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OsETV1 Regulates Early Tillering Vigor and Productive Panicle Number in Rice (Oryza sativa L.)

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OsETV1 Regulates Early Tillering Vigor and Productive Panicle Number in Rice (*Oryza sativa* L.)

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Abstract

Productive panicle number is a major determinant of rice grain yield, and early-emerging low-position tillers are more likely to develop into fruitful panicles. This study examined the role of *OsETV1* (*Os04g0470901*) in the regulation of early tillering vigor in rice. Natural variation in the coding region of *OsETV1* was compared between the early-tillering *indica* cultivar T461 and the *japonica* cultivar Wuyungeng 24, in which allelic differences were associated with a weak early tillering vigor phenotype. Functional analysis was conducted using CRISPR/Cas9-mediated knockout lines and overexpression lines in the Wuyungeng 24 background. Subcellular localization and candidate protein interaction analyses were also used to characterize the gene product. Knockout of *OsETV1* enhanced early tillering capacity, and two independent mutant lines produced on average 2.6 and 2.1 more productive panicles per plant than wild-type Wuyungeng 24, without reducing 1000-grain weight. Overexpression of *OsETV1* likewise accelerated tiller initiation and promoted early tillering vigor, while significantly increasing panicle length and grain length; however, productive panicle number did not change significantly and 1000-grain weight remained stable. *OsETV1* encodes a nucleus-localized protein and may act together with six candidate interacting proteins, including *OsDjA8*, to regulate early tillering vigor at the seedling stage. These findings identify *OsETV1* as a regulator of rice tillering and a potential genetic resource for improving early tillering vigor, productive panicle number, and grain shape in rice breeding.

Key words: Oryza sativa, Early tillering vigor, Panicle development, CRISPR/Cas9, Rice breeding, Tillering capacity

1 Introduction

Rice (*Oryza sativa* L.) is one of the world's three major staple crops and the primary food source for more than half of the global population (Li et al., 2022; Yan et al., 2023). Among the agronomic traits that determine rice productivity, tillering is central because it shapes plant architecture and directly

influences the number of panicles per unit area, thereby affecting yield potential (Chen et al., 2022). Tiller development comprises two major stages, tiller bud formation and tiller bud elongation (Yan et al., 2023). Buds formed earlier generally display stronger early tillering vigor (ETV) and are more likely to develop into productive tillers, whereas later-formed buds often enter dormancy under regulation by the auxin pathway (Chen et al., 2022; Li et al., 2022). For this reason, the timing of early tillering and the rate of early tiller emergence have become important targets in the genetic improvement of modern high-yielding rice cultivars. Despite their agronomic importance, the molecular mechanisms underlying ETV in rice remain poorly understood.

Rice tillering is a typical quantitative trait controlled by multiple genes and characterized by a complex genetic architecture (Wei et al., 2024; Zhang et al., 2025). Numerous regulators of tiller development have been identified. *MONOCULM 1* (*MOC1*), the first cloned tiller-related gene, is required for the initiation and outgrowth of axillary buds (Zha et al., 2022). *MONOCULM 3* (*MOC3*), which encodes a nucleus-localized AP2/ERF family transcriptional repressor, directly binds the promoter of *FLORAL ORGAN NUMBER1* (*FON1*) and activates its transcription (Lu et al., 2015; Shao et al., 2019; Suzaki et al., 2008; G. Wang et al., 2025). *FON1* regulates cell proliferation and organ initiation, and its proper expression is essential for tiller development (Shao et al., 2019; Suzuki et al., 2019).

Transcriptional regulation is a major component of the genetic control of tillering. Transcription factors have pivotal roles in rice growth, development, and environmental adaptation through the modulation of gene expression (Li et al., 2025; Wei et al., 2022; Wu et al., 2024). *OsMADS57*, a MADS-domain transcription factor, promotes tiller bud formation (Li et al., 2025). *OsTB1*, which encodes a TCP family transcription factor, acts as a negative regulator of tillering, as its overexpression markedly reduces tiller number in rice (Takeda et al., 2003). *OsTCP19*, another TCP family member, similarly suppresses tiller outgrowth when overexpressed (Liu et al., 2021). Members of the NAC family are also broadly involved in plant development, and recent work has shown that *OsNAC022* negatively regulates rice tillering by modulating expression of the circadian clock gene CCA1 (Zhai et al., 2025).

Hormonal signaling further refines tiller establishment and outgrowth. Strigolactones are major negative regulators of rice tiller development (Hu et al., 2024). Auxin regulates tiller bud dormancy and outgrowth both by modulating strigolactone biosynthesis and through its direct biological effects (Wu et al., 2025). In contrast, cytokinin promotes tiller bud germination and antagonizes strigolactone action to coordinate tiller bud growth (Zha et al., 2022). Brassinosteroids also contribute to this process by regulating DWARF53 (D53), a core component of the strigolactone signaling pathway, thereby promoting tiller bud elongation and fine-tuning rice tillering (Fang et al., 2020; Zhou et al., 2013).

Although substantial progress has been made in identifying genetic and hormonal regulators of tillering, the molecular basis of early tillering vigor remains insufficiently defined. In this study, we identified *OsETV1*, a gene controlling early tillering vigor, from the early fast-tillering indica rice line T461 derived from the hybrid progeny of Rotation 22/Cript. To investigate its biological function, we generated *OsETV1* knockout and overexpression lines in the japonica cultivar Wuyungeng 24 (WYG) using CRISPR/Cas9-mediated editing and transgenic overexpression. We then evaluated the effects of *OsETV1* on early tiller development, effective panicle number, and panicle and grain-related traits.

2 Materials and Methods

2.1 Materials

In a previous study, the japonica rice lines WYG and Longqingdao3, which showed poor early tillering vigor, and the indica rice line T461, which carried the ETV trait, were used as parental lines to construct three-way cross backcross recombinant inbred line populations. Tiller number was manually investigated at 3-day intervals beginning when 95% of the BIL population had initiated tillering, and the average tiller number per plot was used as the phenotypic index for analysis. Using conjoint analysis of QTL mapping, BSA-seq, and RNA-seq, an unknown gene, *OsETV1* (*Os04g0470901*), on chromosome 4 was identified (Wu et al., 2024).

To investigate the function of *OsETV1* in regulating the rice ETV trait, the wild-type (WT) cultivar WYG was used as the recipient material. Overexpression vectors constructed with the CDS sequence of T461 were introduced via genetic transformation to generate two *OsETV1* overexpression lines, designated *OsETV1*-OE1 and *OsETV1*-OE2. Two *OsETV1* knockout lines, *OsETV1*-CW1 and *OsETV1*-CW2, were generated using the CRISPR-Cas9 gene-editing system. The overexpression lines *OsETV1*-OE1 and *OsETV1*-OE2 and the knockout lines *OsETV1*-CW1 and *OsETV1*-CW2 in this study were T2-generation pure plants, and their genotypes were confirmed by PCR for overexpression lines and DNA sequencing for knockout lines.

