Glabrous Rice 1, encoding a homeodomain protein, regulates trichome development in rice

Jinjun Li1†, Yundong Yuan2†, Zefu Lu2, Liusha Yang2, Rongcun Gao1, Jingen Lu1, Jiayang Li2 and Guosheng Xiong2*

Abstract
Background: Glabrous rice, which lacks trichomes on the rice epidermis, is regarded as an important germplasm resource in rice breeding. Trichomes are derived from aerial epidermal cells and used as a model to study the cell fate determination in plant. In Arabidopsis, the molecular mechanisms of trichome development have been well studied. However, little is known about the molecular basis of trichome development in rice.

Results: In this study, near isogenic lines harboring the glabrous rice 1 locus were developed. By a map-based approach, we narrowed down the locus to a 21-kb DNA region harboring two genes. One of the genes named Glabrous Rice 1 (GLR1), which is most likely the candidate, encodes a homeodomain protein containing the WOX motif. Constitutive Expression of GLR1 could partially complement the glabrous phenotype of NIL glr1. The knock down of GLR1 by RNA interference led to a significant decrease in trichome number on the leaves and glumes of the RNAi transgenic plants.

Conclusion: GLR1 plays an important role in rice trichome development and will contribute to breeding of glabrous elite rice varieties.

Keywords: Glabrous rice, Trichome development, WOX protein

Background
The glabrous feature of rice is considered as a favorite agronomic trait for rice farmers because it has greater packing capability of rice grains and produces less dust that causes itching effect on farmers. Glabrous rice lacks trichomes on leaves and glumes (Khush et al. 2001). Most rice cultivars in America are glabrous and recognized as an important germplasm resource in breeding due to its high yield, good quality, and wide compatibility in crossing with other rice varieties (Guo et al. 1999, Luo et al. 2000). Trichomes are derived from aerial epidermal cells and serve various protective purposes such as insect herbivore resistance, freezing tolerance, and shade of UV irradiation (Ishida et al. 2008). So far, a number of glabrous mutants have been identified in many plant species, including Arabidopsis, tomato, cotton, and maize (Machado et al. 2009, Moose et al. 2004, Rerie et al. 1994, Yang et al. 2011). However, the molecular mechanism underlying trichome development has only been intensively investigated in Arabidopsis.

In Arabidopsis, trichome development has been used as a model system to study the cell fate determination and shown to be regulated by a complex gene network (Ishida et al. 2008). A homeodomain-leucine zipper protein GLABRA2 (GL2) and an R3 Myb protein TRIPYCHON (TRY) play essential roles in trichome initiation and hairless cell differentiation (Rerie et al. 1994, Schellmann et al. 2002). The expression of GL2 and TRY are regulated by the WD-repeat/bHLH/MYB complex including TRANSPARENT TESTA GLABRA1 (TTG1), GLABRA3 (GL3)/ENHANCER OF GLABRA3 (EGL3) and GLABRA1 (GL1). Epidermal cells expressing the GL2 protein are able to differentiate into trichome cells. The TRY protein expressed in trichome cells, however, can move into neighboring cells and compete with GL1 for binding to GL3/EGL3 to repress the GL2 expression. The TRY mediated down regulation of the GL2
expression inhibits trichome formation in neighboring cells (Ishida, et al. 2008). Actually, factors able to modulate this gene network affect the trichome development. Previous studies on mutants defective in the biosynthesis and/or signaling of gibberellins, salicylic acid, jasmonic acid, and cytokinin have shown that phytohormones are involved in trichome initiation (Gan et al. 2006, Gan et al. 2007b, Perazza et al. 1998, Traw and Bergelson 2003, Zhou et al. 2011). It has been turned out that roles of these phytohormones in trichome development are mediated by their effect on the expression or activity of the components of the WD-repeat/bHLH/MYB complexes. Roles of gibberellins and cytokinins in trichome initiation are mainly dependent on C2H2 transcription factors including GIS1, GIS2, ZFP5 and ZFP8. These transcription factors are able to promote the GL1 expression (Gan et al. 2007a, Maes et al. 2008, Perazza, et al. 1998, Zhou, et al. 2011). In addition, JAZ proteins, the key components in the JA signaling pathway, have been shown to interact with bHLH transcription factors (GL3, EGL3 and TT8) and MYB transcription factors (MYB75 and GL1) (Qi et al. 2011). The JA-induced destruction of JAZ proteins results in releasing the transcriptional function of the WD-repeat/bHLH/MYB complex and activating downstream events of trichome initiation. Furthermore, recent studies have shown that the microRNA156 targeted gene SPL9 could bypass the function of GL1 and directly binds to promoters of TCL1 and TRY to activate their expression (Yu et al. 2010).

