 81.70%, and 79.21%, respectively, on the 10th day and by 35.90%, 48.06%, and 59.89%, respectively, on the 18th day. Shoot and root lengths and dry biomass increased with increasing Se concentration. Compared with Se$_0$, shoot and root lengths and dry biomass of Se$_{60}$ decreased by 37.36%, 18.18%, and 27.40%, respectively, on the 10th day and by 24.39%, 15.58%, and 27.41%, respectively, on the 18th day. Notably, Se$_{60}$ significantly reduced the dry biomass of 18-day-old seedlings in FD$_8$. These results indicate that flooding restricted seedling growth, whereas Se priming promoted seedling growth; however, Se$_{60}$ reduced the dry biomass of 18-day-old seedlings in FD$_8$.

#### 3.3 | Biochemical attributes of seeds

Se treatments significantly affected the biochemical attributes of rice seeds (Table 3). MDA and starch contents decreased, whereas soluble sugar content and $\alpha$-amylase activity increased with increasing Se concentration. MDA and starch contents in Se$_{60}$ were 25.11% and 12.88% lower, respectively; however, $\alpha$-amylase activity and soluble sugar content in Se$_{60}$ were 19.52% and 6.69% higher, respectively, compared with the Se$_0$ treatment. These results indicate that Se priming reduced MDA content and accelerated starch hydrolysis.

### TABLE 1 | Effects of selenium (Se) concentration and flooding duration on rice emergence

| FD | Se  | TSE  | $E_{50}$ | MET  | EI   | FEP  |
|----|-----|------|---------|------|------|------|
| 0  | 0   | 2.40 ± .55ab | 3.62 ± .10f | 4.40 ± .05e | 18.71 ± .44ef | 78.40 ± 1.82cd |
| 0  | 30  | 1.60 ± .55cd | 3.53 ± .05gh | 4.07 ± .09g | 21.80 ± 1.33bc | 82.20 ± 3.83bc |
| 0  | 60  | 1.40 ± .55d  | 3.46 ± .04h  | 3.96 ± .06h  | 24.55 ± 1.12a | 88.20 ± 2.05a  |
| 2  | 0   | 2.40 ± .55ab | 4.38 ± .05c  | 4.88 ± .06c  | 18.41 ± 1.35fg | 84.60 ± 5.13ab |
| 2  | 30  | 2.00 ± 0.00bc | 3.71 ± .04e  | 4.33 ± .05e  | 2.66 ± 10.02cd | 84.00 ± 5.20ab  |
| 2  | 60  | 2.00 ± 0.00bc | 3.61 ± .05fg | 4.19 ± .07f  | 22.61 ± 1.10bc | 87.60 ± 4.83ab  |
| 4  | 0   | 2.40 ± .55ab | 4.54 ± .05b  | 5.03 ± .05b  | 17.35 ± .50g  | 83.00 ± 1.22abc |
| 4  | 30  | 2.00 ± 0.00bc | 4.71 ± .04a  | 5.23 ± .03a  | 17.19 ± 10.6g  | 83.60 ± 5.41abc |
| 4  | 60  | 2.00 ± 0.00bc | 4.41 ± .08c  | 4.77 ± .07d  | 19.87 ± .95de  | 88.20 ± 2.95a  |
| 8  | 0   | 2.60 ± .55a  | 4.59 ± .07b  | 5.15 ± .07a  | 14.60 ± .69h  | 72.00 ± 3.39e  |
| 8  | 30  | 2.00 ± 0.00bc | 4.57 ± .07b  | 5.15 ± .14a  | 18.15 ± .52fg  | 84.00 ± 4.00ab  |
| 8  | 60  | 2.00 ± 0.00bc | 4.10 ± 1.11d | 4.68 ± .09d  | 17.32 ± .97g  | 75.20 ± 3.70de |

**F** value

| FD  | Se  | F  | F  | F  | F  |
|-----|-----|----|----|----|----|
| FD  | 3.259** | 751.798** | 499.034** | 82.248** | 14.712** |
| Se  | 14.778** | 173.038** | 201.975** | 78.226** | 1.143** |
| FD × Se | .704ns | 47.411** | 201.975** | 7.033** | 4.958** |

Note: Means ($n = 5$) with different letters differ significantly at the 5% probability level based on Tukey’s test. Abbreviations: $E_{50}$, time taken to 50% emergence; EI, emergence index; FD, flooding duration; FEP, final emergence percentage; MET, mean emergence time; ns, nonsignificance at $p > .05$; TSE, time to start emergence.

*Significant at $p < .05$. **Significant at $p < .001$. 

HU ET AL.
Effects of selenium (Se) concentration and flooding duration on rice morphology

Note: Abbreviation: ns, nonsignificance at p > .05. *Significant at p < .001.

