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Control of a key transition from prostrate to erect growth in rice domestication

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The transition from the prostrate growth of ancestral wild rice (*O. rufipogon* Griff.) to the erect growth of *Oryza sativa* cultivars was one of the most critical events in rice domestication. This evolutionary step importantly improved plant architecture and increased grain yield. Here we find that prostrate growth of wild rice from Yuanjiang County in China is controlled by a semi-dominant gene, *PROG1* (*PROSTRATE GROWTH 1*), on chromosome 7 that encodes a single Cys_2-His_2 zinc-finger protein. *prog1* variants identified in *O. sativa* disrupt the *prog1* function and inactivate *prog1* expression, leading to erect growth, greater grain number and higher grain yield in cultivated rice. Sequence comparison shows that 182 varieties of cultivated rice, including 87 *indica* and 95 *japonica* cultivars from 17 countries, carry identical mutations in the *prog1* coding region that may have become fixed during rice domestication.

Plant domestication is the genetic modification of a wild species to create a new form of a plant altered to meet human needs[1]. Asian cultivated rice (*Oryza sativa* L.) was one of the earliest domesticated crop species and is now a primary staple for billions of people worldwide[2]. As in the domestication of other food crops such as maize and wheat, marked morphological changes have also occurred during rice domestication[3]. Recently, evolutionary mechanisms and genetic factors controlling a few rice domestication-related traits, such as grain shattering and pericarp color, have been characterized[4–7]. The transition from prostrate to erect growth habit was also a critical domestication event. Typical common wild rice (*O. rufipogon* Griff.) tends to have a prostrate growth habit during the vegetative phase (**Fig. 1a**) and develop erect panicle-bearing stalks during the reproductive phase, which may repress the growth of weeds, occupy more space, be more tolerant to trampling and avoid grazing by animals in natural habitats. Cultivated rice has an erect growth habit throughout the entire growth phase (**Fig. 1b**), which may increase plant density, enhance photosynthesis efficiency and improve grain yield. However, the molecular basis for this key evolutionary step remains to be elucidated.

In an attempt to identify the gene responsible for prostrate growth, we constructed a set of introgression lines using an accession of Yuanjiang common wild rice (YJCWR, *O. rufipogon*) from Yuanjiang County of Yunnan Province, China, with prostrate growth habit as a donor, and an elite *indica* cultivar Teqing (*O. sativa*) with erect growth habit as a recipient[8]. We obtained one introgression line (YIL18; **Fig. 2**) displaying prostrate growth (**Fig. 2a**,**b**), which harbored two YJCWR chromosomal segments on the long arm of chromosome 3 and the short arm of chromosome 7 (**Supplementary Fig. 1** online). The tiller angle of YIL18 (**Fig. 2d**) was larger than that of Teqing (**Fig. 2g**). Observing the longitudinal section of the tiller base, we found that the tiller base in YIL18 showed symmetric development and that the length of its near-ground border was similar to that of its far-ground border (**Fig. 2e**,**f**). However, the tiller base in Teqing showed obviously asymmetric growth and the near-ground border was longer than that of the far-ground border (**Fig. 2h**,**i**).

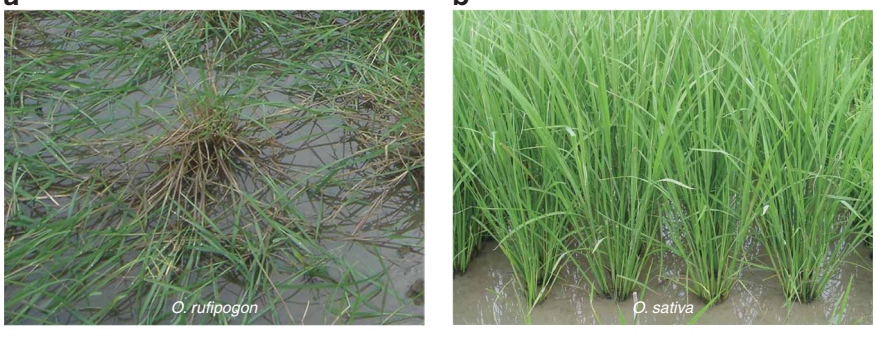

Figure 1 The transition from prostrate growth to erect growth. (**a**) Wild rice (*O. rufipogon*). (**b**) Cultivated rice (*O. sativa*).

