Expression of Potato StDRO1 in Arabidopsis Alters Root Architecture and Drought Tolerance

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Potato (Solanum tuberosum L) is the third important crop for providing calories to a large human population, and is considered sensitive to moderately sensitive to drought stress conditions. The development of drought-tolerant, elite varieties of potato is a challenging task, which can be achieved through molecular breeding. Recently, the DEEPER ROOTING 1 (DRO1) gene has been identified in rice, which influences plant root system and regulates grain yield under drought stress conditions. The potato StDRO1 protein is mainly localized in the plasma membrane of tobacco leaf cells, and overexpression analysis of StDRO1 in Arabidopsis resulted in an increased lateral root number, but decreased lateral root angle, lateral branch angle, and silique angle. Additionally, the drought treatment analysis indicated that StDRO1 regulated drought tolerance and rescued the defective root architecture and drought-tolerant phenotypes of Atdro1, an Arabidopsis AtDRO1 null mutant. Furthermore, StDRO1 expression was significantly higher in the drought-tolerant potato cultivar “Unica” compared to the drought-sensitive cultivar “Atlantic.” The transcriptional response of StDRO1 under drought stress occurred significantly earlier in Unica than in Atlantic. Collectively, the outcome of the present investigation elucidated the role of DRO1 function in the alternation of root architecture, which potentially acts as a key gene in the development of a drought stress-tolerant cultivar. Furthermore, these findings will provide the theoretical basis for molecular breeding of drought-tolerant potato cultivars for the farming community.

Keywords: molecular breeding, root system, branch angle, abiotic stress, food security

INTRODUCTION

Potato (Solanum tuberosum) is indispensable for food security around the globe and the fourth largest food crop in China (Cao et al., 2020). The world potato catalog contains information on approximately 4,500 cultivable varieties from around the globe.¹ These potato cultivars vary by various morphological, physiological, biochemical, and pathological attributes under

¹www.euroseeds.eu/potatoes
ever-changing environmental conditions (Pieczynski et al., 2018). Several classical and molecular studies have been undertaken to understand the genomic regions controlling traits with agricultural and economic importance using diploid and tetraploid potato plants. Kondrak et al. (2012) developed a transgenic White Lady potato cultivar, which expressed the trehalose-6-phosphate synthase gene exhibiting drought tolerance. Similarly, Zaki and Radwan (2022) investigated a set of 21 commercial potato cultivars representing genetic diversity in the Middle East and screened drought tolerance based on morpho-physiological traits and tuber production under in vitro and field trails. The results displayed the upregulation of DRO, ERECTA, ERF, DREB, and SIMYB genes in drought-tolerant cultivars, indicating the possible role of these genes in future molecular breeding programs. Recently, the availability of genome sequence data for most crops, e.g., Arabidopsis (Weigel and Mott, 2009), rice (3,000 rice genomes project, 2014), wheat (Walkowiak et al., 2020), soybean (Xie et al., 2019), maize (Vicki and Volker, 2002), and potato (Leisner et al., 2018; Hoopes et al., 2022) has enabled to understand and improve both quantitative and qualitative traits, especially genes governing abiotic stress tolerance.

Drought is considered the major abiotic stress for crop plants (Sun et al., 2021). The availability of irrigation water will continue to decrease across the globe owing to a surge in human population from 7 to 9 billion by 2050 (Edmeades, 2013). Therefore, it is imperative to use agricultural mechanization and cultivation water-saving techniques, as well as to develop high-yield and high-quality varieties with better resistance to biotic and abiotic stresses to improve agricultural production (Weber et al., 2014; Brito et al., 2016). Potato, being a shallow root crop, is relatively more sensitive to drought stress than other staple crops (Deblonde and Ledent, 2001; Schaeftlener et al., 2007). Long-term or seasonal drought seriously affects the yield and commercial quality of potato (Walworth and Carling, 2002). Moreover, it is notable that some major potato production areas are located in arid and semi-arid regions (Porter et al., 1999; Fabeiro et al., 2001). Accelerating global climate change and associated drought is a threat to potato production (Kumar et al., 2007; Li et al., 2019). Roots are integral in performing a variety of functions, e.g., nutrients and water uptake, serving as a storage organ and helping the plant to anchor in the soil (Smith and De Smet, 2012). The variable interactions of plant roots with the environment depends on root components and root architecture (Lynch and Brown, 2012).