**TABLE 2** Effects of selenium (Se) concentration and flooding duration on rice morphology

| FD | Se | 10th day | 18th day | 10th day | 18th day | 10th day | 18th day |
|----|----|----------|----------|----------|----------|----------|----------|
| 0  | 0  | 5.13 ± 0.2de | 11.28 ± .31bc | 5.52 ± .09c | 1.37 ± .33b | .59 ± .01c | 1.05 ± .03d |
| 0  | 30 | 5.83 ± .26c  | 11.92 ± .64b  | 6.48 ± .07b  | 11.57 ± .50a | .66 ± .03b | 1.21 ± .02b |
| 0  | 60 | 6.48 ± 0.20a | 13.54 ± .38a  | 6.80 ± .23a  | 12.08 ± .42a | .77 ± .02a | 1.33 ± .03a |
| 2  | 0  | 4.89 ± .29e  | 1.65 ± 1.10cd | 4.23 ± .16e  | 9.42 ± .77c | .43 ± .02e | .91 ± .05e |
| 2  | 30 | 5.71 ± .37c  | 11.42 ± .65bc | 5.05 ± .35d  | 1.38 ± .50b | .52 ± .02d | 1.05 ± .05d |
| 2  | 60 | 6.13 ± .25b  | 13.30 ± 1.12a | 5.06 ± .55d  | 9.96 ± .78bc | .58 ± .03c | 1.16 ± .04c |
| 4  | 0  | 3.85 ± .13g  | 9.23 ± .16e  | 3.11 ± .26f  | 7.79 ± .26d | .30 ± .02g | .73 ± .04f |
| 4  | 30 | 4.08 ± .19g  | 1.30 ± .67d  | 3.28 ± .27f  | 8.38 ± .54d | .31 ± .01g | .72 ± .05f |
| 4  | 60 | 5.36 ± .22d  | 11.33 ± .12bc | 3.37 ± .19f  | 1.32 ± .52b | .38 ± .02f | 1.19 ± .03bc |
| 8  | 0  | 2.51 ± .22i  | 6.52 ± .52g  | 1.06 ± .05g  | 5.55 ± .27e | .14 ± .01h | .52 ± .03g |
| 8  | 30 | 3.12 ± .19h  | 8.33 ± .50f  | 1.16 ± .07g  | 6.19 ± .19e | .15 ± .00h | .51 ± .02g |
| 8  | 60 | 4.53 ± .16f  | 8.70 ± .48ef | 1.22 ± .04g  | 5.93 ± .20e | .13 ± .01h | .41 ± .03h |
| F  | FD | 354.739*    | 147.663*    | 1235.500*   | 346.937*   | 2296.481* | 1066.688* |
|    | Se | 224.398*    | 66.026*     | 38.621*     | 8.220*     | 74.146*   | 191.334*  |
|    | FD × Se | 6.577* | 1.663ns | 6.964* | 8.220* | 3.269* | 74.146* |

Note: Means (n = 5) with different letters differ significantly at the 5% probability level based on Tukey’s test. Abbreviations: FD, flooding duration; ns, nonsignificance at p > .05. *Significant at p < .001.

**TABLE 3** Effects of selenium (Se) concentration on biochemical attributes of rice seeds

| Se  | MDA (nm/g seed)  | Starch (% DW)  | α-Amylase (units*) | Sugar (% DW) |
|-----|------------------|----------------|---------------------|-------------|
| 0   | 11.27 ± 1.44a    | 5.24 ± 3.50a   | 8.35 ± .95c         | 7.17 ± .36b |
| 30  | 9.90 ± 1.87b     | 46.68 ± 4.41b  | 9.15 ± .96b         | 7.34 ± .53b |
| 60  | 8.44 ± .57c      | 43.77 ± 2.51c  | 9.98 ± .32a         | 7.65 ± .49a |
| F   | 2.442**          | 16.560**       | 2.635**             | 5.512*      |

Notes: One unit of the enzyme’s activity is the amount of enzyme that released 1 μmol of maltose by 1-ml original enzyme solution in 1 min. Means (n = 5) with different letters differ significantly at the 5% probability level based on Tukey’s test. Abbreviation: ns, nonsignificance at p > .05. *Significant at p < .01. **Significant at p < .001.

