INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
17–1337/2018/20–12–2805–2811
DOI: 10.17957/IJAB/15.0838
http://www.fspublishers.org

Full Length Article

Characterization and Fine Mapping of Two White Panicle Genes with Duplicated Effect in Rice

Wenkai Lv[1†], Hui Hu[1†], Liping He[1†], Xiancheng Zhang[1], Xiaoxue Ou[1], Huoyun Chen[1], Sibin Yu[4], Jianlong Xu[2,3*], Xianjin Qiu[1*], Zhixin Li[1], Junying Xu[1], Xiaoyan Wang[1], Zhangyong Liu[1], Chongrong Wang[5], Jiefeng Jiang[6] and Jue Lou[7]

[1]*Hubei Collaborative Innovation Center for Grain Industry/Hubei Key Laboratory of Waterlogging Disaster and Agricultural Use of Wetland (Yangtze University) /College of Agriculture, Yangtze University, Jingzhou 434025, China*
[2]*Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing 100081, China*
[3]*Shenzhen Institute of Breeding & Innovation, Chinese Academy of Agricultural Sciences, Shenzhen 518120, China*
[4]*National Key Laboratory of Crop Genetic Improvement/College of Plant Science and Technology, Huazhong Agriculture University, Wuhan 430070, China*
[5]*Guangdong Provincial Key Laboratory of New Technology in Rice Breeding, Rice Research Institute, Guangdong Academy of Agricultural Sciences, Guangzhou 510640, China*
[6]*Ningbo Academy of Agricultural Sciences, Ningbo 315040, China*
[7]*Southen Zhejiang Key Laboratory of Crop Breeding, Wenzhou Academy of Agricultural Sciences, Wenzhou 325006, China*
[*]For correspondence: xjqiu216@yangtzeu.edu.cn; hualiandie0119@163.com; xujlcaas@126.com
[†]These authors contributed equally to this work

Abstract

Photosynthesis provides food and energy for all organisms on Earth, but their genetic basis particularly in rice panicle is unknown. In this study, the characterization of GZ-wp, a new rice white panicle mutant from the progeny of *indica* thermo-sensitive genic male sterile line Guangzhan 63-4S (GZ63-4S) with seeds treated by ethylmethane sulfonate was described. The results showed white panicle at heading stage and normal phenotype in other organs at whole developing stages, and some yield related traits decreased. Chlorophyll content accumulation reduced in GZ-wp. Transmission electron microscopy analysis suggested normal chloroplast structure but decreased chloroplast numbers. Genetic analysis indicated the white panicle was controlled by two independent recessive nuclear genes with duplicated effect, designed as *wp5* and *wp6*. Finally, *wp5* and *wp6* were fine mapped to 211 kb and 175 kb regions on chromosome 1 and 7, respectively. The present results will facilitate the cloning of these two genes and help in understanding the genetic basis of chloroplast development in rice panicle.
© 2018 Friends Science Publishers

Keywords: White panicle; Chloroplast number; Duplicated effect; Fine mapping

Introduction

World's population has been sharply increasing since 1960s, and more than half food must be produced in the next half century (Khush, 2005). Starch is the main food and energy supply for world's people, which is the product of photosynthesis. The current average light use efficiency of crops is about 0.5% with the maximum up to 5%. If the light use efficiency increases, the crop yield could enhance largely (Moss and Musgrave, 1974; Zelitch, 1982). This necessitates the illustration of the genetic basis of photosynthesis. The photosynthesis takes place in chloroplast, which is semiautonomous organelle and has its own genome (Kusumi *et al.*, 2004). The development of mature chloroplast starts from proplastid and undergoes three steps (Kusumi *et al.*, 2004; Munekage *et al.*, 2004). In the first step, DNA in the proplastid synthesizes rapidly and proplastid replicates. In the second step, the genetic system is established, and in the last step, photosynthesis activity builds up.

A lot of rice genes taking part in this process are cloned by developing mutants, mainly leaf color mutants (white and yellow). About 160 leaf color mutants have been characterized and more than 30 genes were cloned (Tanaka and Tanaka, 2006; Pogson and Albrecht, 2011; Leng *et al.*, 2017), hence, the genetic basis of chloroplast development and photosynthesis in leaf are relatively clear. Normal panicle color in most leaf color mutants suggested that the

To cite this paper: Lv, W., H. Hu, L. He, X. Zhang, X. Ou, H. Chen, S. Yu, J. Xu, X. Qiu, Z. Li, J. Xu, X. Wang, Z. Liu, C. Wang, J. Jiang and J. Lou, 2018. Characterization and fine mapping of two white panicle genes with duplicated effect in rice. *Int. J. Agric. Biol.*, 20: 2805–2811

genetic basis of chloroplast development and photosynthesis between the two organs are different. However, the genetic basis of these in panicle is still unclear.

