CROP BREEDING AND APPLIED BIOTECHNOLOGY

ARTICLE

Genetic analysis and gene mapping of the purple glume tip trait in rice (*Oryza sativa*)

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Abstract: *The purple glume-tip is an essential morphological marker for selective rice breeding, aiding in assisted selection and variety purification. However, the inheritance of purple glume-tip in japonica rice landrace Donglan Black Rice (DBR) has not yet been explored deeply. The F_2 and F_4 populations were constructed from crossing between Huazhan with colorless glume-tip and DBR to identify the associated genomic region(s). Genetic analysis displayed two highly comparable and perplexing phenotypes in the purple glume-tip of rice. Two significant genes with recessive epistasis predominantly regulated the two phenotypes. The two target gene loci were located in the intervals of 5315163–5316875 bp on chr6 and 27915598-27939357 bp on chr4, respectively, where reported genes associated with the purple color trait in rice, Os06g0205100 and Os04g0557500, are present. The two genes may be potential target genes. However, the role of Os04g0557500 in the glume-tip coloration remains unreported.*

Keywords: *Rice, purple glume tip, gene localization, recessive epistasis*

INTRODUCTION

The rice organ purple trait is a morphological characteristic that is not affected by the environment or other biological indicators and can be used as a marker trait in *assisted* breeding, seed purity identification, stress response, and protection of new plant variety rights (Ithal and Reddy 2004, Du et al. 2022, Teng et al. 2022). Previous studies have indicated that the purple glume tip is partially associated with a wide range of compatibility and photoperiod sensitivity genes (Chandraratna 1953, Yan et al. 2002, Li et al. 2020). Applying glume tip color as a morphological marker can promote the selection of *wide compatibility restorer lines* in field environments (Yan et al. 2002).

Several studies have identified the presence of the gene *LOC_Os06g10350* on chromosome 6, which determines purple or purplish red glume tips, and most have suggested that it alone regulates purple glume tip color (Setty and Misro 1973, Liu et al. 2012, Kim et al. 2020). For example, Kesha and Zhang (2003) found that the purple glume tip gene, *Pa-6*, is monogenic, dominant, and localized on chromosome 6. The gene *LOC_Os06g10350* is responsible for glume tip color and is the chromogen gene *OsC* in rice (Zhao et al. 2016). Tong et al. (2021) localized the purple glume tip of the primary QTL *qPA-1-1* to the short arm of chromosome 6.

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Purple glume tips can be obtained from the anthocyanin pigmentation of rice's lemma and palea tips. The purple glume tip is dominant over colorless glume tip, and the glume tip color exhibits a pair of relative traits (Setty and Misro 1973, Kesha and Zhang 2003, Zhao et al. 2016, Wang et al. 2020). However, some researchers have proposed that glume tip color is not solely influenced by monogenes (Nagai et al. 1962). Regarding the mechanism of anthocyanin pigmentation in rice, previous researchers have proposed genetic systems, such as CAP and C-S-A, and cloned related genes (Mori and Takahashi 1981, Zhou et al. 1996, Sun et al. 2018, Meng et al. 2021). The purple glume tip was regulated by at least one pair of genes. In summary, the inheritance of purple glume tips remains controversial and ambiguous. However, the inheritance mechanism requires further exploration. Further studies on the inheritance patterns and localization of related genes are significant in revealing the glume-tip color determination mechanism. This study constructed an F_2 segregation population by crossing the purple rice cultivar DBR with the conventional japonica rice Huazhan. Genetic analysis was performed through phenotypic identification and statistics, combined with gene chip testing of phenotypic mixing pools, to screen out molecular marker loci with differences and locate possible regions of the target genes. This study provides a theoretical reference for applying purple glume tip traits in molecular breeding programs.

MATERIAL AND METHODS

Plant materials

This study used a conventional indica rice variety (Huazhan) bred by the China National Rice Research Institute, characterized by the absence of purple anthocyanin pigmentation in the panicle. The landrace cultivar Donglan Black Rice (DBR), an ancient variety of rice in Donglan County, Guangxi, belongs to the tropical japonica lineage and is photosensitive glutinous rice. This variety is rich in anthocyanidins, and its leaf margins, auricles, ligules, apiculi, and stem bases are purple-black or purple-red.

