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Mapping of quantitative trait loci for purple stigma and purple apiculus in rice by using a Zhenshan 97B/Minghui 63 RIL population

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Abstract: Anthocyanin pigmentation is an important morphological marker that is commonly used to identify rice varieties and for linkage analysis. The following study investigates the genetic factors involved in the purple stigma (*Ps*) and purple apiculus (*Pa*) traits of an important indica rice cross between Zhenshan 97 (purple stigma and purple apiculus) and Minghui 63 (grey stigma and colourless apiculus). A recombinant inbred line (RIL) population derived from this cross was used for quantitative trait loci (QTL) mapping of the purple stigma and purple apiculus traits. As a result, one major QTL for the purple stigma trait, temporarily designated *qPS-1-1*, and one major QTL for the purple apiculus trait, temporarily designated *qPA-1-1*, were mapped to the short arm of chromosome 6 in the interval between the two markers Y4073L and *P. The LOD peaks of *qPS-1-1* and *qPA-1-1* were 44.0127 and 173.3585, respectively. In addition, *qPS-1-1* and *qPA-1-1* explained 66.7416% and 98.6441% of the total phenotypic variance, respectively. The Zhenshan 97 allele increased the purple stigma trait by approximately 8.0355% (for *qPS-1-1*) and 9.8863% (for *qPA-1-1*). Moreover, since *qPS-1-1* and *qPA-1-1* were strongly correlated, they were also located in the same vicinity of the *C* gene on the short arm of chromosome 6, which suggested that the two QTL might be the same. By comparing these and previous results, it was deduced that *qPS-1-1* or *qPA-1-1* was the *C* gene and was pleiotropic for both the colouration of the apiculus and the colouration of the stigma in rice.

Keywords: colouration of the stigma and apiculus; QTL mapping; recombinant inbred lines (RILs); rice (*Oryza sativa* L.)

Flavonoid derivatives, including anthocyanins, have a variety of biological functions in plants, animals, and bacteria. Flavonoid derivatives are responsible for pigmentation patterns and a wide range of biological functions such as protection against UV radiation, signalling molecules in plant-microbe interactions, and plant defence responses (Dooner et al. 1991; Koes et al. 1994; Reddy 1996; Saitoh et al. 2004). Anthocyanin colouration commonly occurs in the floral organs, stems, leaves, leaf sheaths and other parts of the rice plant. These parts of the rice plant, which are coloured due to the presence of anthocyanin pigments, widely vary in the hue and shade of the colour. The colours include pink, red, reddish purple, purple and purplish black. To date, several studies have investigated the inheritance mode of anthocyanin colouration in rice, and a considerable amount of data concerning the genic interpretation of this colour has accumulated (Takahashi 1957).

Anthocyanin pigmentation in rice is not only an important morphological marker but also an important trait for studying rice domestication (Saitoh et al.

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2004; Fan et al. 2008). Previous studies have revealed that the anthocyanin pigment gene system consists of three basic genes: *C* (chromogen), *A* (activator), and *P* (distributor) (Takahashi 1957, 1982; Nagao & Takahashi 1963; Maekawa & Kita 1987; Reddy 1996).

Quantitative trait loci (QTL) mapping is a common approach used to detect the genetic and molecular architecture underlying complex quantitative traits. This method has been widely applied in crop improvement programmes to create high-quality germplasm resources. Recent progress in this DNA marker technique has provided a powerful tool for quantitative trait loci dissection (McCouch & Doerge 1995; Paterson 1996a, b; Mohan et al. 1997; Mackill et al. 1999; Collard et al. 2005).

In the present paper, we established a molecular marker-based analysis of QTL for the purple stigma and purple apiculus traits by using a recombinant inbred line population derived from an important indica rice cross between Zhenshan 97 and Minghui 63, which are the parents of Shanyou 63, the most widely grown hybrid rice variety in China.

