Phenotypic Characterization and Genetic Analysis of Rice with Pubescent Leaves and Glabrous Hulls (PLgh)

Biaolin Hu, Yong Wan, Xia Li, Fantao Zhang, Wengui Yan,* and Jiankun Xie*

ABSTRACT
Pubescence (hairs or trichomes) of leaves is advantageous against biotic and abiotic stress, and that of hulls is disadvantageous as it interferes with field operations, such as harvesting and processing. Previous phenotypic and genotypic studies on rice (Oryza sativa L.) pubescence used materials that had pubescent or glabrous leaves and hulls. From the National Small Grains Collection (NSGC), two accessions with pubescent leaves and glabrous hulls (PLgh) were identified. These PLgh accessions had more, longer, and softer trichomes on the leaves than traditional pubescent materials. Our objective was to study the inheritance of the PLgh trait. Crosses of PLgh plants with a genotype having glabrous leaves and hulls showed that leaf pubescence in the PLgh material was controlled by a dominant gene because no segregation for glabrous hull in F2 generation occurred. Chi-square values for 3:1 pubescent leaf and glabrous hull:glabrous leaf and hull F2 ratio were 0.283 \((P = 0.626) \) and 0.919 \((P = 0.338) \) in two PLgh crosses, Wells × IARI 6184B and Wells × Padi Pohon Batu, respectively. However, in crosses of PLgh with three genotypes (You I B, Rondo, and Xiqingzao B) having pubescent leaves and hulls, an F2 ratio of 12:3:1 pubescent leaf and hull:pubescent leaf and glabrous hull:glabrous leaf and hull was found in most cases, suggesting two genes were involved in the inheritance. Use of the PLgh germplasm (pubescent leaves) in rice breeding should be advantageous as a defense mechanism against biotic and abiotic stresses while avoiding the disadvantages of pubescent hulls in transportation and storage.

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Rice is one of the most important food crops as it feeds more than half of the world’s population (Yu et al., 2002). It is a model monocot for genetic and genomic research (Lee et al., 2011). Improvement of rice cultivars depends on the discovery and use of valuable genes from germplasm collections available in the world.

Trichomes, also called hairs or pubescence, are unicellular or multicellular epidermal structures present on the surface of various plant organs, for example, leaves, hulls (glumes), roots, stems, and flowers (Yu et al., 2010). Rice cultivars are classified as pubescent (trichomes present) or glabrous (trichomes absent). In rice, trichomes on the leaf surface are important for plant development and productivity because they contribute to photosynthesis and are involved in transpiration, respiration, and grain-yield formation (Zhu et al., 2008; Angeles-Shim et al., 2009; Li et al., 2010a). Two types of pubescence are commonly present on the surface of rice
leaves, macro-hair that are located on silica cells over a thin vascular bundle and oriented perpendicular or parallel to the leaf blade and micro-hair that are located beside motor cells or stomata cells and aligned parallel to leaf venation.

Pubescent or hairy hulls of rice are a disadvantage in transportation (Dat et al., 1978; Zhu et al., 2008; Wang et al., 2009a; Li et al., 2010a). Besides their prickly nature, they reduce weight per unit volume vis-à-vis glabrous or smooth hulls. Thus transportation costs are increased.

Glabrous cultivars or mutants have been developed in numerous crop species, including cucumber (Cucumis sativus L.) (Yang et al., 2011), soybean (Glycine max (L.) Merr.) (Hunt et al., 2011), pepper (Capsicum annuum L.) (Kim et al., 2010, 2011), squash (Cucurbita pepo L.) (Xiao and Loy, 2007), Chinese cabbage [Brassica rapa (L.) (Nawab et al., 2011)], and processors. However, pubescent leaves provide allergic reactions and itching caused to handlers (farmers and processors). Further, pubescent leaves provide resistance to biotic stress (insects and diseases) (Zhang et al., 2003; Xu et al., 2002; Kim et al., 2011) and abiotic stress (weather and soil stresses) (Saltveit and Hepler, 2004; Du et al., 2009; Angeles-Shim et al., 2012). Leaf pubescence is reportedly associated with glufosinate herbicide resistance (Zhang et al., 2003), brown planthopper (Nilaparvata lugens Stål) resistance (Xu et al., 2002), and light reflectance and lower transpiration rate (Yoo et al., 2011; Angeles-Shim et al., 2012) in comparison to leaf glabrousness.