3.4 | Biochemical attributes of seedlings

Flooding duration, Se concentration, and their interaction significantly affected seedling biochemical attributes, although the interaction had no significant effect on GPx activity (Table 4). Antioxidant enzyme activities first increased and then decreased with increasing flooding duration. SOD and POD activities were highest in FD₄ and lowest in FD₈. Furthermore, SOD and POD activities in FD₂ were 14.63% and 26.15% lower, respectively, compared with FD₄. In turn, CAT and GPx activities were highest in FD₂ and lowest in FD₈, whereas SOD and POD activities in FD₈ were 25.74% and 19.20% lower, respectively, compared with FD₂. Additionally, soluble protein and total chlorophyll contents decreased with increasing flooding duration. Thus, compared with FD₀, soluble protein and total chlorophyll contents in FD₈ increased by 35.51% and 44.72%, respectively. In contrast, SOD, POX, CAT, and GPx activities and soluble protein and total chlorophyll contents increased with increasing Se concentration. Thus, compared with Se₀, these six physiological indicators increased by 55.53%, 129.00%, 225.68%, 9.72%, 75.86%, and 46.02%, respectively, in Se₆₀. Se priming tended to increase antioxidant enzyme activities, as well as soluble protein and total chlorophyll contents, although the extent of such increase was different under different flooding duration treatments. In summary, short-term flooding stimulated antioxidant enzyme activities. Conversely, long-term flooding damaged the physiology of seedlings, but Se restored and in fact enhanced the physiology of seedlings under conditions of 0–8 days of flooding.
Effects of selenium (Se) concentration and flooding duration on biochemical attributes of rice seedlings

**Table 4** Effects of selenium (Se) concentration and flooding duration on biochemical attributes of rice seedlings

| FD | Se  | SOD (units/g protein) | POD (µmol min⁻¹ g⁻¹) | CAT (µmol min⁻¹ g⁻¹) | GPx (µmol min⁻¹ g⁻¹) | Protein (mg/g FW) | Total chlorophyll (mg/g FW) |
|----|-----|----------------------|-----------------------|----------------------|----------------------|------------------|--------------------------|
| 0  | 0   | 565.38 ± 19.80g      | 1.04 ± .03j           | .66 ± .01i           | 152.18 ± 5.21fg      | .27 ± .01f       | 3.32 ± .08f              |
| 0  | 30  | 663.74 ± 16.60cd     | 1.68 ± .05g           | 1.32 ± .03f          | 199.03 ± 15.05de     | .36 ± .01c       | 4.32 ± .07b              |
| 0  | 60  | 673.99 ± 55.53cd     | 2.25 ± .09f           | 1.66 ± .04d          | 289.77 ± 13.82a      | .44 ± .01a       | 5.06 ± .21a              |
| 2  | 0   | 612.50 ± 27.39ef     | 1.23 ± .05i           | .73 ± .04i           | 176.08 ± 7.77ef      | .24 ± .02g       | 3.23 ± .12f              |
| 2  | 30  | 682.47 ± 50.76cd     | 2.36 ± .08de          | 1.48 ± .07e          | 231.87 ± 10.83bc     | .35 ± .01c       | 4.28 ± .22b              |
| 2  | 60  | 923.54 ± 49.13a      | 2.77 ± .05b           | 2.49 ± .07a          | 307.70 ± 15.62a      | .41 ± .02b       | 5.01 ± .41a              |
| 4  | 0   | 587.32 ± 27.17fg     | 1.42 ± .05h           | .68 ± .05i           | 122.54 ± 69.06g      | 0.20 ± .01h      | 2.79 ± .16g              |
| 4  | 30  | 708.49 ± 16.45c      | 2.41 ± .06d           | 1.21 ± .05g          | 211.88 ± 13.36cd     | .30 ± .01e       | 3.73 ± .08d              |
| 4  | 60  | 933.46 ± 21.75a      | 2.90 ± .12a           | 2.24 ± .10b          | 280.34 ± 6.19a       | .36 ± .01c       | 4.01 ± .25c              |
| 8  | 0   | 457.42 ± 6.40h       | .93 ± .04k            | .50 ± .03j           | 137.15 ± 5.96g       | .16 ± .01i       | 2.09 ± .10h              |
| 8  | 30  | 645.79 ± 18.68de     | 2.30 ± .09ef          | 1.01 ± .02h          | 197.60 ± 11.11d      | 0.21 ± .01h      | 2.32 ± .12h              |
| 8  | 60  | 877.01 ± 44.14b      | 2.66 ± .07c           | 1.98 ± .13c          | 243.53 ± 16.61b      | .32 ± .02d       | 2.61 ± .19g              |

**Table 5** Effects of selenium (Se) concentration and flooding duration on rice seedlings

| FD | Se  | Total Se  | Organic Se |
|----|-----|-----------|------------|
|    |     | mg/kg     | mg/kg      |
| 0  | 0   | .165 ± .002d | .082 ± .002h |
| 0  | 30  | 1.506 ± .068c | .828 ± .024e |
| 0  | 60  | 2.653 ± .069a | 1.746 ± .062a |
| 2  | 0   | .151 ± .003d | .071 ± .003h |
| 2  | 30  | 1.499 ± .029c | .814 ± .061e |
| 2  | 60  | 2.545 ± .084b | 1.620 ± .044b |
| 4  | 0   | .130 ± .002d | .063 ± .004h |
| 4  | 30  | 1.468 ± .048c | .725 ± .029f |
| 4  | 60  | 2.481 ± .123b | 1.446 ± .039c |
| 8  | 0   | 0.101 ± .003d | .051 ± .003h |
| 8  | 30  | 1.490 ± .059c | .664 ± .031g |
| 8  | 60  | 2.494 ± .0108b | 1.271 ± .070d |