Root architecture defines the spatial configuration of roots and helps the plant to respond to ever-changing environmental conditions. Understanding root architecture is important for agricultural productivity because mostly soils have an uneven distribution of resources (Zhao et al., 2018). The spatial distribution of roots allow the plant to exploit available soil resources efficiently. Plant roots function in the absorption and transport of water and nutrients, and root architecture is known to strongly contribute for plant’s ability to tolerate abiotic stresses, especially drought condition (Manschadi et al., 2006; Mansoor-khani et al., 2014; Bartlett et al., 2022; Ranjan et al., 2022; Rasool et al., 2022). Several studies have shown that drought (or the lack of irrigation in the topsoil) can promote the formation of deeper roots to allow crops to access water and nutrients from the deeper soil (Shahnazari et al., 2007; Chimungu et al., 2014). In recent years, extensive efforts have been observed to harness deep rooting architecture as a screening and evaluation index for drought-tolerance breeding in some cereal crops (Wasson et al., 2012; Lynch, 2013; Liao et al., 2022). Genetic information focused on root architecture, and its role to counter abiotic stresses especially drought in tuber crops is less available (Villordon et al., 2014a).

In rice, a major quantitative trait locus, OsDRO1 (DEEPER ROOTING 1), was functionally characterized by map-based cloning of two varieties with apparent differences in their root architecture. The DRO1 protein was shown to regulate both root angle and drought tolerance (Uga et al., 2012, 2013; Arai-Sanoh et al., 2014). Subsequently, DRO1 orthologs in Arabidopsis (Arabidopsis thaliana), plum (Prunus domestica), and wheat (Triticum aestivum) were also found to function in regulating root architecture; however, it is notable that the specific root traits regulated by this gene were distinct in these plants (Hollender and Dardick, 2015; Ge and Chen, 2016, 2019; Guseman et al., 2017; Taniguchi et al., 2017; Ashraf et al., 2019; Furutani et al., 2020; Waite et al., 2020). In addition, DRO1 orthologs in Arabidopsis were placed within the larger IGT gene family, with the LAZY and TILLER ANGLE CONTROL genes (Yoshihara et al., 2013; Hollender and Dardick, 2015; Guseman et al., 2017; Taniguchi et al., 2017; Ge and Chen, 2019). Keeping in view, the present study was designed to analyze the role of DRO1 orthologs in potato (S. tuberosum) exerting similar functions, we initially cloned StDRO1 and conducted a series of functional analyses to study the function of StDRO1 for the alternation of root architecture and improvement for the drought stress tolerance.

**MATERIALS AND METHODS**

**Plant Materials and Mutant Detection**

Arabidopsis ecotype Columbia (Col.) was used for the present investigation. The Arabidopsis T-DNA insertion mutant (SALK_201221C, Col. background) Atdro1 was obtained from the Arabidopsis Biological Resource Center (Ohio State University, United States). Heterozygous mutants of Atdro1 were first identified, and the homozygous mutants were obtained from self-crossed progenies of the heterozygous parent. The gene-specific primers of left genomic primer (LP) and right genomic primer (RP) were utilized for genotyping; moreover, LB1 was used as border primer of T-DNA (Supplementary Table 1). The potato cultivars Atlantic and Unica for tissue culture seedlings were provided by the Key Laboratory of Crop Genetic Improvement and the Germplasm Innovation of Gansu Agricultural University whereas, virus-free potato mini-tubers of both drought-sensitive “Atlantic” and drought-tolerant “Unica” cultivars were provided by the Dingxi Academy of Agricultural Sciences, the Gansu province.
Cloning, Vector Construction, and Subcellular Localization Analysis of StDRO1

Gene-cloning primers of StDRO1 were designed according to the 35 s promoter and Supplementary Table 1 gene-specific as reverse primer (PCR) was used to identify T1 method (Clough and Bent, 1998). Polymerase chain reaction (Murashige and Skoog, 1962). After 2 weeks of growth, 75 mM mannitol to simulate drought stress conditions, MS plates with 0.8% (w/v) agar, 1% (w/v) sucrose, and Arabidopsis seeds were surface-sterilized with the similar indexes under drought stress.