2.2 Bioinformatic Analysis for *OsETV1*

The genomic DNA sequence of *OsETV1* and its encoded protein sequence were retrieved from the Ensemble Plants database (http://plants.ensembl.org) using the *indica* rice cultivar 9311 (*Oryza sativa* L. ssp. *indica*) and the *japonica* rice cultivar Nipponbare (*Oryza sativa* L. ssp. *japonica*) as reference genomes. Gene structure was visualized using GSDS 2.0 (http://gsds.gao-lab.org/). Homologous protein sequences of *OsETV1* were identified by BLASTP searches against the NCBI non-redundant protein database.

Putative cis-regulatory elements in the 2,000 bp promoter region upstream of the *OsETV1* initiation

codon (ATG) were predicted using the Plant CARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/). Signal peptides and transmembrane domains in the *OsETV1* protein were predicted using SignalP-6.0 (https://services.healthtech.dtu.dk/service.php? SignalP-6.0) and TMHMM-2.0 (https://services.healthtech.dtu.dk/service.php?TMHMM-2.0), respectively.

2.3 Vector Construction and Genetic Transformation

2.3.1 Overexpression Vector Construction and Transformation

The full-length *OsETV1* CDS (576 bp) was amplified by PCR using cDNA from the indica rice cultivar T461 as the template. The amplified product was digested with *Bsa*I and *Eco31*I and cloned into the corresponding site of the overexpression vector pBWA(V)HS-ccdB. The recombinant plasmid was sequenced to verify the integrity of the inserted *OsETV1* CDS, and sequencing confirmed that the insert matched the expected sequence without nucleotide substitutions or frameshift mutations. The verified overexpression plasmid was introduced into the japonica cultivar WYG by Agrobacterium tumefaciens-mediated transformation to generate *OsETV1* OE lines. Primer sequences used for vector construction are provided in Supplementary Table S1.

2.3.2 CRISPR/Cas9 Knockout Vector Construction and Transformation

A single-guide RNA target sequence was designed within an exon of *OsETV1*. The corresponding oligonucleotide pair was cloned into the U3 sgRNA expression vector to generate the intermediate vector pYLsgRNA-*OsETV1*. The ligation product was transformed into Escherichia coli competent cells, and positive clones were identified by colony PCR followed by plasmid extraction. The pYLsgRNA-*OsETV1* plasmid was then ligated with the CRISPR/Cas9 vector pYLCRISPR/Cas9 using T4 DNA ligase to generate the final knockout vector pYLCRISPR/Cas9:*OsETV1*. This construct was introduced into the rice cultivar WYG by Agrobacterium tumefaciens-mediated transformation to produce *OsETV1* CW lines. Primer sequences used for vector construction are provided in Supplementary Table S1.

2.4 Cultivation and Field Management

All rice genotypes, including WT, *OsETV1*-OE1, *OsETV1*-OE2, *OsETV1*-CW1, and *OsETV1*-CW2, were transplanted into paddy fields at the two-week-old seedling stage. The experiment was arranged in a randomized complete block design with three biological replicates. Each replicate plot contained 60 individually planted hills at a spacing of 16.5 × 22.1 cm.

The field trial was conducted at Jiangxi Agricultural University, China (28.75° N, 115.83° E). After

transplanting, a 3-cm water layer was maintained, and slow-release compound fertilizer (N:P:K = 17:15:15) was applied at 150 kg ha^{-1}.

2.5 qRT-PCR Analysis

2.5.1 Total RNA Extraction and cDNA Synthesis

Leaves were collected separately from WT and *OsETV1* OE lines. Total RNA was extracted using TRIzol® Reagent (Vazyme Biotech Co., Ltd., Nanjing, China). First-strand cDNA was synthesized using the PrimeScript™ RT Reagent Kit with gDNA Eraser (Perfect Real Time) (Takara Bio Inc., Japan) according to the manufacturer's protocol.

2.5.2 qRT-PCR Analysis

qRT-PCR was performed using 2× SYBR® Premix Ex Taq™ (Tli RNaseH Plus; TIANGEN Biotech) on an Applied Biosystems QuantStudio 5 real-time PCR system (Thermo Fisher Scientific, USA). Rice *OsActin* (*Os03g0718100*) was used as the internal reference gene. Relative expression levels were calculated using the $2^{-\Delta\Delta Ct}$ method (Livak & Schmittgen, 2001). Sequences of all qRT-PCR primers are listed in Table S1.

2.6 Analysis of Tillering Dynamics and Agronomic Traits Investigation

2.6.1 Analysis of Tillering Dynamics

At the 3-leaf stage, 9 days after transplanting (DAT), 10 uniformly growing plants were randomly selected from the internal area of each plot for WT, *OsETV1* CW, and *OsETV1* OE lines. These plants were tagged for tillering dynamics analysis. Tiller number per plant was recorded every 3 days. Monitoring continued until the end of the peak tillering stage and included at least seven consecutive observations. A tiller was counted when its leaf had emerged at least 1 cm from the sheath of the main stem or mother tiller at the tillering node. Three independent field plots served as biological replicates.

2.6.2 Major Agronomic Trait Investigation

At the yellow ripening stage, five plants were harvested individually from each plot that had been used for tiller dynamics analysis. Ear length of the main panicle and all tiller panicles per plant was measured and recorded manually. Plants were then threshed individually, and grains were separated into filled and unfilled grains. The numbers of filled and unfilled grains per plant, 1000-grain weight, grain length, and grain width of filled grains were determined using a multi-functional automatic seed analyzer (Jieyu Technology, Fujian, China). Three independent field plots served as biological

replicates.

2.6.3 Data Processing

Differences among the genotype groups WT (T461 and WYG), CW, and OE were analyzed by one-way analysis of variance (ANOVA) after confirmation of homogeneity of variances by Levene's test and normality by the Shapiro-Wilk test. When ANOVA indicated significant differences among groups ($P < 0.05$), Tukey's honestly significant difference (HSD) test was used for multiple comparisons. Data were visualized using GraphPad Prism 10 software (GraphPad Software, San Diego, CA, USA).

2.7 Subcellular Localization Analysis

To determine the subcellular localization of *OsETV1*, the full-length CDS without the stop codon was amplified by PCR using cDNA from T461. The PCR product was digested with *Bsa*I and *Eco31*I and directionally cloned into the corresponding restriction sites of the pAN580-ccdb-eGFP vector to generate the C-terminal eGFP fusion construct pAN580:*OsETV1*-eGFP, abbreviated *OsETV1*-GFP.

After sequence verification, the *OsETV1*-GFP plasmid was introduced into rice leaf protoplasts by polyethylene glycol-mediated transfection. Protoplasts transfected with the empty pAN580-eGFP vector served as the negative control. Transfected protoplasts were incubated at 26℃ in darkness for 18-24 h. eGFP fluorescence was then observed using a confocal laser scanning microscope (Nikon AXR) with a 63× oil immersion objective. The eGFP signal was excited at 488 nm, and emission was detected at 510 nm. All experiments were performed with three biological replicates. Primer sequences are listed in Table S1.