**Note:** Means (n = 5) with different letters differ significantly at the 5% probability level based on Tukey’s test.

**Abbreviations:** CAT, catalase; FD, flooding duration; GPx, glutathione peroxidase; nonsignificance at p > .05; POD, peroxidase; SOD, superoxide dismutase.

*Significant at p < .01. **Significant at p < .001.

### 3.5 Effect of Se concentration in seed soaking solution on seedlings

Flooding duration and Se treatments considerably affected seedling total Se and organic Se contents, although the interaction between them significantly affected only organic Se content (Table 5). Total Se and organic Se contents decreased with increasing flooding time, being 5.53% and 25.23% lower in FD0, respectively, compared with FD5. Conversely, total Se and organic Se contents increased with increasing Se concentration; indeed, they increased by 2.407 and 1.454 mg kg⁻¹, respectively, in Se50, compared with Se0. Se content of polished rice ranged between .101 and .121 mg kg⁻¹ across treatments. These results indicate that flooding reduced the transport of Se from the seed to the growing seedling, whereas Se priming significantly increased Se content in seedlings.

### 3.6 Total dry weight, yield, and Se content in polished rice

Flooding duration, Se concentration, and their interaction significantly affected total dry weight and yield in both years, but the interaction had no significant effect on Se content in polished rice in 2018 (Table 6). In 2018–2019, total dry weight and yield first increased and...
Effects of selenium (Se) concentration and flooding duration on total dry weight, yield, and Se content in Polish rice in 2018

Furthermore, except for Se60 in FD8, Se seed priming accelerated seed germination and seedling growth were promoted by seed priming with low Se concentrations (Moulick et al., 2019); consistently, our data showed that Se60 reduced 18-day-old seedling dry weight in FD8 (Table 2). Although Se60 enhanced the anaerobic stress-escape mechanism by accelerating seed germination and promoting shoot and root growth, shoot elongation reportedly consumes more endosperm nutrients and reduces seedling dry weight under prolonged flooding (Nishiuchi et al., 2012). These results indicate that Se seed priming at a high concentration entails certain risks in the case of prolonged flooding in the field.

### TABLE 6 Effects of selenium (Se) concentration and flooding duration on total dry weight, yield, and Se content in Polish rice in 2018–2019

| FD | Se | 2018 | 2019 |
|----|----|------|------|
|    |     | Total dry weight t/ha | Yield t/ha | Se content mg/kg | Total dry weight t/ha | Yield t/ha | Se content mg/kg |
| 0  | 0  | 1.30 ± .55bc | 5.15 ± 0.21efg | .101 ± .003d | 10.34 ± .66cde | 4.93 ± 0.15f | 0.108 ± .003g |
| 0  | 30 | 9.85 ± .45cd | 5.06 ± 0.12gh | .106 ± .004c | 10.44 ± .30cde | 5.11 ± .07def | 0.112 ± .003f |
| 0  | 60 | 10.11 ± .40bc | 5.30 ± 0.19cde | 0.108 ± .003abc | 10.35 ± .14cde | 5.51 ± .21bc | 0.113 ± .002ef |
| 2  | 0  | 10.28 ± .51bc | 5.13 ± 0.11efg | 0.109 ± .004abc | 10.25 ± .62de | 5.05 ± .14ef | 0.114 ± .003def |
| 2  | 30 | 10.66 ± .26b | 5.37 ± 0.15bcd | .110 ± .002abc | 11.02 ± .48bc | 5.61 ± .12ab | 0.123 ± .002a |
| 2  | 60 | 12.01 ± .90a | 5.50 ± 0.08bc | .111 ± .004ab | 11.48 ± .88b | 5.67 ± .16ab | 0.118 ± .002bc |
| 4  | 0  | 10.33 ± .68bc | 5.16 ± .22efg | 0.107 ± .002bc | 10.81 ± .26bcd | 5.22 ± .18de | 0.117 ± .002bcd |
| 4  | 30 | 11.35 ± .42a | 5.56 ± 0.15b | .106 ± .003c | 11.40 ± .22b | 5.80 ± .24a | 0.121 ± .004ab |
| 4  | 60 | 11.67 ± .52a | 5.77 ± 0.15a | 0.107 ± .004abc | 12.35 ± .55a | 5.82 ± .14a | 0.116 ± .002cde |
| 8  | 0  | 9.38 ± .71d | 4.88 ± .16h | 0.112 ± .002a | 9.70 ± .57ef | 5.13 ± .13def | 0.119 ± .002bc |
| 8  | 30 | 9.92 ± .37bcd | 5.25 ± .05def | 0.108 ± .005abc | 10.79 ± .63bcd | 5.33 ± .21cd | 0.119 ± .003bc |
| 8  | 60 | 9.59 ± .53cde | 4.96 ± 0.15gh | .111 ± .003ab | 9.49 ± .33f | 4.98 ± .26ef | .116 ± .003cde |

Note: Means (n = 5) with different letters differ significantly at the 5% probability level based on Tukey’s test.