MATERIAL AND METHODS

Plant material and field planting. A population of 241 recombinant inbred lines (RILs) was used in this study. The RILs were derived from a cross between Zhenshan 97B and Minghui 63, which are also the parents of Shanyou 63, the most widely grown hybrid rice variety in China. The RIL population was planted in the field during the 2009 rice-growing season at the experimental stations in Tianjin, China. Seeds were planted in a seedbed in mid-May and transplanted to the field in mid-June. The planting density was 13.3 cm between plants in a row, and the rows were 16.7 cm apart. Field management, including irrigation, fertilizer application and pest control, essentially followed normal agricultural practices.

Trait measurement. The colouration of the stigma and apiculus was recorded 7–10 days after heading, and five normal panicles from five representative plants were sampled from each RIL to investigate the colouration of the stigma and apiculus. In a bright room, the sampled panicles were placed neatly, the colouration of the stigma and apiculus was recorded by visual measurement method.

Molecular markers and linkage map construction. The molecular marker data including 168 RFLPs and 52 SSRs were as described previously by Xing et al. (2002). Another 34 SSR markers located in certain regions were added to reduce the gaps in the map. The RFLP marker assay followed the method described by Liu et al. (1997), and the SSR assay was conducted as described by Wu and Tanksley (1993). The linkage map consisted of 254 DNA markers covering a total of 1 796 cM with an average interval of approximately 7.1 cM between adjacent marker loci.

QTL analysis. The purple stigma and purple apiculus traits exhibit discontinuous variation, typical of qualitative characters. There are two methods of mapping for this type of character. One method is to take the character as a morphological marker and map it to the linkage group; another is to convert the colouration values to specific digits and treat the trait as a continuous quantitative character in the mapping of quantitative trait loci. The second method was adopted in this research.

(1) Colouration of the stigma: RILs showing a purple stigma were assigned a phenotypic value of 30; RILs showing colouration segregation were assigned a phenotypic value of 20; and RILs showing a grey stigma were assigned a phenotypic value of 10. RILs without phenotypic data for stigma colour were treated as missing.

(2) Colouration of the apiculus: RILs showing a purple apiculus were assigned a phenotypic value of 30; RILs showing colouration segregation were assigned a phenotypic value of 20; and RILs showing a colourless apiculus were assigned a phenotypic value of 10. RILs without original phenotypic data for apiculus colour were treated as missing.

Molecular marker linkage maps were constructed, and QTL analysis was performed by using QTL IciMapping Ver. 4.0.1.0 (Meng et al. 2015). The putative QTLs for the colouration of the stigma and colouration of the apiculus were estimated with a calculated logarithm of the odds (LOD) score after 1000 permutation tests (Meng et al. 2015).

RESULTS

Performance of the traits. The phenotypic values of the colouration of the stigma and the colouration of the apiculus for the RIL population are presented in Table 1, and the phenotype of their parents are presented in Figure 1. Similar to qualitative traits, the colouration of the stigma and colouration of the apiculus showed discontinuous variation in the RIL population (Table 1).

QTL mapping analysis. The mapping results revealed only one major QTL for the purple stig-

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Table 1. Colouration of the stigma and colouration of the apiculus data for the recombinant inbred line population (n = 241)

Organ	Colour			
	purple	grey/ colourless	segregating	missing
Stigma	89	136	1	15
Apiculus	94	129	2	16

Figure 1. Phenotype of the stigma colouration and apiculus colouration of Zhenshan 97B (left) and Minghui 63 (right)

ma trait, temporarily designated *qPS-1-1*, on the short arm of chromosome 6 in the interval between the two markers Y4073L and *P. The LOD peak of *qPS-1-1* was 44.0127, and *qPS-1-1* explained 66.7416% of the total phenotypic variance. In addition, the Zhenshan 97B allele increased the purple stigma trait by approximately 8.0355% (Table 2; Figure 2).

Furthermore, the result of the QTL analysis of the purple apiculus trait indicated only one major QTL, temporarily designated *qPA-1-1*, on the short arm of chromosome 6 in the interval between the two markers Y4073L and *P. The LOD peak of *qPA-1-1* was 173.3585, and *qPA-1-1* explained 98.6441% of the total phenotypic variance. Additionally, the Zhenshan 97B allele increased the purple stigma trait by approximately 9.8863% (Table 2; Figure 2).