Phenotype Observation and Determination of Physiological and Biochemical Indexes of Transgenic Plants

Root Phenotype Observation
Arabidopsis seeds were surface-sterilized with 75% (v/v) ethanol for 40 s, followed by 1% (v/v) NaClO for an additional 8 min and then washed with desterilized water six times. The washed seeds were placed on one-half-strength MS plates containing 0.8% (w/v) agar and 1% (w/v) sucrose. Seeds were vernalized at 4°C for 3 days and transferred to a growth chamber under a long-day condition (16 h of light and 8 h of dark) at 22°C. After 2 weeks of growth, the images of the root system were taken. Stable homozygous transgenic lines were identified and studied for subsequent phenotypic observation and drought tolerance analysis.

Phenotypic Observation of Aerial Parts
Nutrient soil and vermiculite were mixed at a 2:1 volume ratio and supplied to 10-cm diameter pots. Sterilized and vernalized Arabidopsis seeds were sown in pots containing nutrient soils, and the pots were placed in a greenhouse under a long-day condition (16 h of light and 8 h of dark) at 22°C. After 5 weeks of growth, aerial parts' images were taken.

RNA Extraction and Quantitative Real-Time Polymerase Chain Reaction of StDRO1

Potted Potato Growth Conditions
Nutrient soil and vermiculite were mixed at a 2:1 volume ratio and put into a 38-cm diameter pot. Virus-free mini-tubers were sown 5 cm below the soil surface. The pots were placed under field conditions at Gansu Agricultural University, normal agronomic practices were carried out throughout the growing period. After 65 days of growth, the whole plant, including roots, was carefully uprooted from the soil. Various tissues were quickly frozen in liquid nitrogen and stored at −80°C. The same procedure was repeated for all plants under investigation.

Potato Tissue Culture Growth and Treatment Condition
Stems (approximately 2 cm) of 1-month-old tissue culture plantlets were cut and transferred to sterilized glass jars containing MS medium. The jars were placed in a greenhouse under long-day conditions (16 h of light and 8 h of dark) at 22°C. After 4 weeks of growth, potato seedlings were collected and grown with 200 mM mannitol in liquid medium for 0, 2, 6, 12, and 24 h. After treatment, seedlings were quickly frozen in liquid nitrogen and stored at −80°C.

RNA Extraction and Quantitative Real-Time Polymerase Chain Reaction

The RNA extraction kit (Tiangen) was used for the extraction of total RNAs from various potato tissues. About 5 µg of RNA was transcribed to cDNA using the ReverTra Ace® qPCR RT Master Mix kit (TOYOBO). The resulting cDNAs, corresponding to 100 ng of total RNA, were then used as templates for quantitative real-time PCR by the StepOnePlusTM Real-Time PCR System (Applied Biosystems) utilizing the TB Green® Premix Ex Taq II kit (Takara). The relative expression level was calculated utilizing the −∆∆Ct method, and ACTIN2 was used as an internal control. The primers used for real-time PCR are listed in Supplementary Table 1. The experimental procedures were the same as those reported previously by Sun et al. (2017).

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Statistical Data Analysis
All experiments were repeated independently at least three times, and each sampling was analyzed separately. SPSS 20.0 software was used for statistical analyses, and statistically significant differences were measured by using Student’s t-test at *p < 0.05; **p < 0.01; ***p < 0.001.

RESULTS
Subcellular Localization and Tissue-Specific Expression Analysis of StDRO1
In the model plant Arabidopsis and some other plant species, DRO1 was found to play an integral role for regulating the growth and development of the root system; however, its function in potatoes has not been reported (Uga et al., 2012; Guseman et al., 2017; Ashraf et al., 2019). The potato StDRO1 was cloned, and an overexpression vector containing a StDRO1-GFP fusion was constructed. The vector was transiently transformed into tobacco leaves, and the GFP signals were observed under a laser confocal microscope. The StDRO1-GFP fusion protein was mainly located at the plasma membrane, whereas GFP control appeared in both the plasma membrane and the nucleus (Figure 1A). Moreover, the yeast two-hybrid assay displayed no interaction between potato StDRO1 (or StDRO1ΔEAR) and StTOPLESS (Supplementary Figure 1).