In contrast to the sophisticated mechanisms revealed in Arabidopsis, little is known about the molecular mechanisms of trichome development in other plants. It has been noted that a couple of homeodomain-leucine zipper proteins, which are specifically expressed in epidermal cells, are essential in differentiation of epidermal cells. Outer Cell Layer 4 (OCLA), a maize HD-ZIP transcription factor, has been suggested to involve in the repression of macrohair differentiation (Vernoud, et al. 2011). In addition, another subfamily of the homeobox gene, known as WUS-like homeobox genes (WOX), may also play roles in division or differentiation of epidermal cells. Pressed Flower (PRS) is involved in activation of the proliferation of marginal cells. It has been observed that multicellular bulges with trichomes formed on stems and epidermal cells outgrow on sepal of 3SS:PRS transgenic plants (Matsumoto and Okada 2001). Moreover, Narrow sheath 1 (NS1) and Narrow sheath 2 (NS2), which are duplicated relatives of PRS in maize, have been suggested to play a role in a lateral domain of shoot apical meristems (Nardmann et al. 2004). In addition, OsWOX3 has been found to repress the expression of OsYAB3, which is required for cell differentiation during rice leaf development (Dai et al. 2007).

Previous study showed that macrohairs on the leaf blade are greatly reduced in the maize macrohairless 1 (mhl1) mutant (Moose, et al. 2004). A major QTL controlling macrohairs in Teosinte has been found to locate near the maize gene MHL1 (Lauter et al. 2004). In rice, previous genetic analysis has identified a couple of loci that control trichome development. For example, gl may regulate glabrous leaf and hull traits, Hl, and Hl could be related to long hair development on rice leaves and Hg may be responsible for the extreme long hairs on auricles and glumes (Nagao et al. 1960). However, no gene controlling these traits has been cloned in rice as yet. Recently, glabrous leaf and hull mutant (gl1) has been reported to locate within a 54-kb region at the short arm of chromosome 5 (Li et al. 2010, Wang et al. 2009, Yu et al. 1995), but the gene has not been identified yet.

Here, we report the identification and characterization of the Glabrous Rice 1 (GLR1), which controls the trichome development in rice. Our work extends an insight into the molecular mechanism of trichome development in rice. The identification and characterization of GLR1 will facilitate breeders to develop elite glabrous rice varieties via marker-assisted-selection and genetic modification approaches.

Results
Phenotype of the near isogenic line of glabrous rice
The glabrous variety Jia64 is derived from the American rice variety Rico No.1 and near isogenic lines (NIL) of glabrous rice developed by backcrossing Jia64 with a pustulent variety Jia33 for 5 generations. There are no obvious differences of the overall morphology between NIL GLR1 and NIL glr1 plants (Figure 1a). However, the leaves of NIL glr1 plants are smooth whereas leaves of NIL GLR1 plants are rough with many hairs. In contrast to glumes of the NIL GLR1 plant (Figure 1b), the glumes of the NIL glr1 plant showed no trichome or only a few trichomes growing on margins of the hull (Figure 1c). On rice leaves, there are two types of trichomes, macrohairs and microhairs. Scan Electronic Microscope (SEM) analysis showed that both macrohairs and microhairs on the abaxial and adaxial sides of NIL GLR1 leaves are able to be observed (Figure 1d and Figure 1e). However, neither macrohairs nor microhairs could be observed on both sides of NIL glr1 leaves (Figure 1f and Figure 1g).