Till now, twelve white panicle mutants and twelve genes for chloroplast development in panicle have been characterized (Sanchez and Khush, 1994; Li *et al.*, 2003; Jin *et al.*, 2011; Chen *et al.*, 2012; Li *et al.*, 2014; Song *et al.*, 2014; Chen *et al.*, 2015; Wang *et al.*, 2015b; Wang *et al.*, 2016; Wei *et al.*, 2017; Zhang *et al.*, 2017). wp1 and wp2 were used as two morphological markers, located on chromosome 7 and 1, respectively (Sanchez and Khush, 1994). wp(t) displays white stripe on the basal leaves and white panicle at heading stage (Li *et al.*, 2003). It's controlled by a single recessive gene in a 3 cM region on chromosome 1. wslwp and st-wp exhibit stripe leaf at seedling stage and white panicle at heading stage (Jin *et al.*, 2011; Chen *et al.*, 2015). These both are controlled by single recessive nuclear genes. *wslwp* is located in a 87 kb region on chromosome 7, with 11 candidate genes. *st-wp* was fine mapped to a 9.2 kb region on chromosome 6, in which region a single-nucleotide mutation was found for Ribonucleoside-diphosphate reductase small chain, and it's allelic to *St1* and *Gws* (Yoo *et al.*, 2009; Xu *et al.*, 2010). st-fon exhibits white stripe leaf and shoot at whole developing stage, white panicle at heading stage and abnormal glumous flower. Genetic analysis indicates that *st-fon* is a cytoplasm gene (Chen *et al.*, 2012). zebra254 exhibits zebra leaf at seedling stage and white panicle in heading stage. Single-nucleotide mutation was found for *β-OsLCY* in mutant, which may be the responsible gene for the mutant (Li *et al.*, 2014). wp4 displays yellow green leaf at whole developing stage and white panicle at heading stage (Wang *et al.*, 2015b). *wp4* was fine mapped to a 79 kb region on chromosome 8, with 14 candidate genes. Transmission electron microscopy shows that chloroplast appears no well-structured lamellar structure in above mutants, indicating that these genes take part in the first step of chloroplast development. Besides, the yield and related traits of mutants decrease.

Among these twelve genes, only four have been cloned. *WLP1* encodes a 50S ribosome L13 protein, localized to the chloroplast (Song *et al.*, 2014). It mainly expresses in green tissues and particularly in the early seedling leaves, and the expression level is induced by low temperature. *WP1* encodes a Vat-tRNA synthetase (OsValRS2) targeted to both chloroplast and mitochondria (Wang *et al.*, 2016). Mutation of *WP1* causes virescent to albino phenotypes at seedling stage and white panicle at heading stage. This gene plays an important role in regulating chloroplast ribosome biogenesis and is essential for chloroplast development. *WSP1* encodes a protein similar with multiple organellar RNA editing factors (*MORFs*), localized to chloroplasts (Zhang *et al.*, 2017). Mutation of *WSP1* affects the editing of multiple organellar RNA sites, chloroplast ribosome biogenesis and *ndhA* splicing. *OsAK1* encodes a rice adenylate kinase localized to chloroplast (Wei *et al.*, 2017). Hypermethylation at promoter region caused silencing of *OsAK1* and resulted in albino in young leaf and panicle. Many genes associated with photosynthesis processes are downregulated in mutant.

In this study, a new white panicle mutant from the progeny of *indica* thermo-sensitive genic male sterile line Guangzhan 63-4S (GZ63-4S) with seeds treated by ethylmethane sulfonate (EMS) was reported and termed it as GZ-wp. The mutant displayed only white panicle at heading stage and mutation trait was controlled by two independent recessive nuclear genes (*wp5* and *wp6*) with duplicated effect. Using Simple Repeat Sequence (SSR) markers, these were fine mapped to 211 kb and 175 kb on chromosome 1 and 7, respectively. The present results will facilitate the cloning of these two genes and help understanding the genetic basis of chloroplast development in rice panicle.

Materials and Methods

Plant Materials and Field Experiments

The mutant GZ-wp was isolated from the progeny of *indica* thermo-sensitive genic male sterile line GZ 63-4S with seeds treated by EMS. The mutant was crossed with two *indica* varieties (Huanghuazhan and 93-11) and two *japonica* varieties (02428 and Beilu130) to construct four F_2 segregating populations for the inheritance pattern analysis. Among them, the F_2 population derived from GZ-wp and 02428 was used for gene mapping. For fine mapping *wp5* and *wp6*, a large segregating population containing 30534 individuals was grown at experimental farm of Yangtze University, Jingzhou, China (30.18°N, 112.15°E). All field management followed local farmers' practices.

Agronomic Traits Evaluations

The mutant GZ-wp and wide type GZ63-4S were planted at Lingshui, China (18.51°N, 109.83°E). Ten plants of each line were used to evaluate yield related traits following the methods described in Qiu *et al.* (2012), including heading date, plant height, panicle number, panicle length, primary branch number, spikelet number per panicle, grain number per panicle, seed setting ratio, 1000-grain weight and grain yield per plant. To measure the mutation effect for agronomic traits in hybrid state, GZ-wp was crossed with 93-11, and Yangliangyou 6, a widely cultivated variety at Yangtze River valley derived from GZ63-4S and 93-11, was used as control. The two hybrid lines were also measured for yield and related traits as described above at Jingzhou, China.