We also evaluated StDRO1 expression in the roots, stems, and leaves of the drought-tolerant potato cultivar (Unica) and the drought-sensitive potato cultivar (Atlantic). In both Atlantic and Unica, StDRO1 expression was observed to be non-significant in leaves, whereas approximately 1.5-fold higher expression was observed in the stem of the Unica cultivar. However, the StDRO1 expression level in the roots of Unica was highly significantly more than Atlantic (p < 0.001; t-test) (Figure 1B).

StDRO1 Regulates Plant Root Architecture
To investigate the capacity of potato StDRO1 to affect root architecture, we first obtained the Arabidopsis T-DNA insertion mutant AtDRO1 (Col. background) and confirmed the homozygous mutant (Figure 2A). Compared with Col. plants, AtDRO1 plants showed a significant increase in lateral root angle and a significant decrease in lateral root number, confirming that AtDRO1 regulates root architecture. Moreover, we overexpressed StDRO1 in both wild-type (Col.) and AtDRO1 mutant plants (Figure 2B). The results displayed that overexpressed StDRO1 homozygous plants had significant reductions in lateral root angle and a significant increase in the number of lateral roots compared to Col [p < 0.05; analysis of variance (ANOVA)] (Figures 2C–E). In addition, we found complementary AtDRO1 mutant plants based on transgenic overexpression of StDRO1 rescued root phenotypes as wild-type [p < 0.05; analysis of variance (ANOVA)] (Figures 2C–E). Thus, beyond confirming that Arabidopsis AtDRO1 regulates root architecture, the results also indicated that potato StDRO1 can regulate the angle and number of lateral roots.

Therefore, we observed the aerial organs of the different transgenic plants and found that the overexpression of StDRO1 in the Col. background caused a significant decrease in the lateral

![Figure 1](image-url)
StDRO1 Regulates the Drought Tolerance of Plants

It has been reported that OsDRO1 regulates the root architecture of rice and also influences rice to develop drought tolerance (Uga et al., 2013). Therefore, to examine the role of potato StDRO1 in drought tolerance, we measured physiological and biochemical indicators of stress tolerance, including the activities of the antioxidant enzymes SOD, POD, and CAT, and the Pro content of the four aforementioned Arabidopsis genotypes, under both normal growth conditions and drought treatments (75 mM mannitol in the growth medium). For Col. plants, drought stress increased the activities of the examined antioxidant enzymes and increased the Pro content ($p < 0.05$; t-test) (Figure 4). It was noteworthy that drought stress caused an increase in four indicators, namely, SOD, POD, CAT, and Pro content, and a highly significant increase in these indicators was observed in StDRO1 overexpression line (35s:StDRO1 in Col.) plants than in Col. ($p < 0.05$; t-test). Moreover, our analysis of Atdro1 plants showed no differences for SOD, POD, and CAT activities under normal and drought stress conditions; however, it detected a slight increase in Pro content in drought-stressed plants ($p < 0.05$; t-test). In contrast, complementation of Atdro1 mutant plants based on transgenic StDRO1 overexpression rescued the response for SOD, POD, CAT, and Pro content ($p < 0.05$; ANOVA).
FIGURE 3 | StDRO1 regulates the branch angle of plant aerial organs. Images of (A) quantified branch angles (B) and silique angles (C) of 5-week-old plants of Col., homozygous of 35s::StDRO1 in Col., Atdro1, and homozygous of 35s::StDRO1 in Atdro1. Statistical analysis (ANOVA) was carried out to evaluate the significance of differences between these four genotypes. Different letters indicate significant differences ($p < 0.05$).

StDRO1 Gene Expression Is Induced by Drought Stress

Based on the recorded observation, StDRO1 can regulate drought tolerance, we further expanded our research objective to investigate StDRO1 gene expression under induced drought stress conditions. The real-time quantitative PCR (qRT-PCR) analysis results showed that drought treatment (mannitol), coupled with increasing treatment time, caused a slow elevation in the expression level of StDRO1 for drought-sensitive Atlantic cultivar plants; however, it gradually increased by 10-fold with an additional 24-h sampling time point (Figure 5). In contrast, the drought-tolerant cultivar Unica showed that the expression level of StDRO1 first increased and decreased subsequently, reaching its maximum at 6 h (with a 4-fold increase) (Figure 5). Thus, the StDRO1 expression response to drought stress occurs earlier in the drought-tolerant cultivar Unica compared to the drought-sensitive cultivar Atlantic, and a significant difference of StDRO1 expression at 6 h was detected between the two cultivars, ($p < 0.01$, $t$-test) (Figure 5).

