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RESEARCH ARTICLE

OsFKBP42b Regulates Rice Growth and Development Through Interacting with OsABCB1 and OsABCB14

Di Wang[1,2] · Yingjie Wang[3] · Gen Pan[4] · Yanyan Wang[3] · Guizhi Wang[3] · Wenjing Chen[3] · Yating Feng[3] · Xi Liu[2,3]

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Abstract

FK506 binding proteins, a member of peptidyl-prolyl cis-trans isomerase (PPIase), are essential for plant growth; however, the molecular function of FKBPs remains largely unknown. In this report, we isolated and identified an FK506 binding protein, OsFKBP42b, that regulates rice growth and development. The *OsFKBP42b* mutation led to reductions in plant height, panicle length, and seed setting rate. Scanning electron microscopy of the wild-type and the mutant stems showed no difference in cell size. *OsFKBP42b* was expressed in rice various organs, especially in panicles, leaves, and stems. Subcellular localization suggested that OsFKBP42b was a plasma membrane protein. Furthermore, we found that OsFKBP42b interacted with the ATP binding cassette B proteins, OsABCB1 and OsABCB14, by yeast two-hybrid and bimolecular fluorescence complementation assays. Taken together, our results provide new insights into OsFKBP42b in rice.

Keywords Rice · OsFKBP42b · Growth and development · OsABCBs

Introduction

Global extreme weathers, including drought, high temperature, and flood, occur frequently and seriously affect agricultural production. Rice, a food for two-thirds of the world's population, has a small genome and can be used as a model crop for genomics research (Yang et al. 2022). Identification of rice gene function is helpful to rice molecular design and breeding and to ensure global food security.

The FK506 binding proteins (FKBPs) are the superfamily of peptidyl-prolyl cis-trans isomerases (PPIases) (Schiene and Fischer 2000; He et al. 2004; Ahn et al. 2010). Members of the FKBP family have different molecular weights from 12 kDa (hFKBP12) to over 77 kDa (wFKBP77) (Ahn et al. 2010). There are 23 and 29 members of the FKBP family in the genome of *Arabidopsis thaliana* and rice, respectively (Ahn et al. 2010; Gollan and Bhave 2010). In plants, FKBP members are reported to be involved in regulating cell differentiation, stress responses, brassinosteroid signaling, and auxin transport (Ahn et al. 2010; Cheung et al. 2020). Disruption of the *Arabidopsis AtFKBP42*, named as a *twisted dwarf* (*TWD1*), exhibited dwarfism, epinastic growth of leaves and cotyledons, shorter hypocotyls in the light, and reduced BR sensitivity (Geisler et al. 2003; Henrichs et al. 2012; Chaiwanon et al. 2016). AtFKBP42 functionally interacts with the BR receptor kinases BRI1 and BAK1 to regulate brassinosteroid signaling in *Arabidopsis* (Chaiwanon et al. 2016). In *Arabidopsis*, overexpression of *PaFKBP12* from *Polytrichastrum alpinum* increased the plant size, and had enhanced tolerance towards heat, salt, and drought stresses (Alavilli et al. 2018). AtFKBP12 was shown to interact with an ATPase, AtFIP37, in vitro, which was proposed to participate in RNA splicing (Faure et al. 1998). Recently, AtFKBP12 was identified to be a positive regulator of flowering time in *A. thaliana* by interacting with CONSTANS (CO, Serrano-Bueno et al. 2020). Ectopically expressing *OsFKBP12* in *A. thaliana* was found to increase the susceptibility of the plant to the pathogen and

✉ Xi Liu
1240623244@qq.com

1 Huaiyin Institute of Agricultural Sciences of Xuhuai Region in Jiangsu, Huai'an 223001, China

2 Key Laboratory of Eco-Agricultural Biotechnology around Hongze Lake, Regional Cooperative Innovation Center for Modern Agriculture and Environmental Protection, Huai'an 223300, China

3 School of Life Sciences, Huaiyin Normal University, Changjiang West Road 111, Huai'an City 223300, Jiangsu Province, China

4 Institute of Bast Fiber Crops, Chinese Academy of Agricultural Sciences, Changsha 410205, China

salt stress (Cheung et al. 2020). Furthermore, the unconventional GTPase, OsYchF1, an interactor of OsFKBP12, was involved in both biotic and abiotic stress responses (Cheung et al. 2020). The expression level of *OsFKBP20* was induced by heat, and over-expression of *OsFKBP20* in yeast enhanced the tolerance of yeast to high temperatures (Nigam et al. 2008). However, the function of FKBPs in rice has many unknowns, especially in the molecular level.

In this study, we confirmed that *OsFKBP42b* positively regulates plant growth and development in rice. Compared with the wild type, the *osfkbp42b* mutant showed dwarfism, shorter panicles, and decreased seed setting rate. *OsFKBP42b* was expressed in rice various organs and encodes a plasma membrane protein. Yeast two-hybrid and bimolecular fluorescence complementation assays indicated that OsFKBP42b interacted with the ATP binding cassette B proteins, OsABCB1 and OsABCB14.

