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Genetic control of rice plant architecture under domestication

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The closely related wild rice species *Oryza rufipogon* is considered the progenitor of cultivated rice (*Oryza sativa*)[1–5]. The transition from the characteristic plant architecture of wild rice to that of cultivated rice was one of the most important events in rice domestication; however, the molecular basis of this key domestication transition has not been elucidated. Here we show that the *PROG1* gene controls aspects of wild-rice plant architecture, including tiller angle and number of tillers. The gene encodes a newly identified zinc-finger nuclear transcription factor with transcriptional activity and is mapped on chromosome 7. *PROG1* is predominantly expressed in the axillary meristems, the site of tiller bud formation. Rice transformation experiments demonstrate that artificial selection of an amino acid substitution in the PROG1 protein during domestication led to the transition from the plant architecture of wild rice to that of domesticated rice.

Rice (*Oryza sativa*) is an essential cereal crop, providing a carbohydrate source for more than one-third of the world's population, and it is widely cultivated in arable land worldwide. Cultivated rice is considered to be domesticated from the closely related wild species *Oryza rufipogon*, which distributed from southeastern Asia to India through artificial selection during the long history of domestication[1–5]. Through the course of domestication, several important traits have been artificially selected, including the loss of seed shattering and color, and changes in seed shape and plant architecture[3,5–11]. Recently, two genes (*Sh4* and *qSH1*) responsible for seed shattering have been identified and cloned in order to explore the evolutionary history of rice[9,10].

O. rufipogon shows a prostrate growth habit with a wider tiller angle and short stature with many tillers (**Supplementary Fig. 1** online). This plant architecture increases leaf shade and therefore decreases photosynthetic efficiency, prohibiting dense plantings. Such undesirable plant architecture was targeted and continuously selected against by ancient humans, which gradually resulted in the more desirable plant architecture of domesticated rice (*O. sativa*). Domesticated rice shows relatively erect growth (a narrow tiller angle) and fewer tillers, which allows for effective high-yield cultivation. Therefore, plant-architecture selection was a pivotal event in rice domestication. However, to date, the molecular basis of selection has remained unknown.

We constructed a set of chromosome segment substitution lines (CSSLs) from backcross progenies derived from a cross between Teqing (*O. sativa* L. ssp. *indica* variety) as the recurrent parent and wild rice (*O. rufipogon*) as the donor parent (obtained from Hainan province, China)[12]. We found a CSSL line (CSSL68) that carried a wild-rice genomic segment of the short arm of chromosome 7. The line showed plant architecture similar to that of wild rice, including a prostrate growth (a wider tiller angle) and many tillers. The F_1 derived from the cross between CSSL68 and Teqing also had plant architecture similar to wild rice, and 47 out of 192 F_2 plants showed Teqing plant architecture (3:1 ratio; $\chi^2 = 0.03$; $P > 0.90$). These mendelian inheritance patterns indicated that a single dominant gene controls wild-rice plant architecture. We mapped this gene on the short arm of chromosome 7 and termed it *PROG1* (*PROSTRATE GROWTH 1*).

We further developed a near-isogenic line, NIL(*PROG1*), that contained a very short *PROG1* chromosomal segment from wild rice in the Teqing genetic background and characterized the plant architecture (**Fig. 1**). During the early seedling stage, both tiller bud formation and tiller outgrowth in NIL(*PROG1*) were earlier than that in Teqing (**Fig. 1a**,**b**). After the tillering stage, NIL(*PROG1*) produced many tillers, but Teqing produced very few (**Fig. 1c**,**d**,**f**). Furthermore, NIL(*PROG1*) showed increased tiller spread with a wider tiller angle, whereas Teqing had a compact plant architecture with a narrower tiller angle (**Fig. 1c**,**e**). These results show that NIL(*PROG1*) possesses plant architecture similar to that of wild rice, including a prostrate growth (a wider tiller angle) and many tillers, suggesting that *PROG1* may be a key domestication gene responsible for plant architecture.

To clone *PROG1*, we carried out a large-scale linkage analysis and fine mapped *PROG1* to a 14-kb region between markers S3204 and P71 (**Fig. 2a**,**b**). In this region, only one predicted ORF was identified, and we considered it a good candidate gene for *PROG1*. To confirm whether the candidate gene was in fact *PROG1*, we carried out a genetic complementation test. We were unable to regenerate shoots from Teqing callus tissue; therefore, we chose *O. sativa* subsp. *japonica* variety Zhonghua 11 for the transformation because the variety is easily regenerated[13]. A 2.677-kb wild-rice DNA fragment containing the *PROG1* promoter region and the entire ORF was transferred into