Transmission Electron Microscopy (TEM) Analysis

Rice hull of both GZ-wp and GZ63-4S at heading stage were harvested to examine chloroplast development using transmission electron microscopy (TEM) following the

method as described in Inada *et al*. (1998). The samples were fixed in 2.5% glutaraldehyde at 4℃ for 4 h, rinsed, then incubated overnight in 1% osmium tetroxide (OsO_4) at 4℃, dehydrated in a series of ethanol, and finally embedded in Suprr's medium prior to ultrathin sectioning. Then, the samples were stained and examined using a Hitachi H-7650 transmission electron microscope (Tokyo, Japan).

Chlorophyll Content Measurement

The panicle chlorophyll content was determined as described previously (Arnon, 1949) with minor modification. A 0.1 g sample was ground to powders in liquid nitrogen and transferred to a 2 mL centrifuge tube. Then 2 mL buffer (ethanol: acetone: water=4.5: 4.5: 1) was added to the tube, and mixed thoroughly. After that, mixture stood for 12 h in dark. Finally, the supernatant was analyzed by spectrophotometric scanning at 663 nm and 645 nm.

DNA Extraction and Marker Analysis

Young seedling leaves were harvested and DNA was extracted using the CTAB method (Murray and Thompson, 1980) with minor modification. A bulked segregant analysis (BSA) approach was used for screening the responsible genes (Michelmore *et al.*, 1991). DNA of ten individuals with green and white panicles respectively from the F_2 population derived from GZ-wp and 02428 were pooled into two DNA bulks. 531 SSR markers evenly distributed on 12 chromosomes were used to survey polymorphic markers between two parents. The polymorphic markers were then used for evaluating polymorphism between two DNA bulks. Using the latter polymorphic markers, all individuals from F_2 population were genotyped for linkage analysis. For fine mapping, all white panicle individuals from the large F_2 population were genotyped with two ends of the candidate region to identify recombinants. All SSR markers in the candidate region were designed according GRAMENE database (http://www.gramene.org/) and also used to survey polymorphic markers between two parents. The polymorphic markers were then used to genotype the recombinants. The 10 μL PCR reaction volume contained 50 ng of template DNA, 1.0 μL 10× PCR buffer, 0.1 m*M* dNTP, 0.1 μM of each primer, and 0.1 U Taq DNA polymerase. The PCR protocol included an initial denaturation step of 95℃/3 min, followed by 32 cycles of 95℃/30 s, 55℃/30 s, and 72℃/40 s, and final extension step of 72℃/5 min. Finally, the amplicons were separated in 4% polyacrylamise gels and visualized by silver staining.

Data Analysis

Likage map was constructed by MAPMAKER 3.0 software (Lander *et al.*, 1987). Difference analysis was performed in Statistica 5.5 (Morales, 2001).

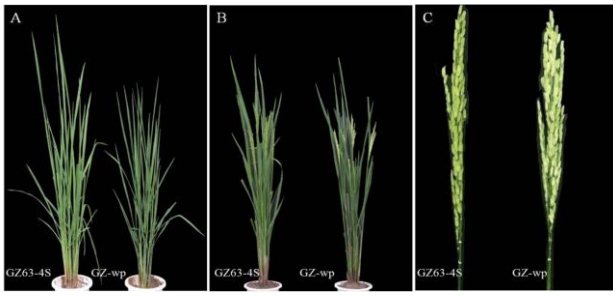

Fig. 1: Phenotypic comparison of GZ63-4S and GZ-wp
A Comparison of plants between GZ63-4S and GZ-wp at seedling stage; **B** Comparison of plants between GZ63-4S and GZ-wp at heading stage; **C** Comparison of panicles between GZ63-4S and GZ-wp at heading stage

Results

Effect on Chlotophyll Content and Agronomic Traits in GZ-wp Mutant

The rice mutant GZ-wp was identified from the progeny of GZ63-4S with seeds treated by EMS. Under normal field condition, leaves of GZ-wp mutant were green like wild-type GZ63-4S at all developing stages (Fig. 1A, B), while the panicles of GZ-wp were white at heading stage (Fig. 1B, C). Consistent with this observation, the chl *a*, chl *b* contents and total chlorophyll contents in panicles of GZ-wp mutant was significantly lower than those of GZ63-4S (Fig. 2F). Compared with GZ63-4S, most agronomic traits in GZ-wp slightly reduced, but it was significantly decreased for grain number per panicle, seed setting ratio, 1000-giran weight and yield per plant (Table 1). To measure the mutation effect for agronomic traits in hybrid state, two hybrid lines (GZ-wp/93-11 and GZ63-4S/9311) measured for yield and related traits (Table 1). All agronomic traits displayed no significant difference between two hybrids.

Chloroplast Development

The chloroplast changes were compared by the chloroplast ultrastructures of hulls between GZ-wp mutant and GZ63-4S using TEM method. Under field conditions, the lamellar structure of GZ63-4S chloroplasts was well developed (Fig. 2A) and grana stacks and stroma lamellae normal (Fig. 2C). Similarly, the development of lamellar structure of GZ-wp chloroplasts was also normal (Fig. 2B), with normal-looking grana stacks and stroma lamellae (Fig. 2D). In contrast, chloroplast number of panicle in GZ-wp was significantly less than in GZ63-4S (Fig. 2E). These results suggested that the white panicle phenotype and reduced chlorophyll contents of GZ-wp mutant were due to reduced chloroplast number.