Results

Characterization of OsFKBP42a and OsFKBP42b

There are two *OsFKBP42* genes (*OsFKBP42b* and *OsFKBP42a*) located on chromosomes 11 and 12 in rice (Ahn et al. 2010). OsFKBP42a and OsFKBP42b were predicted to contain 375 and 370 amino acids, respectively (Fig. 1). OsFKBP42a and OsFKBP42b have a mitochondrial precursor proteins import receptor domain, a TPR repeat region and an FKBP-type peptidyl-prolyl cis-trans isomerase domain (Fig. 1). The homologous protein BLAST revealed that FKBP42 exists among rice, *Zea mays*, *A. thaliana* and *Sorghum bicolor*. OsFKBP42a and OsFKBP42b showed approximately 90% amino acid identity, indicating that these two proteins may have similar functions or are functionally redundant.

Expression Pattern and Subcellular Localization of OsFKBP42a and OsFKBP42b

Based on the public gene expression database the Rice eFP Browser (http://bar.utoronto.ca/efp rice/cgi-bin/efpWeb.cgi) and the RiceXPro (https://ricexpro.dna.affrc.go.jp/Zapping/), we found that *OsFKBP42a* and *OsFKBP42b* had similar expression patterns and were expressed in various rice tissues (e.g., roots, stems, leaves, seeds) (Figs. S1–S4). To verify the expression pattern of *OsFKBP42a* and *OsFKBP42b*, we used the qRT-PCR method to analyze these two genes with different organs of the *japonica* rice Nipponbare. As shown in Fig. 2, *OsFKBP42a* and *OsFKBP42b* have similar spatial–temporal expression patterns. Transcripts of *OsFKBP42a* and *OsFKBP42b* were expressed in roots, panicles, leaves, stems, and sheaths (Fig. 2).

To examine the subcellular localization of the OsFKBP42a and OsFKBP42b proteins, we fused the OsFKBP42a and OsFKBP42b coding sequences with a GFP tag, respectively. Then, OsFKBP42a-GFP and OsFKBP42b-GFP were introduced into rice protoplasts. Laser confocal microscope observation indicated that GFP fluorescence could be observed in the plasma membrane (Fig. 3), which is similar to the location of the plasma membrane protein OsCAMP (Lam et al. 2007).

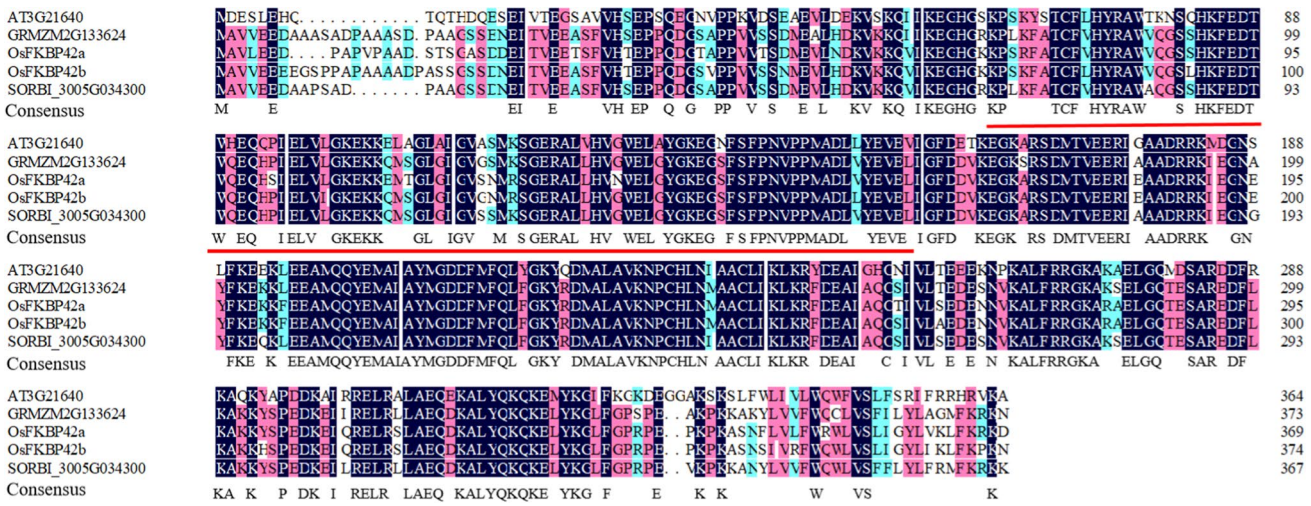

Fig. 1 Amino acid sequence alignment of OsFKBP42b and its homologs OsFKBP42a (*Oryza sativa*), GRMZM2G133624 (*Zea mays*), SORBI_3005G034300 (*Sorghum bicolor*), AT3G21640 (*Arabidopsis thaliana*). Black and pink indicate that fully or partially conserved amino acids, respectively. Red underline represents the domain of FKBP-type peptidyl-prolyl cis-trans isomerase