So far, five genes, namely two duplicate genes (gl1 and gl2), two complementary genes (Hla and Hlb) that are responsible for long pubescence on leaves, and Hg that is responsible for long pubescence on hulls (Gramene database [http://www.gramene.org/, accessed 7 Jan. 2012] and Oryzabase – Integrated Rice Science Database [http://www.shigen.nig.ac.jp/rice/oryzabase/, accessed 7 Jan. 2012]), have been identified and mapped in rice. These genes are responsible for trichome initiation and morphogenesis, resulting in pubescence or glabrousness of both leaf and hull. Gene gl1 responsible for glabrous leaves and hulls was mapped to the short arm of chromosome (chr.) 5 (Yu et al., 1995; Yoshimura et al., 2001; Wang et al., 2009a). The gl1 is linked to both Nk gene (notched kernel) (Sobrizal and Yoshimura, 2007) and QBphr5a gene (brown planthopper resistance) (Xu et al., 2002). Recently, Li et al. (2010a) fine mapped gl1 to a 54-kb region on chr. 5. Angeles-Shim et al. (2009) also located gl1 gene in a 64-kb region on chr. 5 using chromosome segment substitution lines derived from a cross between O. sativa subsp. japonica Kato ‘Koshihikari’ and Oryza glaberrima Steud. (African cultivated rice).

All the glabrous cultivars in rice have glabrous leaves and hulls; similarly, all the pubescent rice cultivars have pubescent leaves and hulls (Yu et al., 1995; Yoshimura et al., 2001; Rutger and Mackill, 2001; Rutger and Tai, 2005). We discovered rice germplasm that had pubescent leaves and glabrous hulls (PLgh) and conducted initial studies in the United States and completed the research in China. This germplasm with pubescent leaves could be used in breeding programs as a defense mechanism against abiotic and biotic stresses while avoiding the disadvantages of pubescent hulls in transportation. Our objective was to study the inheritance and phenotypically and genotypically characterize the PLgh trait for its potential use in rice breeding programs.

**MATERIALS AND METHODS**

**Germplasm Discovery**

A total of 752 “low inventory” accessions derived from the U.S. National Small Grains Collection (NSGC) were field grown for seed increase at the Dale Bumpers National Rice Research Center (DBNRRRC) near Stuttgart, AR, in 2009. An accession becomes low inventory when the seed stock is 50 g or less in the NSGC. Because all 752 accessions had red pericarp and because of concerns that the red pericarp rice could contaminate rice fields, their seed was increased in the field in an isolated area. During phenotyping and harvesting,
the accession IARI 6184B (PI 353693), introduced from India in 1970 (USDA-ARS, 2009b), was found to have pubescent leaves but glabrous hulls (PLgh).

In 2009, 217 accessions in the USDA rice mini-core collection (Agrama et al., 2009) were evaluated in the field, and Padi Pohon Batu was identified to be PLgh as well. Padi Pohon Batu was introduced from Malaysia in 1972 (PI 373816 [USDA-ARS, 2009c] and Genetic Stock Oryza [GSOR] 310354 [USDA-ARS, 2009a]). Padi Pohon Batu belongs to O. sativa subsp. japonica (Li et al., 2010b).

Experimental Materials

Ten F2 populations and a BC1F1 population were developed from seven parents, including two PLgh accessions (cultivars Padi Pohon Batu and IARI 6184B), two O. sativa subsp. japonica (cultivars Wells and P1017) with glabrous leaves and hulls, and three O. sativa subsp. indica (cultivars Rondo, Xieqingzao B [B represents maintainer line in hybrid rice], and You I B) with pubescent leaves and hulls. IARI 6184B has purple pericarp and is aromatic. Wells was bred by the University of Arkansas (Moldenauer et al., 2007) and has been popularly grown in the United States (Yan and McClung, 2010). P1017 was developed by RiceTec Inc. in Texas. Rondo was registered by ARS, USDA, located at the DBNRRC in Arkansas (Yan and McClung, 2010). Xieqingzao B was bred by Hunan Hybrid Rice Research and Development Center, Hunan, China. You I B was bred by the Institute of Agricultural Sciences of Deyang, Anhui, China.