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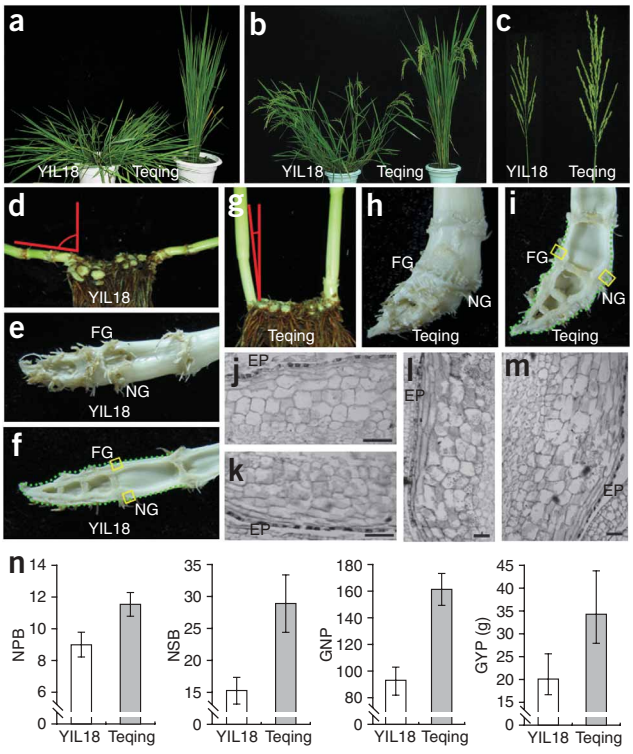

Figure 2 Phenotype of YIL18 and Teqing. (**a**) Introgression line YIL18 and the recipient parent Teqing at 60 days after sowing. (**b**) YIL18 and Teqing at 15 days after heading. (**c**) Main panicle of YIL18 and Teqing. (**d**–**f**) The tiller base of YIL18. (**d**) The base of two primary tillers; the tiller angle is marked in red lines. (**f**) The longitudinal section of **e**. FG, far-ground border marked with green broken line; NG, near-ground border marked with green broken line. (**g**–**i**) The tiller base of Teqing. (**g**) The base of two primary tillers; the tiller angle is marked in red lines. (**i**) The longitudinal section of **h**. (**j**–**m**) Histological graphs of the longitudinal section. (**j**) The YIL18 tissue from yellow box of FG in **f**. (**k**) The YIL18 tissue from yellow box of NG in **f**. (**l**) The Teqing tissue from yellow box of FG in **i**. (**m**) The Teqing tissue from yellow box of NG in **i**. EP, epiderm. Scale bars, 100 μm. (**n**) Comparison of the number of primary branches (NPB), secondary branches (NSB) and grain number (GNP) on main panicle, and grain yield per plant (GYP) between YIL18 and Teqing. Data are means ± s.d. ($n = 20$).

Further examination at the histological level showed that there was no significant difference in cell size between the far-ground and the near-ground tissue in Teqing (**Fig. 2j–m**). These results indicate that the longer near-ground border, which led to erect growth in Teqing, should be attributable to an increase in cell number (**Fig. 2j–m**). In addition, we found that the grain number on the main panicle (GNP) in YIL18 was only 57.6% of that in the recipient Teqing, a result of the lesser number of primary branches (NPB) and second branches (NSB) on the main panicle (**Fig. 2c**,**n**).