Genetic population construction

Using DBR as the female parent and Huazhan as the male parent, the hybrid combination DBR × Huazhan was artificially demulinized to produce F_1 hybrid seeds. These hybrid seeds were planted to obtain the F_1 generation plants. The F_1 plants were self-pollinated to obtain F_2 generation and then cultivated via the progeny lineage method, resulting in segregated populations of F_3, F_4, and other subsequent generations. The F_2 and F_4 generation were planted individually in Plot 68 and Plot 88 in the summer of 2019.

Phenotypic observation, identification, and statistical analysis

The color of the glume tip of each rice spike was observed during the tasseling stage to determine the location, extent, and degree of anthocyanin pigmentation. The phenotype of each glume tip color was assessed, and the number of individuals with each phenotype in the population was recorded. The proportion of each phenotype was then calculated, and the genetic segregation proportion model was estimated. The predicted proportion was tested for suitability using chi-square (χ^2), and genetic law was analyzed.

High-density genome-wide SNP microarray analysis

Based on phenotypic classification, the leaves of individual plants with different glume tip colors were collected. A total of 30–40 individuals of each phenotype were used to generate phenotypic mixing pools according to the classification. DNA was extracted to construct DNA mixing pools. A high-density single-nucleotide polymorphism (SNP) microarray (rice GSR40K) was used for SNP detection. Based on microarray data, Genome Studio analyzed the base differences between phenotypic mixing pools.

Interval localization and candidate gene analysis

The Nipponbare genome was used as a reference genome in the sample pairwise comparison method to analyze differences in SNP markers. The positions and interval sizes of the differential loci were visually displayed based on the positions of the differential loci on the chromosome. Homozygous SNP sites were labeled AA or BB, and heterozygous SNPs were labeled AB. These differential SNPs were plotted according to their chromosomal locations, with the difference

interval as the possible interval for the target genes. Genes related to anthocyanin synthesis within the target region were analyzed to predict the target genes.

RESULTS AND DISCUSSION

Rice glume tip color phenotype observation

In this study, the rice glume tip color of individual plants during the tasseling stage was highly consistent with that of single spikes and glumes within each plant. Three glume tip color phenotypes were identified in the F_2 segregated population. These included colorless (or pale green), purple-spiked, and diffuse purple glume tips. The colorless glume tip was pale yellow or light green and recorded as colorless. The spiked purple glume tip is the purple glume apex of the palea and lemma, with a small purple area. It was concentrated at the tip apex, and the colored area was spotted. Another relative trait was the diffuse purple glume tip, where purple diffused from the glume apex downward to some extent, and the entire apical part of the glume was purple. Both purple-spiked and diffuse purple glume tips showed a purple color at the glume tips but differed significantly and consistently within populations, with no intermediate phenotype or qualitative traits (Figure 1).

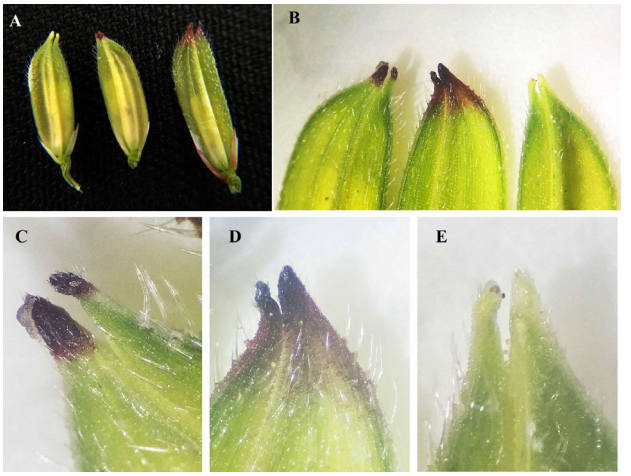

Figure 1. Three glume tip color phenotypes of rice. Three relative traits of glume tip color (A and B). C, purple-spiked glume tip; D, diffuse purple glume tip. E, colorless (or pale green) glume tip.

Glume tip color is a useful morphological marker-trait (Yue et al. 2006). In the past, glume tip color was often linked to traits such as wide compatibility *(Yan et al. 2002)*. This aids in selecting sterile or restorer lines with wide compatibility. In the present study, we found that this trait was not just a pair of relative traits (colorless or purple) but two types of purple glume tips with similar traits, namely purple-spiked and diffuse purple. These are very similar but distinctly different. Therefore, at least three relative traits of the glume tip color: colorless, purple-spiked, and diffuse purple. No other similar reports on the three types of glume tip colors have been published to date.