Preliminary Mapping of *wp5* and *wp6*

For genetic analysis of white panicle phenotype in GZ-wp mutant, four crosses were made between GZ-wp and green

Table 1: Agronomic traits analysis of GZ63-4S, GZ-wp, GZ63-4S/9311 and GZ-wp/9311

Trait	GZ63-4S	GZ-wp	GZ63-4S/9311	GZ-wp/9311
Heading date (d)	94.55 ± 1.67	93.21 ± 1.33	96.67 ± 0.33	97.25 ± 1.25
Plant height (cm)	83.20 ± 3.27	79.2 ± 4.55	126.33 ± 2.86	122.75 ± 3.70
Panicle number	11.00 ± 3.52	12.00 ± 4.85	14.33.00 ± 2.19	16.00 ± 3.21
Panicle length (cm)	25.04 ± 0.58	24.80 ± 1.92	27.73 ± 0.55	26.10 ± 0.42
Primary branch number	9.80 ± 0.84	10.80 ± 1.48	11.89 ± 0.11	11.00 ± 0.33
Spikelet number per panicle	163.80 ± 14.31	177.00 ± 17.93	225.33 ± 20.17	259.44 ± 14.59
Grain number per panicle	143.09 ± 15.24	105.81 ± 13.53**	187.89 ± 18.46	237.44 ± 16.63
Seed setting ratio (%)	85.05 ± 6.99	61.27 ± 8.26*	88.24 ± 3.84	91.37 ± 3.35
1000-grain weight (g)	18.32 ± 1.08	15.73 ± 2.01**	27.05 ± 0.52	26.68 ± 0.77
Yield per plant (g)	23.25 ± 7.04	15.13 ± 5.13**	56.43 ± 6.11	70.84 ± 11.93

*, ** represent $p < 0.05$ and 0.01

Table 2: Phenotype of F_1 plants and segregating F_2 populations from the crosses between GZ-wp and four white panicle varieties

cross	Panicle color of F_1 plants	Panicle color in F_2 population			χ^2（15:1）
		green	white	Total	
GZ-wp/02428	green	871	70	941	1.76
GZ-wp/Beilu130	green	596	48	644	1.18
GZ-wp/93-11	green	887	53	940	0.55
GZ-wp/Huanghuazhan	green	1195	85	1280	0.26

$\chi^2_{0.05}$=3.84

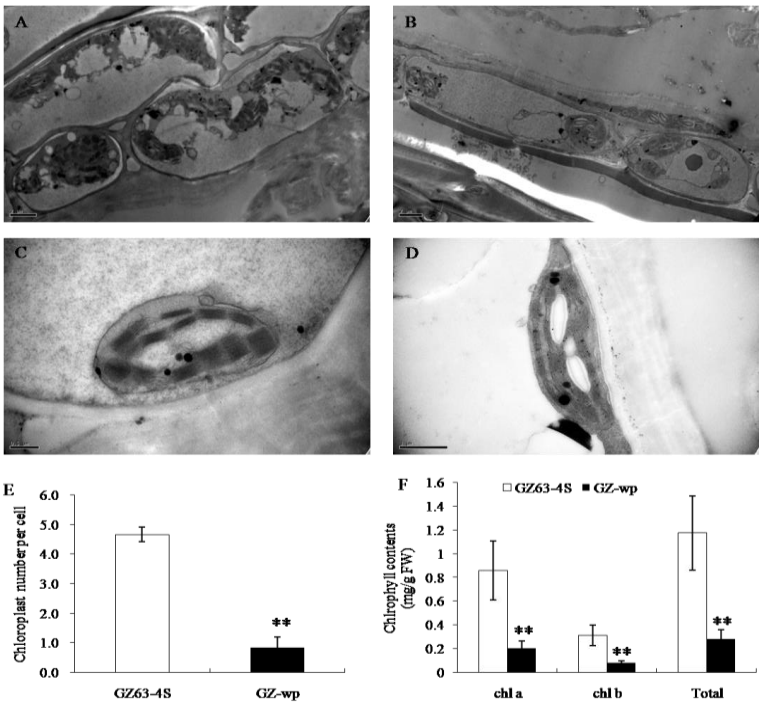

Fig. 2: Ultra-structure of chloroplasts and chlorophyll contents in GZ63-4S and GZ-wp

A and C Ultra-structure of chloroplasts of panicle in GZ63-4S at heading stage; B and D Ultra-structure of chloroplasts of panicles in GZ63-wp at heading stage; E Comparison of chloroplast number per cell of panicles between GZ63-4S and GZ-wp at heading stage; F Comparison of Chl *a*, chl *b*, and total chlorophyll contents of panicles between GZ63-4 S and GZ-wp at heading stage. *, ** represent $p < 0.05$ and 0.01

panicle varieties of 02428, Beilu130, 9311 and Huanghuazhan (two *japonica* and two *indica*), respectively. All the F_1 individuals displayed green panicles, and the panicle color segregated in all F_2 populations (Table 2). Moreover, panicle color of all four populations segregated at 15: 1 ratio of green panicle plants to white panicle plants. These results indicated that the white panicle phenotype was caused by two independent recessive nuclear genes, which had duplicated effect on white panicle, and were designed as *wp5* and *wp6*.