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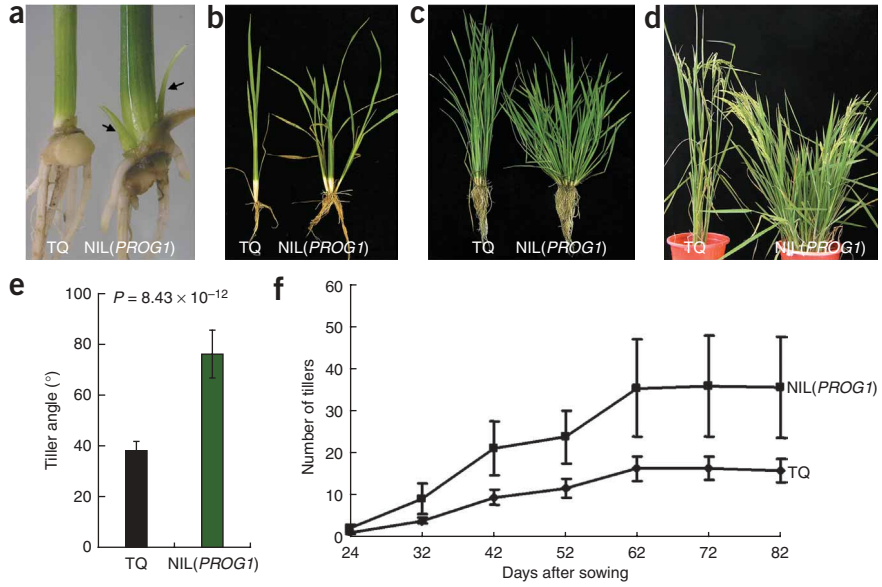


Figure 1 Plant architecture phenotypic characterization in Teqing and NIL(*PROG1*). (**a**–**c**) Tiller number and tiller angle comparisons between Teqing (TQ) and NIL(*PROG1*) plants at early seedling stage (**a**), seedling stage (**b**) and tillering stage (**c**). Arrows show emerging tiller bud formation in NIL(*PROG1*) plants. (**d**,**e**) Tiller number and tiller angle comparisons between Teqing and NIL(*PROG1*) plants at heading stage (**d**), and quantitative measurement of tillering angle at tillering stage (**e**, $n = 12$). The tiller angle was measured between the outermost tiller in the left side and the outermost tiller in the right side. There was significant difference in the tiller angle between Teqing and NIL(*PROG1*) (Student's *t*-test). (**f**) Changes in tiller number during development in Teqing and NIL(*PROG1*) ($n = 30$). Data are presented as means ± s.d.

Zhonghua 11 (**Fig. 2b**,**c**). We obtained 21 independent transgenic lines containing the wild-rice DNA fragment, and all of them showed plant architecture similar to wild rice, including a prostrate growth and many tillers (**Fig. 2c**,**d**). These results confirmed that the candidate gene was *PROG1*, which is primarily responsible for wild-rice plant architecture. We predicted that *PROG1* encodes a 167-residue polypeptide containing a C2H2-type zinc-finger motif (**Fig. 3a**) with unknown function. Recently, genes that control tiller angle but not tiller number in cultivated rice have been identified, including *LA1* and *TAC1*, both of which are grass-specific genes[14,15]. *PROG1*, together with these two genes, will be of value to further explore the molecular mechanisms controlling rice tiller angle.

A comparison of a 2.679-kb sequence containing the *PROG1* promoter and the ORF between Teqing and wild rice revealed six mutations (**Fig. 3b**). Two nucleotide substitutions were detected in the ORF, including a 1-bp substitution (M5) that did not result in amino acid variation, and another 1-bp substitution (M6) in Teqing, where threonine in wild rice was replaced by serine (T152S). Four additional mutations, including three 1-bp substitutions (M1, M2, M3) and one 2-bp insertion in Teqing (M4) were located in the *PROG1* promoter region. We subsequently carried out rice transformations to test the role of the two mutations in the ORF. We constructed two site-directed-mutation constructs containing the M5 and M6 substitutions; that is, we changed the guanosine (G) and thymidine (T) nucleotides at the M5 and M6 sites of Teqing to the adenosine (A) nucleotides of wild rice (**Fig. 3b**). In the resulting M5 or M6 construct, the Teqing *PROG1* promoter drove the coding region containing the adenosine nucleotide of wild rice at the M5 or M6 site (**Fig. 3b**). The mutant constructs were transformed into Zhonghua 11. We obtained 21 independent transgenic lines with the M5 construct and 25 with the M6 construct. All transgenic lines that expressed the M6 construct, but none with the M5 construct, showed plant architecture similar to that of wild rice (**Fig. 3c**–**e**). These results demonstrated that threonine (Thr152) at the M6 site of the PROG1 protein was primarily responsible for wild-rice plant architecture. The phenotypes of all transgenic lines with the M5 construct were unchanged, consistent with the fact that this mutation does not lead to amino acid change in the ORF.