Phenotypic identification of rice glume tip color and statistical analysis

The number of individual plants with each phenotype was counted to identify the glume tip color of each plant in the plots (68A and 68B) of the F_2 generation. In plots 68A and 68B, three glume tip color phenotypes were isolated, with 545 diffuse, 193 purple-spiked, and 241 colorless glume tips, respectively (Table 1). The ratio of individual plants with diffuse purple, purple-spiked, and colorless glume tips was approximately 9:3:4. A chi-square (χ^2) test was at a significance level, and the predicted ratio (9:3:4) was confirmed as appropriate. This genetic segregation ratio was consistent with the model of recessive epistatic interactions between two pairs of genes that produce three relative phenotypes. This suggests that two pairs of genes interacting via recessive epistatic effects regulate the three rice glume tip phenotypes.

GSR40K gene chip assay

The GSR40k SNP microarray was used to detect differential SNPs in three phenotypes (diffuse purple glume tip, purple-spiked glume tip, and colorless glume tip) of mixed-pooled samples in plot no.68, and two extreme phenotypes (diffuse

Table 1. Separation conditions of glume tip traits from F_2 population in different plots

Rice plot	Individual number			Predicted genetic ratios	χ^2	$\chi^2_{0.05,\ 2}$
	Diffuse purple	Purple-spiked	Colorless			
68A	330	132	149	9:3:4	3.29	5.99
68B	215	61	92	9:3:4	1.24	5.99
Total	545	193	241	/	/	/

Note: $\chi^2<\chi^2_{0.05,\ 2}$, at significant level 0.05.

purple glume tip and colorless glume tip) of mixed-pooled samples in plot no.88 (Figure 2). A total of 134 differential SNPs between colorless glume tips and diffuse purple glume tip samples, 251 SNPs between colorless glume tips and purple-spiked glume tip samples, and 75 SNPs between purple-spiked glume tips and diffuse purple glume tip samples were detected in plot no.68. In total, 33 differential SNPs were detected between the mixed pools of phenotypes in plot no.88.

Allelic homozygosity

The Genome Studio software was used to map the genotyped heterozygous loci to the reference genome to obtain a visual heterozygosity graph. According to the heterozygosity analysis, three mixed pools in plot no.68 had large heterozygous and few homozygous regions, whereas two phenotypic mixed pools in plot no.88 (F_4) had relatively fewer heterozygous and larger homozygous regions (Figure 2). This corresponded to the generation of the genetic population in this study. Plot 68 was from the low generation (F_2), which showed high heterozygosity in the genome. Plot 88 was from the higher generation (F_4), resulting in a larger proportion of homozygous regions.