The F_2 population derived from GZ-wp and 02428 was used to determine the locations of *wp5* and *wp6*.

Firstly, 531 SSR markers evenly distributed on 12 chromosomes were used to survey polymorphic markers between GZ-wp and 02428. Among them, 295 SSR markers showed polymorphism between them. Secondly, ten individuals with green and white panicles respectively were selected to create two DNA bulk pools. BSA showed seven polymophic markers detected between two bulked DNAs, three (RM243, RM581 and RM580) closed linked on the short arm of chromosome 1 and four (RM214, RM432, RM11 and RM336) linked on the long arm of chromosome 7. Then, the 70 recessive phenotype (white panicle) plants were genotyped for all seven polymorphic markers to construct the linkage map of *wp5* and *wp6* (Fig. 3). Finally, *wp5* was flanked between RM581 and RM580, while *wp6* was flanked between RM432 and RM336, and co-segregated with RM11.

Fine Mapping of *wp5* and *wp6*

To further fine mapping *wp5* and *wp6*, a large F_2 segregating population containing 30534 individuals derived from GZ-wp and 02428 was planted and a total of 1871 white panicle plants were selected. These were then screened with four SSR flanking markers (RM581, RM580, RM432 and RM336) for *wp5* and *wp6*, respectively. Sixty, one hundred and ninety recombinants were identified in the regions of RM581-RM580 and RM432-RM336, respectively. All SSR markers in the two regions were used for evaluating polymorphism between two parents. Then two and seven markers were used to genotype all recombinants and construct high-resolution map of *wp5* and *wp6* (Fig. 3), respectively. According to their genotypes, sixty recombinants were grouped into five groups for *wp5* (Fig. 3A). The group M5 contained the heterozygous genotype downstream of RM580 and displayed white panicle, so it was eliminated. Using the same procedure, the RM8132-RM580 region was also eliminated by M4. Of the most important were M1, M2 and M3. All of them recombined between RM581 and RM1032, indicating that *wp5* was located in the recombinant region of approximately 211 kb between RM581 and RM1032.

A total of one hundred and ninety recombinants were detected for *wp6*, and grouped into nine groups. The group M6 was heterozygous upstream of RM432, thus it was eliminated. Using the same procedure, the region of RM432-RM11 and downstream of RM3404 were also eliminated by M7, M10, M11, M12, M13 and M14. The great important recombinant groups were M8 and M9, which both recombined between RM21690 and RM21706, suggested that *wp6* was fine mapped in the region of approximately 175 kb between RM21690 and RM21706 (Fig. 3B).

Discussion

wp5 and *wp6* were Two New Genes for White Panicle

In present study, a white panicle mutant (GZ-wp) was characterized and two responsible genes, *wp5* and *wp6*, were fine mapped to 211 kb and 175 kb regions respectively. GZ-wp exhibited only white panicle at heading stage and other organs were normal. Differently, most mutants displayed both white panicle and white/stripe/zebra/yellow leaves (Li *et al.*, 2003; Jin *et al.*, 2011; Li *et al.*, 2014; Song *et al.*, 2014; Chen *et al.*, 2015; Wang *et al.*, 2015b; Wang *et al.*, 2016; Wei *et al.*, 2017; Zhang *et al.*, 2017). Besides, TEM analysis indicated that chloroplast developed normally in GZ-wp, but chloroplast number was significantly less than GZ63-4s, while other mutants except Epi-AK1 showed abnormal chloroplast development. These evidences indicated that GZ-wp was a new white panicle mutant. Moreover, all mutation phenotypes were controlled by single recessive nuclear gene or cytoplasmic gene in previous studies (Sanchez and Khush, 1994; Li *et al.*, 2003; Jin *et al.*, 2011; Chen *et al.*, 2012; Li *et al.*, 2014; Song *et al.*, 2014; Chen *et al.*, 2015; Wang *et al.*, 2015b; Wang *et al.*, 2016; Wei *et al.*, 2017; Zhang *et al.*, 2017), and these genes were located on chromosome1, 2, 6, 7 and 8. In contrast, white panicle of GZ-wp was controlled by two independent recessive nuclear genes (*wp5* and *wp6*) with duplicated effect on white panicle. Of the most importance, *wp5* and *wp6* were fine mapped on chromosome 1 and 7 respectively with no same or similar regions of all above genes. All evidences suggested that *wp5* and *wp6* were new genes for white panicle.