**Significant at p < .05.**

***Significant at p < .01.***

### DISCUSSION

In Southern China, rice seedling quality is ensured by the wet direct-seeding method, which involves soaking the seeds until the embryo breaks through the husk and leaks white spots (Liu et al., 2014). During the sowing period, in which the seeds are generally in the second phase of germination, anaerobic stress caused by rain, uneven fields, or flooding for weed control will cause anaerobic respiration to replace aerobic respiration, thereby reducing the efficiency of starch hydrolysis into soluble sugars (Ella et al., 2011). In the experiments reported herein, seed germination and seedling growth were restricted with increasing duration of flooding conditions (Tables 1 and 2), consistently with results of a previous study (Ella et al., 2011). Furthermore, except for Se60 in FD8, Se seed priming accelerated seed germination, increased EI and FEP, and promoted seedling growth (Tables 1 and 2). Reportedly, rice germination and growth are promoted by seed priming with low Se concentrations (Moulick et al., 2016) but are inhibited at high Se concentrations (Du et al., 2019); consistently, our data showed that Se60 reduced 18-day-old seedling dry weight in FD8 (Table 2). Although Se60 enhanced the anaerobic stress-escape mechanism by accelerating seed germination and promoting shoot and root growth, shoot elongation reportedly consumes more endosperm nutrients and reduces seedling dry weight under prolonged flooding (Nishiuchi et al., 2012). These results indicate that Se seed priming at a high concentration entails certain risks in the case of prolonged flooding in the field.

The level of MDA, an important biochemical indicator of plant stress, increased significantly under conditions of extended flooding duration but decreased markedly with increasing Se concentration (Table 3). This indicates that seeds subjected to Se priming show higher antioxidant capacity and whole-cell membranes to resist flooding stress damage. Flooding induces oxidative stress, which in turn induces an increase in the production of MDA (Gautam et al., 2014). Concomitantly, the ability of α-amylase to hydrolyze starch into soluble sugars provides energy for coleoptile growth under limiting O2 conditions and is therefore directly related to the ability of rice to resist flooding stress (Vijayan et al., 2018). This study showed that Se application accelerated starch hydrolysis (Table 3) and, consistently, seed priming with Se reportedly increases the activity of...
yield. Among them, the highest seedling total dry weight and grain weight, yield, and Se content in polished rice (except 2018) at different flooding duration and selenium treatments, which could promote seed germination, improve emergence rate and better seedling stand production, and thus improved effective tillering and seed setting. In the future, it is necessary to further study the effects of the interaction between flooding duration and selenium on rice yield and grain selenium content in order to provide more guidance for Se-rich rice planting in direct seeding fields.

ACKNOWLEDGMENTS
This work was supported by the National Natural Science Foundation of China (U21A2039) and National Public Welfare Industry Project (201303106).

CONFLICT OF INTEREST
The authors declare that they have no known competing financial interests or personal relationships that might have influenced the work reported in this paper. The results/data/figures in this manuscript have not been published elsewhere, nor are they under consideration by any other publisher. The corresponding author has read Food Policy’s author responsibilities and submits this manuscript in accordance with these policies. All the material is owned by the authors, and/or no permissions were required. In addition, the manuscript has been revised by many of our colleagues, but if the editor believes that the manuscript still needs English editing services, we fully agree and will pay the relevant fees.

AUTHOR CONTRIBUTIONS
F.Q.H. was the principal investigator who designed and implemented the research. S.C.J. wrote the English version of the manuscript. D.Y.X. provided guidance during the experimentation process.
J.O.Z. reviewed the final version of the manuscript prior to submission for peer review. B.D. oversaw the study and performed statistical analysis. W.Z. provided English guidance in the process of revising the manuscript. K.H. provided help in completing the experiment. Y.M.X. & L.Z. helped with selenium testing.

**DATA AVAILABILITY STATEMENT**

The datasets analyzed in this study are available from the corresponding author upon reasonable request.