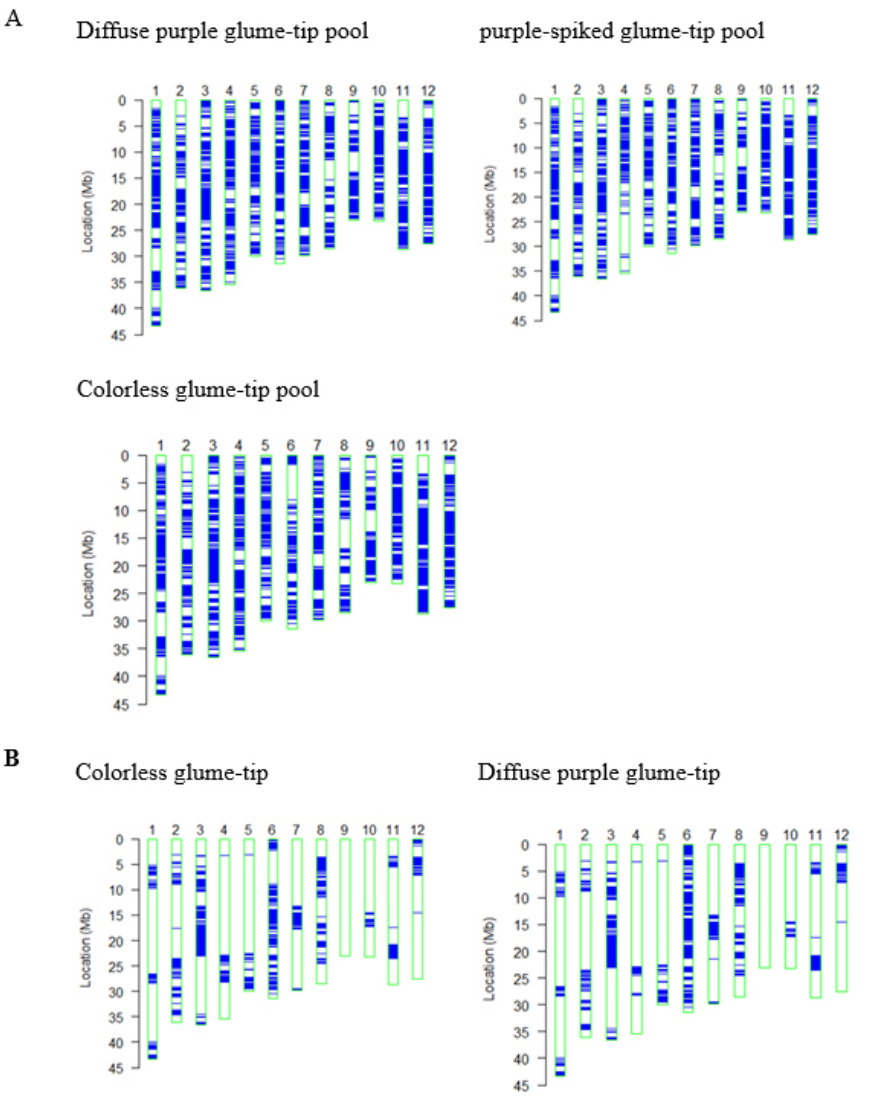

Figure 2. Analysis of heterozygosity among phenotypic pools. A: Plot 68; B: Plot 88.

Shaded areas indicate heterozygous base sites and blank areas indicate homozygous sites in the bar chart.

SNP differences between phenotypic mixed pool

Differences in SNP markers between samples were determined using pairwise comparisons. The positions and homozygosity of these differential markers are displayed in the reference genome. In plot no.68, a large and relatively concentrated number of SNP marker differences were observed on chromosomes 4 and 6 between the mixed pools of colorless glume tips and the purple-spiked glume tip phenotypes (Figure 3). All the highly concentrated differential SNP markers on chromosome 4 in the colorless glume tip samples were heterozygous, whereas all highly concentrated