To assess the evolutionary direction of these six mutations during rice domestication, we analyzed 13 rice (*O. sativa*) varieties, including

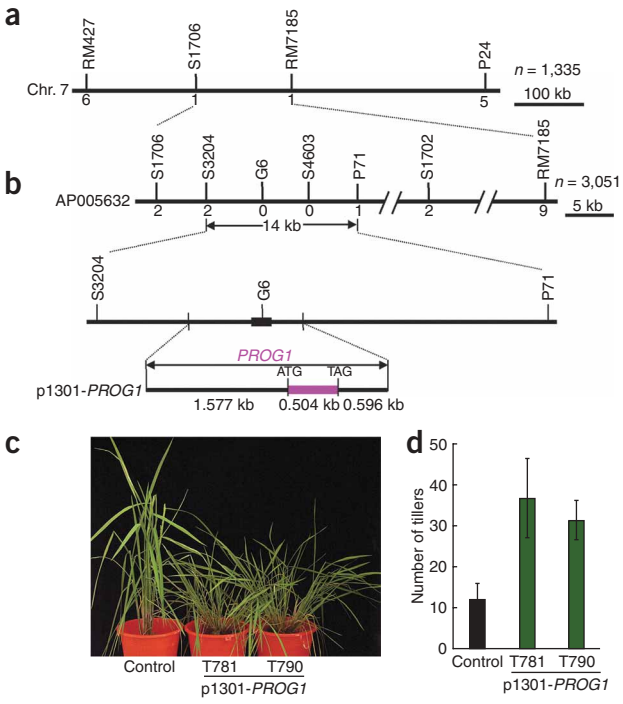
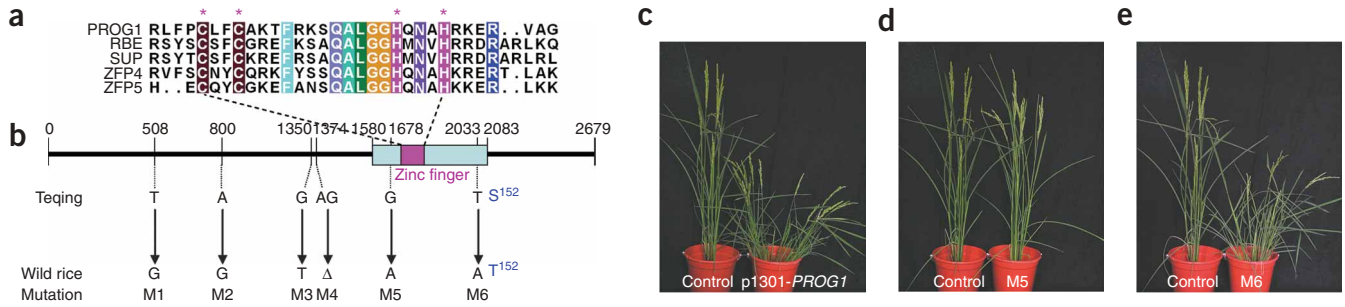


Figure 2 Map-based cloning of *PROG1* and genetic complementation test. (**a**) Mapping of *PROG1* using 1,335 F_2 plants (BC_3F_2). (**b**) Top panel: the large-scale linkage analysis for fine mapping of *PROG1* using 3,051 F_2 plants (BC_3F_2). *PROG1* was delimited to a 14-kb genomic DNA region between markers S3204 and P71. Numbers below lines indicate the number of recombinants between *PROG1* and each marker in **a** and **b**. Bottom panel: a 2.677-kb DNA fragment containing *PROG1* from wild-rice genomic DNA, inserted into the binary vector pCAMIA1301 to generate the transformation vector p1301-*PROG1*. (**c**,**d**) Complementation test of the *PROG1* gene. Plant architecture (**c**) and tiller number (**d**) of T2 transgenic lines at the tillering stage; p1301-*PROG1* vector with the wild-rice fragment was transformed into Zhonghua 11. Data are presented as means ± s.d. ($n = 11$).