Genetic linkage analysis within 246 F_2 individuals derived from the cross between YIL18 and Teqing showed that prostrate growth was completely associated with a marked decrease of GNP and controlled by a single semi-dominant gene, *PROG1* (*PROSTATE GROWTH 1*), located between SSR markers RM298 and RM481 on short arm of chromosome 7 (**Fig. 3a**). Using a total of 3,600 recessive homozygote plants with erect growth from the F_2 population, we further delimited *prog1* within an 8.8-kb region between the pr5 and pr7 markers (**Fig. 3b**). Within this region, there is only one hypothetical gene (LOC_Os07g05900) in the Nipponbare genome (the TIGR Rice Genome Annotation Database)[9] (**Fig. 3c**). One positive BAC clone (YJ0710308) covering this region was isolated from genomic BAC library of YJCWR (**Fig. 3d**). We screened the YJ0710308 subclone library and identified two subclones, p*PROG1-1* and p*PROG1-2*, containing the entire *O. rufipogon* LOC_Os07g05900 with 596-bp and 2,914-bp 5′-flanking regions, respectively (**Fig. 3e**). Another construct containing only the 2,914-bp 5′-flanking region (p*TCK*), was developed as a control. We introduced these three constructs into a *japonica* cultivar, Zhonghua 17, using *Agrobacterium*-mediated transformation. We found that 21 independent transgenic lines for p*PROG1-1* and 25 lines for p*PROG1-2* all showed complementation of the prostrate growth phenotype, similar to introgression line YIL18 (**Fig. 3f**,**g**), whereas 30 independent transgenic lines of the control construct p*TCK* still showed the erect growth habit (**Fig. 3h**). Taken together, these results demonstrate that LOC_Os7g05900 in the *O. rufipogon* genome was a key gene (*PROG1*) controlling prostrate growth.

In addition to showing prostrate growth, all the transgenic plants for p*PROG1-1* and p*PROG1-2* had shorter plant height, less branches and lower grain number and yield than control transgenic plants for p*TCK* (**Fig. 3i**). The numbers of primary branches, secondary branches and grains on the main panicle of p*PROG1-1* transgenic lines were 7.3, 3.7 and 44.3, respectively, whereas those of control plants were 11.3, 28.0 and 149.3, respectively. Grain yield per plant of p*PROG1-1* transgenic lines was only 47.7% of that in control plants. These results indicate that the *PROG1* gene can decrease the number of primary and secondary branches, grain number and grain yield, and also suggest that the *PROG1* gene was a key pleiotropic gene controlling plant architecture and yield-related traits in rice.

Sequence analysis of 5′- and 3′-RACE cDNA products indicated that the *PROG1* cDNA in *O. rufipogon* is 833-bp long, with an ORF of 486 bp, a 147-bp 5′ untranslated region (UTR), and a 200-bp 3′ UTR, and encodes a 161 amino-acid protein (**Supplementary Fig. 2a** online). The *PROG1* gene encodes a putative single Cys_2-His_2 zinc-finger protein containing a highly conserved QALGGH motif specific to EPF zinc-finger proteins in plants[10] and a leucine-rich motif that is similar to an EAR-like active repression domain at the C-terminal region[11] (**Fig. 3j–l**). When we introduced the *PROG1-GFP* fusion gene under control of the rice *Act1* (actin) promoter into the *japonica* cultivar Zhonghua 17, we found that the PROG1-GFP fusion protein localized to the nucleus (**Fig. 4a**). This result supports the bioinformatic prediction that *PROG1* may function as a transcriptional factor. To study the tissue specificity of *PROG1* expression, we introduced the constructs consisting of the *PROG1* promoter regions fused to the *GUS* or *GFP* reporter gene into the *japonica* cultivar Zhonghua 17. We detected GUS expression in the tiller base (**Fig. 4b**,**c**), leaf-sheath pulvinus (**Fig. 4d**,**e**) and lamina joint (**Fig. 4f**), but not in the root, leaf blade and culm. We also observed GFP activity and found that *PROG1* was expressed strongly in the vascular bundles of the leaf-sheath pulvinus (**Fig. 4g**,**h**). Consistent with the expression patterns shown by GUS staining, we detected higher expression of *PROG1* in the leaf-sheath pulvinus, tiller base and lamina joint by real-time quantitative PCR (**Fig. 4i**); these organs might directly respond to the development and maintenance of plant structure, consonant with previous observations of similar expression patterns for *LAZY1* (refs. 12,13) and *TAC1* (ref. 14) controlling tiller angle of rice.