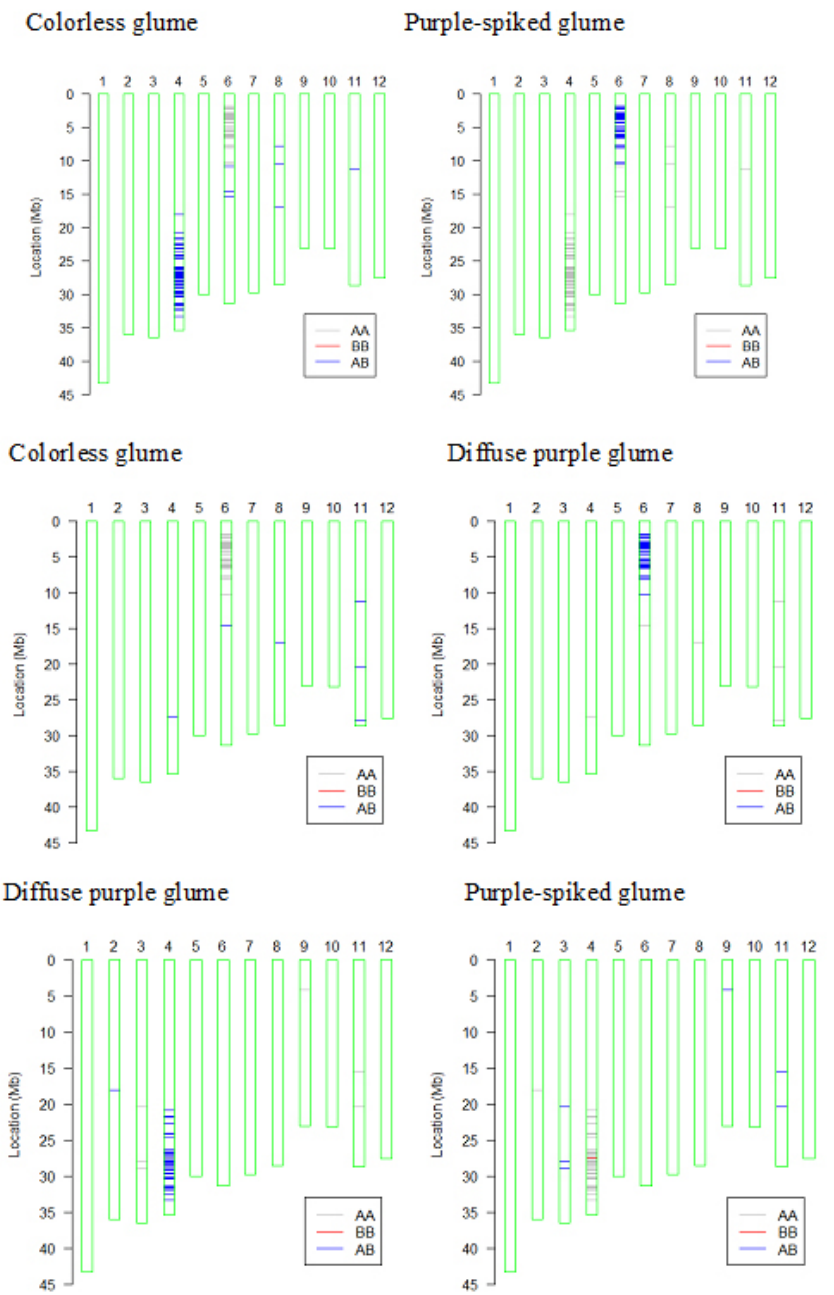

Figure 3. SNP differential locus analysis by microarray in Plot 68.

differential SNP markers on chromosome 6 were homozygous. All highly concentrated differential SNP markers on chromosome 4 in the purple-spiked glume tip samples were homozygous, whereas all highly concentrated differential SNP markers on chromosome 6 were heterozygous. Many highly concentrated differential SNP differences on chromosome 6 between colorless and diffuse purple glume tips were observed in the former homozygous and latter heterozygous. Many highly concentrated differential SNP on chromosome 4 existed between diffuse purple and purple-spiked glumes, with former heterozygosity and latte homozygosity.

The results showed two pairs of reciprocal gene loci: one allele locus (A/a) located on chromosome 6 and the other allele locus (B/b) located on chromosome 4. The glume tip was diffuse purple when both A and B were dominant, and the genotype was AxBx. When locus A showed heterozygosity, whereas locus B showed recessive homozygosity, that is, genotype Axbb, a purple-spiked glume tip was observed. The glume tip was colorless when the allele locus on chromosome 6 was homozygous and recessive (aaxx). A large number of highly concentrated SNP differences on chromosome 6 between colorless and diffuse purple glume tips in plot no.88 were identified, with former homozygosity and latter heterozygosity.

Preliminary localization of genes for the purple glume trait

After combining the differential SNP distribution among samples to analyze the location of the target gene loci, the regions where the differential SNPs were located and their genotypic characteristics were analyzed to clarify further the regions where the target genes were located, the phenotypic mixed-sample pool of differential SNPs for colorless and purple-spiked glume tips in plot no.68 was highly concentrated on chromosomes 4 and 6 (Figure 3). Differential SNPs on chromosome 4 of the colorless glume tip-sample were labeled heterozygous, whereas differential SNPs on chromosome 6 were labeled homozygous. The purple-spiked glume tip samples showed higher concentrations of differential SNP markers that were homozygous for chromosome 4 and heterozygous for chromosome 6. The screening was conducted contiguously with SNP loci intervals consistent with this characterization: Chr4:18083552-33309544, Chr6:1824125-8110690. Many highly concentrated differential SNP markers were observed on chromosome 6 between the colorless glume tip and the diffuse purple glume tip, with the former homozygous and the latter heterozygous. The interval of consecutive SNP loci that fit this characterization was Chr6:1824125-8110690. Many highly concentrated SNP differences were observed between diffuse purple and purple-spiked glumes on chromosome 4, with the former being heterozygous and the latter homozygous. The consecutive SNP locus interval consistent with this characterization was Chr4:20920636-33309544 (Table 2). A large number of highly concentrated SNP were observed on chromosome 6 between the colorless glume tips and diffuse purple glume tips in plot no.88. The former was homozygous, and the latter was heterozygous. The interval of contiguous SNP loci consistent with this characterization was Chr 6:2926795-8039284 (Table 2).

These results indicated that the color of the glume tip was controlled by at least two genes in the studied population. The glume tip is colorless (or pale green) when the purple apiculus P locus is homozygous and recessive; otherwise, it appears diffuse purple or purple-spiked. Purple apiculus P exhibited a recessive epistatic effect on Purple apiculus C (Table 2). *In the present study, the interval located on chromosome 6 contained genes for wide compatibility, indica-japonica hybrid sterility, and other traits, such as S5-ORF5, S5-ORF4, and S5-ORF3, in line with previous studies* (Chen et al. 2008).