Population Development and Field Evaluation

All the populations for genetic analysis were developed either at the DBNRRC, USDA-ARS, in Arkansas or the Rice Research Institute (RRRI), Jiangxi Academy of Agricultural Sciences (JAAS), Nanchang, China. In 2009, three types of cross were made using PLgh type (cultivars IARI 6184B and Padi Pohon Batu) with glabrous leaf (GL) and glabrous hull (GH) type (cultivars Wells and P1017) and pubescent leaf (PL) and pubescent hull (PH) type (cultivars Rondo, Xieqingzao B, and You I B) at the DBNRRC. Specifically, the crosses were Xieqingzao B × Padi Pohon Batu, Xieqingzao B × IARI 6184B, You I B × Padi Pohon Batu, You I B × Wells, Rondo × Padi Pohon Batu, Rondo × IARI 6184B, Wells × Padi Pohon Batu, Wells × IARI 6184B, and Padi Pohon Batu × IARI 6184B. Pubescent leaf and PH line Xieqingzao B was crossed to GL and GH line P1017 at RRRI, JAAS in China. The emasculation and pollination during the crossing followed a standard procedure. The resulting F1, seeds of all crosses were harvested 20 d or more after pollination.

In 2010, seven parents and their F1 hybrids were grown in plastic buckets (18 cm depth by 20 cm diameter) filled with clay soil for generating F2 seeds in a greenhouse at the DBNRRC. The resulting F1 seeds of all crosses were harvested 20 d or more after pollination. The emasculation and pollination during the crossing followed a standard procedure. The resulting F1, seeds of all crosses were harvested 20 d or more after pollination.

In 2009, 217 accessions in the USDA rice mini-core collection (Agrama et al., 2009) were evaluated in the field, and Padi Pohon Batu was identified to be PLgh as well. Padi Pohon Batu was introduced from Malaysia in 1972 (PI 373816 [USDA-ARS, 2009c] and Genetic Stock Oryza [GSOR] 310354 [USDA-ARS, 2009a]). Padi Pohon Batu belongs to O. sativa subsp. japonica (Li et al., 2010b).

Phenotypic Characterization

Four parental lines, that is, Rondo, Wells, Padi Pohon Batu, and IARI 6184B, and two pairs of reciprocal F1 hybrids were characterized in experiments conducted at the DBNRRC. At flowering, leaf samples were collected from flag leaves (main culm) of five different plants and immediately placed in a labeled plastic bag to maintain moisture. Leaf blades were rinsed twice with distilled water and softly dried with a paper towel. An area of 7.068 mm2 (π × 1.5 2) was punched out from the top, middle, and bottom of each leaf blade using a round puncher (3 mm diameter), observed for pubescence or glabrousness, and photographed using a Leica S8 APO stereoZoom microscope equipped with Leica DC300 digital camera at 100× magnification and Photoshop 6.0 (Adobe Systems Incorporated, 2000) according to manufacturer’s protocol. At maturity, five plants of Rondo, IARI 6184B, Padi Pohon Batu, and Wells were sampled for agronomic evaluation, including plant height, panicle length, filled grains, total grains per panicle, seed set percentage, 100-grain weight, number of grains per centimeter of panicle, kernel width, length and length:width ratio.

Statistical Analyses

One-way ANOVA and mean comparisons of the four lines were conducted using the IBM SPSS (Statistical Product and Service Solutions) package (version 19) (IBM Corporation, 2010). Fisher’s least significant difference test was conducted to determine significant (P = 0.05) differences among mean values. The segregation ratios in the F2 and BC1F1 populations were tested using χ2 procedure of the IBM SPSS (version 19).

RESULTS AND DISCUSSION

Phenotypic Performance of PLgh Rice

Comparisons of IARI 6184B and Padi Pohon Batu with pubescent leaves and glabrous hulls (PLgh), Wells with glabrous leaves and hulls, and Rondo with pubescent leaves and hulls showed variation for 10 agronomic and kernel characteristics (Table 1). More than 65% of the variation was attributable to the differences among the four parents, ranging from 65.77 to 97.93% for different traits (Table 2). Therefore, the segregating populations derived from these parents were justified for genetic analysis of other traits of interest, such as yield components. IARI 6184B exhibited many prominent phenotypic characteristics, such as white inflorescence (panicle), white hull, purple leaf auricle, dark-purple stigma, dark-purple lemma tip (apiculi), and purple sterile lemma at flowering stage and purple pericarp at maturity (Fig. 1 and 2d). Photos of the abaxial (lower) and adaxial (upper) epidermis of leaf and hull in the four parents and their F1 progenies,
taken under a dissecting microscope, are displayed in Fig. 2. Usually, for pubescent leaves, adaxial surfaces had more and longer trichomes or hairs than abaxial surfaces. The trichomes on hulls started to appear at flowering and grew with the development of rice grains.