Through comparison of the coding sequences of *PROG1* in YJCWR and *prog1* in Teqing (**Supplementary Fig. 2b**), we detected 15 SNPs and 6 insertion/deletions (indels) that encoded 23 amino-acid changes between *PROG1* and *prog1* (**Supplementary Fig. 2c**). In order to compare the function of *PROG1* from YJCWR with that of *prog1* from

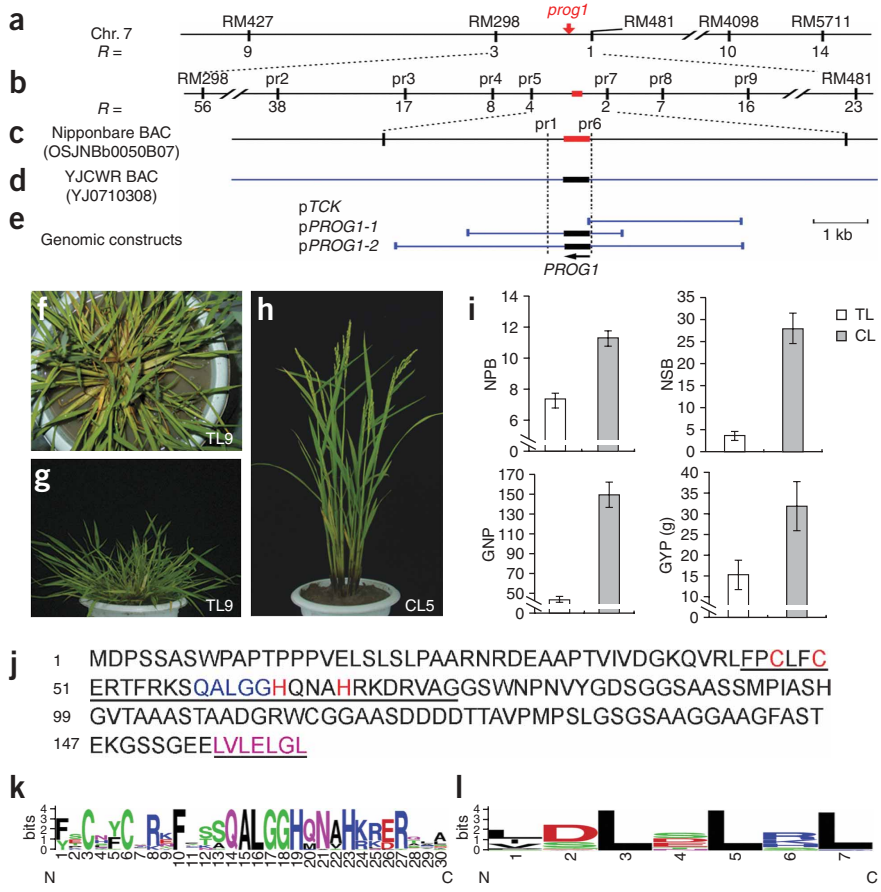

Figure 3 Molecular identification of *PROG1*. (**a**) *prog1* was mapped in the interval of RM298 and RM481 on short arm of chromosome 7. *R* is the number of recombinants. (**b**) The *prog1* locus was delimited to an 8.8-kb region between the pr5 and pr7 markers. (**c**) Nipponbare BAC. (**d**) YJCWR BAC. (**e**) Genomic fragments containing the entire or truncated *PROG1* gene from the YJCWR genomic BAC were cloned into a plant transformation vector, resulting in p*PROG1-1* and *pPROG1-2* constructs for complementation, respectively. The p*TCK* construct was a control containing only the 5-flanking region of *PROG1*. (**f**,**g**) The phenotype of transgenic plant (TL9) harboring the genomic construct p*PROG1-1*. (**h**) The phenotype of the control plant (CL5) harboring the construct p*CTK*. (**i**) Comparison of the number of primary branches (NPB), secondary branches (NSB) and grains (GNP) on main panicle, and grain yield per plant (GYP) between transgenic plants (TL) harboring the genomic construct p*PROG1-1* and the control plants (CL). Data are means ± s.d. ($n = 50$). (**j**) Predicted amino acid sequence of *PROG1*. Red letters show position of the Cys_2-His_2 zinc-finger domain; blue letters indicate conserved QALGGH motif; and pink letters show position of the EAR-like domain. The regions of motif analysis are underlined. (**k**,**l**) Motif analysis of Cys_2-His_2 zinc-finger domain, QALGGH domain and EAR-like domain. The logo for the consensus sequence graphically depicts the sequence conservation at that position and the height of symbols within the stack indicates the relative frequency of each amino acid at that position.