Map-based cloning of GLR1
Previous genetic analysis has shown that the glabrous phenotype of America rice was controlled by a single recessive nuclear gene (Li et al. 1993). To map the GLR1 locus, an F2 mapping population was generated from a cross
between Jia64 and a polymorphic *japonica* variety Jia33. Linkage analysis of 44 F$_2$ plants having the glabrous phenotype showed that the GLR1 locus located between the InDel marker M1 and the SSR marker M2 on chromosome 5 (Figure 2a and Table 1). This region is consistent with the previously mapped gl1 locus on the short arm of chromosome 5 (Li, et al. 2010, Wang, et al. 2009). To fine-map GLR1, 1,447 F$_2$ glabrous plants were analyzed using 7 newly developed markers (Figure 2b and Table 1) and GLR1 was finally pinpointed within an interval of 21-kb DNA fragment between the markers M6 and M7. Within this region, there are 2 predicted genes, LOC_Os05g02720 (Os05g0118600) and LOC_Os05g02730 (Os05g0118700) (Figure 2c). The former encodes a hypothetic protein and the latter encodes a homeobox-containing protein. Sequence analysis showed that LOC_Os05g02730 shares similarity to PRS in *Arabidopsis*, NS1 and NS2 in maize, and OsWOX3 in rice (Dai, et al. 2007, Matsumoto and Okada 2001, Nardmann, et al. 2004). There are a conserved homeodomain at the N terminal and a conserved WOX motif at the C terminal of these proteins (Figure 3). Phylogenetic analysis indicated that LOC_Os05g02730 belongs to a small NS/WOX3 subgroup consisting of OsWOX3, PRS, NS1 and NS2 (Dai, et al. 2007). We sequenced and compared the 21-kb DNA fragments between markers M6 and M7 from the NIL$_{GLR1}$ and NIL$_{glr1}$. There is no difference in this region between NIL$_{GLR1}$ and NIL$_{glr1}$ plants. To understand which gene, LOC_Os05g02720 or LOC_Os05g02730, is responsible for the phenotype, we analyzed their expression levels by RT-PCR. Compare to NIL$_{GLR1}$, the expression level of LOC_Os05g02720 decreased in the NIL$_{glr1}$ plant (Figure 2d). However, the expression of LOC_Os05g02730 was dramatically reduced in the NIL$_{glr1}$ plant (Figure 2d). The previous studies showed that the NS/WOX3 subgroup
Figure 2 Map-based cloning of GLR1. (a) The GLR1 locus was mapped in chromosome 5 between markers M1 and M2. Recombinants were identified from 1,447 F2 glabrous plants. (b) Fine mapping of the GLR1 locus. The GLR1 locus was narrowed to a 21-kb genomic DNA region between markers M6 and M7. (c) The LOC_Os05g02720 (green) and LOC_Os05g02730 (red) are predicted in the candidate region. The annotated gene of LOC_Os05g02730 consists of two exons and one intron. (d) The relative expression levels of LOC_Os05g02720, LOC_Os05g02730 and LOC_Os05g02754 in young panicles of NILGLR1 and NIGLR1 plants (T-test, P<0.05).

| Primer | Primer sequence(5’-3’) | Primer types | Genetic distance(cm) |
|--------|-------------------------|--------------|----------------------|
| M1     | TGGTTATTTGTTATTTTAGTTGGGTG | InDell       | 1.38                 |
|        | TGGTTATTTGTTATTTTAGTTGGGTG | Reverse      | 1.38                 |
| M2     | ACGCACGCCATTACAAAC       | SSR          | 0.44                 |
|        | ACGCACGCCATTACAAAC       | Reverse      | 0.44                 |
| M3     | ACGACCCACCAGCAGATA       | InDell       | 9.43                 |
|        | ACGACCCACCAGCAGATA       | Reverse      | 9.43                 |
| M4     | GCCCTTGATCAGGCGGCTCT     | InDell       | 1.07                 |
|        | GCCCTTGATCAGGCGGCTCT     | Reverse      | 1.07                 |
| M5     | GGGGAGCTCTTGGTCGG        | InDell       | 0.10                 |
|        | GGGGAGCTCTTGGTCGG        | Reverse      | 0.10                 |
| M6     | GTAGTAGTAGAGAGACACAGC    | InDell       | 0.07                 |
|        | GTAGTAGTAGAGAGACACAGC    | Reverse      | 0.07                 |
| M7     |AACAAATCCCTCCTGGTTCC | CAPS         | 0.07                 |
|        |AACAAATCCCTCCTGGTTCC | Reverse      | 0.07                 |
| M8     | ATGGACTGCCACATTTTCT     | InDell       | 0.07                 |
|        | ATGGACTGCCACATTTTCT     | Reverse      | 0.07                 |
| M9     | CTAGGACGTGACCTGTGAAT    | InDell       | 0.07                 |
|        | CTAGGACGTGACCTGTGAAT    | Reverse      | 0.07                 |
| M10    | TCTGGTTGTTGATTAGT       | InDell       | 0.04                 |
|        | TCTGGTTGTTGATTAGT       | Reverse      | 0.04                 |
WOX genes are specifically expressed in the epidermal cells and play important roles in their differentiation (Dai et al., 2007; Ishida et al., 2008; Matsumoto and Okada, 2001; Nardmann et al., 2004; Vernoud et al., 2009). Therefore, LOC_Os05g02730 is most likely the candidate gene responsible for the rice glabrous phenotype.