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Accession name	Species	M1	M2	M3	M4	M5	M6	Phenotype
Hainan Lingshang	Wild rice (*Oryza rufipogon*)	G	G	T	–	A	A	Many tillers, tiller spread
Hainan Yanfeng	Wild rice (*Oryza rufipogon*)	G	G	T	–	A	A	Many tillers, tiller spread
Guangdong	Wild rice (*Oryza rufipogon*)	G	G	T	–	A	A	Many tillers, tiller spread
Teqing (TQ)	*indica* rice (*Oryza sativa*)	T	A	G	AG	G	T	Fewer tillers, tiller compact
Guangluai-4	*indica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact
Guichao-2	*indica* rice (*Oryza sativa*)	T	A	G	AG	G	T	Fewer tillers, tiller compact
Fengaizhan-1	*indica* rice (*Oryza sativa*)	T	A	G	AG	G	T	Fewer tillers, tiller compact
IR28	*indica* rice (*Oryza sativa*)	T	A	G	AG	G	T	Fewer tillers, tiller compact
Kasalath	*indica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact
Zhonghua-11	*japonica* rice (*Oryza sativa*)	T	A	G	AG	G	T	Fewer tillers, tiller compact
Nipponbare	*japonica* rice (*Oryza sativa*)	T	G	T	AG	G	T	Fewer tillers, tiller compact
Koshihikari	*japonica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact
Wuyuging-7	*japonica* rice (*Oryza sativa*)	T	G	T	AG	G	T	Fewer tillers, tiller compact
Xueheaizao	*japonica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact
CB	*japonica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact
Lemont	*japonica* rice (*Oryza sativa*)	T	G	G	AG	G	T	Fewer tillers, tiller compact

Figure 3 *PROG1* structure and mutation analysis. (**a**) Amino acid sequence alignments of the zinc finger domain. Identical residues are shown in colored boxes. Asterisks indicate cysteine and histidine in C2H2-type zinc finger domain. (**b**) Comparison of the 2.679-kb sequence between Teqing and wild rice revealed six mutations (M1–M6). Two and four mutations are located in the ORF (shown by box) and promoter region of the *PROG1*, respectively. Five mutations are 1-bp substitutions, and one is a 2-bp deletion (M4) in the promoter region of wild-rice *PROG1* (2.677-kb sequences for the wild rice). (**c**–**e**) Plant architecture of T2 transgenic lines with M5 or M6 mutation constructs. The two site-mutation mutants from Teqing to wild rice containing M5 (**d**) and M6 (**e**) were constructed and transformed into Zhonghua 11. (**f**) The sequences of 13 rice varieties including six *indica* and seven *japonica* varieties, and three accessions of *O. rufipogon* at six mutation sites.

six *indica* and seven *japonica* varieties, and three accessions of wild rice (*O. rufipogon*) (**Fig. 3f**). We found that all *O. sativa* varieties shared the same M5 and M6 mutation sequences in the ORF and differed from those of *O. rufipogon*. The M5 mutation was not functional; therefore, we suggested that the amino acid substitution (functional mutation) at the M6 site had been the target of artificial selection for the development of desirable plant architecture of *O. sativa* during rice domestication. In addition, all 13 *O. sativa* varieties had the same M1 and M4 mutation sequences at the promoter region, which were different from those of *O. rufipogon* (**Fig. 3f**). However, at the remaining two mutation sites (M2 and M3) in the promoter region, sequence polymorphisms were detected within the *O. sativa* varieties (**Fig. 3f**); that is, some of *O. sativa* varieties shared the same sequence with the *O. rufipogon* accessions.

Protein sequence analysis showed that PROG1 contains a single highly conserved C2H2-type zinc-finger motif at its N-terminal region (**Fig. 3a**), suggesting that PROG1 serves as a transcription factor[16–19]. Database searches indicated that with the exception of the zinc-finger motif, PROG1 shows no substantial similarity to any protein identified or predicted in rice or any other organism, indicating that PROG1 is a newly identified zinc-finger protein. To investigate whether PROG1 is a transcription factor, we carried out a subcellular localization experiment and transcriptional activation assay. The transient expression experiment in onion epidermal cells showed that GFP-PROG1 (*PROG1* from wild rice) was specifically localized in the nucleus (**Fig. 4a**), supporting a role for PROG1 as a nuclear transcription factor. The transcriptional activation assay showed that expression of the PROG1 (wild rice) and BD (GAL4 binding domain) fusion protein in yeast resulted in high reporter gene expression (**Fig. 4b**), implying that PROG1 has strong transcriptional activity as a transcription factor. We did not observe any differences in activation levels between PROG1 in wild rice and PROG1 in Teqing, suggesting the amino acid substitution at the M6 site is not responsible for transcriptional activity and that this amino acid substitution may affect the interactions between the PROG1 protein and other proteins. In addition, we carried out deletion analysis to ascertain the transcriptional activation domain of PROG1. Deletion of the region between amino acids 1 and 69 of the N terminus maintained relatively high activation, whereas deletion of the region between amino acids 70 and 167 of the C terminus resulted in a large reduction in activation (**Fig. 4b**), indicating that the C terminus of PROG1 is required for transcriptional activation. Taken together, these results demonstrated that PROG1 is a nuclear transcription factor with transcriptional activity and that the activation domain is localized in the C terminus.