Table 2. Information on markers related to purple glume tip traits in rice

Interval name	Chromosomes	Marker interval	Interval size (M)
Purple apiculus P	4	20920636-33309544	12.34
Purple apiculus C	6	2926795-8110690	5.18

Table 3. Control genes for anthocyanin biosynthesis

Gene	Gene location	Role description
Os04g0557500	chr04:27915598 ~ 27939357	Maize R/B gene homologs that regulate anthocyanin pigment deposition
Os06g0205100	chr06:5315163 ~ 5316875	Determinants of anthocyanin content of leaf, glume tip, and leaf sheath color in rice

Many genes are involved in the regulation of the purple glume tips. For example, Choudhury et al. (2014) found that other genes may determine the coloration of glume tips in addition to *OsC1*, and Mori and Takahashi (1981) proposed a C-A-P polygene model. Zhou et al. (1996) suggested that at least four genes, the dominant chromogen gene *C* and activation gene *A*, and two dominant *P* genes, are required for the purplish-red coloration of the glume tip. Based on the C-S-A gene system, three genes determine the coloration of anthocyanin pigmentation in rice organs (Sun et al. 2018). In this study, two genes were found to interact and determine the color of the glume tips, consistent with the C-A-P gene system hypothesis. Although other genes may be involved, there was no segregation of other possible genes that affected phenotypic segregation within the population.

Prediction of target genes within intervals

Located in the interval Chr4:20920636–33309544, 162 genes were present, of which *Os04g0557500* was located on Chr4:27915598–27939357 and regulated anthocyanin pigmentation. The locus Chr6:2926795-8110690 interval contains 125 genes, of which *Os06g0205100* is a determinant of leaf, glume tip, leaf sheath color, and anthocyanin content in rice (Table 3). *Os06g0205100* and *Os04g0557500* may be target genes.

The complementary hypothesis of the C-A-P gene system suggests that the differences in rice organ coloration are due to anthocyanin metabolism. The three dominant genes are the chromogen gene *C*, the gene *A* for the activation of anthocyanin, and the complementary gene *P* (which determines the tissue of pigment deposition) (Mori and Takahashi 1981, Zhou et al. 1996). In this study, two gene loci that control the color of the glume tip were subjected to primary localization analysis. The Purple apiculus C segment overlapped with the results of the localization of the *C* gene, and the Purple apiculus P segment coincided with the functional description of the gene *P*. Sun et al. (2018) proposed a C-S-A genetic system for the anthocyanin synthesis pathway. In the C-S-A genetic system of the anthocyanin synthesis pathway, the *C* gene acts as a color-producing gene, *S* determines the tissue specificity of pigmentation, and *C* interacts with *S* to activate the expression of *A*. The glume tip was green when no *C* gene existed, but the *S* and *A* genes, or both, coexisted. The *C* gene is located on chromosome 6 between RM5754 and RM19565 as *Os06g0205100* (Ithal and Reddy 2004, Wang et al. 2020, Du et al. 2022). The *S* gene is located on chromosome 4, between RM3820 and MM2687 as *Os04g0557500* (Sakamoto et al. 2001, Oikawa et al. 2015). The *A* gene is located on chromosome 1 near 49kb as *Os01g0633500*. These data suggest that the *C* gene is the switch that controls color production, which is consistent with most anthocyanin studies in rice. In this study, the major acting gene loci were located on chromosomes 6 and 4, where the purple apiculus C region overlapped with the *C* gene localization, and the purple apiculus P region overlapped with the *P* gene localization. Therefore, in combination with previous studies on CAP, C-S-A, and other genic systems using the DNA marker localized in this study, it was speculated that Purple apiculus C corresponds to the *C* gene, with a high probability of *Os06g0205100* and Purple apiculus P corresponds to the *P* gene, with a high probability of *Os04g0557500*.

CONCLUSION

The rice glume tip color has three relative traits: colorless (green), diffuse purple, and purple-spiked. Three relative phenotypes of glume tip color existed instead of two. The diffuse purple and purple-spiked glume tips are very similar but distinctly different and are mainly regulated by two pairs of alleles in the recessive epistatic reciprocal mode, likely *Os06g0205100* and *Os04g0557500* genes.

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DATA AVAILABILITY

The datasets generated and/or analyzed during the current research are available from the corresponding author upon reasonable request.

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