DISCUSSION

Potato tubers are rich in starch, protein, vitamin C, crude fiber, potassium, calcium, and have an excellent nutritional profile (Zaheer and Akhtar, 2016; Robertson et al., 2018). Potatoes are grown worldwide and are of great significance for global nutrition and food security (Friedman, 2006). A series of studies have indicated that the spatial distribution of crop roots largely determines the ability of plants to obtain soil resources, regulating crop water, and nutrient use efficiency as well as crop adaptability to abiotic stress conditions (Malekpoor et al., 2014). In cereal crops, root traits have been extensively studied as an informative breeding index (Wasson et al., 2012; Lynch, 2013; Henry et al., 2014). In recent years, research on tuber crops has found that the optimization of root system architecture can confer substantial yield increases (Villordon et al., 2014b). However, drought is one of the principal abiotic stress limiting potato production around
FIGURE 4 | StDRO1 regulates plant drought tolerance. (A–D) Responses of SOD, POD, and CAT activity along with proline (Pro) content under drought stress treatment. Two-week-old seedling of Col., homozygous 35s:StDRO1 in Col., Atdro1, and homozygous of 35s:StDRO1 in Atdro1 grown with or without 75 mM mannitol were used. Student's t-test was carried out to evaluate the significant difference among control and drought treatment. ∗p < 0.05; ∗∗p < 0.01; ∗∗∗p < 0.001; and ns, not significant.

FIGURE 5 | StDRO1 gene expression is induced by drought stress. At the indicated time point, the effect of drought stress (by mannitol treatment) on StDRO1 gene expression. Four-week-old seedlings of the drought-tolerant potato cultivar (Unica) and the drought-sensitive potato cultivar (Atlantic) grown under long-day-condition treated with or without 200 mM mannitol were used. StACTIN2 was used as a reference gene. Error bars represent SD (n = 3). Student’s t-test was carried out to evaluate significance at each time point between Unica and Atlantic. ∗, p < 0.05; ∗∗, p < 0.01; ∗∗∗, p < 0.001; and ns, not significant.

the globe (Deblonde and Ledent, 2001; Toubiana et al., 2020). For instance, the lack of water in the upper soil layers caused by irregular rainfall and high-intensity sunlight is common for

rainfed potato planting areas. Therefore, maintaining tuber yield and commercial quality under such production conditions that have uneven distribution of water resources across different soil layers has been hotspot among researchers (Fabeiro et al., 2001; Liu et al., 2006; Kifle and Gebretsadikan, 2016; Li et al., 2019). In addition to studying and developing water-retaining and efficient cultivation techniques, researchers have sought to identify genes that help optimize root architecture and improve drought tolerance, which can be used in future potato molecular breeding programs.

In a study, map-based cloning was conducted on the shallow root rice variety “IR64” and the deep root variety “KP” for the DRO1 gene, sequencing analysis revealed that a nucleotide deletion mutation occurred in the DRO1 gene of “IR64” that caused premature cessation of DRO1 protein translation causing the deletion of C-terminal EAR motif (Uga et al., 2013; Guseman et al., 2017). For further verification, the near-isogenic line DRO1-NIL was constructed (having the “KP” DRO1 allele in the “IR64” genetic background). Compared with “IR64,” DRO1-NIL has significantly smaller root angles at different growth stages, and higher yield under drought conditions without affecting root dry weight. The outcome of the study supported the hypothesis that OsDRO1 participates in regulating the root angle and drought tolerance of rice (Uga et al., 2013). Furthermore, another group examined Arabidopsis and reported that single-gene mutations of AtDRO1 can enlarge
lateral root angles, showing that AtDRO1 overexpression causes smaller lateral root and lateral branch angles. Taken together, this could indicate that AtDRO1 regulates root architecture in Arabidopsis. The C-terminal EAR motif of the AtDRO1 protein was proven to be an essential element controlling root architecture (Guseman et al., 2017).

The construction, screening, and identification of transgenic lines in potato may took considerably longer time compared to Arabidopsis, therefore the Atdrol (Col. background) mutant was used to assess the potato StDRO1 gene function. We found that the expression of potato StDRO1 reduced the angles of lateral roots, side branches, and siliques; however, StDRO1 expression increased lateral root numbers. In addition, transgenic expression of StDRO1 could successfully rescue the defective phenotype of Atdrol mutant plants. We also observed that, under drought stress, the ability of Atdrol mutants to activate antioxidant enzymes and osmotic stress protection decreased, indicating that AtDRO1 functions in drought stress responses in Arabidopsis, a result that has not been reported in previous studies.