Teqing, we introduced two constitutive-expression constructs (p*Act1*::*PROG1* and p*Act1*::*prog1*), harboring *PROG1* ORF of YJCWR and *prog1* ORF of Teqing under control of the rice *Act1* promoter, respectively, into the *japonica* cultivar Zhonghua 17. All p*Act1*::*PROG1* plants showed prostrate growth and shorter stature, whereas all p*Act1*::*prog1* plants showed erect growth. We detected similar expression of *PROG1* and *prog1* in transgenic plants for the two constitutive-expression constructs by RT-PCR (**Supplementary Fig. 3** online). These results demonstrate that the mutations in the coding region of *prog1* might cause the loss of protein function.

To determine the origin of the *prog1* mutation in Asian cultivated rice, we sequenced the *prog1* coding regions of 182 erect-growth varieties of cultivated rice, including 87 *indica* and 95 *japonica* cultivars from 17 countries. We found that all the cultivars contained identical mutations as *prog1* in Teqing, including 15 SNPs and 6 indels (**Supplementary Table 1** online). These data imply that all domesticated rice varieties have exactly the same haplotype as defined by the 15 SNPs and 6 indels and that the favored *prog1* allele might have been singly originated and strongly selected during rice domestication.

We further sequenced the coding regions of 30 accessions of prostrate-growth wild rice, including 25 perennial *O. rufipogon* and 5 annual *O. nivara*. We found that 11 *O. rufipogon* and 5 *O. nivara* harbored the same or similar nucleotide sequences to *PROG1* in YJCWR. However, the remaining 14 *O. rufipogon* contained identical or similar mutations to *prog1* in Teqing (**Supplementary Table 1**). The prostrate growth of these 14 *O. rufipogon* accessions might be controlled by a gene(s) other than *PROG1*. Systematic comparison of the coding regions from these 182 varieties of cultivated rice and 30 accessions of wild rice showed that 5 (SNP3, SNP4, SNP8, SNP9 and SNP11) out of the 15 SNPs were not responsible for loss of the *prog1* function, as SNP4 and SNP11 were synonymous mutations and SNP3, SNP8 and SNP9 were not associated with disruption of *prog1* function (**Supplementary Table 1**). The remaining 10 SNPs and 6 indels, which resulted in the change of 20 amino acids (**Supplementary Table 1**), might be the mutations causing inactivation of *prog1* function.

Investigation of the endogenous transcriptional level of *PROG1* and *prog1* from the leaf-sheath pulvinus of YJCWR, YIL18 and Teqing by RT-PCR, 5′-RACE and 3′-RACE showed that the transcripts were present only in YJCWR and YIL18, but not in Teqing (**Fig. 4j**,**k**), suggesting that the regulatory region of *prog1* may harbor some mutations that affect *prog1* expression. We then compared the 600-bp 5′-flanking regions of *PROG1* in YJCWR and *prog1* in Teqing and identified 32 SNPs and 3 indels (**Supplementary Fig. 2d**). Large-scale sequence verification of the 32 SNPs and 3 indels from 161 varieties of cultivated rice and 29 accessions of wild rice indicated that five SNPs (PS3, PS10, PS23, PS25 and PS32) and one indel (PID2) had no effect on *prog1* expression (**Supplementary Table 2** online), and that the remaining 27 SNPs and 2 indels in the 5′-flanking region of *prog1* might be responsible for the inactivation of *prog1* expression. We speculate that, taken together, the marked genome variation of *prog1* in *O. sativa*, including 10 SNPs and 6 indels in the coding region and 27 SNPs and 2 indels in the 5′-flanking region, disrupt *prog1* function and inactivate *prog1* expression, which led to erect growth and higher grain number and yield in cultivated rice relative to its ancestor species, *O. rufipgon*.