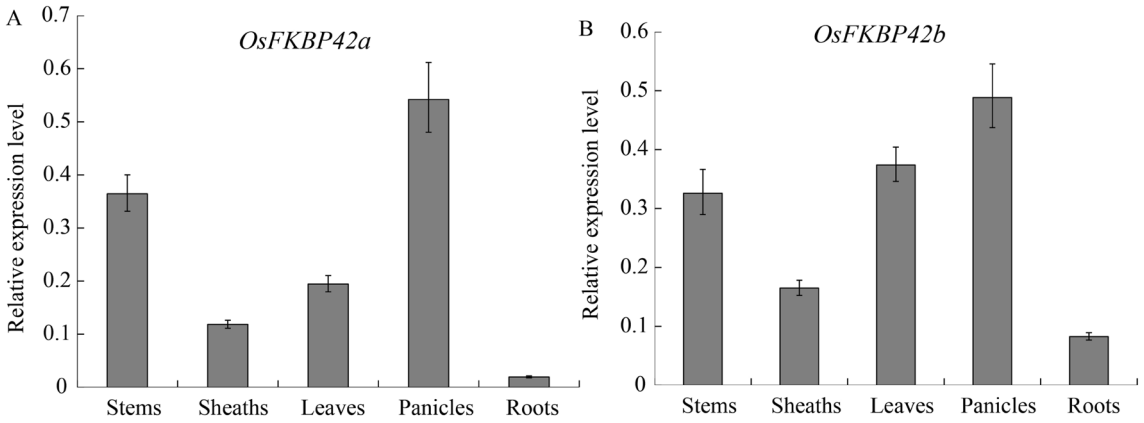

Fig. 2 Expression patterns of *OsFKBP42a* and *OsFKBP42b*. **A** Expression of *OsFKBP42a* in roots, stems, leaves, panicles, and sheaths of the Nipponbare plants. **B** Expression of *OsFKBP42b* in various tissues of the Nipponbare plants. Three biological repeated experiments were performed

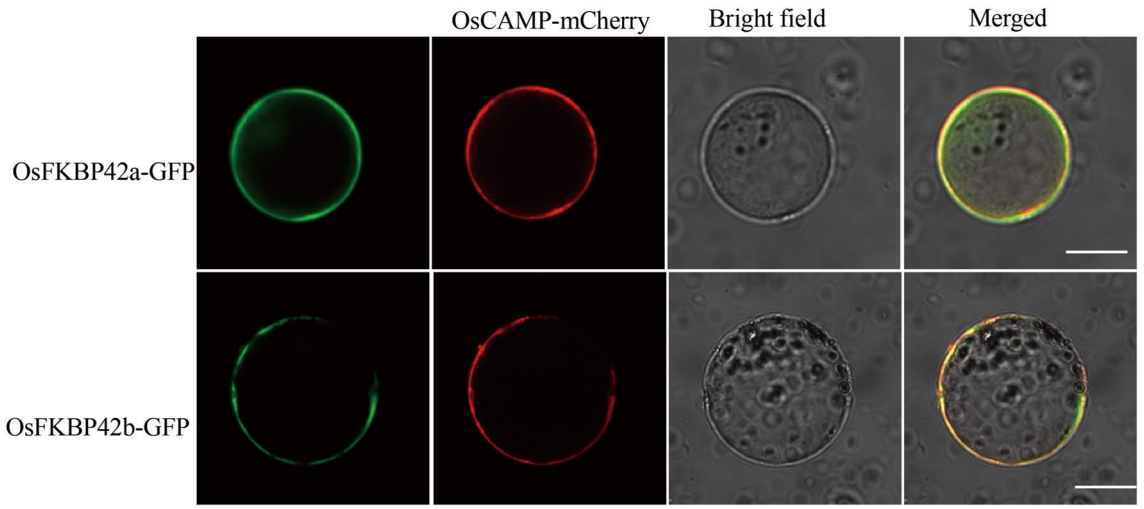

Fig. 3 Subcellular localization of OsFKBP42a and OsFKBP42b. OsFKBP42a and OsFKBP42b were inserted into the pAN580-GFP vector, respectively, and then were transferred into rice protoplasts. The OsCAMP protein was used as the plasma membrane protein marker. Scale bar, 10 μm

Disruption of OsFKBP42b Resulted in Defects of Rice Growth and Development

To study the function of *OsFKBP42* on rice growth and development, we isolated an *OsFKBP42b* mutant *osfkbp42b* from the CRISPR-Cas9 library of Nipponbare (*Oryza sativa*), but not obtained an *OsFKBP42a* mutant. The *osfkbp42b* mutant plants contained two bases 'TA' deletion in the second exon of *OsFKBP42b* (Fig. 4A), which resulted in premature termination of the OsFKBP42b protein translation (Fig. S5). Compared with the wild type, the *osfkbp42b* mutant plants showed dwarfism, short panicles, and low grain setting rate (Fig. 4B–E). However, tiller number, grain size, and grain weight were not altered in the *osfkbp42b* mutant (Fig. S6). To further confirm the OsFKBP42b function, we performed genetic complementation experiments using the pCUBi1390 vector. As shown in Fig. 4F, pCUBi1390-*OsFKBP42b* complemented the *osfkbp42b* mutant phenotypes.