Altering the expression levels of GLR1 could partially change the glabrous phenotype

To confirm LOC_Os05g02730 is the GLR1 gene, we generated transgenic plants in a pubescent japonica variety Nipponbare background by the RNA interference (RNAi) method (Figure 4a). SEM analysis showed that much fewer trichomes on leaves of the RNAi transgenic lines have been observed (Figure 4b), and a further statistical analysis showed that the macrohair number on the RNAi transgenic leaves was significantly decreased (Figure 4c). When constitutively express GLR1 in NIL_{glr1}, it can partially rescue glabrous phenotype of NIL_{glr1} of T0 transgenic plants (Figure 4 d-g). These results indicate that LOC_Os05g02730 is the gene responsible for the glabrous phenotype of the NIL_{glr1} plant.

DNA methylation may be involved in the expression of GLR1

The findings that no mutation was found in the GLR1-containing mapping region and that the expression of LOC_Os05g02730 was unable to be detected in the NIL_{glr1} plant strongly suggests that GLR1 may be regulated epigenetically through a DNA methylation mechanism. We therefore carried out a bisulfite sequencing experiment to examine whether DNA methylation are involved in the regulation of GLR1. As shown in Figure 5, the bisulfite sequencing of the 2.0-kb promoter region of GLR1 revealed some apparent methylation differences between NIL_{glr1} and NIL_{GLR1}, suggesting that an epigenetic mechanism may involve in the regulation of the GLR1 expression.

Discussion

In Arabidopsis, trichomes have been served as an excellent model system to study plant cell differentiation (Ishida et al. 2008). Glabrous mutants that are defective in leaf hair or trichome have been identified in many plant species. However, genes controlling trichome development in rice have not been identified up to date yet. GL1 was previously mapped on the short arm of chromosome 5 (Li, et al. 2010, Wang et al. 2009, Yu et al. 1995) and it was proposed that a single nucleotide mutation (A to T) in the 5’UTR of LOC_Os05g02754 (Os05g0118900), which encode an unknown protein, might be responsible for the gl1 trait (Li, et al. 2010). Our mapping data suggested that glr1 may be allelic to gl1. We compared the sequences of 5’UTR of LOC_Os05g02754 (Os05g0118900) of NIL_{GLR1} and NIL_{glr1} and found that the indicated position of 5’ UTR of LOC_Os05g02754 (Os05g0118900) in the NIL_{GLR1} plant is A and that in the NIL_{glr1} plant is T. However, our data indicate that instead of LOC_Os05g02754 (Os05g0118900)
LOC_Os05g02730 (Os05g0118700), which encode a WUS-like homeodomain protein, controls the glabrous phenotype. First, the mapping data has pinpointed the GLR1 locus within a 21-kb region that contains only two predicted genes, LOC_Os05g02720 (Os05g0118600) and LOC_Os05g02730 (Os05g0118700). Second, comparison of the gene expression levels of LOC_Os05g02720 and LOC_Os05g02730 between NIL\textsuperscript{GLR1} and NIL\textsuperscript{glr1} plants showed that LOC_Os05g02730 is dramatically increased in the NIL\textsuperscript{glr1} plant, however, change of LOC_Os05g02720 in the NIL\textsuperscript{glr1} plant is not very significant. In contrast, no difference of expression levels of LOC_Os05g02730 has been detected between NIL\textsuperscript{GLR1} and NIL\textsuperscript{glr1} plants (Figure 2d). Third, an apparent decrease in the trichome number on leaves and glumes of GLR1 RNAi transgenic plants have been obtained. Overexpression of GLR1 in NIL\textsuperscript{glr} partially rescues glabrous phenotype of the NIL\textsuperscript{glr1} plant. Fourth, the sequence alignment showed that GLR1 has high
similarity to previously identified homeodomain proteins, whose functions are essential for the differentiation of epi-
dermal cells (Dai, et al. 2007, Matsumoto and Okada 2001, 
Nardmann, et al. 2004). Taken all these together, we 
strongly suggest that the WUS-like homeodomain protein 
encoded by LOC_Os05g02730 is the GLR1 gene and is es-
sential for the trichome development in rice.