Here we show that the selection of *prog1* led to the critical transition from prostrate to erect growth. The tiller base in common wild rice

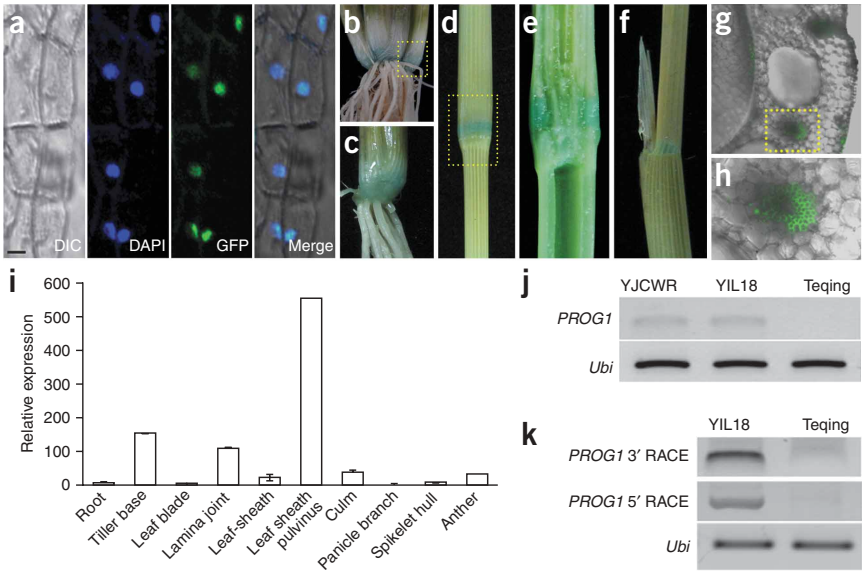

Figure 4 Expression of *PROG1* and *prog1*. (**a**) The PROG1-GFP fusion protein is localized to the nucleus. DIC, a differential interference contrast image; DAPI, the same cells showing the DAPI-stained nuclei; GFP, the same cells showing PROG1-GFP green fluorescence in the nuclei; merge, the merged image. Scale bar, 10 μm. (**b**–**h**) Tissue localization of *PROG1*. The expression of *PROG1* is detected in tiller base (**b**,**c**), leaf-sheath pulvinus (**d**,**e**) and lamina joint (**f**) by GUS staining and in vascular bundles of leaf-sheath pulvinus (**g**,**h**) by GFP visualization. (**c**) Magnification from yellow box in **b**. (**e**) Magnification of longitudinal section from yellow box in **d**. (**h**) Magnification from yellow box in **g**. (**i**) Real-time quantitative PCR estimates the relative expression of *PROG1*. (**j**) Analysis of *PROG1* expression using RT-PCR in leaf-sheath pulvinus of YJCWR, YIL18 and Teqing. *Ubi*, rice *Ubiquitin* as a control. (**k**) 5′ and 3′ RACE of *PROG1* and *prog1* in the leaf-sheath pulvinus of YIL18 and Teqing.

showed symmetric growth resulting in prostrate growth, and the possible roles of *PROG1* in regulating symmetric growth are yet to be investigated. A similar transition from prostrate to erect growth also occurred in the domestication of wheat[15], and the cloning of *PROG1* might provide a new tool for understanding the domestication of plant architecture in other crops. In addition to leading to erect growth, selection of *prog1* also resulted in higher grain number and yield in cultivated rice relative to its ancestor species. This evidence suggests that mutation of a single gene can improve plant architecture and yield in crop domestication; indeed, such an improvement also resulted from the selection of *tb1* (*teosinte branched1*) in maize[16,17].

METHODS

Plant materials. The 182 varieties of cultivated rice, including 87 *indica* and 95 *japonica* varieties, and the 34 accessions of wild rice used in this study are listed in **Supplementary Table 3** online.

Primers. The primers used in this study are listed in **Supplementary Table 4** online.