To investigate the cytological cause of the dwarf phenotype in the *osfkbp42b* mutant, we observed the first internode at the heading stage by the scanning electron microscope (SEM) (Fig. S7A). The cell length and width in *osfkbp42b* were similar to the wild type (Fig. S7A). Four cell cycle-related genes, *H1*, *E2F2*, *CYCA2.1*, and *CYCA2.2* were remarkably repressed in *osfkbp42b* (Fig. S7B). This result indicated that the dwarf phenotype in the *osfkbp42b* mutant might be caused by decreased cell number but not cell size.

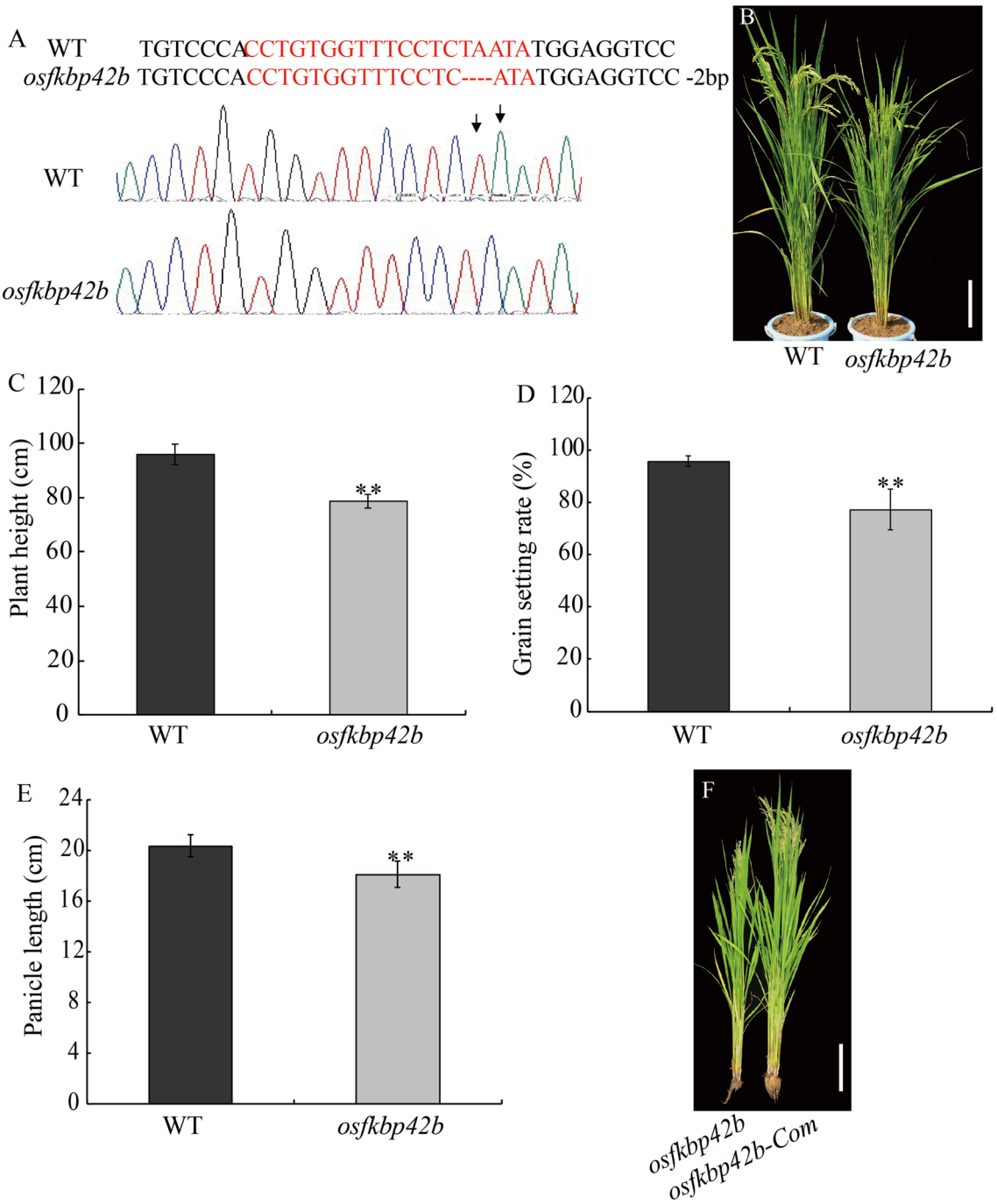

Fig. 4 OsFKBP42b influenced plant morphology and grain setting rate. **A** Diagram of the *OsFKBP42b* mutation site. The mutation position of *OsFKBP42b* was highlighted in red. *sativa*)Plant morphologies of the wild type and *osfkbp42b* plants at the mature stage. Scale bar, 10 cm. **C** Plant height of the wild type and *osfkbp42b* plants at the mature stage. **D** Grain setting rate of the wild type and *osfkbp42b* plants. **E** Panicle length of the wild type and *osfkbp42b* plants. **F** Complementation of the *osfkbp42b* mutant plants. Scale bar, 10 cm. ** indicated the significance of differences between the wild type and *osfkbp42b* as determined by Student's *t*-test analysis