The RNAi of GLR1 reduced the trichome number in 
transgenic lines, while the trichome is almost completely 
lost in NILglr1. This discrepancy could result from the 
different genetic background of plant materials or from 
incomplete suppression of the target gene in transgenic 
plants. Alternatively, the expression LOC_Os05g02720 is 
also decreased in the NILglr1 plant, which implies that 
LOC_Os05g02720 may be also involve in trichome develop-
ment, thus knockdown of LOC_Os05g02730 alone cannot 
completely suppress the trichome development. Further knockdown 
LOC_Os05g02720 along or knock-
down it together with LOC_Os05g02730 will clarify the 
role of LOC_Os05g02720.

Chromatin state controls gene expression and plays crit-
ical roles in development. In plant, trimethylated K9 of 
histone H3 (H3K9me3) indicates an open chromatin 
state, while monomethylated and dimethylated H3K9s 
(H3K9me1 and H3K9me2) indicate a closed state (Liu et al. 
2010). The identification of GL2 EXPRESSION MODULA-
TOR (GEM) indicates that the regulation of GL2 expres-
sion is more complicated than previously expected 
(Caro, et al. 2007). Trichome density increased in gem-1 
mutant whereas decrease in GEM-overexpressing plants 
(Caro, et al. 2007). It has been observed that H3K9me3 increases and H3K9me2 decreases 
in the GL2 promoter in the gem-1 background, but 
H3K9me3 decreases and H3K9me2 increases in GEM-
overexpressing plants (Caro, et al. 2007). This kind of epi-
getic control may also be involved in rice trichome 
development. Rice SET Domain Group Protein 714 (SDG714) 
functions as a histone H3K9 methyltransferase, which is 
involved in histone H3K9 methylation, DNA methylation 
and genome stability (Ding et al. 2007). Loss of macrohairs 
but not microhairs on leaves of the SDG714 RNAi trans-
genic plants indicated that regulation of chromatin status 
of some unidentified regulators may play an important role 
in the trichome development in rice (Ding et al. 2007). In 
agreeable to these findings, the genomic bisulfite sequen-
cing of GLR1 showed that the DNA methylation pattern at 
several sites of the GLR1 promoter region in the NILglr1 
plants is different from that in the NILGLR1 plants, though 
no sequence difference of GLR1 was found between the 
NILGLR1 and NILglr1 plants. These results indicated that the epigenetic mechanism may be involved in the regula-
tion of the GLR1 expression and the trichome develop-
ment in rice. Although, different patterns of the DNA 
methylation in upstream region of LOC_Os05g02730 
(OS05g0118700) between NILGLR1 and NILglr1 has been 
observed, we are unable to determine which sites are re-
sponsible for suppression of LOC_Os05g02730. Moreover, 
the GLR1 expression driven by a constitutive promoter

Figure 5 Comparison of the DNA methylation between NILGLR1 and NILglr1. DNA methylation levels (%) of the GLR1 and glr1 DNA sequences 
of the NILGLR1 (red) and NILglr1 (blue) plants are analyzed. The numbers indicate the position in the 2-kb upstream region starting from the start 
codon.
dramatically increased the expression of GLR1, but cannot completely rescue the glabrous phenotype in T0 transgenic plants (Figure 4 d-g). It indicates that the regulation of the GLR1 expression and the trichome development in rice is more complicated than expected. Further investigation is needed to uncover the molecular mechanism of GLR1 expression regulation.