2.8 Yeast Two-Hybrid Assay

2.8.1 Bait and Prey Vector Construction

The full-length *OsETV1* CDS was amplified by PCR, digested with *EcoR*I and *BamH*I, and cloned into the corresponding restriction sites of the bait vector pGBKT7 carrying the GAL4 DNA-binding domain to generate pGBKT7-*OsETV1*. Candidate interacting protein sequences identified from a yeast two-hybrid cDNA library of rice cultivar ZhongHua11 (ZH11) were digested with *EcoR*I and *BamH*I and cloned into the prey vector pGADT7 carrying the GAL4 activation domain to generate AD-candidate protein fusion constructs.

2.8.2 Yeast Two-Hybrid Screening to Identify OsETV1 Interacting Candidates

The bait plasmid pGBKT7-*OsETV1* and prey plasmids pGADT7-candidate protein were

co-transformed into the reporter yeast strain AH109. Co-transformants were plated on triple dropout medium (SD/-Leu/-Trp/-His) supplemented with 40 μg/mL X-α-Gal and incubated at 30°C for 3–5 days.

The following controls were included: positive control, a known interacting protein pair; and negative controls, bait plus empty pGADT7 and prey plus empty pGBKT7. Protein interactions were assessed by colony growth and blue color development, which indicated a positive interaction through α-galactosidase activity. All experiments were performed with three independent biological replicates. Primer sequences are listed in Table S1.

3 Results

3.1 Sequence and Bioinformatic Analysis of *OsETV1*

Comparative sequencing of the coding sequence (CDS) of *OsETV1* between the early-tillering *indica* cultivar T461 and the *japonica* cultivars WYG and Longqingdao3, both exhibiting poor early tillering vigor (ETV), revealed three conserved non-synonymous mutations in WYG and Longqingdao3 (Figure 1A). These mutations—c.298G>T, c.523G>A, and c.716G>T—result in the amino acid substitutions p.Q100W, p.D175N, and p.R239L, respectively.

Cis-regulatory element analysis of the *OsETV1* promoter region identified multiple hormone-responsive elements, as well as elements associated with meristem-specific expression, suggesting potential hormone-regulated and tissue-specific regulation of this gene (Figure 1B). Transmembrane domain prediction identified a putative transmembrane helix spanning residues 65–87 (Figure 1C), whereas signal peptide prediction detected no signal peptide, indicating that *OsETV1* is likely a non-secretory protein (Figure 1D).

3.2 Generation of Transgenic Lines and Expression Analysis of *OsETV1*

To investigate the function of *OsETV1*, the coding sequence was amplified from the T461 background and introduced into the WYG variety under the control of the 35S promoter, generating two independent overexpression lines designated *OsETV1*-OE1 and *OsETV1*-OE2. Sequencing confirmed that the *OsETV1* coding sequence was inserted in the sense orientation downstream of the 35S promoter (Figure 2A). qRT-PCR analysis confirmed that *OsETV1* transcript levels were significantly upregulated in both overexpression lines relative to WYG (Figure 2B).

In parallel, two *OsETV1* knockout lines, *OsETV1*-CW1 and *OsETV1*-CW2, were generated in the WYG background using the CRISPR/Cas9 system. Sequence analysis of the target sites revealed that *OsETV1*-CW1 carried a 1 bp deletion (G) at the first target site and a 35 bp deletion at the second target site within the exon, whereas *OsETV1*-CW2 carried a 1 bp insertion (T) at the first target site and the

same 35 bp deletion at the second target site (Figure 2C).

3.3 *OsETV1* Positively Regulates Early and Rapid Tillering in Rice

To assess the effect of *OsETV1* on early tillering vigor, tiller dynamics were monitored throughout the tillering stage in both overexpression and knockout lines. In the overexpression lines, *OsETV1*-OE1 and *OsETV1*-OE2 exhibited earlier tiller initiation and a higher tillering rate relative to wild-type (WT) WYG during the early stage (0–18 days after transplanting, DAT). During the middle and late stages (21–30 DAT), the tillering rate of WT gradually approached that of the overexpression lines (Figure 3A). Similarly, the knockout mutants *OsETV1*-CW1 and *OsETV1*-CW2 had already entered the tillering stage by 9 DAT, whereas WT had not yet initiated tillering. During the critical growth period of 15–18 DAT, the tillering rate of the knockout mutants was markedly higher than that of WT, and the average tiller number per plant in the mutants remained consistently higher than that of WT throughout the 30 DAT observation period (Figure 3B).

Tiller numbers per plant were further quantified at 9 DAT and 18 DAT. At 9 DAT, *OsETV1*-OE lines exhibited a highly significant increase in tiller number compared with WT, while *OsETV1*-CW lines showed a significant increase (Figure 3C and E). At 18 DAT, the *OsETV1*-OE lines showed a significant increase and the *OsETV1*-CW lines showed a highly significant increase in tiller number relative to WT (Figure 3D). Together, these results indicate that *OsETV1* positively regulates both the rate and the number of tillers during early rice development.

3.4 Agronomic Traits of *OsETV1* Transgenic Lines

To determine whether the early tillering advantage in OE and CW lines translated into differences in yield-related traits at maturity, agronomic parameters were evaluated at the yellow ripening stage in WT, *OsETV1*-OE1, *OsETV1*-OE2, *OsETV1*-CW1, and *OsETV1*-CW2. The traits assessed included effective panicle number per plant, panicle length, number of filled grains per panicle, number of filled grains per plant, grain length, grain width, 1000-grain weight, and grain weight per plant.

Compared with WT, the overexpression lines *OsETV1*-OE1 and *OsETV1*-OE2 showed no significant change in effective panicle number but exhibited significantly longer panicles (Figure 4B) and significantly increased grain length (Figure 4E). No significant differences were detected between the overexpression lines and WT in the number of filled grains per panicle, number of filled grains per plant, grain width, 1000-grain weight, or grain weight per plant (Figure 4A, C, D, F, G, H).

In the knockout lines, the average number of effective panicles per plant was 12.5 for *OsETV1*-CW1 and 12.0 for *OsETV1*-CW2, representing significant increases of 2.6 and 2.1 panicles per plant, respectively, compared with WT (Figure 4C). No significant differences between the knockout lines and WT were observed for panicle length, number of filled grains per panicle, number of filled grains

per plant, grain length, grain width, 1000-grain weight, or grain weight per plant (Figure 4A, B, D, E, F, G, H). Collectively, these results indicate that *OsETV1* differentially affects panicle architecture depending on the direction of genetic perturbation: overexpression increases panicle length and grain length, whereas knockout increases effective panicle number, with neither manipulation resulting in a significant change in 1000-grain weight or grain weight per plant.

3.5 *OsETV1* Localizes to the Nucleus

To determine the subcellular localization of the *OsETV1* protein, a 35S:*OsETV1*:GFP fusion expression vector was constructed and introduced into rice protoplasts alongside a 35S:GFP control. In protoplasts expressing the 35S:GFP control, green fluorescence was distributed in the cytoplasm and at the plasma membrane. In contrast, protoplasts expressing 35S:*OsETV1*:GFP exhibited green fluorescence exclusively in the nucleus (Figure 5). These results indicate that *OsETV1* is predominantly localized to the nucleus, suggesting that the putative transmembrane domain predicted by bioinformatic analysis may represent a false positive.