The *OsFKBP42b* Mutation Affected Auxin Pathway

In *Arabidopsis*, the *OsFKBP42b* homologous gene *FKBP42* regulates auxin transport, and the *FKBP42* mutant *twd1* exhibited dwarfism (Geisler et al. 2003). We predicted that the disruption of *OsFKBP42b* affects the auxin pathway. Firstly, we treated the wild-type and the *osfkbp42b* mutant with exogenous different concentrations of IAA. As shown in Fig. 5A, IAA inhibited the growth of the wild-type and the mutant seedlings.

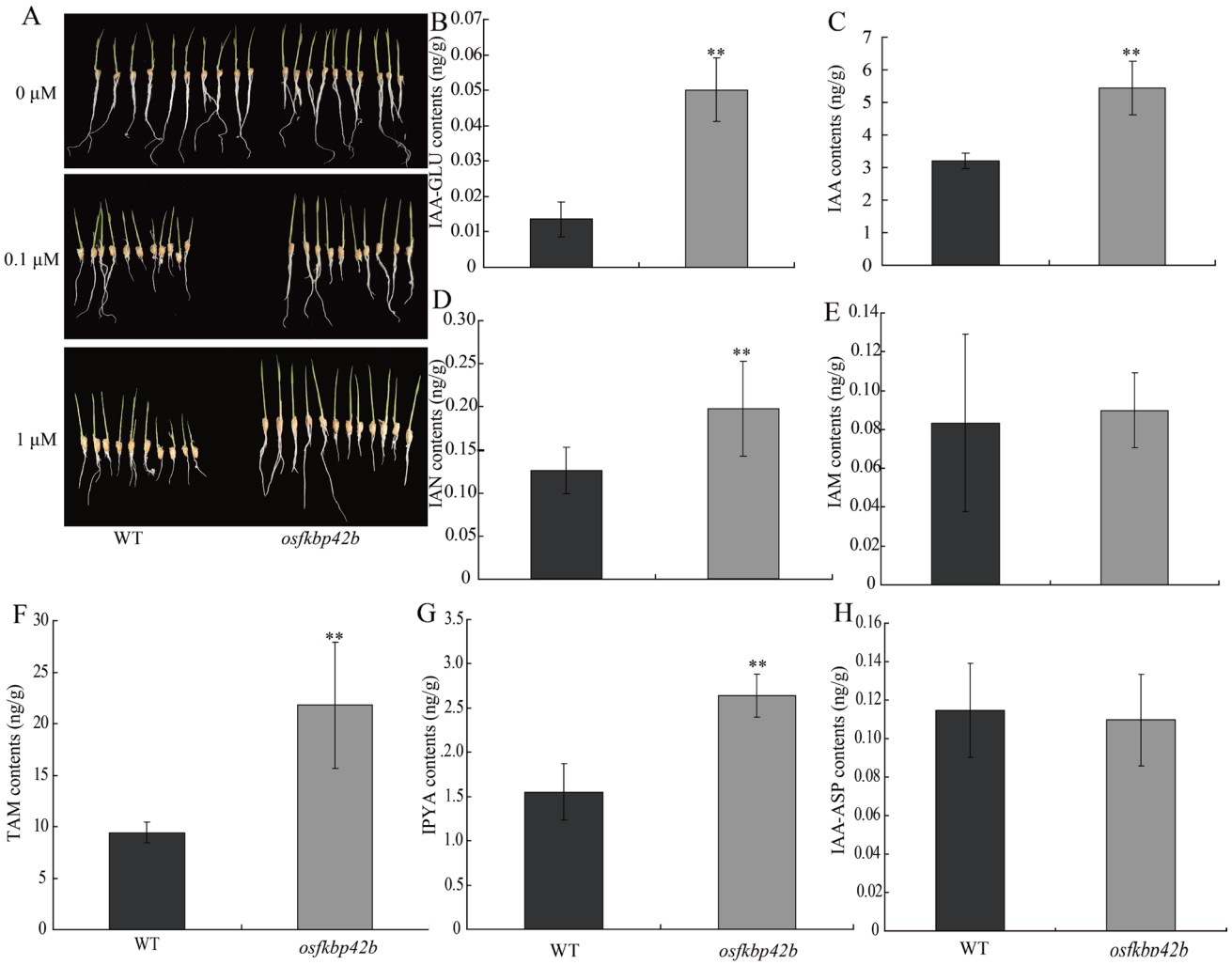

Fig. 5 Auxin contents were increased in the *osfkbp42b* plants. **A** Seedling phenotypes of the wild type and *osfkbp42b* treated with 0, 0.1 and 1 μM IAA. Bars, 1 cm. **B** IAA-GLU contents in the wild type and *osfkbp42b* plants. **C** Contents of IAA in the wild type and *osfkbp42b* plants. **D** IAN contents in the wild type and *osfkbp42b* plants. **E** IAM contents in the wild type and *osfkbp42b* plants. **F** TAM contents in the wild type and *osfbkp42b* plants. **G** IPYA contents in the wild type and *osfkbp42b* plants. **H** IAA-ASP contents in the wild type and *osfkbp42b* plants. *Error bars* indicate SD with biological triplicates. Asterisks indicate the significance of differences between the wild type and *osfkbp42b* as determined by Student's *t*-test analysis: $^{**}P < 0.01$

To determine whether the disruption of *OsFKBP42b* alters auxin concentration in rice, we measured the auxin concentration in the wild type and *osfkbp42b* mutants. The results showed that the free auxin concentration of *osfkbp42b* was significantly higher than in the wild type (Fig. 5C). In addition, the concentrations of IAA-GLU, IAN, TAM, and IPYA were also significantly higher than those of the wild type, but IAA-ASP and IAM contents had no difference between the wild type and *osfkbp42b* (Fig. 5B, D–H).