Glabrous rice varieties are widely cultivated in America and Africa, while most varieties cultivated in Asia are pubescent (Khush, et al. 2001). In higher plants, although trichomes are thought to be important for plant defense against biotic and abiotic stresses, glabrous trait may be a selectively neutral trait in rice. Previous studies have indicated that the introduction of glabrous trait into japonica varieties may not cause any obvious disadvantages in plant defense (Li et al. 2011). In agriculture, the interest of breeding glabrous elite rice varieties is mainly due to its practical advantages of greater packing capability and less itching effect during the harvest process. The cloning of GLR1 will not only help to understand the molecular mechanism of trichome development in rice but also improve the efficiency of breeding glabrous elite rice varieties by marker-assisted selection and genetic modification approaches.

Conclusions
GLR1 plays an important role in rice trichome development and will contribute to breeding of glabrous elite rice varieties

Methods
Plant materials
Jia64 is a glabrous variety derived from American rice variety Rico No.1 and Jia33 is a pubescent variety in southeast China. Rice plants were cultivated in the experimental field of Jiaxing Academy of Agricultural Science in growing seasons from May to October.

Scanning electron microscopy
Samples were prepared as described previously (Li et al. 2009). Briefly, samples were fixed with 2.5% (v/v) glutaraldehyde in 0.1 M sodium phosphate buffer (PBS, pH 7.2) at 4°C overnight. After being rinsed with 0.1 M PBS twice, samples were post-fixed in 1% (w/v) osmium tetroxide for 2 h at 4°C. Samples were rinsed with the same buffer for 2 more times and then dehydrated in a graded series of ethanol. For scanning electron microscopy, samples were critical-point dried (Hitachi HCP-2) and observed under a scanning electron microscope (Hitachi S-3000N).

Genetic mapping of GLR1
An F2 mapping population was generated from a cross between Jia64 and Jia33. 24 molecular markers were used for genetic linkage analysis of 44 F2 plants that show the glabrous phenotype. To fine-map GLR1, new PCR-based markers were developed and 1,447 F2 glabrous plants were analyzed using markers as given in Table 1. The GLR1 locus was further narrowed within an interval of 21-kb DNA fragment between the M6 and M7 markers. To sequence the GLR1 locus, the entire genomic region was amplified from NILGLR1 and NILstr by PCR with LA-Taq (TaKaRa).

RNA extraction and reverse transcription-polymerase chain reaction (RT-PCR)
Total RNA was isolated from rice plants by Trizol extraction method (Invitrogen Life Technologies). To conduct RT-PCR analyses, cDNA strands are synthesized by the SuperScript III RT kit (Invitrogen Life Technologies). Real-time PCR analysis were performed using the SYBR Green RT-PCR kit (Biorad). Primers RT1-F and RT1-R were used to amplify LOC_Os05g02720, RT2-F and RT2-R to LOC_Os05g02730 and primers RT3-F and RT3-R to LOC_Os05g02754 (Table 2).

Plasmid construction and rice transformation
To generate the RNAi construct, two DNA fragments RNAi 1-1 and RNAi 1-2 were amplified respectively by primers RNAi 1-1f and RNAi1-1r, RNAi1-2f and RNAi1-2r (Table 2). The construct 1460-RNAi 1-1 was generated by digesting the RNAi 1-1 fragment with BamH I and Kpn I and ligated to the binary vector 1460 by T4 DNA ligases. The hairpin cassette was generated by digesting the RNAi 1-2 fragment with BamH I and Spe I and ligated in reversed direction of fragment RNAi 1-1 to construct 1460-RNAi 1-1. For construction of the overexpression cassette, the coding region of GLR1 was amplified and ligated to the 1460 vector by BamH I and Spe I. The constructs were confirmed by sequencing and introduced into Agrobacterium tumefaciens strain EHA105 by electroporation. The rice (Nipponbare)
transformation was performed as described previously (Hiei et al. 1994). For RNAi transgenic plants, T2 lines derived from individual transgenic lines were used for further analysis. T2 Lines RNAi 4-8-7, RNAi 4-8-11 and RNAi 4-8-17 were derived from line RNAi 4-8. T2 Lines further analysis. T2 Lines RNAi 4-8-7, RNAi 4-8-11 and derived from individual transgenic lines were used for of LOC_Os05g02730 (59104). The candidate 2-kb upstream of the coding region DNA was bisulfite treated using the Bisulfite kit (Qiagen pGEM-T easy vector (Promega) for sequencing.