Rondo (Fig. 2a) possessed fewer trichomes or pubescence (5.79 trichomes mm⁻²) on the leaves than IARI 6184B (11.83 trichomes mm⁻²) (Fig. 2d) and Padi Pohon Batu (12.20 trichomes mm⁻²) (Fig. 2e). The differences in pubescence density were highly significant (Table 3). While IARI 6184B and Padi Pohon Batu had glabrous hulls, Rondo had pubescent hulls. The F₁ progenies of Wells (glabrous hulls) crossed with Padi Pohon Batu (glabrous hulls) and IARI 6184B (glabrous hulls) exhibited glabrous hulls. Both F₁ progenies (Wells × Padi Phonon Batu and Wells × IARI 6184B) displayed leaf pubescence (7.88 and 7.85 trichomes mm⁻², respectively), indicating that the genes for pubescent leaves in IARI 6184B and Padi Pohon Batu were dominant over the genes for glabrous leaves in Wells. The F₁ progenies of pubescent-leaved Rondo with glabrous-leaved Padi Phonon Batu and IARI 6184B had pubescent leaves, with 7.85 and 11.02 trichomes mm⁻², respectively. Trichomes were observed on the hulls of both the Fₛ (Rondo × Padi Phonon Batu and Rondo × IARI 6184B), indicating that the genes for pubescent hulls in Rondo were dominant over the genes for glabrous hulls in IARI 6184B and Padi Phonon Batu.

When evaluated by touch, the hairs on the PLgh leaves felt soft whereas the hairs on the traditional pubescent leaves felt firm and caused an itch. Such morphological differences of the PLgh germplasm (Padi Pohon Batu and IARI 6184B) from a traditional pubescent cultivar (Rondo) have not been reported in previous studies, such as Hu et al. (1999), Luo et al. (2000), Rutger and Mackill (2001), and Li et al. (2010a). Plant leaf pubescence or trichomes play an important role in biotic (insects and diseases stresses [Xu et al., 2002; Pfeiffer et al., 2003; Zhang et al., 2003; Kim et al., 2011]) and abiotic stress (weather and soil stresses) tolerance (Saltveit and Hepler 2004; Du et al., 2009; Angeles-Shim et al., 2012). Pfeiffer et al. (2003) observed a delay of aphid infection in soybean cultivars with high density of pubescence, which functioned

### Table 2. Analysis of variance of agronomic traits and yield components among four parental lines.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Plant height (cm)</th>
<th>Panicle length (cm)</th>
<th>Filled grains per panicle</th>
<th>Total grains per panicle</th>
<th>Seed set (%)</th>
<th>Grains cm⁻¹ panicle</th>
<th>100-grain weight (g)</th>
<th>Kernel length (mm) (L)</th>
<th>Kernel width (mm) (W)</th>
<th>L:W ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replications</td>
<td>4</td>
<td>7.68</td>
<td>0.79</td>
<td>514.45</td>
<td>9.35</td>
<td>0.44</td>
<td>0.01**</td>
<td>0.01**</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01**</td>
</tr>
<tr>
<td>Lines</td>
<td>3</td>
<td>2,241.13**</td>
<td>16.79**</td>
<td>28,138.98**</td>
<td>15.22</td>
<td>53.31</td>
<td>1.11**</td>
<td>0.72**</td>
<td>0.72**</td>
<td>0.53**</td>
<td>0.63**</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>15.34</td>
<td>1.92</td>
<td>1,007.32</td>
<td>14.69</td>
<td>1.23</td>
<td>0.002</td>
<td>0.01</td>
<td>0.003</td>
<td>0.002</td>
<td>0.002</td>
</tr>
</tbody>
</table>