Reverse-transcriptase PCR (RT-PCR) analysis showed that the expression of *PROG1* in both NIL(*PROG1*) and Teqing was detected at the unelongated basal internodes where tiller buds are produced, but was more abundant in the NIL(*PROG1*) compared with Teqing (**Fig. 4c**). Quantitative real-time PCR data further confirmed that the expression of *PROG1* in NIL(*PROG1*) was higher than that in Teqing at the unelongated basal internodes (**Supplementary Fig. 2** online). On the other hand, the expression of *PROG1* was very low in matured leaves and roots of both NIL(*PROG1*) and Teqing (**Supplementary Fig. 3** online). These results led us to suggest that the identified mutations in the promoter region might not affect the spatial mRNA expression pattern of *PROG1*, but might affect only the quantitative variation in mRNA expression at the unelongated basal internodes. A previous study has also reported that mutations in the promoter region of *sh4*, another gene associated with rice domestication, affect the quantitative variation in *sh4* expression, which was higher in wild rice than in cultivated rice, although an amino acid substitution in the sh4 protein primarily controlled grain shattering[9]. In our study, the

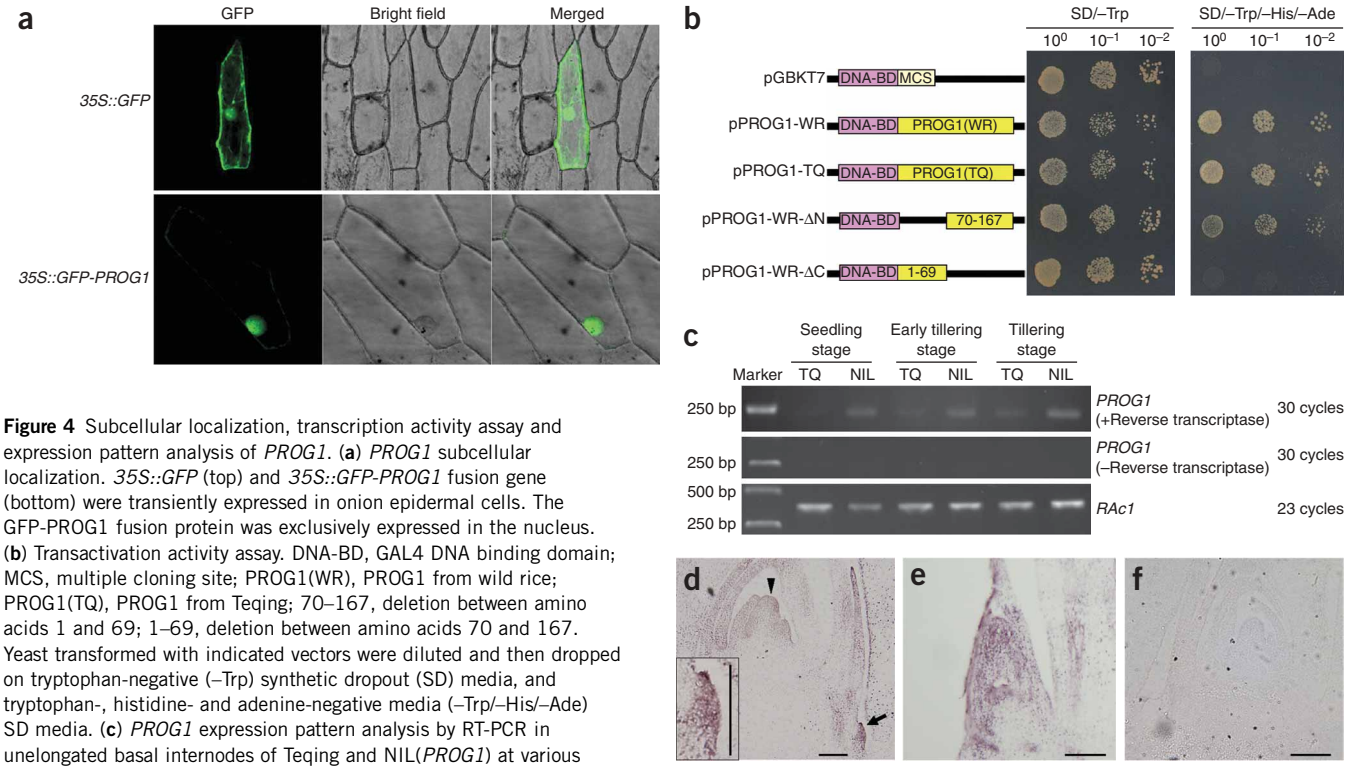

Figure 4 Subcellular localization, transcription activity assay and expression pattern analysis of *PROG1*. (**a**) *PROG1* subcellular localization. *35S::GFP* (top) and *35S::GFP-PROG1* fusion gene (bottom) were transiently expressed in onion epidermal cells. The GFP-PROG1 fusion protein was exclusively expressed in the nucleus. (**b**) Transactivation activity assay. DNA-BD, GAL4 DNA binding domain; MCS, multiple cloning site; PROG1(WR), PROG1 from wild rice; PROG1(TQ), PROG1 from Teqing; 70–167, deletion between amino acids 1 and 69; 1–69, deletion between amino acids 70 and 167. Yeast transformed with indicated vectors were diluted and then dropped on tryptophan-negative (–Trp) synthetic dropout (SD) media, and tryptophan-, histidine- and adenine-negative media (–Trp/–His/–Ade) SD media. (**c**) *PROG1* expression pattern analysis by RT-PCR in unelongated basal internodes of Teqing and NIL(*PROG1*) at various stages. TQ, Teqing; NIL, NIL(*PROG1*); Reverse transcriptase (Rever Tra Ace, ToYoBo, Japan). RAc1 (actin) was used as a control. (**d**,**e**) Expression of *PROG1* at early tillering stage is detected by *in situ* hybridization with an antisense probe. (**d**) The mRNA hybridization signals are detected in axillary meristem (close-up inset of right corner), as well as in the shoot apical meristem (SAM) and developing leaves (young leaves). Arrow and triangle show axillary meristem and SAM, respectively. (**e**) The strong expression of *PROG1* is maintained in a matured tiller bud. (**f**) A negative control using the sense probe. Scale bars, 100 μm.