ME-3F: AAGATTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTTT
Maes L, Inze D, Goossens A (2008) Functional specialization of the TRANSPARENT TESTA GLABRA1 network allows differential hormonal control of laminal and marginal trichome initiation in Arabidopsis rosette leaves. Plant Physiol 148:1453–1464

Matsumoto N, Okada K (2001) A homeobox gene, PRESSED FLOWER, regulates lateral axis-dependent development of Arabidopsis flowers. Genes Dev 15:3355–3364

Moose SP, Lauter N, Carlson SR (2004) The maize macrohairless1 locus specifically promotes leaf blade macrohair initiation and responds to factors regulating leaf identity. Genetics 166:1451–1461

Nagao S, Takahashi M-E, Kinoshita T (1960) Genetical studies on rice plant, XXV: inheritance of threemorphological characters, pubescence of leaves and floral glumes, and deformation of empty glumes. Journal of the Faculty of Agriculture, Hokkaido University, pp 299–314

Nardmann J, Ji J, Werr W, Scalon MJ (2004) The maize duplicate genes narrow sheath1 and narrow sheath2 encode a conserved homeobox gene function in a lateral domain of shoot apical meristems. Development 131:2827–2839

Perazza D, Vachon G, Herzog M (1998) Gibberellins promote trichome formation by up-regulating GLABROUS1 in Arabidopsis. Plant Physiol 117:375–383

Qi T, Song S, Ren Q, Wu D, Huang H, Chen Y, Fan M, Peng W, Ren C, Xie D (2011) The Jasmonate-ZIM-domain proteins interact with the WD-Repeat/ bHLH/MYB complexes to regulate Jasmonate-mediated anthocyanin accumulation and trichome initiation in Arabidopsis thaliana. Plant Cell 23:1795–1814

Reeke WG, Feldmann KA, Marks MD (1994) The GLABRA2 gene encodes a homeo domain protein required for normal trichome development in Arabidopsis. Genes Dev 8:1388–1399

Schellmann S, Kirik SA, V Wada T, Okada K, Beermann A, Thumbahrt J, Jurgens G, Hulskamp M (2002) TRIPTYCHON and CAPRICE mediate lateral inhibition during trichome and root hair patterning in Arabidopsis. EMBO J 21:5036–5046

Traw MB, Bergelson J (2003) Interactive effects of jasmonic acid, salicylic acid, and gibberellin on induction of trichomes in Arabidopsis. Plant Physiol 133:1367–1375

Vernoud V, Laigle G, Rozier F, Meeley RB, Perez P, Rogowsky PM (2009) The HD-ZIP IV transcription factor OCL4 is necessary for trichome patterning and anther development in maize. Plant J 59:883–894

Wang D, Sun S-X, Gao F-Y, Lu X-J, Li Z-H, Ren G-J (2009) Mapping a rice Glabrous gene using simple sequence repeat markers. Rice Sci 16:93–98

Yang C, Li H, Zhang J, Luo Z, Gong P, Zhang C, Li J, Wang T, Zhang Y, Lu Y, Ye Z (2011) A regulatory gene induces trichome formation and embryo lethality in tomato. Proc Natl Acad Sci USA 108:11836–11841

Yu N, Cai WJ, Wang S, Shan CM, Wang L, Chen XY (2010) Temporal control of trichome distribution by microRNA156-targeted SPL genes in Arabidopsis thaliana. Plant Cell 22:2322–2335

Yu ZH, McCouch SR, Tankesley SD, Kinoshita T, Sato S (1995) Association of morphological and RFLP markers in rice (Oryza sativa L.). Genome 38:566–574

Zhou Z, An L, Sun L, Zhu S, Xi W, Broun P, Yu H, Gan Y (2011) Zinc finger protein S is required for the control of trichome initiation by acting upstream of zinc finger protein B in Arabidopsis. Plant Physiol 157:673–682

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