**Significant at the 1% level of probability.

### Table 1. Mean comparisons of agronomic traits and yield components among four parental lines.

<table>
<thead>
<tr>
<th>Parental lines</th>
<th>Plant height (cm)</th>
<th>Panicle length (cm)</th>
<th>Filled grains per panicle</th>
<th>Total grains per panicle</th>
<th>Seed set (%)</th>
<th>100-grain weight (g)</th>
<th>Kernel length (mm) (L)</th>
<th>Kernel width (mm) (W)</th>
<th>L:W ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wells</td>
<td>99.6 c</td>
<td>22.44 b</td>
<td>244.0 a</td>
<td>289.0 a</td>
<td>89.04 a</td>
<td>12.73 a</td>
<td>2.72 c</td>
<td>8.88 c</td>
<td>3.04 b</td>
</tr>
<tr>
<td>Rondo</td>
<td>138.8 a</td>
<td>24.22 b</td>
<td>213.6 a</td>
<td>235.2 b</td>
<td>93.02 a</td>
<td>8.91 b</td>
<td>2.78 c</td>
<td>9.94 a</td>
<td>3.00 b</td>
</tr>
<tr>
<td>IARI 6184B</td>
<td>141.8 a</td>
<td>26.38 a</td>
<td>106.0 b</td>
<td>120.2 c</td>
<td>90.36 a</td>
<td>4.98 c</td>
<td>3.72 a</td>
<td>9.52 b</td>
<td>3.78 a</td>
</tr>
<tr>
<td>Padi Pohon Batu</td>
<td>109.0 b</td>
<td>22.60 b</td>
<td>133.4 b</td>
<td>163.0 c</td>
<td>89.71 a</td>
<td>7.26 b</td>
<td>2.86 b</td>
<td>8.92 c</td>
<td>3.02 b</td>
</tr>
</tbody>
</table>

†Means followed by different letters within a column are significantly different at 5% level of probability according to Fisher’s least significant difference test.

Figure 1. IARI 6184B (PI 353693) with pubescent leaves and glabrous hulls has white panicles (A) and (B), purple leaf auricle (C), and purple grain pericarp (D).
as a mechanical barrier to aphid probing. The spread of soybean mosaic virus (SMV) depends on aphids feeding on infected plants so that high density of pubescence offers a non-strain-specific resistance and/or avoidance mechanism to SMV spread. Du et al. (2009) reported that soybean cultivars with high density of pubescence had lower temperature on leaves during drought because the pubescences restricted loss of water via transpiration, thus enhancing photosynthesis in comparison to the cultivars with low density of pubescence. Therefore, the pubescent leaves in our newly discovered PLgh germplasm may provide tolerance to biotic (insects and diseases) and abiotic (weather and soil) stresses. In addition, the glabrous hulls of our PLgh rice certainly provide a comfortable operation and economical transportation described by Dat et al. (1978), Rutger and Mackill (2001), Wang et al. (2009a), and Li et al. (2010a). This useful germplasm should be valuable in developing rice cultivars with improved resistance and/or tolerance to biotic and abiotic stresses.

**Genetic Analysis of PLgh Rice**

Among F1 progenies of seven crosses, hulls were pubescent when pubescent Rondo, You I B, and Xieqingzao B were crossed with PLgh IARI 1684B and Padi Pohon Batu and glabrous Wells, indicating that pubescence hull was dominant over glabrous hull (Fig. 2; Table 4). All leaves were pubescent when pubescent Rondo, You I B, and Xieqingzao B were crossed with glabrous Wells, indicating that the

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**Table 3. Mean comparisons of adaxial leaf pubescence density (hairs mm⁻²) among four parental lines and their F1 progeny.**

<table>
<thead>
<tr>
<th>Lines or crosses</th>
<th>IARI 6184B</th>
<th>Padi Pohon Batu</th>
<th>Rondo × Padi Pohon Batu</th>
<th>Wells × IARI 6184B</th>
<th>Rondo × IARI 6184B</th>
<th>Wells × Padi Pohon Batu</th>
<th>Rondo</th>
<th>Wells</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>11.83 a†</td>
<td>12.20 a</td>
<td>11.02 ab</td>
<td>9.83 b</td>
<td>7.85 c</td>
<td>7.88 c</td>
<td>5.79 d</td>
<td>0 e</td>
</tr>
</tbody>
</table>

†Means followed by different letters within the row are significantly different at 5% level of probability according to Fisher’s least significant difference test.
gene for pubescent leaf was dominant over the gene controlling glabrous leaf. As for coloration of the hull and pericarp, IARI 6184B had white hulls at flowering stage and purple pericarp at maturity whereas Wells and Rondo had green hulls at flowering stage and white pericarp at maturity. The F1s of Wells × IARI 6184B and Rondo × IARI 6184B crosses showed green hulls at flowering and purple pericarp at maturity, indicating that green hull was dominant over white hull whereas purple pericarp was dominant over white pericarp.