Since *qPS-1-1* and *qPA-1-1* were strongly correlated, they were also located in the same vicinity on the short arm of chromosome 6, which suggested that the two QTL were the same locus. All the LOD scores of QTL for the purple stigma and purple apiculus traits are listed in Table 2.

Based on these and previous results, it was deduced that *qPS-1-1* or *qPA-1-1* was the *C* gene and was pleiotropic for the colouration of the apiculus and the colouration of the stigma in rice.

DISCUSSION

Biosynthesis of anthocyanin pigments in maize, wheat and rice. The biosynthesis of anthocyanin pigments in maize requires complex interactions between genes with both structural and regulatory roles (Dooner et al. 1991). Structural genes encode the biosynthetic enzymes in the pathway. Expression of the structural genes is controlled at the transcriptional

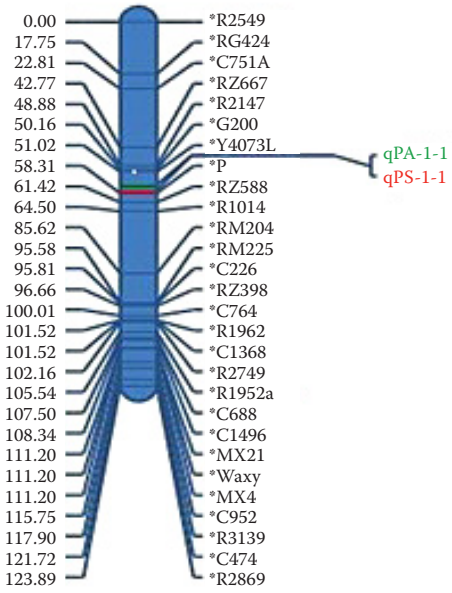

Figure 2. Quantitative trait loci for the purple stigma and purple apiculus was mapped to between the two markers Y4073L and *P on the rice short arm of chromosome 6 by using the RIL population of Zhenguan 97B/ Minghui 63

Table 2. The LOD score of quantitative trait loci for the purple stigma and purple apiculus traits

Trait name	Chromosome	Position	Interval	LOD	PVE (%)	Add
PA	6	56	Y4073L–*P	173.3585	98.6441	–9.8863
PS	6	58	Y4073L–*P	44.0127	66.7416	–8.0355

PVE – phenotypic variation explained; Add – additive effect; LOD – logarithm of the odds

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level by the products of regulatory genes belonging to the two gene families *R/B* and *C1/Pl*. Transcriptional activation of the structural genes in any particular tissue of the plant requires a functional allele of the *R/B* family and a functional allele of the *C1/Pl* family. The *R/B* genes encode related proteins homologous to the basic-helix-loop-helix (bHLH) DNA-binding protein dimerization domain of Myc proteins (Chandler et al. 1989), while the *C1/Pl* genes encode related proteins homologous to the DNA-binding domain of Myb proteins (Paz-Ares et al. 1987; Saitoh et al. 2004).

In wheat, the regulatory role of the *Pp* genes has been confirmed by functional analysis of the anthocyanin synthesis structural genes in wheat near-isogenic lines (NILs) differing by the allelic state of the *Pp-1* and *Pp3* genes (Tereshchenko et al. 2013; Shoeva et al.2014). Comparative mapping has shown that the *Pp-1* genes are orthologs of both maize *C1* and rice *OsC1*, which encode MYB-like transcription factors (TFs) responsible for the activation of structural genes encoding various enzymes participating in anthocyanin synthesis (Li et al. 1999; Saitoh et al. 2004; Khlestkina 2013; Shoeva et al.2014). Similarly, *Pp3* is orthologous to both *Pb/Ra* in rice and *Lc/R* in maize, which encode MYC-like TFs underlying the regulation of anthocyanin synthesis (Ludwig et al. 1989; Hu et al. 1996; Wang & Shu 2007; Shoeva et al. 2014).

In rice, an extensive genetic study revealed that *C* and *A* are the two basic genes necessary for the production of anthocyanin pigments. These two genes are required for colouration in all rice tissues, where a series of multiple alleles at these loci contribute to varying degrees to apiculus colouration, resulting in continuous variation among cultivated forms (Takahashi 1957, 1982).