**ORCID**

Zhun Wang https://orcid.org/0000-0002-5949-3191  
Kang Hu https://orcid.org/0000-0002-2527-3799  
Yi-mei Xie https://orcid.org/0000-0001-6616-1286  
Bin Du https://orcid.org/0000-0003-0182-7942

**REFERENCES**

Bradford, M. M. (1976). A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry*, 72, 248–254. https://doi.org/10.1016/0003-2697(76)90527-3  
Candan, N., & Tarhan, L. (2012). Tolerance or sensitivity responses of *Mentha pulegium* to osmotic and waterlogging stress in terms of antioxidant defense systems and membrane lipid peroxidation. *Environmental and Experimental Botany*, 75, 83–88. https://doi.org/10.1016/j.envexpbot.2011.08.014  
Chamara, B. S., Marambe, B., Kumar, V., Ismail, A. M., Septiningsih, E. M., & Chauhan, B. S. (2018). Optimizing sowing and flooding depth for anaerobic germination-tolerant genotypes to enhance crop establishment, early growth, and weed management in dry-seeded rice (*Oryza sativa* L.). *Frontiers in Plant Science*, 9, 1654. https://doi.org/10.3389/fpls.2018.01654  
Deng, X., Liu, K., Li, M., Zhang, W., Zhao, X., Zhao, Z., & Liu, X. (2017). Difference of selenium uptake and distribution in the plant and selenium form in the grains of rice with foliar spray of selenium or selenate at different stages. *Field Crops Research*, 211, 165–171. https://doi.org/10.1016/j.fcr.2017.06.008  
Du, B., Luo, H., He, L., Zhang, L., Liu, Y., Mo, Z., Pan, S., Tian, H., Duan, M., & Tang, X. (2019). Rice seed priming with sodium selenate: Effects on germination, seedling growth, and biochemical attributes. *Scientific Reports*, 9, 1–9. https://doi.org/10.1038/s41598-019-40849-3  
Ella, E. S., Dionisio-Sese, M. L., & Ismail, A. M. (2011). Seed pre-treatment in rice reduces damage, enhances carbohydrate mobilization and improves emergence and seedling establishment under flooded conditions. *AoB Plants*, 2011. https://doi.org/10.1093/aobpla/plr007  
Farooq, M., Basra, S., Cheema, M. A., & Afzal, I. (2006). Integration of presowing soaking, chilling and heating treatments for vigour enhancement in rice (*Oryza sativa* L.). *Seed Science and Technology*, 34, 499–506. https://doi.org/10.15258/sst.2006.34.2.24  
Farooq, M., Ullah, A., Rehman, A., Nawaz, A., Nadeem, A., Wakeel, A., Nadeem, F., & Siddique, K. H. (2018). Application of zinc improves the productivity and biofortification of fine grain aromatic rice grown in dry seeded and puddled transplanted production systems, *Field Crops Research*, 216, 53–62. https://doi.org/10.1016/j.fcr.2017.11.004  
Feng, R., Wei, C., & Tu, S. (2013). The roles of selenium in protecting plants against abiotic stresses. *Environmental and Experimental Botany*, 87, 58–68. https://doi.org/10.1016/j.envexpbot.2012.09.002  
Filek, M., Keskinnen, R., Hartikainen, H., Szarejko, I., Janiak, A., Miszalski, Z., & Golda, A. (2008). The protective role of selenium in rape seedlings subjected to cadmium stress. *Journal of Plant Physiology*, 165, 833–844. https://doi.org/10.1016/j.jplph.2007.06.006  
Gautam, P., Lal, B., Raja, R., Baig, M. J., Haldar, D., Rath, L., Shahid, M., Tripathi, R., Mohanty, S., & Bhattacharyya, P. (2014). Post-flood nitrogen and basal phosphorus management affects survival, metabolic changes and anti-oxidant enzyme activities of submerged rice (*Oryza sativa*). *Functional Plant Biology*, 41, 1284–1294. https://doi.org.org/10.1071/FP14093  
Ge, D., Long, H., Zhang, Y., & Tu, S. (2018). Analysis of the coupled relationship between grain yields and agricultural labor changes in China. *Journal of Geographical Sciences*, 28, 93–108. https://doi.org/10.1007/s11442-018-1461-5  
Gupta, M., & Gupta, S. (2017). An overview of selenium uptake, metabolism, and toxicity in plants. *Frontiers in Plant Science*, 7, 2074. https://doi.org/10.3389/fpls.2016.02074  
Ismail, A. M., Ella, E. S., Vergara, G. V., & Mackill, D. J. (2009). Mechanisms associated with tolerance to flooding during germination and early seedling growth in rice (*Oryza sativa*). *Annals of Botany*, 103, 197–209. https://doi.org/10.1093/aob/mcn211  
Kaur, N., Sharma, S., Kaur, S., & Nayar, H. (2014). Selenium in agriculture: A nutrient or contaminant for crops? *Archives of Agronomy and Soil Science*, 60, 1593–1624. https://doi.org/10.1080/03650340.2014.918258  
Kennedy, D. (2002). The importance of rice. *Science*, 296, 13. https://doi.org/10.1126/science.296.5565.13  
Khaliq, A., Aslam, F., Matloob, A., Hussain, S., Geng, M., Wahid, A., & ur Rehman, H. (2015). Seed priming with selenium: Consequences for emergence, seedling growth, and biochemical attributes of rice. *Biological Trace Element Research*, 166, 236–244. https://doi.org/10.1007/s12011-015-0260-4  
Kieliszek, M., & Błażejek, S. (2016). Current knowledge on the importance of selenium in food for living organisms: A review. *Molecules*, 21, 609. https://doi.org/10.3390/molecules21050609  
Lal, B., Gautam, P., Nayak, A. K., Raja, R., Shahid, M., Tripathi, R., Singh, S., Septiningsih, E. M., & Ismail, A. M. (2018). Agronomic manipulations can enhance the productivity of anarobic tolerant rice sown in flooded soils in rainfed areas. *Field Crops Research*, 220, 105–116. https://doi.org/10.1016/j.fcr.2016.08.026  
Li, Y., Liu, K., & Chen, F. (2016). Effect of selenium enrichment on the quality of germinated brown rice during storage. *Food Chemistry*, 207, 20–26. https://doi.org/10.1016/j.foodchem.2016.03.080  
Lidon, F. C., Oliveira, K., Ribeiro, M. M., Pelica, J., Pataco, I., Ramalho, J. C., Leitão, A. E., Almeida, A. S., Campos, P. S., & Ribeiro-Barros, A. I. (2018). Selenium biofortification of rice grains and implications on macronutrients quality. *Journal of Cereal Science*, 81, 22–29. https://doi.org/10.1016/j.jcres.2018.03.010  
Liu, K., Chen, F., Zhao, Y., Gu, Z., & Yang, H. (2011). Selenium accumulation in protein fractions during germination of Se-enriched brown rice and molecular weights distribution of Se-containing proteins. *Food Chemistry*, 127, 1526–1531. https://doi.org/10.1016/j.foodchem.2011.02.010  
Liu, S., Zhang, Y., Lin, F., Zhang, L., & Zou, J. (2014). Methane and nitrous oxide emissions from direct-seeded and seedling-transplanted rice paddies in southeast China. *Plant and Soil*, 374, 285–297. https://doi.org/10.1007/s11104-013-1878-7  
Lu, H., Xie, H., & Yao, G. (2019). Impact of land fragmentation on marginal productivity of agricultural labor and non-agricultural labor supply: A case study of Jiangsu, China. *Habitat International*, 83, 65–72. https://doi.org/10.1016/j.habitatint.2018.11.004  
Ma, M., Cen, W., Li, R., Wang, S., & Luo, J. (2020). The molecular regulatory pathways and metabolic adaptation in the seed germination and early seedling growth of rice in response to low O2 stress. *Plants*, 9, 1363. https://doi.org/10.3390/plants9101363
Mahakham, W., Sarmah, A. K., Maensiri, S., & Theerakulpisut, P. (2017). Nanopriming technology for enhancing germination and starch metabolism of aged rice seeds using phytosynthesized silver nanoparticles. *Scientific Reports*, 7, 1–21. https://doi.org/10.1038/s41598-017-08669-5