In the F2 populations derived from PLgh IARI 6184B and Padi Pohon Batu with glabrous Wells, segregation ratios of the PLgh phenotypes (PL and GH) and glabrous phenotypes (GL and GH) were 181:56 and 103:28, respectively, ideally fitting a single-gene model (3:1 ratio) ($c^2 = 0.283$, $P = 0.626$ and $c^2 = 0.919$, $P = 0.338$) (Table 4). However, in the F2 populations derived from PLgh phenotypes (IARI 6184B and Padi Pohon Batu) with pubescent Rondo, You i B, and Xieqingzao B, segregation ratios of pubescent phenotypes (PL and PH), PLgh phenotypes (PL and GH), and glabrous phenotypes (GL and GH) did not deviate significantly from 12:3:1 ratio, except for Rondo × IARI 6184B probably due to segregation distortion in F2 progenies caused by partial fertility of its F1's, suggesting that two genes were involved in the inheritance of leaf and hull pubescences. When only leaf or hull was considered independently, leaf pubescence and hull pubescence showed 15:1 and 3:1 ratios for two-gene and one-gene models, respectively, which indicated that the gene for leaf pubescence was different from the gene for hull pubescence.

Table 4. Phenotype of parents, F1, and F2 (or BC1) segregation for leaf pubescence and pericarp from crosses between two new glabrous lines with pubescent and glabrous lines.

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Observed</td>
<td>Expected</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>Xieqingzao B × Padi Pohon Batu</td>
<td>PL and PH</td>
<td>12:3:1</td>
<td>187:41:15</td>
<td>182:46:15</td>
<td>0.583</td>
</tr>
<tr>
<td>You i B × Padi Pohon Batu</td>
<td>PL and PH</td>
<td>12:3:1</td>
<td>154:40:21</td>
<td>161:40:14</td>
<td>4.584</td>
</tr>
<tr>
<td>Rondo × Padi Pohon Batu</td>
<td>PL and PH</td>
<td>12:3:1</td>
<td>74:18:12</td>
<td>78:19:7</td>
<td>4.975</td>
</tr>
<tr>
<td>Xieqingzao B × IARI 6184B</td>
<td>PL and PH</td>
<td>12:3:1</td>
<td>142:23:16</td>
<td>136:34:11</td>
<td>6.63</td>
</tr>
<tr>
<td>Rondo/IARI 6184B</td>
<td>PL and PH</td>
<td>12:3:1</td>
<td>253:25:16</td>
<td>221:55:18</td>
<td>21.78</td>
</tr>
<tr>
<td>You i B/Wells</td>
<td>PL and PH</td>
<td>3:1</td>
<td>166:0:53</td>
<td>164:55</td>
<td>0.075</td>
</tr>
<tr>
<td>P1017 × Xieqingzao B</td>
<td>PL and PH</td>
<td>13:3</td>
<td>126:0:26</td>
<td>124:29</td>
<td>0.31</td>
</tr>
<tr>
<td>P1017/IARI 6184B</td>
<td>PL and PH</td>
<td>3:1</td>
<td>138:0:47</td>
<td>139:46</td>
<td>0.016</td>
</tr>
<tr>
<td>Wells × Padi Pohon Batu</td>
<td>PL and GH</td>
<td>3:1</td>
<td>181:56</td>
<td>178:59</td>
<td>0.283</td>
</tr>
<tr>
<td>Wells × IARI 6184B</td>
<td>PL and GH</td>
<td>3:1</td>
<td>103:28</td>
<td>98:33</td>
<td>0.919</td>
</tr>
<tr>
<td>Padi Pohon Batu × IARI 6184B</td>
<td>PL and GH</td>
<td>3:1</td>
<td>No segregation</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Phenotype of parents, F1, and F2 (or BC1) segregation for leaf pubescence and pericarp from crosses between two new glabrous lines with pubescent and glabrous lines.