Generation of constructs. The BAC clone YJ0710308, containing the *PROG1* gene, was identified from the BAC library of Yuanjiang common wild rice[18]. The 2,921-bp and 6,669-bp fragments from YJ0710308, harboring the entire *PROG1* gene, were inserted into the binary vector p*CAMBIA1300* to form p*PROG1-1* and p*PROG1-2*, respectively. The construct p*TCK* contained the 2,914-bp 5′-flanking region of *PROG1*, the constructs *pAct1*::*PROG1* and *pAct1*::*prog1* harbored the *PROG1* ORF of YJCWR and *prog1* ORF of Teqing under the control of rice *Act1* promoter, respectively, and the construct p*Act1*::*PROG1-GFP* contained *PROG1* fused with *GFP* driven by an *Act1* promoter. To investigate the expression pattern of *PROG1*, we made constructs in which the *PROG1* promoter (2,914 bp) fused with *GUS* or *GFP* were inserted into the binary vector p*CAMBIA1300*. All plasmid constructs were introduced to *Agrobacterium tumefaciens* strain LBA4404 and subsequently transferred into the *japonica* cultivar Zhonghua 17.

Phenotypic evaluation. For the introgression line YIL18 and the recipient parent Teqing, we used 20 plants to measure the number of primary branches (NPB), secondary branches (NSB) and grains (GNP) on main panicle, and grain yield per plant (GYP). For transgenic plants, phenotypic measurements were done using five independent lines (ten plants from each line) harboring the construct p*PROG1-1* and p*TCK*, respectively.

RT-PCR, 5′ and 3′ RACE and real-time quantitative PCR. We extracted total RNAs using an RNeasy Plant Mini Kit (Qiagene). First-stand cDNA synthesis was done with *Bca*BEST RNA PCR Kit (TaKaRa). We carried out RT-PCR to amplify the *PROG1* transcripts with the primers RPG1F and RPG1R, and 5′ and 3′ RACE with the GeneRacer Kit (Invitrogen Life Technologies) following the manufacturer's instructions. Real-time RT-PCR was done on the ABI Prism 7900 Sequence Detection System (Applied Biosystems). Diluted cDNA was amplified with primers QZF1F and QZF1R using the SYBR Green Master Mix (Applied Biosystems). We normalized the levels of *PROG1* transcripts by endogenous 18S rRNA transcripts amplified with primers 18SF and 18SR. Each set of experiments was repeated three times, and the relative quantification method (DDCT) was used to evaluate quantitative variation.

Subcellular and tissue localization. Roots of the transgenic plants harboring the p*Act1*::*PROG1-GFP* construct were frozen and cut, stained with 4,6-diamidino-2-phenylindole (DAPI, 5 μg ml^{-1} in PBS) and examined with a Nikon C1 Si confocal laser microscope. GUS staining of tissues from plants harboring the p*PROG1*::*GUS* construct was performed as previously described[19].

Conserved motif analysis. We selected 13 rice and 23 *Arabidopsis* single Cys_2-His_2 zinc-finger genes by searching the TIGR database. Multiple sequence alignments were done using CLUSTAL X[20] and edited manually to reserve only the consensus sequence (**Supplementary Fig. 4** online). Motif analyses were done using the web tool WebLogo[21].

Sequencing and data analysis. We purified and sequenced PCR-amplified products from genomic DNA with primers ZF11F and ZF11R for the coding region of *PROG1* and *prog1* and with primers PPG1F and PPG1R for the 5′-flanking region of *PROG1* and *prog1*. Multiple sequence alignments were done using CLUSTAL X[20].

Accession codes. GenBank: EU554631, *PROG1* promoter of YJCWR C4; EU556718, *PROG1* cDNA of YJCWR C4; EU556719, *PROG1* cds of YJCWR C4; EU556720, *PROG1* allele of Guangxi common wild rice YD2-0772; EU556721, *prog1* allele of Jiangxi common wild rice 94W1; EU556722, *PROG1* allele of India *O. nivara* W1987; EU556723, *prog1* allele of Teqing.

Note: Supplementary information is available on the Nature Genetics website.