Misra, S., Boylan, M., Selvam, A., Spallholz, J. E., & Björnstedt, M. (2015). Redox-active selenium compounds—From toxicity and cell death to cancer treatment. *Nutrients*, 7, 3536–3556. https://doi.org/10.3390/nu7053536

Mondal, S., Khan, M. I. R., Entila, F., Dixit, S., Cruz, P. C. S., Ali, M. P., Pittendrigh, B., Septiningsih, E. M., & Ismail, A. M. (2020). Responses of AG1 and AG2 QTL introgression lines and seed pre-treatment on growth and physiological processes during anaerobic germination of rice under flooding. *Scientific Reports*, 10, 1–15. https://doi.org/10.1038/s41598-020-67240-x

Moulick, D., Ghosh, D., & Santra, S. C. (2016). Evaluation of effectiveness of seed priming with selenium in rice during germination under arsenic stress. *Plant Physiology and Biochemistry*, 109, 571–578. https://doi.org/10.1016/j.plaphy.2016.11.004

Moulick, D., Santra, S. C., & Ghosh, D. (2018). Effect of selenium induced seed priming on arsenic accumulation in rice plant and subsequent transmission in human food chain. *Ecotoxicology and Environmental Safety*, 152, 67–77. https://doi.org/10.1016/j.ecoenv.2018.01.037