The occurrence of tissue-specific pigmentation is determined by the *C-A-P* control system, in which *C* (chromogen) is the basic gene for the production of chromogen, *A* (activator) exerts its activation effect on *C* and turns the chromogen into anthocyanin, and *P* (distributor) is responsible for the distribution of colour in specific tissues (Takahashi 1957, 1982; Fan et al. 2008).

Advanced mapping of the *C* gene, purple stigma trait and purple apiculus trait in rice. Numerous studies have focused on the anthocyanin pigmentation of rice. It has been reported that the *C* gene responsible for the colouration of the apiculus, stigma and leaf sheath is linked to the waxy gene in rice (Zhao 1928). Extensive studies on anthocyanin pigmentation in rice plants have led to the description of the *C-A-P* control system, where the *C* gene is located in Group I of the Japanese classical linkage rice map (Kinoshita 1984). Since the publication of the first molecular linkage rice map by McCouch et al. (1988), Japanese researchers have constructed another map and aligned it with the classical map (Kishimoto et al. 1992). The *C* locus was mapped to between G165 and G200 on rice chromosome 6. In another development, through the synteny of maps between rice and maize, a rice homologue (*OsC1*) of the maize *C1* anthocyanin regulatory gene was cloned from the cDNA library (Reddy et al. 1996). In a comparative sequence study between tawny-coloured and colourless apiculi, Mikami et al. (2000) showed that this *OsC1* might be responsible for the coloured apiculus trait. In addition, through comparison of coloured and colourless NILs, it has been shown that the *OsC1* locus is located on chromosome 6 at a distance of 6.2 cM from the linked RFLP marker RZ588. More studies have located *C* in the same region, with slight variation (Li et al. 1995; Wang et al. 1998). Saitoh et al. (2004) mapped the rice homologue *OsC1* of the maize *C1* anthocyanin regulatory gene between the RFLP markers RZ588 and G200. Recently, the *C* locus was delimitated to a 59.3 kb region in which *OsC1* was located (Fan et al. 2008). Based on the syntenic relationship between maize and rice, Zhao et al. (2016) identified *LOC_Os06g10350* as the candidate for the rice homologue (*OsC*) of maize *C1*. *LOC_Os06g10350* encodes proteins of R2R3-Myb factors that activate the transcription of genes encoding enzymes involved in the biosynthesis of anthocyanin pigments (Martin & Paz-Ares 1997).

In Asian cultivated rice, a total of 8 purple stigma-related genes were mapped to chromosomes 3, 6, and 11. Four of these genes, namely, *Ps-1*, *Ps-2*, *Ps-3*, and *Ps-4(t)*, were regulatory genes, and *IPs-1*, *IPs-2*, *IPs-3*, and *IPs-4* were inhibitor genes (Han et al. 2006). Li et al. (2012) reported a recessive purple-stigma mutant, *ps-5*, and mapped it to the interval between the two SSR markers LR41 and LRM43 on chromosome 8 with a genetic distance of 0.12 cM to each marker. The physical distance between LR41 and LRM43 was approximately 125 kb. Liu et al. (2012) mapped the purple-stigma gene *Pa-6* (*Purple apiculus-6*) to an interval of 41.7 kb between L02 and RM19561 on chromosome 6. Sequence analysis revealed that ORF5 *in the target region* is the *C* (chromogen for anthocyanin) gene, and it is presumed to be the candidate

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gene for *Pa-6*. Using a RIL population derived from a cross between Zhenshan 97 and IRAT109, Yue et al. (2006) dissected the genetic bases of grain apiculus colour (GAC), finding that the trait is controlled by a single gene. Using a single-segment substitution line (SSSL), Fan et al. (2008) further mapped the *C* locus for the purple apiculus of Zhenshan 97B to a 59.3-kb region between RM111 and RM253 on chromosome 6.

The results of this study were consistent with those of related reports (Yue et al. 2006; Fan et al. 2008; Liu et al. 2012; Zhao et al. 2016), suggesting that *qPS-1-1* and *qPA-1-1* were the *C* (chromogen for anthocyanin) gene in rice. Moreover, the *OsC1* locus appeared to be a pleiotropic gene for the colouration of the apiculus and the colouration of the stigma.

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