OsFKBP42b Interacted with OsABCB1 and OsABCB14

To understand the molecular mechanism by which OsFKBP42b regulates rice growth and development, we performed a yeast-two hybrid (Y2H) screen assay. Among the proteins we identified, two were OsABCB1 and OsABCB14, which encode the ATP Binding Cassette B (ABCB) subfamily proteins (Fig. 6). We further confirmed the protein interaction with bimolecular fluorescence complementation (BiFC) assays (Fig. 7). OsABCB14 was shown to function in rice auxin transport and Fe homeostasis (Xu et al. 2014). Knock-down of *OsABCB14* has decreased auxin concentrations and polar auxin transport rates (Xu et al. 2014). *OsABCB1* and *OsABCB14* were expressed in leaves, stems, roots, panicles, and seeds (Figs. S8 and S9).

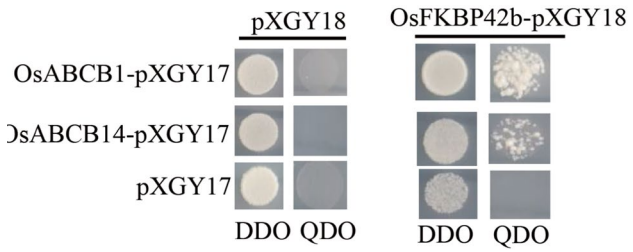

Fig. 6 Interaction among OsFKBP42b, OsABCB1 and OsABCB14 by the yeast two-hybrid assay. OsFKBP42b was fused to the pXGY18 vector, and OsABCB1 and OsABCB14 were fused to the pXGY17 vector

Discussion

OsFKBP42a and OsFKBP42b are Two Conserved FKBP Proteins in *O. sativa*

Compared to the extensive studies on mammalian FKBPs function, little is known about FKBP function in plants, especially crops. In *A. thaliana*, FKBP domain-containing proteins were reported to regulate cell differentiation, abiotic stresses, redox signaling, auxin transport, and photosystem assembly (Pérez-Pérez et al. 2004; Lima et al. 2006; Aviezer-Hagai et al. 2007). In rice, OsFKBP42a and OsFKBP42b have approximate 90% amino acid identity