3.6 Identification of *OsETV1*-Interacting Proteins by Yeast Two-Hybrid Screening

To investigate the molecular pathway through which *OsETV1* regulates early tillering vigor, the full-length CDS of *OsETV1* was fused to the pGBKT7 bait vector, and its capacity for transcriptional self-activation was assessed. The AH109 yeast strain was co-transformed with the combinations pGADT7-T × pGBKT7-p53 (positive control), pGADT7-T × pGBKT7-Lam (negative control), and pGADT7 × pGBKT7-*OsETV1* (self-activation test), and plated on SD/−Trp/−Leu (DDO), SD/−Trp/−Leu/−His (TDO/X), and SD/−Trp/−Leu/−His/−Ade (QDO/X) media. All strains grew on DDO plates, confirming successful co-transformation. On QDO/X plates, only the positive control grew, whereas neither the negative controls nor the *OsETV1* bait strain produced colonies, indicating that the *OsETV1* protein does not possess intrinsic transcriptional activation activity (Figure 6A).

Using BD-*OsETV1* as bait, a cDNA library derived from the rice variety ZH11 (library titer: 1.5×10^6 CFU) was screened on SD/−Leu/−Trp/−His/−Ade medium, yielding a total of 17 positive clones (Figure 6B). Following sequencing, NCBI BLAST analysis, and removal of redundant sequences, six high-confidence candidate interacting proteins were identified: DnaJ protein *OsDjA8* (*Os05g0334400*), and five expressed proteins encoded by *Os06g0316300*, *Os02g0109800*, *Os11g0146700*, *Os03g0123600*, and *Os04g0674100* (Table 1).

4 Discussion

The number of panicles, effective tillers, grains per panicle, panicle size, grain weight, and grain size are the primary determinants of rice yield (Li et al., 2026). However, simultaneous optimization of

these traits is often constrained by trade-offs among yield components (Song et al., 2022; Wang et al., 2017). Tiller formation, which comprises tiller bud initiation and outgrowth, is a key agronomic trait influencing panicle number (Li et al., 2003). In this study, we identified *OsETV1* as a gene that regulates rice tiller development. Both overexpression and knockout of *OsETV1* promoted earlier and faster tiller emergence compared to the WT (Figure 3), yet the two types of transgenic lines diverged markedly at maturity. OE lines significantly increased panicle length and grain length (Figure 4B, E) without altering effective panicle number (Figure 4C), whereas CW lines significantly increased effective panicle number (Figure 4C) without corresponding changes in panicle length or grain length (Figure 4B, E). The 1000-grain weight remained unchanged in both sets of lines (Figure 4G), and neither manipulation significantly affected grain weight per plant (Figure 4H). These contrasting phenotypes suggest that *OsETV1* regulates tiller initiation and panicle architecture through distinct, potentially allele-dependent mechanisms and that an early tillering advantage does not necessarily translate into increased effective panicles at maturity.

Effective panicle number, which is largely determined by tillering during the vegetative stage, is a key determinant of grain yield in rice (Jiao et al., 2010; Ma et al., 2020). In our study, both *OsETV1*-OE and *OsETV1*-CW lines exhibited earlier tiller initiation and higher early tiller numbers than the WT (Figure 3A, D). However, at maturity, OE lines showed only a non-significant increase in effective panicle number, whereas CW lines exhibited a significant increase (Figure 4C). In the OE lines, the tiller production rate gradually became comparable to that of the WT during the late tillering stage (Figure 3A), suggesting that premature cessation of tillering upon the vegetative-to-reproductive transition may have shortened the window for productive tiller formation, thereby preventing the early tillering advantage from translating into more effective panicles. Since tiller initiation ceases in most rice cultivars upon this developmental transition (Ma et al., 2020; Wang et al., 2018), the shift from vegetative to reproductive growth may partly explain the reduced tillering rate observed in the OE lines at later stages. Trade-offs among yield components are common in rice (Song et al., 2022; Yano et al., 2019). For example, *GS2* increases panicle length and grain size but reduces spikelet number per panicle (Wang et al., 2025), the *GNP6* allele of *MOC1* increases tiller number while reducing panicle length (Zhang et al., 2021), and Gnp4/LAX2 overexpression increases grain length and 1000-grain weight but reduces spikelets per panicle (Zhang et al., 2018). In this context, the significantly increased panicle length and grain length in *OsETV1*-OE lines with unchanged 1000-grain weight (Figure 4B, E, G) may reflect reallocation of assimilates from non-productive tillers to surviving panicles, promoting longitudinal growth rather than increasing sink number.

By contrast, *OsETV1*-CW lines maintained higher tiller numbers than the WT throughout the entire tillering observation period (Figure 3D), and this sustained advantage translated into a significant increase in effective panicle number at maturity (Figure 4C). The 1000-grain weight remained

unchanged (Figure 4G), suggesting that the increase in effective panicle number did not compromise grain-filling capacity of individual grains. The Results indicate that no significant difference in filled grains per panicle was detected between the knockout lines and the WT (Figure 4A), which suggests that the yield trade-off between panicle number and grains per panicle, though expected, was not statistically evident in these lines. The difference in phenotypic responses between the two knockout lines may be attributable to allelic variation arising from their distinct mutation types. The relatively stable 1000-grain weight across all transgenic lines further indicates that genetic perturbation of *OsETV1* primarily alters sink number rather than the grain-filling capacity of individual grains.

Given that OE lines express the T461 allele, whereas CW lines disrupt the WYG allele, the divergent mature phenotypes may reflect allele-specific functional differences rather than a simple dose-dependent switch. In the OE lines, the T461 allele promotes tiller initiation but appears to lead to premature cessation of tillering, whereas in the CW lines, loss of the WYG allele enhances early tillering vigor and sustains tiller production, favoring the formation of productive panicles. Notably, the increase in effective panicle number without a reduction in 1000-grain weight in the CW lines suggests that knockout of *OsETV1* genuinely promotes tiller formation rather than merely shifting assimilate allocation. However, further evidence is required to confirm the allele- and dose-dependent regulation proposed here.

In light of this phenotypic divergence, we next investigated the molecular characteristics of *OsETV1* to explore the basis of its regulatory role. Subcellular localization demonstrated that *OsETV1* is nuclear-localized (Figure 5), a finding that is inconsistent with the bioinformatically predicted transmembrane domain and suggests that this prediction may represent a false positive. Despite its nuclear localization, yeast two-hybrid assays revealed that *OsETV1* lacks transcriptional autoactivation activity (Figure 6A), indicating that it is unlikely to function as a typical transcriptional activator. Rather, *OsETV1* may act as a nuclear regulatory component, possibly a transcriptional repressor or part of a larger protein complex. This is consistent with the allele- and dose-dependent model proposed above, in which *OsETV1* fine-tunes downstream pathways rather than acting as a simple on/off switch (T. Wang et al., 2024).