quantitative differences in *PROG1* expression might be a result of selection in the regulatory region of the gene for a minor adjustment of the plant architecture. A comparison of *PROG1* expression among diverse wild-rice accessions and rice cultivars in future studies will provide further insights into the genetic basis for finer adjustment of plant architecture during rice domestication.

To determine the expression pattern of *PROG1*, we carried out an RNA *in situ* hybridization experiment (**Fig. 4d–f**). We found that transcripts of *PROG1* predominantly accumulated in the axillary meristems (the site of tiller bud formation), as well as in the shoot apical meristem (SAM) and the developing leaves (young leaves) (**Fig. 4d**). The strong expression of *PROG1* was maintained throughout the entire tiller bud (**Fig. 4e**). Such expression pattern of *PROG1* is consistent with its role in the control of plant architecture.

Previous studies have cloned domestication-related genes and found mutations in regulatory genes that are responsible for marked morphological improvements during maize and tomato domestication[20–26]. *Teosinte branched1* (*tb1*) is thought to be a key gene in the domestication of maize plant architecture. Alterations in its regulatory region, but not coding region, brought about the change from wild Mexican grass (teosinte) to the maize plant architecture in maize domestication[20,21]. Here we show that *PROG1* is a key domestication-related gene involved in rice plant architecture. Alteration in the *PROG1* coding region led to the transition from the plant architecture of wild rice to that of cultivated rice in rice domestication. The map-based cloning and molecular characterization of *PROG1* not only shed light on plant development and evolution, but also provide an opportunity to optimize crop plant architecture by molecular design and improve grain yield in future crop breeding.

METHODS

Plant materials. We constructed a set of chromosome segment substitution lines (CSSLs) from repetitive backcross progeny derived from a cross between Teqing (*O. sativa* L. ssp. *indica* variety) as the recurrent parent and wild rice (*O. rufipogon*) as the donor parent (obtained from Hainan province, China) using marker-assisted selection (MAS)[12]. We selected a CSSL (No. 68) to backcross with Teqing and obtained F_1 plants. The resulting F_1 were selfed to produce a large F_2 population for fine mapping. A NIL(*PROG1*) with a very small wild-rice chromosomal segment containing the *PROG1* locus in the Teqing genetic background was developed from the BC_4F_2 generation.

Fine mapping of *PROG1*. We used the F_2 (BC_3F_2) population segregating for the *PROG1* region to fine map *PROG1*. Phenotypic evaluation of *PROG1* in selected recombinants was confirmed using the F_3 progeny. To further determine the location of the recombinations nearest *PROG1*, we developed markers on the basis of the PAC clone (AP005632) sequence and determined genotypes of the recombinants using these markers (**Supplementary Table 1** online). The candidate *PROG1* gene from Teqing and wild-rice genomic DNA were sequenced and compared.