†GH, glabrous hull; GL, glabrous leaf; PH, pubescent hull; PL, pubescent leaf; PP, purple pericarp; WP, white pericarp.
Glabrous parent P1017 (GL and GH) showed a pubescent:glabrous segregation ratio of 3:1 in the BC₁F₁ populations and of 13:3 in the F₂ populations (Table 4), which implied that GL and GH P1017 was controlled by two recessive genes with dominant and recessive epistasis interactions. In the F₂ population of GL and GH Wells and PL and PH You I B, the GL and GH was controlled by a single recessive gene, however. These results demonstrated that one or two genes were involved in determining leaf glabrousness. Therefore, inheritance pattern of glabrousness in rice would appear to be dependent on genetic background. The single-gene model has been well studied (Li et al., 2010a). Extensive studies on the two-gene model of glabrousness at the molecular and metabolic levels should be conducted for a full understanding of the biological mechanisms conditioning this important trait.

In the F₂ progenies derived from IARI 6184B and Wells, a segregation ratio of green panicle (green rachis and hulls and white pericarp, the same as the Wells phenotype) and white panicle (white rachis and hulls and purple pericarp, the same as the IARI 6184B phenotype) was 176:61, ideally fitting the 3:1 ratio for a single-gene model ($X^2 = 0.069$, $P = 0.792$). To date, two white panicle mutants, $wp1$ and $wp2$, have been reported to be on chr. 1 and chr. 7, respectively (Sanchez and Khush, 1994; Li et al., 2003). Both of them exhibit white-striped leaves at the seedling stage. The rachis and pedicel of the $wp1$ mutant are green at flowering and its hulls are normal, straw colored at maturity, but the rachis, pedicel, and hulls of the $wp2$ mutant are white at flowering and maturity. IARI 6184B displayed the same phenotype as the panicle and hulls of the $wp2$ mutant, but it did not show white-striped leaves at the seedling stage. The recessive white inflorescence (panicle) in IARI 6184B has ornamental significance and it could serve as a marker in the hybrid rice system before flowering during hybrid seed production. Similarly, pubescent leaf and glabrous hull of the $PLgh$ germplasm could also serve as such a marker in the hybrid rice system so that the unwanted plants (off-type or volunteer plants) can be visually identified and rogued out before flowering during hybrid seed production. Similarly, pubescent leaf and glabrous hull of the $PLgh$ germplasm could also serve as such a marker in the hybrid rice system.

As for pericarp color, a 9:7 purple pericarp:white pericarp ratio was noted for four F₂ populations where purple pericarp parents were crossed with white pericarp parents (Table 4). This implied that pericarp color was controlled by two genes with complementary interaction. Two genes, $Pp$ (Prp-a) and $Pb$ (Prp-b), were reported to be on chr. 1 and chr. 4, respectively, for pericarp pigmentation in purple rice where $Pb$ was recessively epistatic to gene $Pp$ by Hsien and Chang (1964), Wang and Shu (2007), and Wang et al. (2009b). Rice grains appear brown in the presence of the $Pb$ gene but without the $Pp$ gene whereas they appear white in the absence of the $Pb$ gene. A 9:3:4 purple pericarp:brown pericarp:white pericarp ratio was reported in F₂ populations (Hsien and Chang, 1964; Wang et al., 2009b). Thus, our results show another mode of inheritance for purple pericarp.

### Allelic Analysis of $PLgh$ Rice

The reciprocal F₁ crosses of $PLgh$ IARI 6184B and Padi Pohon Batu with other PL and PH and GL and GH parents showed identical phenotypes of pericarp color, leaf and hull pubescence, or glabrousness, indicating no cytoplasmic effects existed for these traits. Furthermore, there were no segregations for pubescence and glabrousness of leaf and hull in the F₂ populations when both parents had the same leaf and hull phenotype. Thus, the genes controlling $PLgh$, that is, pubescent leaf and glabrous hull, were allelic to those in PL and PH and in GL and GH parents (Table 4).

Therefore, the $PLgh$ germplasm could be valuable not only for enriching the gene pool to regulate trichome expression but also for other uses in rice breeding programs. We plan to map and clone the $PLgh$ gene for cultivar development.

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### References