Dual regulation of tillering and grain shape is not unprecedented in rice. *GLW9* negatively regulates tillering angle while positively regulating grain length (Shi et al., 2025), and *DTG1* regulates tillering through auxin and ABA pathways and interacts with *GW2* to control grain size (Li et al., 2024). These examples suggest that co-regulation of tiller development and grain morphology may be a common feature of rice regulatory networks, and *OsETV1* may act through a similar integrative mechanism. Yeast two-hybrid screening identified *OsDjA8* (*Os05g0334400*), a chloroplast-localized DnaJ protein essential for chloroplast development (Lim et al., 2023; Zhu et al., 2015), and *Os06g0316300*, a putative glycine-rich cell wall structural protein (Li et al., 2024), as candidate interacting partners of

OsETV1. Given its nuclear localization and lack of autoactivation, *OsETV1* may serve as a nuclear regulatory node integrating chloroplast development—ensuring the energy supply for tiller bud emergence—and cell wall biogenesis—providing the structural support for cell proliferation and remodeling in tiller internodes—to modulate tiller initiation and elongation. This model provides a testable framework linking the molecular function of *OsETV1* to the observed tillering and panicle phenotypes. However, these interactions require validation by BiFC, Co-IP, and genetic epistasis analysis, and the downstream targets of *OsETV1* remain to be identified.

5 Conclusions

This study identifies *OsETV1* as a positive regulator of early tillering in rice, with both overexpression and knockout accelerating tiller initiation relative to the WT. Importantly, the two genetic perturbations produced divergent effects at maturity: overexpression of the T461 allele enhanced panicle length and grain length, whereas knockout of the WYG allele increased effective panicle number, with neither manipulation altering 1000-grain weight or grain weight per plant. These findings point to an allele-dependent regulatory role for *OsETV1* in coordinating tiller development and panicle architecture. The nuclear localization of *OsETV1*, its lack of transcriptional autoactivation, and its candidate interactions with proteins involved in chloroplast development and cell wall biogenesis suggest that it functions as a regulatory node integrating energy metabolism and structural growth processes during tillering. Validation of these protein interactions and identification of downstream targets will be essential for elucidating the precise molecular mechanism and for assessing the potential of *OsETV1* as a target for improving rice yield architecture.

Supplementary Materials: Supplementary data associated with this article can be found in the online version.

Author Contributions: Jianglin Liao designed and supervised the experiments and edited the draft. Wei Wu, Tiantian Zhang, Pingan Zhong, performed the experiments and prepared the original draft, and contributed equally to this paper. Yu Feng, Yulun- Wen, analyzed and curated the experimental data. Xiao-Bing Xie, Yong-qi Fu and Wei-Xing Li Guided the draft process. All authors contributed to the article and approved the submitted version.

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Figure 1 Nucleotide and amino acid variations and bioinformatics characterization of the *OsETV1* mutation site. (A) CDS sequence alignment of *OsETV1*; (B) Distribution of core cis-acting elements in the promoter region of *OsETV1*, the detailed biological functions of the abbreviations are listed in Table S2; A-box indicate cis-acting regulatory element, ABRE indicate cis-acting element involved in the abscisic acid responsiveness, AE-box indicate part of a module for light response, LTR indicate cis-acting element involved in low-temperature responsiveness, CGTCA-motif indicate cis-acting regulatory element involved in the MeJA-responsiveness, TGACG-motif indicate cis-acting regulatory element involved in the MeJA-responsiveness, G-box indicate cis-acting regulatory element involved in light responsiveness, TC-rich repeats cis-acting element involved in defense and stress responsiveness, GT1-motif indicate light responsive element, chs-CMA1a indicate part of a light responsive element; (C) Analysis of Transmembrane Domains of the Protein Encoded by *OsETV1*; (D) Prediction of the signal peptide of the *OsETV1* protein.

Figure 2 Construction and identification of the *OsETV1* overexpression vector and transgenic rice lines. (A) Construction of the *OsETV1* overexpression vector and molecular identification of transgenic rice lines (*OsETV1*-OE1 and *OsETV1*), the representative sequencing chromatograms confirm the identity of the transgene in overexpression lines.; (B) qRT-PCR analysis of *OsETV1* expression levels

in T461 and two overexpression lines (*OsETV1*-OE1 and *OsETV1*-OE2). Data are presented as means ± SD (n=3). ****P < 0.0001 (Student's t-test). Representative sequencing chromatograms confirm the identity of the transgene in overexpression lines, relative mRNA levels of *OsETV1* were normalized relative to *OsActin*; (C) Alignment of the *OsETV1* target sequence in WYG and two knock out lines (*OsETV1*-CW1 and *OsETV1*-CW2). Dashed red lines indicate deletions, and the green base indicates a point mutation.

Figure 3 The effect of *OsETV1* gene overexpression and knockout on early tillering of rice WYG. (A) Investigation on tillering dynamics of wild-type strain WYG and two *OsETV1* gene overexpressing strains, with the slope representing the rate of tillering increase; (B) Investigation on tillering dynamics of wild-type strain WYG and two homozygous *OsETV1* gene knockout strains, with the slope representing the rate of tillering increase; (C) The average number of tillers per plant in wild-type strain WYG, *OsETV1* gene overexpression and homozygous knockout strains at 9 d after rice transplantation; (D) The average number of tillers per plant in wild-type strain WYG, *OsETV1* gene overexpression and homozygous knockout strains at 18 d after rice transplantation; (E) Tiller number of WYG and mutant rice at 18 DAT, Scale bar = 5cm; The asterisk indicates the significance of the difference between WYG and other transgenic strains (*: 0.01< P <0.05, **: 0.001< P< 0.01).

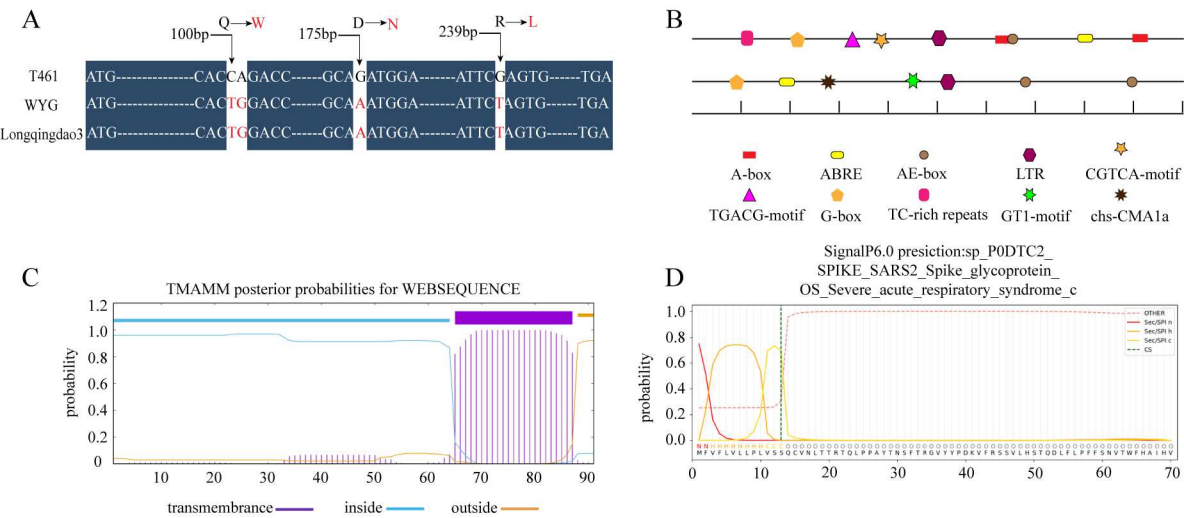
Figure 4 The effects of *OsETV1* gene overexpression and knockout on agronomic traits of rice WYG. (A) Filled grain number per panicle; (B) panicle length; (C) Effective panicle number; (D) Filled grain number per plant; (E) Grain length; (F) Grain width; (G) Thousand-grain weight; (H) Grain weight per plant. WYG: wild-type control; *OsETV1*-OE1, *OsETV1*-OE2: two overexpressing strains of *OsETV1* gene in WYG; *OsETV1*-CW1，*OsETV1*-CW2: two homozygous strains with *OsETV1* gene knockout in WYG. Data are presented as the mean of 15 non-border rows plants (three plots × 10 plants each). Error bars represent the standard deviation (SD), n = 15. Significant differences between the WT and each transgenic line were analyzed by one-way ANOVA followed by Dunnett's test (*: 0.01< P <0.05, **: 0.001< P <0.01).