Vector construction and complementation test. We created a complementation construct by PCR amplification of a 2.677-kb DNA fragment containing the *PROG1* promoter region (1.577-kb sequence before ATG), the entire ORF (0.504 kb) and the 3′-untranslated region (0.596-kb sequence after TAG) from wild-rice genomic DNA. The DNA fragment was inserted into the pMD18-T vector (TaKaRa, Japan) and subsequently subcloned into the binary vector pCAMIA1301 *Pst*I-*Kpn*I site. The primer sequences are listed in **Supplementary Table 2** online. The two mutants (M5 and M6) were obtained using the

site-directed mutagenesis method. We generated the mutants by amplification of the pMD18-T vector (TaKaRa, Japan) inserted with a 2.679-kb Teqing DNA fragment, including *PROG1*, using primers designed with mutated nucleotides (**Supplementary Table 2**). PCR products were digested with *Dpn* I and then transformed into *E. coli* strain DH5α. The *PROG1* mutated sequences were subcloned into the pCAMIA1301 vector *Pst*I-*Kpn*I site for transformation. We confirmed all resultant constructs by sequencing and then transformed them into the *japonica* variety Zhonghua 11 using an *Agrobacterium*-mediated method as previously described[27].

Subcellular localization. Subcellular localization of *PROG1* was determined using the coding sequence of a green fluorescent protein (GFP) fused in-frame to the *PROG1* coding sequence of wild rice and transcribed from a 35S promoter. The resulting plasmid was bombarded into onion epidermal cells using a helium biolistic device (Bio-Rad PDS-1000). We examined bombarded tissues with a confocal laser-scanning microscope (Carl Zeiss LAM510). The primer sequences are listed in **Supplementary Table 2**.

Transactivation activity assay. We carried out the transactivation activity assay using the Matchmaker GAL4 Two-Hybrid System 3 (Clontech). To construct pPROG1, pPROG1ΔN$_{1\text{-}69}$ and pPROG1ΔC$_{70\text{-}167}$, the full-length coding sequence and the N-terminal and C-terminal deletions of *PROG1* were amplified by PCR. The PCR products were digested with *Eco*RI and *Pst*I and cloned into pGBKT7 to fuse to the GAL4 binding domain. We transformed all vectors into yeast strain AH109. The yeast colonies were diluted to an OD_{600} of 0.5, serially diluted and dropped on either tryptophan-negative synthetic dropout media or tryptophan-, histidine- and adenine-negative synthetic dropout media.

RNA extraction, RT-PCR and quantitative real-time PCR. We extracted total RNA from Teqing and NIL(*PROG1*) plant tissues at various stages using TRIzol (Invitrogen) reagent. RNA was converted into first-strand cDNA, and RT-PCR was carried out to amplify the *PROG1* transcripts with 30 PCR cycles using the first-strand cDNA as the template. Actin was amplified as the control. Quantitative real-time PCR was performed on ABI 7500 (Applied Biosystems) using SYBR Green. We conducted data analysis following the previously reported method[28]. The sequences of the primers are listed in **Supplementary Table 2**.

***In situ* hybridization experiment.** We synthesized the sense and antisense probes with T3 and T7 RNA polymerase from an 253-bp unique sequence from the *PROG1* cDNA clone. Tissue fixation and RNA *in situ* hybridization were carried out essentially as described previously[29,30]. The primer sequences are listed in **Supplementary Table 2**.

Accession codes. GenBank: *PROG1*, FJ155665; *RBE*, NP_568161.1; *SUP*, NP_188954.1; *ZFP4*, NP_176788.1; *ZFP5*, NP_172518.1.

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

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AUTHOR CONTRIBUTIONS

H.-X.L. designed the experiments. J.J. performed most of the experiments. W.H., J.-P.G., J.Y., M.S., M.-Z.Z., D.L. and H.-X.L. performed some of the experiments. H.-X.L. wrote the manuscript.