Implication of *wp5* and *wp6*

Color is very important for identifying different varieties. Besides, it can be morphological marker for other important traits, and most of these were derived from mutations (Sanchez and Khush, 1994). There are numerous yield and quality genes linked with *wp6* on chromosome 7, such as *Ghd7* (Xue *et al.*, 2008), *qPGWC-7* (Zhou *et al.*, 2009), *Ghd7.1* (Yan *et al*., 2013), *GLW7* (Si *et al.*, 2016), *GL7*/*GW7* (Wang *et al.*, 2015a, c) and *SGDP7* (Bai *et al.*, 2017). By mutating *wp5* and *wp6* in the carrier varieties of above genes, white panicle can be an important morphological marker. Moreover, similar to most other white panicle mutants, mutation of *wp5* and *wp6* displayed decrease of yield related traits, such as grain number per panicle, seed setting ratio, 1000-grain weight and yield per plant (Table 1). After further fine mapping and cloning of *wp5* and *wp6*, their novel alleles to enhance rice yield related traits can be found. Of the most important, *wp5* and *wp6* can be important morphological marker for identifying and increasing purity of hybrid seed. Rice yield was sharply increased due to use of heterosis at 1970s, and high purity of

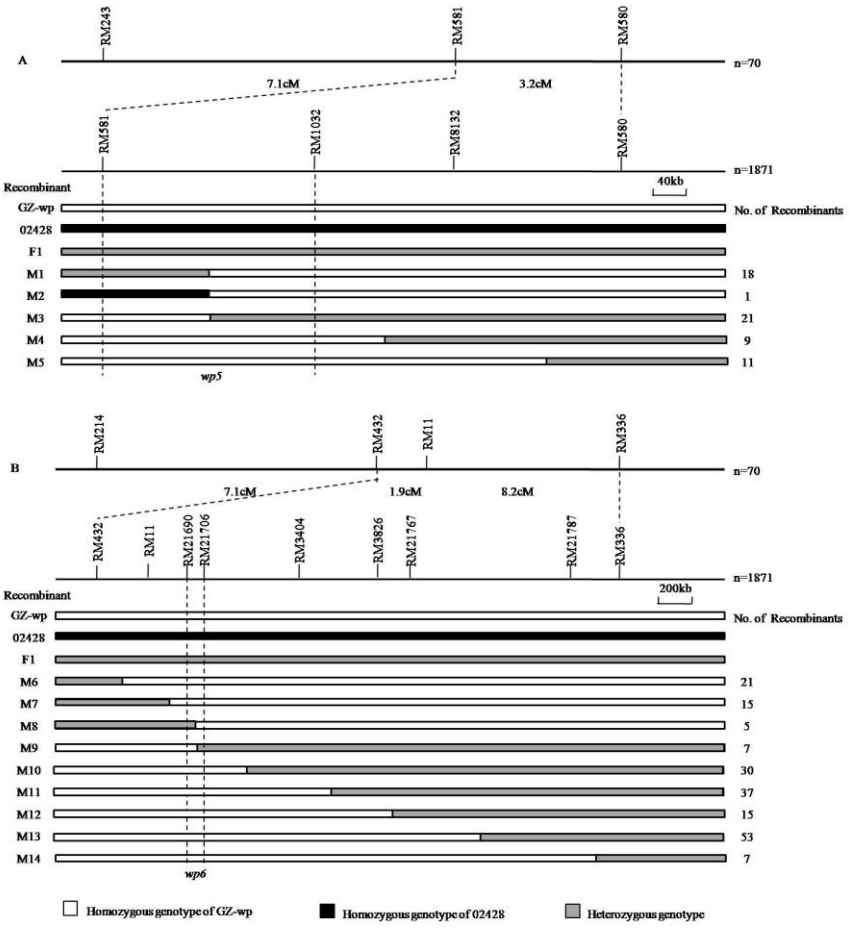

Fig. 3: Fine mapping of *wp5* and *wp6*
A Fine mapping of *wp5*; B Fine mapping of *wp6*

hybrid seed is the basis of its high yield. The conventional method to identify purity of hybrid seed is to plant the hybrid in another season or another place, which must use more time and money (Zhu *et al.*, 2015). Using white panicle phenotype, other plants mixed in sterile population can be eliminated rapidly to increase the hybrid purity at seed production stage, and sterile lines can be easily distinguished from hybrid progenies to identify seed purity. Thus, white panicle controlled by *wp5* and *wp6* had large advantages for increasing and identifying hybrid seed purity without negative effect on hybrid's yield (Table 2). In summary, *wp5* and *wp6* had large valuable implication for high yield breeding and hybrid seed production.

Conclusion

In this study, a new rice white panicle mutant named GZ-wp was characterized. It displayed white panicle at heading stage and normal phenotype for other organs, some yield related traits decreased, and chlorophyll accumulation was reduced. Chloroplast structure was normal in white panicle but chloroplast number decreased. White panicle was controlled by two independent recessive nuclear genes with duplicated effect. They were fine mapped to 211 kb and 175 kb regions on chromosome 1 and 7, respectively.

Acknowledgements

This work was partially supported by National Key Research and Development Program of China (2016YFD0300208), open funds of the National Key Laboratory of Crop Genetic Improvement (ZK201603), Hubei Collaborative Innovation Center for Grain Industry (LXT-16-08, LXT-16-17), the Yangtze Fund for Youth Teams of Science and Technology Innovation (2015cqt02), Ningbo Science and Technology Project (2017C10062), Southern Zhejiang Key Laboratory o Crop Breeding (2018SZCB03), Guangdong Provincial Key Laboratory of New Technology in Rice Breeding, and Innovation and entrepreneurship training project for college students of Yangtze University (2016095, 2017169).