Niishichi, S., Yamauchi, T., Takahashi, H., Kotula, L., & Nakazono, M. (2012). Mechanisms for coping with submergence and waterlogging in rice. *Rice*, 5, 1–14. https://doi.org/10.1186/1939-8433-5-2

Oraby, M. M., Allababidy, T., & Ramadan, E. M. (2015). The bioavailability of selenium in *Saccharomyces cerevisiae*. *Annals of Agricultural Sciences*, 60, 307–315. https://doi.org/10.1016/j.aas.2015.10.006

Pappas, A. C., Zoidis, E., & Chadio, S. E. (2019). Maternal selenium and developmental programming. *Antioxidants*, 8, 145. https://doi.org/10.3390/antiox8050145

Pedrero, Z., Madrid, Y., Hartikainen, H., & Cámara, C. (2008). Protective effect of selenium in broccoli (*Brassica oleracea*) plants subjected to cadmium exposure. *Journal of Agricultural and Food Chemistry*, 56, 266–271. https://doi.org/10.1021/jf072266w

Rayman, M. P. (2012). Selenium and human health. *The Lancet*, 379, 1256–1268. https://doi.org/10.1016/S0140-6736(11)61452-9

Rehman, H. U., Rasool, F., Awal, M. I., Mahmood, A., Wakeel, A., & Hajiboland, R. (2018). Irrigation and Zn fertilizer management improves Zn phyto-availability in various rice production systems. *Journal of Plant Nutrition and Soil Science*, 181, 374–381. https://doi.org/10.1002/jpln.201700412

Sadeghzadeh, B., & Rengel, Z. (2011). Zinc in soils and crop nutrition. In M. J. Hawkesford & P. Barracough (Eds.), *The molecular and physiological basis of nutrient use efficiency in crops* (pp. 335–375). John Wiley & Sons.

Sarkar, R. K. (2012). Seed priming improves agronomic trait performance under flooding and non-flooding conditions in rice with QTL SUB1. *Rice Science*, 19, 286–294. https://doi.org/10.1016/S1672-6308(12)60053-5

Tao, Y., Chen, Q., Peng, S., Wang, W., & Nie, L. (2016). Lower global warming potential and higher yield of wet direct-seeded rice in Central China. *Agronomy for Sustainable Development*, 36, 24. https://doi.org/10.1007/s13593-016-0361-2

Vijayan, J., Senapati, S., Ray, S., Chakraborty, K., Molla, K. A., Basak, N., Pradhan, B., Yeasmin, L., Chattopadhyay, K., & Sarkar, R. K. (2018). Transcriptomic and physiological studies identify cues for germination stage oxygen deficiency tolerance in rice. *Environmental and Experimental Botany*, 147, 234–248. https://doi.org/10.1016/j.envexpbot.2017.12.013

Wang, C., Ji, J., & Zhu, F. (2017). Characterizing Se transfer in the soil-crop systems under field condition. *Plant and Soil*, 415, 535–548. https://doi.org/10.1007/s11104-017-3185-1

Wang, Y., Wang, X., & Wong, Y. (2012). Proteomics analysis reveals multiple regulatory mechanisms in response to selenium in rice. *Journal of Proteomics*, 75, 1849–1866. https://doi.org/10.1016/j.jprot.2011.12.030

Yamauchi, M., & Winn, T. (1996). Rice seed vigor and seedling establishment in anaerobic soil. *Crop Science*, 36, 680–686. https://doi.org/10.2135/cropsciresearch1996.0011183X003600030027x

Yang, P., Huang, Q., Qin, G., Zhao, S., & Zhou, J. (2014). Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. *Photosynthetica*, 52, 193–202. https://doi.org/10.1007/s11109-014-0020-2

Zhang, M., Tang, S., Huang, X., Zhang, F., Pang, Y., Huang, Q., & Yi, Q. (2014). Selenium uptake, dynamic changes in selenium content and its influence on photosynthesis and chlorophyll fluorescence in rice (*Oryza sativa* L.). *Environmental and Experimental Botany*, 107, 39–45. https://doi.org/10.1016/j.envexpbot.2014.05.005

Zulfiqar, U., Hussain, M., Maqsood, M., Ishfaq, M., & Ali, N. (2021). Zinc nutrition to enhance rice productivity, zinc use efficiency, and grain biofortification under different production systems. *Crop Science*, 61, 739–749. https://doi.org/10.1002/csc2.020381

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**How to cite this article:** Hu, F., Jiang, S., Wang, Z., Hu, K., Xie, Y., Zhou, L., Zhu, J., Xing, D., & Du, B. (2022). Seed priming with selenium: Effects on germination, seedling growth, biochemical attributes, and grain yield in rice growing under flooding conditions. *Plant Direct*, 6(1), e378. https://doi.org/10.1002/pld3.378