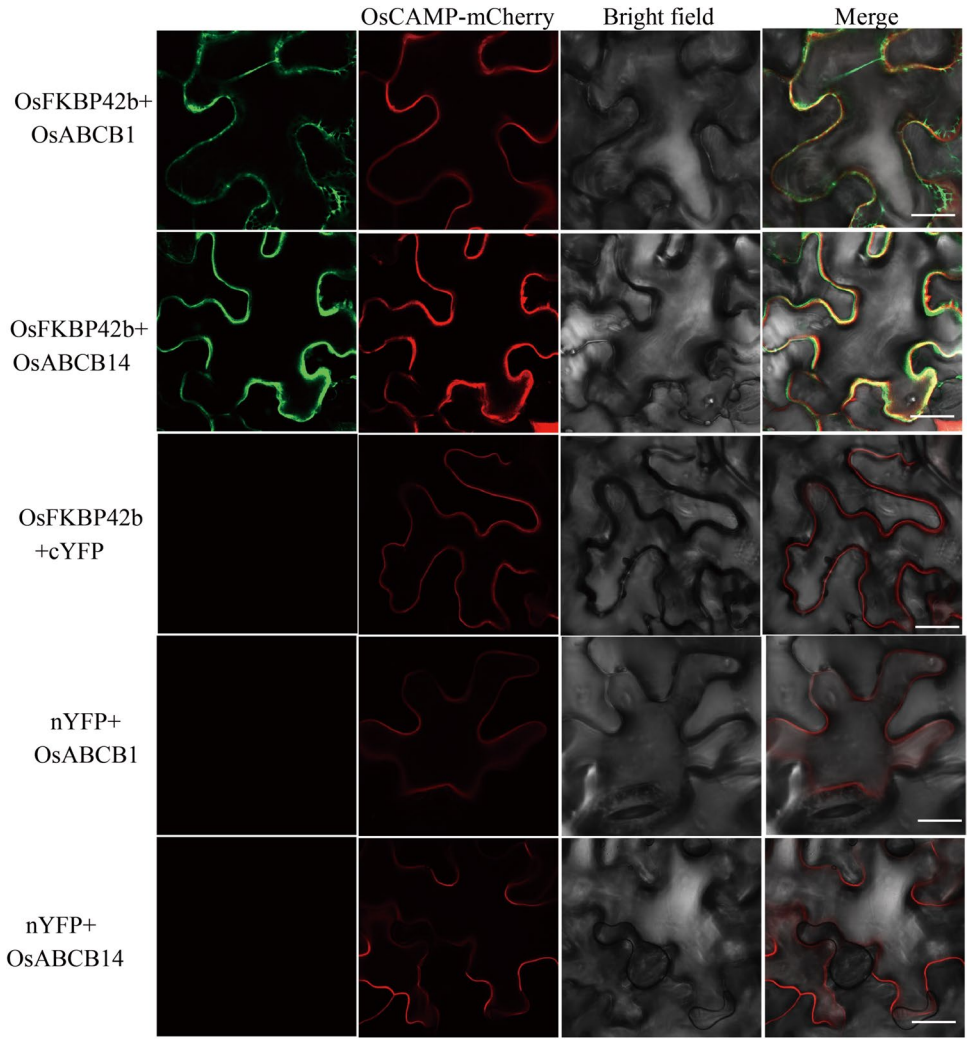

Fig. 7 Interaction among OsFKBP42b, OsABCB1, and OsABCB14 by BiFC assay. Scale bars, 10 μm

(Fig. 1). Similar to its homologs in *Zea mays*, *A. thaliana*, and *Sorghum bicolor*, the FKBP domain was conserved (Fig. 1). OsFKBP42a and OsFKBP42b have similar expression patterns (Fig. 2), and subcellular localization indicated that OsFKBP42a and OsFKBP42b are two plasma membrane proteins (Fig. 3). These results implied that OsFKBP42a and OsFKBP42b may have functional redundancy.

OsFKBP42b Influenced Rice Growth and Development

In *Arabidopsis*, the *FKBP42* mutant *twd1* exhibited dwarfism, and *FKBP42* regulates auxin transport and BR signaling (Geisler et al. 2003). FKBP42 shares 65.25% amino acid sequence identity with OsFKBP42b (Fig. 3). Compared with the wild type, the *osfkbp42b* mutant showed some defects in growth and development, such as dwarfism, short panicles, and reduced grain setting rate (Fig. 4), but not as severe as the *TWD1*/*FKBP42* mutation phenotype. This may be due to the functional redundancy between OsFKBP42a and OsFKBP42b. As shown in Fig. 5A, IAA inhibited the growth of the wild-type and the *osfkbp42b* mutant seedlings, but auxin concentrations (e.g., free IAA, IAA-GLU, IAN, TAM, and IPYA) in *osfkbp42b* were significantly increased (Fig. 5B–H). This implies rice and *Arabidopsis* FKBP42s both act as regulators in the auxin pathway.

OsFKBP42b Interacts with Two ABCB Subfamily Proteins, OsABCB1 and OsABCB14

Yeast two-hybrid and in vivo bimolecular fluorescence complementation assays were employed in our study to detect the protein interacting partners of OsFKBP42b. Two OsFKBP42b interacting proteins were identified, OsABCB1 and OsABCB14 (Fig. 6). We further confirmed the protein interaction with bimolecular fluorescence complementation (BiFC) assays (Fig. 7). OsABCB1 and OsABCB14 belong to the ATP Binding Cassette B subfamily protein (Xu et al. 2014). In *Arabidopsis thaliana*, the first identified ABCB subfamily protein is AtPGP1/AtABCB1, which regulates hypocotyl cell elongation in the light (Dudler and Hertig 1992; Sidler et al. 1998). AtABCB4, AtABCB6, and AtABCB19 are all involved in auxin transport and root development (Kaneda et al. 2011; Kamimoto et al. 2012). According to recent studies, AtFBKP42/TWD1 controls auxin transport and plant development by differential activation of multiple ABCB transporters (Jenness et al. 2022; Liu et al. 2022). In rice, OsABCB14, a homology of AtABCB19, is highest expressed in the tubular tissues and regulates auxin transport and Fe homeostasis (Xu et al. 2014). In addition, *OsABCB11*, *OsABCB8*, *OsABCB13*, *OsABCB23*, and *OsABCB24* were induced by drought stress, whereas *OsABCB6*, *OsABCB9*, and *OsABCB8* were induced by salt stress (Saha et al. 2015), suggesting that they are potentially involved in abiotic stresses.