References

Arnon, D.I., 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. *Plant Physiol*., 24: 1–15

Bai, X.F., Y. Huang, Y. Hu, H.Y. Liu, B. Zhang, C. Smaczniak, G. Hu, Z.B. Han and Y.Z. Xing, 2017. Duplication of an upstream silencer of *FZP* increases grain yield in rice. *Nat. Plants*, 3: 885–893

Chen, D.X., T. Li, G.L. Qu, W.J. Huang, Z.Q. He and S.G. Li, 2012. Characterization and genetic analysis of a streaked and abnormal glumous flower mutant st-fon. *Chin. J. Rice Sci*., 26: 677–685

Chen, Y.P., Z. Zhai, W.J. Yang, J. Sun, X.L. Shu and D.X. Wu, 2015. Genetic analysis and fine mapping of *St-wp* gene in mutant rice with stripe white leaf and white panicle. *J. Nucl. Agric. Sci*., 29: 1246–1252

Inada, N., A. Sakai, H. Kuroiwa and T. Kuroiwa, 1998. Three-dimensional analysis of the senescence program in rice (*Oryza sativa* L.) coleoptiles. *Planta*, 206: 585–597

Jin, Y., H.Q. Liu, D.K. Wang and Y.Z. Tao, 2011. Genetic analysis and gene mapping of a white stripe leaf and white panicle mutant in rice. *Chin. J. Rice Sci*., 25: 461–466

Khush, G.S., 2005. What it will take to feed 5.0 billion rice consumers in 2030. *Plant Mol*., 59: 1–6

Kusumi, K., A. Yara, N. Mitsui, Y. Tozawa and K. Iba, 2004. Characterization of a rice nuclear-encoded plastid RNA polymerase gene *OsRpoTp*. *Plant Cell Physiol.*, 9: 1194–1201

Lander, E.S., P. Green, J. Abrahamson, A. Barlow, M.J. Daly, S.E. Lincoln and L.A. Newberg, 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics*, 1: 174–181

Leng, Y., D. Xue, L. Huang, L. Chen, D. Ren, Y. Yang, G. Zhang, J. Hu, L. Zhu, L. Guo, Y. Lin, Q. Qian and D. Zeng, 2017. Mapping QTL with main effect, digenic epistatic and QTL × environment interactions of panicle related traits in rice (*Oryza sativa*). *Int. J. Agric. Biol*., 19: 1608–1614

Li, H., Q. Qian, Y. Wang, X. Li and J. Xu, 2003. Characterization and mapping of a white panicle mutant gene in rice. *Chin. Sci. Bull.*, 48: 457–459

Li, Y.Q., P. Zhong, Z.Y. Gao, B.Y. Zhu, D. Chen, C.H. Sun, P.R. Wang and X.J. Deng, 2014. Morphological characterization and candidate gene analysis of zebra leaf mutant zebre254 in rice. *Sci. Agric. Sin*., 47: 2907–2915

Michelmore, R.W., I. Oaran and R.V. Kesseli, 1991. Identification of markers linked to disease-resistance genes by bulk analysis: a rapid method to detect markers in specific genomic region by using segregating population. *Proc. Natl. Acad. Sci. U.S.A.*, 88: 9828–9832

Morales, M., 2001. Statistica, Version 5.5. *Bull. Ecol. Soc. Amer*., 82: 126–127

Moss, D.N. and P.B. Musgrave, 1974. Photosynthesis and crop production. *Adv. Agron*., 23: 317–336

Munekage, Y., M. Hashimoto, C. Miyake, K., Tomizawa, T. Endo, M. Tasaka and T. Shikanai, 2004. Cyclic electron flow around phtosystem I is essential for photosynthesis. *Nature*, 429: 579–582

Murray, M.G. and W.F. Thompson, 1980. Rapid isolation of high molecular-weight plant DNA. *Nucl. Acids Res.*, 8: 4321–4326

Pogson, B.J. and V. Albrecht, 2011. Genetic dissection of chloroplast biogenesis and development: an overview. *Plant Physiol*., 155: 1545–1551

Qiu, X.J., R. Gong, Y.B. Tan and S.B. Yu, 2012. Mapping and characterization of the major quantitative trait locus *qSS7* associated with increased length and decreased width of rice seeds. *Theor. Appl. Genet.*, 125: 1717–1726

Sanchez, A.C. and G.S. Khush, 1994.Chromosome location of some marker genes in rice using the primary trisomics. *J. Hered*., 85: 297–300

Si, L.Z., J.Y. Chen, X.H. Huang, H. Gong, J.H. Luo, Q.Q. Hou, T.Y. Zhou, T.T. Lu, J.J. Zhu, Y.Y. Shangguan, E.W. Chen, C.X. Gong, Q. Zhao, Y.F. Jing, Y. Zhao, Y. Li, L.L. Cui, D.L. Fan, Y.Q. Lu, Q.J. Weng, Y.C. Wang, Q.L. Zhan, K.Y. Liu, X.H. Wei, K. An, G. An and B. Han, 2016. *OsSPL13* controls grain size in cultivated rice. *Nat. Genet.*, 48: 447–456