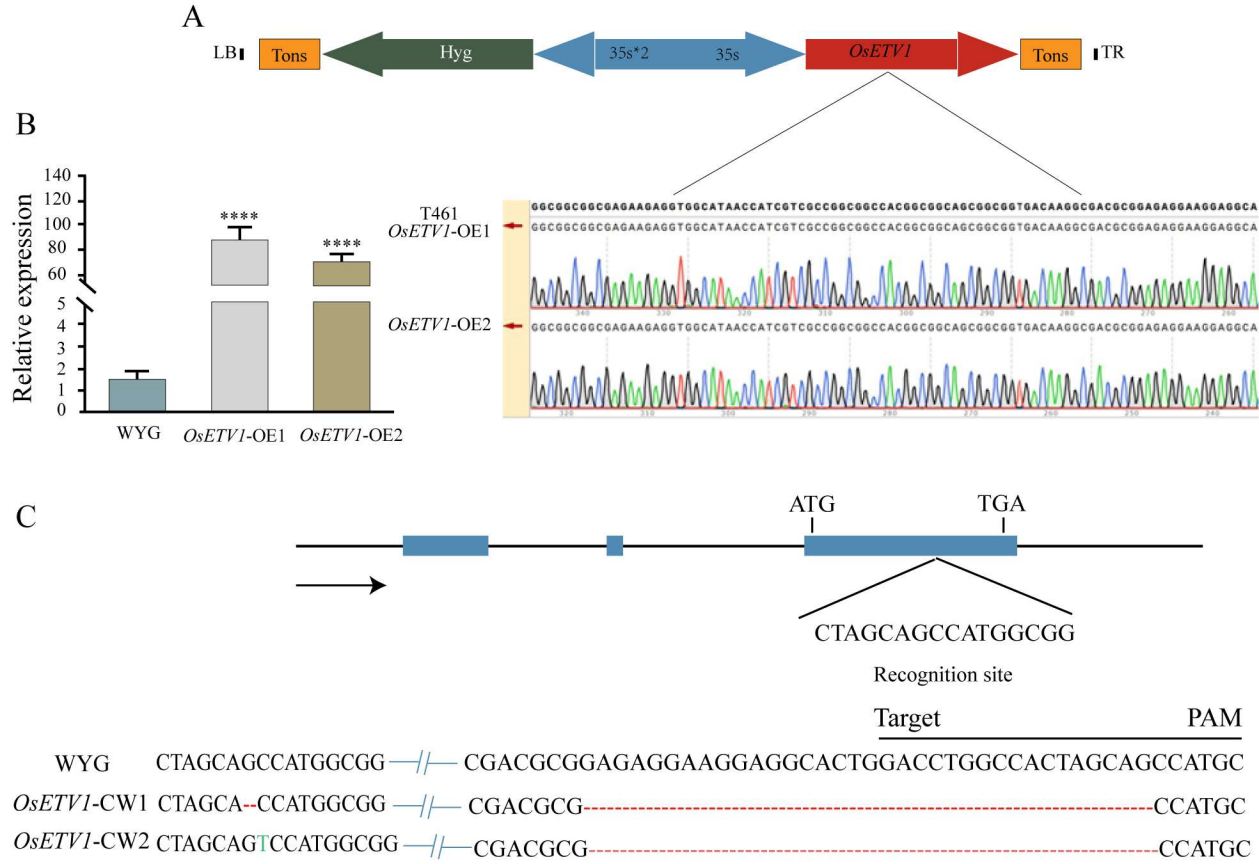
Figure 5 Subcellular localization of *OsETV1* in rice protoplast, GFP fluorescence was observed with excitation at 488 nm and emission at 510 nm. Scale bar = 10μm.

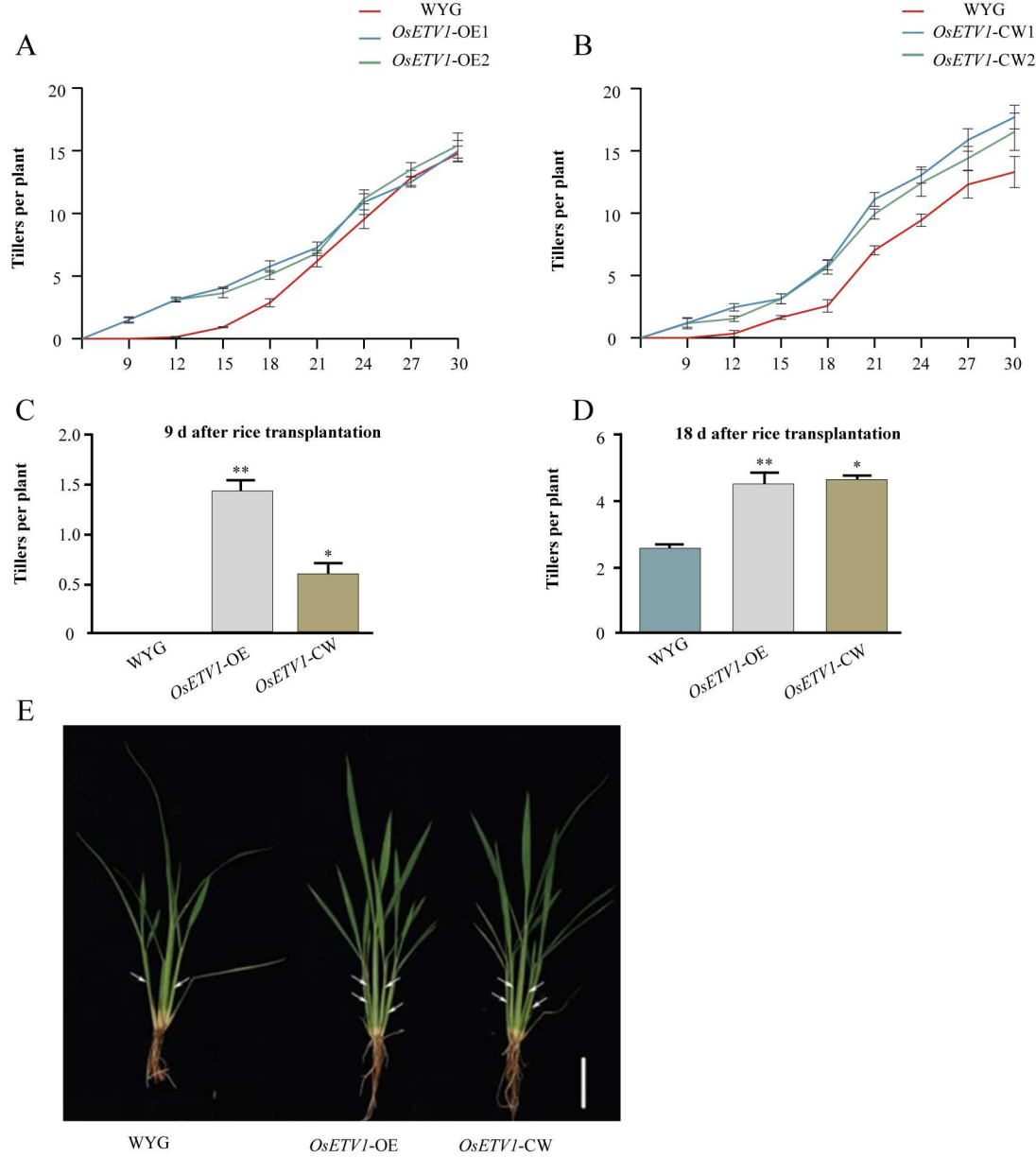
Figure 6 Screening the interacting proteins of *OsETV1*. (A) Autoactivation and toxicity detection of pGBKT7- *OsETV1* bait vector; （B） X-α-Gal analysis and screening of positive clones from *OsETV1* yeast screening library；+: positive；-: negative；15: *Os05g0334400* (*OsDjA8*); 1: *Os06g0316300*; 7: *Os02g0109800*; 14: *Os11g0146700*; 4, 5, 8, 9 and 10: *Os03g0123600*; 13: *Os04g0674100*.