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AUTHOR CONTRIBUTIONS

L.T. conducted characterization of introgression line, genetic mapping, gene cloning and gene expression analysis; X.L. constructed the genomic BAC library of YJCWR and screened the positive clone; F.L. helped L.T. with genetic mapping and gene expression analysis; X.S. maintained plant materials and performed the field management; C.L. performed the genetic transformation; Z.Z., Y.F., H.C. and X.W. conducted the collection of rice garmplasm and phenotypic data; C.S and D.X. designed and supervised this study; C.S., D.X. and L.T. analyzed the data and wrote the paper.

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1. Doebley, J., Gaut, B. & Smith, B. The molecular genetics of crop domestication. *Cell* **127**, 1309–1321 (2006).
2. Khush, G. Origin, dispersal, cultivation and variation of rice. *Plant Mol. Biol.* **35**, 25–34 (1997).
3. Kovach, M., Sweeney, M. & McCouch, S. New insights into the history of rice domestication. *Trends Genet.* **23**, 578–587 (2007).
4. Li, C., Zhou, A. & Sang, T. Rice domestication by reducing shattering. *Science* **311**, 1936–1939 (2006).
5. Lin, Z. *et al.* Origin of seed shattering in rice (*O. sativa* L.). *Planta* **226**, 11–20 (2007).
6. Konishi, S. *et al.* An SNP caused loss of seed shattering during rice domestication. *Science* **312**, 1392–1396 (2006).
7. Sweeney, M. *et al.* Caught red-handed: *Rc* encodes a basic helix-loop-helix protein conditioning red pericarp in rice. *Plant Cell* **18**, 283–294 (2006).
8. Tan, L. *et al.* Development of *Oryza rufipogon* and *Oryza sativa* introgression lines and assessment for yield-related quantitative trait loci. *J. Integr. Plant Biol.* **49**, 871–884 (2007).
9. Yuan, Q. *et al.* The TIGR rice genome annotation resource: annotating the rice genome and creating resources for plant biologists. *Nucleic Acids Res.* **31**, 229–233 (2003).
10. Takatsuji, H. Zinc-finger proteins: the classical zinc finger emerges in contemporary plant science. *Plant Mol. Biol.* **39**, 1073–1078 (1999).
11. Hiratsu, K., Ohta, M., Matsui, K. & Ohme-Takagi, M. The SUPPERMAN protein is an active repressor whose carboxy-terminal repression domain is required for the development of normal flowers. *FEBS Lett.* **514**, 351–354 (2002).
12. Yoshihara, T. & Iino, M. Identification of the gravitropism-related rice gene *LAZY1* and elucidation of LAZY1-dependent and –independent gravity signaling pathways. *Plant Cell Physiol.* **48**, 678–688 (2007).
13. Li, P. *et al. LAZY1* controls rice shoot gravitropism through regulating poplar auxin transport. *Cell Res.* **17**, 402–410 (2007).
14. Yu, B. *et al. TAC1*, a major quantitative trait locus controlling tiller angle in rice. *Plant J.* **52**, 891–898 (2007).
15. Waisel, Y. Evolution of erect growth forms in domesticated wheats: possible effects of grazing. *Oecologia* **73**, 630–632 (1987).
16. Doebley, J., Stec, A. & Hubbard, L. The evolution of apical dominance in maize. *Nature* **386**, 485–488 (1997).
17. Clark, R., Wagler, T., Quijada, P. & Doebley, J. A distant upstream enhancer at the maize domestication gene *tb1* has pleiotropic effects on plant and inflorescent architecture. *Nat. Genet.* **38**, 594–597 (2006).
18. Li, X. *et al.* Construction of a bacterial artificial chromosome (BAC) library of common wild rice (*Oryza rufipogon* Griff.) for map-based cloning of genes selected during the domestication of rice. *Biotechnol. Lett.* **30**, 555–561 (2008).
19. Scarpella, E., Rueb, S. & Meijer, A.H. The *RADICLELESS1* gene is a required for vascular pattern formation in rice. *Development* **130**, 645–658 (2003).
20. Thompson, J., Gibson, T., Plewniak, F., Jeanmougin, F. & Higgins, D. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res.* **25**, 4876–4882 (1997).
21. Crooks, G., Hon, G., Chandonia, J. & Brenner, S. WebLogo: a sequence logo generator. *Genome Res.* **14**, 1188–1190 (2004).