In this report, OsFKBP42b is characterized as a positive regulator in rice growth and development, and interacts with OsABCB1 and OsABCB14. Our study provides a new insight into the function of the rice *OsFKBP42b* gene.

Materials and Methods

Plant Materials

The *OsFKBP42b* mutant was isolated from the CRISPR/Cas9 mutant library of Nipponbare (*O. sativa*). All plants were grown in a natural field condition in Huai'an cCty, Jiangsu Province, China. For auxin measurement and gene expression analysis, the mutant and Nipponbare were grown in a growth chamber with 14 h light and 10 h dark at 30/25 °C.

Scanning Electron Microscopy (SEM)

Stem samples of the wild type and the mutant at the heading stage were collected and fixed in 2.5% glutaraldehyde. The fixed samples were picked up the suction for 1.5 h and then were dehydrated with alcohol solutions. The samples were observed and photographed by JSM-840 (JEOL, Tokyo, Japan).

Sequence Analysis

The Blastp search program of the National Center for Biotechnology Information (NCBI, http://www.ncbi.nlm.nih.gov/) was used to identify the homologous proteins of OsFBKP42b. The homologous proteins and OsFBKP42b were compared with the DNAMAN software

Subcellular Localization

For examining the subcellular localization of OsFKBP42b, OsABCB1(*LOC_Os08g45030*), and OsABCB14 (*LOC_Os04g38570*), the complete ORF of *OsFKBP42b*, OsABCB1, and OsABCB14 without the stop codon was amplified and inserted into pAN580-GFP at the XbaI and BamHI sites. Then, the recombinant plasmid was transformed into rice protoplasts as previously described (Liu et al. 2020). Plasma membrane protein *OsCAMP1*-mCherry was used as a control. The GFP fluorescence was imaged with a Zeiss confocal laser scanning microscopy LSM700.

Gene Expression Analysis

Various tissues of Nipponbare at the heading stage, such as roots, stems, sheaths, leaves, and panicles, were collected and ground by liquid nitrogen. Total RNA was extracted with an RNA Prep Pure Plant kit (#CW0591S, CWBIO, Jiangsu, China). First-strand cDNA was reverse transcribed using an oligo(dT)18 primer for nuclear-encoded genes. Quantitative Real-time PCR was performed using an SYBR Premix Ex TaqTM kit (TaKaRa) on a CFX96 Touch Real-time PCR Detection System (Bio-rad, America) with three biological replicates. The primers for qRT-PCR are listed in Table S1. The primers used for cell cycle-related genes were listed in the reference (Zhang et al. 2016). The rice *UBQ* gene was used as a reference gene.

Auxin Treatment and Determination

For auxin treatment, the seeds of the wild type and the mutant were sterilized with 75% ethanol for 5 min and rinsed with sterile water. Sterilized seeds were plated in Yoshida rice nutrient salt mixture (Coolaber, NSP1040, Beijing, China) with different concentrations of IAA and grown under 30℃ at a photoperiod of 14-h light/10-h dark in a growth chamber for 10 d.

For auxin measurement, ~1 g of fresh shoots or of 14-day-old wild type and the mutant seedlings grown on Yoshida rice nutrient solution was collected and washed using sterile deionized water, respectively. The samples were ground into powder in liquid nitrogen. IAA concentrations were measured by gas chromatography-selected reaction monitoring mass spectrometry (Nanjing WEBiolotech Biotechnology Co., Ltd).

Yeast Two-Hybrid and Bimolecular Fluorescence Complementation (BiFC) Assays

The coding sequences of *OsFBKP42b*, *OsABCB1*, and *OsABCB14* were amplified and inserted into the bait vector pXGY18 and the prey vector pXGY17 using a ClonExpress II One Step Cloning Kit (#C112-02, Nanjing Vazyme Biotech Co., Ltd.), respectively. Five combinations of plasmids were transformed into the yeast strain, NMY51 as previously described (Xu et al. 2017). The primers for the pXGY18 and pXGY17 vector constructs are listed in Table S1.

For the bimolecular fluorescence complementation assay, *OsFBKP42b*, *OsABCB1*, and *OsABCB14* were cloned into pVYNE and pVYCE, respectively. The recombinant plasmids were transformed into *Agrobacterium* EHA105 and co-transformed into tobacco (*Nicotiana benthamiana*) leaves as previously described (Waadt et al. 2008).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12374-023-09396-3.

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Author contributions LX, WD, and WYJ designed the research. WD is responsible for rice field planting. WYJ, WYY, WGZ, and WD performed the qRT-PCR experiment, yeast two-hybrid assays and BiFC assay. PG, CWJ, FYT, and LX are responsible for scanning electron microscope and subcellular localization. LX and WD wrote and revised the manuscript.

Data availability All data supporting this article are provided within the article (and its supplementary files).

Declarations

Conflict of interest All authors declare no conflict of interest.

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