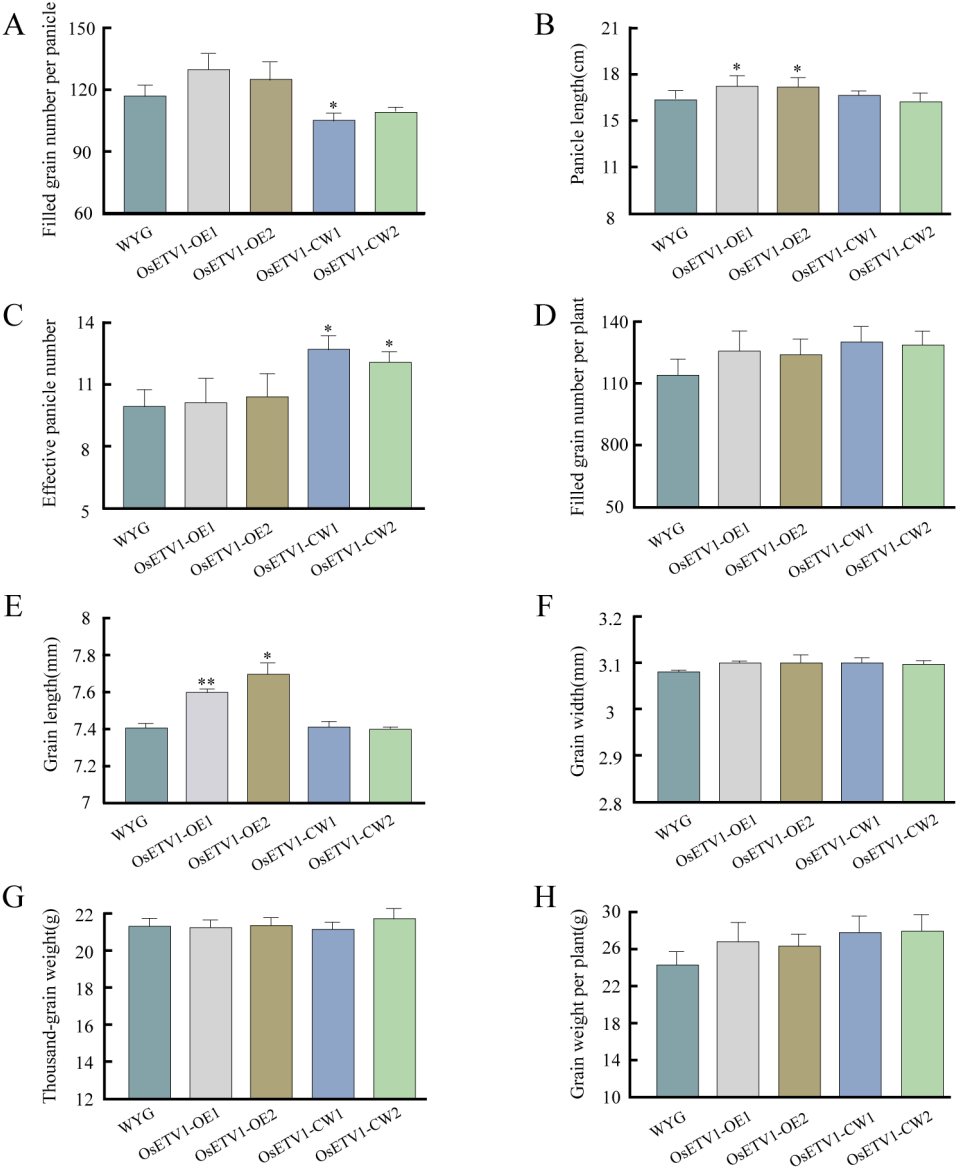
Additional file

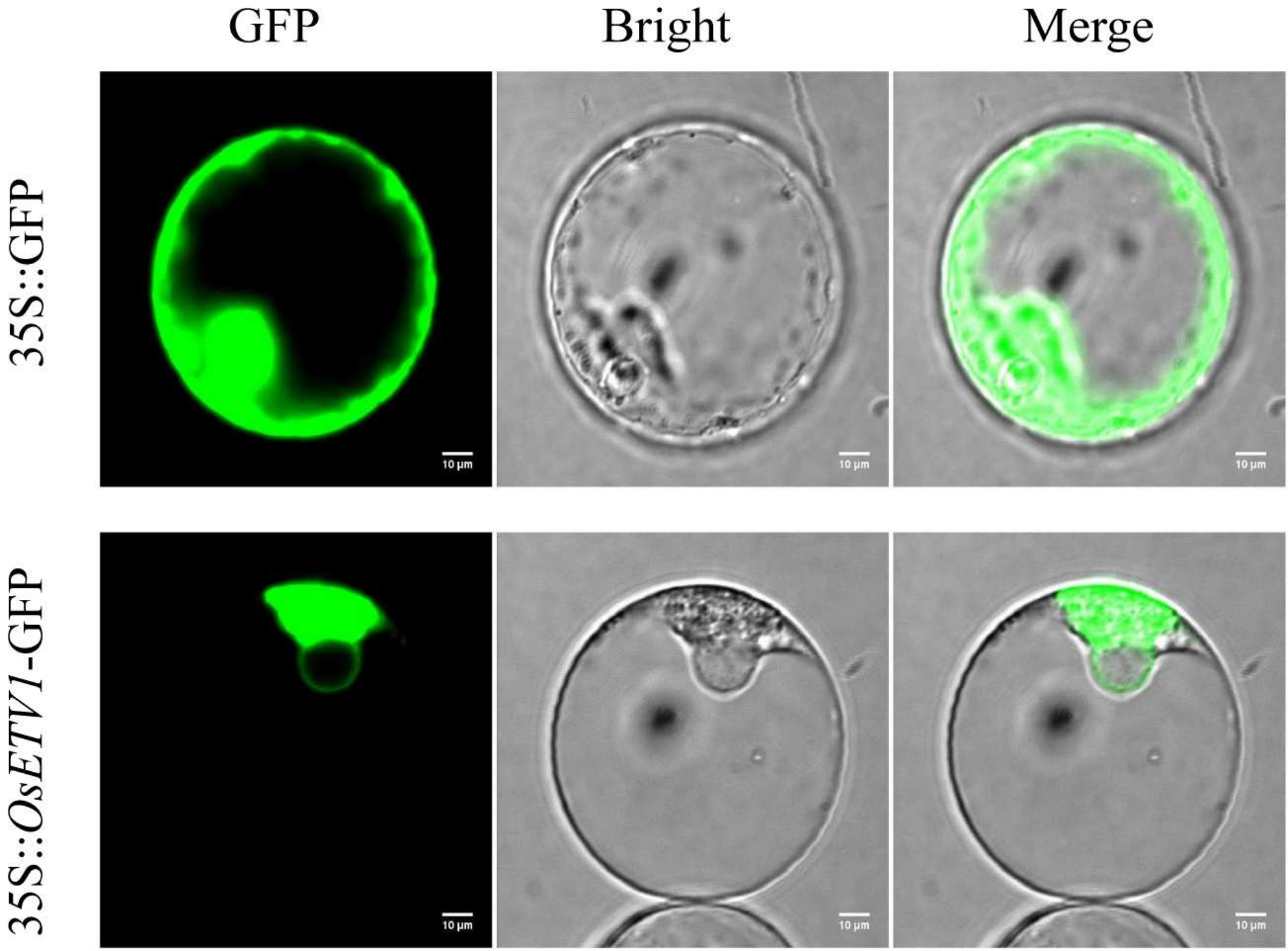
Table S1 The primers used in this study.

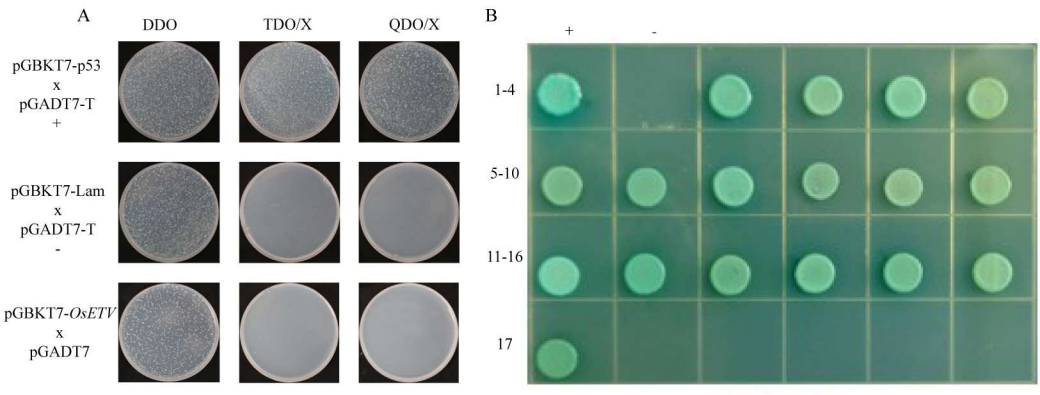

A
100bp
Q→W
175bp
D→N
239bp
R→L
T461 ATG----------CACCAGACC------GCAGATGGA------ATTCGAGTG------TGA
WYG ATG----------CACTGGACC------GCAAATGGA------ATTCTAGTG------TGA
Longqingdao3 ATG----------CACTGGACC------GCAAATGGA------ATTCTAGTG------TGA
B
A-box
ABRE
AE-box
LTR
CGTCA-motif
TGACG-motif
G-box
TC-rich repeats
GT1-motif
chs-CMA1a
C
TMAMM posterior probabilities for WEBSEQUENCE
probability
transmembrance
inside
outside
D
SignalP6.0 presiction:sp_P0DTC2_
SPIKE_SARS2_Spike_glycoprotein_
OS_Severe_acute_respiratory_syndrome_c
probability
OTHER
Sec/SPI n
Sec/SPI h
Sec/SPI c
CS


A
LB
Tons
Hyg
35s*2
35s
OsETV1
Tons
TR
B
Relative expression
140
120
100
80
60
5
4
3
2
1
0
****
****
WYG
OsETV1-OE1
OsETV1-OE2
T461
OsETV1-OE1
OsETV1-OE2
C
ATG
TGA
CTAGCAGCCATGGCGG
Recognition site
Target
PAM
WYG CTAGCAGCCATGGCGG CGACGCGGAGAGGAAGGAGGCACTGGACCTGGCCACTAGCAGCCATGC