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1. Oka, H.I. *Origin of Cultivated Rice* (Japan Scientific Society Press, Tokyo, 1988).
2. Chang, T.T. in *Evolution of Crop Plants* 2nd edn. (eds. Smartt, J. & Simmonds, N.W.) Rice: *Oryza sativa* and *Oryza glaberrima* (*Gramineae-Orzeae*) 147–155 (Longman Scientific and Technical, Essex, UK, 1995).
3. Khush, G.S. Origin, dispersal, cultivation and variation of rice. *Plant Mol. Biol.* **35**, 25–34 (1997).
4. Sharma, S.D., Tripathy, S. & Biswal, J. in *Rice Breeding and Genetics: Research Priorities and Challenges* (ed. Nanda, J.S.) 349–369 (Science Publications, Enfield, New Hampshire, 2000).
5. Kovach, M.J., Sweeney, M.T. & McCouch, S.R. New insights into the history of rice domestication. *Trends Genet.* **23**, 578–587 (2007).
6. Vaughan, D.A., Morishima, H. & Kadowaki, K. Diversity in the *Oryza* genus. *Curr. Opin. Plant Biol.* **6**, 139–146 (2003).
7. Cheng, C. *et al.* Polyphyletic origin of cultivated rice: based on the interspersion pattern of SINEs. *Mol. Biol. Evol.* **20**, 67–75 (2003).
8. Vitte, C., Ishii, T., Lamy, F., Brar, D. & Panaud, O. Genomic paleontology provides evidence for two distinct origins of Asian rice (*Oryza sativa* L.). *Mol. Genet. Genomics* **272**, 504–511 (2004).
9. Li, C., Zhou, A. & Sang, T. Rice domestication by reducing shattering. *Science* **311**, 1936–1939 (2006).
10. Konishi, S. *et al.* An SNP caused loss of seed shattering during rice domestication. *Science* **312**, 1392–1396 (2006).
11. Sweeney, M.T., Thomson, M.J., Pfeil, B.E. & McCouch, S. Caught red-handed: Rc encodes a basic helix-loop-helix protein conditioning red pericarp in rice. *Plant Cell* **18**, 283–294 (2006).
12. Hao, W., Jin, J., Sun, S.Y., Zhu, M.Z. & Lin, H.X. Construction of chromosome segment substitution lines carrying overlapping chromosome segments of the whole wild rice genome and identification of quantitative trait loci for rice quality. *J. Plant Physiol. Mol. Biol.* **32**, 354–362 (2006).
13. Ren, Z.H. *et al.* A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nat. Genet.* **37**, 1141–1146 (2005).
14. Li, P.J. *et al. LAZY1* controls rice shoot gravitropism through regulating polar auxin transport. *Cell Res.* **17**, 402–410 (2007).
15. Yu, B. *et al. TAC1*, a major quantitative trait locus controlling tiller angle in rice. *Plant J.* **52**, 891–898 (2007).
16. Miller, J., McLachlan, A.D. & Klug, A. Repetitive zinc-binding domains in the protein transcription factor IIIA from *Xenopus* oocytes. *EMBO J.* **4**, 1609–1614 (1985).
17. Wolfe, S.A., Nekludova, L. & Pabo, C.O. DNA recognition by Cys2His2 Zinc finger proteins. *Annu. Rev. Biophys. Biomol. Struct.* **29**, 183–212 (2000).
18. Sakamoto, H. *et al. Arabidopsis* Cys2/His2-type zinc-finger proteins function as transcription repressors under drought, cold, and high-salinity stress conditions. *Plant Physiol.* **136**, 2734–2746 (2004).
19. Lin, R. *et al.* Transposase-derived transcription factors regulate light signaling in *Arabidopsis*. *Science* **318**, 1302–1305 (2007).
20. Doebley, J., Stec, A. & Hubbard, L. The evolution of apical dominance in maize. *Nature* **386**, 485–488 (1997).
21. Wang, R.L., Stec, A., Hey, J., Lukens, L. & Doebley, J. The limits of selection during maize domestication. *Nature* **398**, 236–239 (1999).
22. Frary, A. *et al.* fw2.2: a quantitative trait locus key to the evolution of tomato fruit size. *Science* **289**, 85–88 (2000).
23. Liu, J., Van Eck, J., Cong, B. & Tanksley, S.D. A new class of regulatory genes underlying the cause of pear-shaped tomato fruit. *Proc. Natl. Acad. Sci. USA* **99**, 13302–13306 (2002).
24. Wang, H. *et al.* The origin of the naked grains of maize. *Nature* **436**, 714–719 (2005).
25. Doebley, J.F., Gaut, B.S. & Smith, B.D. The molecular genetics of crop domestication. *Cell* **127**, 1309–1321 (2006).
26. Cong, B., Barrero, L.S. & Tanksley, S.D. Regulatory change in YABBY-like transcription factor led to evolution of extreme fruit size during tomato domestication. *Nat. Genet.* **40**, 800–804 (2008).
27. Hiei, Y., Ohta, S., Komari, T. & Kumashiro, T. Efficient transformation of rice (*Oryza sativa* L.) mediated by *Agrobacterium tumeficience* and sequence analysis of the boundaries of the T-DNA. *Plant J.* **6**, 271–282 (1994).
28. Pfaffl, M.W. A new mathematical model for relative quantification in real-time RT-PCR. *Nucleic Acids Res.* **29**, e45 (2001).
29. Coen, E. *et al.* Floricaula: a homeotic gene required for flower development in *Antirrhinum majus*. *Cell* **63**, 1311–1322 (1990).
30. Li, X. *et al.* Control of tillering in rice. *Nature* **422**, 618–621 (2003).