Song, J., X.J. Wei, G.N. Gao, Z.H. Sheng, D.B. Chen, C.L. Liu, G.A. Jiao, L.H. Xie, S.Q. Tang and P.S. Hu, 2014. The rice nuclear gene *WLP1* encoding a chloroplast ribosome L13 protein is needed for chloroplast development in rice grown under low temperature conditions. *Plant Mol. Biol.*, 84: 301–Tanaka, A. and R. Tanaka, 2006. Chlorophyll metabolisom. *Curr. Opin. Plant Biol.*, 9: 248–255

Wang, S.K., S. Li, Q. Liu, K. Wu, J.Q. Zhang, S.S. Wang, Y. Wang, X.B. Chen, Y. Zhang, C.X. Gao, F. Wang, H.X. Huang and X.D. Fu, 2015a. The *OsSPL16-GW7* regulatory module determines grain shape and simultaneously improves rice yield and grain quality. *Nat. Genet.*, 47: 949–954

Wang, X.W., Y.D. Jiang, H.X. Liao, B. Yang, S.Y. Zou, X.Y. Zhu, G.H. He and X.C. Sang, 2015b. Identification and gene fine mapping of white panicle mutant *wp4* in *Oryza sativa*. *Acta Agron. Sin*., 41: 838–844

Wang, Y.X., G.S. Xiong, J. Hu, L. Jiang, H. Yu, J. Xu, Y.X. Fang, L.J. Zeng, E.B. Xu, J. Xu, W.J. Ye, X.B. Meng, R.F. Liu, H.Q. Chen, Y.H. Jing, Y.H. Wang, X.D. Zhu, J.Y. Li and Q. Qian, 2015c. Copy number variation at the *GL7* locus contributes to grain size diversity in rice. *Nat. Genet.*, 47: 944–948

Wang, Y., C. Wang, M. Zheng, J. Liu, Y. Xu, X. Li, M. Niu, W. Long, D. Wang, H.Y. Wang, W. Terzaghi, Y. Wang and J. Wan, 2016. *WHITE PANICLE1*, a Val-tRNA synthetase regulating chloroplast ribosome biogenesis in rice, is essential for early chloroplast development. *Plant Physiol*., 170: 2110–2123

Wei, X.J., X.W. Song, L.Y. Wei, S.Q. Tang, J. Sun, P.S. Hu and X.F. Cao, 2017. An epiallele for rice *AK1* affects photosynthetic capacity. *J. Integr. Plant Biol.*, 59: 158–163

Xu, F.H., Z.J. Chen, J.L. Wang, Z.M. Wu, W. Sun, X, Zhang, C.L. Lei, J. Wang, F.Q. Wu, X.P. Guo, L.L. Liu and J.M. Wan, 2010. Genetic analysis and fine mapping of *Gw* gene using *green-white-stripe* rice mutant. *Acta Agron. Sin.*, 36: 713–720

Xue, W.Y., Y.Z. Xing, X.Y. Weng, Y. Zhao, W.J. Tang, L. Wang, H.J. Zhou, S.B. Yu, C.G. Xu and Q.F. Zhang, 2008. Natural variation in *Ghd7* is an important regulator of heading date and yield potential in rice. *Nat. Genet.*, 40: 761–767

Yan, W., H. Liu, X. Zhou, Q. Li, J. Zhang, L. Lu, T. Liu, H. Liu, C. Zhang, Z. Zhang, G. Shen, W. Yao, H. Chen, S. Yu, W. Xie and Y. Xing, 2013. Natural variation in *Ghd7.1* plays an important role in grain yield and adaptation in rice. *Cell Res.*, 23: 969–971

Yoo, S.C., S.H. Cho, H. Sugimoto, J. Li, K. Kusumi, H.J. Koh, K. Iba and N.C. Paek, 2009. Rice *virescent3* and *stripe1* encoding the large and small submits of ribonucleotide reductase are required for chloroplast biogenesis during early leaf development. *Plant Physiol.*, 150: 388–401

Zelitch, I., 1982. The close relationship between net photosynthesis and crop yield. *Bioscience*, 32: 796–802

Zhang, Z., X. Cui, Y. Wang, J. Wu, X. Gu and T. Liu, 2017. The RNA editing factor *WSP1* is essential for chloroplast development in rice. *Mol. Plant*, 10: 86–89

Zhou, L.J., L.M. Chen, L. Jiang, W.W. Zhang, L.L. Liu, X. Liu, Z.G. Zhang, S.J. Liu, L.J. Zhang, J.K. Wang and J.M. Wan, 2009. Fine mapping of the grain chalkiness QTL *qPGWC-7* in rice (*Oryza sativa* L.). *Theor. Appl. Genet*., 118: 581–590

Zhu, G.Q., J.P. Chen, Y.J. Zhan, D. Xue and Q.C. Zhan, 2015. Analysis on seed purity difference of same hybrid rice variety identified by different SSR primers. *Hybr. Rice*, 30: 81–84

(Received 24 November 2017; Accepted 16 July 2018)