OsETV1-CW1 CTAGCA--CCATGGCGG CGACGCG CCATGC
OsETV1-CW2 CTAGCAGTCCATGGCGG CGACGCG CCATGC


A
WYG
OsETV1-OE1
OsETV1-OE2
Tillers per plant
20
15
10
5
0
9
12
15
18
21
24
27
30
B
WYG
OsETV1-CW1
OsETV1-CW2
Tillers per plant
C
9 d after rice transplantation
Tillers per plant
2.0
1.5
1.0
0.5
0
**
*
WYG
OsETV1-OE
OsETV1-CW
D
18 d after rice transplantation
Tillers per plant
6
4
2
0
**
*
WYG
OsETV1-OE
OsETV1-CW
E
WYG
OsETV1-OE
OsETV1-CW


A
Filled grain number per panicle
150
120
90
60
*
WYG
OsETV1-OE1
OsETV1-OE2
OsETV1-CW1
OsETV1-CW2
B
Panicle length(cm)
21
18
15
11
8
*
*
C
Effective panicle number
14
11
8
5
*
*
D
Filled grain number per plant
140
110
800
50
E
Grain length(mm)
8
7.8
7.6
7.4
7.2
7
**
*
F
Grain width(mm)
3.2
3.1
3
2.9
2.8
G
Thousand-grain weight(g)
22
20
18
16
14
12
H
Grain weight per plant(g)
30
26
24
22
18
14
10


GFP
Bright
Merge
35S::GFP
35S::OsETV1-GFP
10 μm


A
DDO
TDO/X
QDO/X
pGBKT7-p53
x
pGADT7-T
+
pGBKT7-Lam
x
pGADT7-T
-
pGBKT7-OsETV
x
pGADT7
B
+
-
1-4
5-10
11-16
17

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.docx
- TableS1.xlsx