Our findings based on transient expression in tobacco leaves indicated that the DRO1 protein is mainly localized at the plasma membrane. This membrane localization for StDRO1 was reported in OsDRO1 (rice) and TaDRO1 (wheat) (Figure 1A) (Uga et al., 2013; Ashraf et al., 2019). A recent study reported that for Atdrol null mutant plants complemented with a VENUS-tagged AtDRO1 driven by the native AtDRO1 promoter, the reporter protein was localized in the nuclei of root tip cells (Waite et al., 2020). Further, the deletion of the EAR motif of DRO1 was reported to alter the localization of this protein in rice protoplasts (cell membrane with the full-length protein; cell nucleus and cytoplasm with the ΔEAR mutant variant) (Uga et al., 2013; Weber et al., 2014). EAR motifs are present in numerous transcriptional co-repressor proteins in plants, some of which have been shown to function by recruiting TOPLESS, a repressor of auxin-regulated, root-promoting genes (Kell, 2011). Previous reports in wheat complemented the interaction of TaDRO1-like with TaTOPLESS through the EAR motif with in vitro experiments (Ashraf et al., 2019). However, in the present investigation, the yeast two-hybrid assay displayed no interaction between potato StDRO1 (or StDRO1ΔEAR) and StTOPLESS, indicating that DRO1 can putatively exert distinct molecular functions in different plant species. The detailed function and molecular mechanism of StDRO1 in potato need to be further analyzed.

It is noteworthy to mention that in rice, Arabidopsis, and wheat, DRO1 is mainly expressed in the root tips and basal part of shoots; however, in the present investigation we observed that StDRO1 expression was low in leaves whereas it was strong in the stem part of the plant. In potato roots, the StDRO1 expression level of the drought-tolerant cultivar Unica was significantly higher than that of the drought-sensitive cultivar Atlantic. Moreover, we also observed that the gene expression of StDRO1 could be induced by drought stress, the transcriptional response of StDRO1 to drought stress occurred significantly earlier in Unica than in the Atlantic cultivar. The findings were consistent with previous studies (Schaffeitner et al., 2007; Kashiwagi et al., 2015; Li et al., 2019). These results strongly imply that StDRO1 exerts the function of drought tolerance in potato; however, related molecular mechanism(s) await further characterization. Previous studies on Arabidopsis indicated that other members of the IGT gene family (to which DRO1 belongs) are involved in the regulation of root and shoot branching angles (Yoshihara et al., 2013; Taniguchi et al., 2017; Yoshihara and Spalding, 2017; Ge and Chen, 2019). Thus, our findings showing that the function of potato StDRO1 for the regulation of root architecture and drought stress tolerance further support that StDRO1 can be considered as an attractive gene for molecular breeding efforts to obtain robust-rooting and drought-tolerant potato varieties.

**CONCLUSION**

In this study, DRO1 function for the regulation of root architecture and drought tolerance was investigated. In addition, StDRO1 expression was several-fold higher in the stem and root of the Unica (drought-tolerant) cultivar, whereas, overexpression rescued the aerial organ and root phenotypes of the Arabidopsis Atdrol null mutant. The ectopic expression of StDRO1 in Arabidopsis revealed a significant increase in biochemical indicators (e.g., SOD, POD, and CAT), along with Pro content under drought stress conditions, indicating that StDRO1 is potentially a key player for potato drought stress tolerance. These results provide additional evidence that StDRO1 functions during drought stress, thus laying a foundation for future studies focusing on DRO1 and related genes in the drought responses of other crops under drought stress conditions.

**DATA AVAILABILITY STATEMENT**

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

**AUTHOR CONTRIBUTIONS**

CS designed the experiments and wrote the original draft of this manuscript and revision. CS, WL, KY, DX, and TQ performed the experiments and analyzed the data. SF, PK, ZB, YL, ZL, and JZ contributed to the review and editing. JB developed the research concept and managed the funding for the publication. All authors have read and agreed to the published version of this manuscript.

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**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.836063/full#supplementary-material
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