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Genetic Analysis and Gene Mapping of a Rice White Stripe Leaf Mutant (*st10*)

Yinghong He¹, Guoxing Zou^{1,2}, Yuchun Rao¹, Jiang Hu^{1,2}, Jian Liu¹, Zhenyu Gao¹, Longbiao Guo¹, Li Zhu¹, Qian Qian¹

1. China National Rice Research Institute, Chinese Academy of Agricultural Sciences, Hangzhou, 31006, P.R. China

2. Rice Research Institute, Jiangxi Academy of Agricultural Sciences, Nanchang, 330200, P.R. China

✉ Corresponding authors email: qianqian188@hotmail.com; zhuli@caas.net.cn; Authors

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Abstract A temperature-sensitive white-stripe leaf mutant *st10* was identified from rice mutant library generated by EMS mutagenesis in our previous work, which has a genomic background of elite japonica variety Nipponbare. The leaves of mutant *st10* appears white-stripe fore and aft in two or three leaf stages, then the white color gradually weakens as the plant grows, leaf color returns to normal during heading stage, besides the leaf vein continuing to show white color. The white strip trait is obviously affected by temperature change. All of mutants would well exhibit their mutant traits growing under the high temperature condition, which appear white strip leaves and even full white panicles, whereas the white-stripe of leaf becomes narrow and the color of panicles appears normal growing the low temperature condition. The results of genetic analysis revealed that white-stripe phenotype was controlled by a single recessive nucleic gene. The F₂ population was developed from a across between peiai64s (a male sterility line) and *st10*. *St10* gene was mapped in 150 kb region between marker STR19 and marker STR24 on chromosome 3. In this research we assayed the chlorophyll contents of mutant leaves growing under the temperatures at 24°C, 28°C and 32°C, the result showed that the content of chlorophyll b and chlorophyll a were significantly reduced at the temperature of 32°C, while there is no obviously change at 24°C or at 28°C. Chlorophyll Fluorescence data revealed that maximum photosynthetic quantum capacity of the mutant was less than that of the wild-type, which would contribute the decrease of chlorophyll contents of the mutant. In this study, we constructed the genetic separate population by using Pei-Ai 64, an elite sterile line, as maternal parent and *st10* mutant as paternal parent to further analyze the genetic basis, the result demonstrated that the phenotype of the mutant trait was controlled with a single recessive locus that was mapped on chromosome 3 within the 150 kb region framed between STR19 and STR 24.

Keywords Rice (*Oryza sativa* L); Semidwarf; Green Revolution; *sd1*; Transcription; RNA diagnosis; Trait performance; Lodging resistance

Background

Chlorophyll affects crop photosynthetic efficiency through involving in capturing the light energy, charge separation and electron transfer in antenna complexes (Tanaka and Tanaka, 2006). The current study has shown that leaf color mutant gene could be directly or indirectly affect the synthesis and degradation of chlorophyll to alter chlorophyll content of mutant, consequently leading to decrease of photosynthetic efficiency to reduce crop yield and even to result in plant death (He et al., 2006). Leaf color mutations can be divided into many different types according to the

colors of seedling leaves, such as yellow, albino, light green, stripes, zebra, etc. (Wu, 1995). The studies of plant leaf color mutations have great significances to in-depth understand the relationships of chlorophyll synthesis and degradation pathways as well as to understand plant photosynthesis to further explore the mechanism of plant photosynthesis.

In recent years, it has been reported on mutations of the uneven leaf color in rice, such as the white stripe leaf, zebra leaves and so on, and most of the reported mutants were associated with temperature, the mutant phenotypes were different under the different

temperature conditions. Therefore, the studies of temperature-sensitive leaf color mutation will help to further clarify the mechanism of leaf color change, which might be the basis for in-depth exploring the relationship between photosynthesis and temperature response. Xie et al found leaf color mutant 11035 from the rice field population of TGMS 89025, a Photo-thermoperiod Sensitive Genic Male Sterile Lines, in which is characterized by the changes of intermittent loss of green happening in leaves and leaf sheaths in the low temperature whether in the seedling stage, the "zebra-type stripes" with permutation of yellow and white in whole plant occurred prior to recovering normal green as temperature had gone up again in a few days later (Xie et al., 1995). Genetic analysis of the zebra leaf B411 mutant showed the mutant trait was controlled by one pair of recessive gene. Chloroplast ultrastructure observations of yellow zone and green zone of zebra leaf revealed that development of chloroplast in green zone of zebra leaf was normal, while the shape of the chloroplast in the yellow zone was abnormal, and inner-membrane systems of the chloroplast was also incomplete, the chloroplast contained osmiophilic bodies, with the yellow zone gradually re-greening, normal chloroplast structure will being recovered (Li et al., 2008). Rice zebra leaf gene, ZEBRA2, encodes carotenoid isomerase, of which the key is the enzyme to convert cis-lycopene into trans-lycopene, mainly expressed in mesophyll cells of mature leaves, involving in the process of photo-protection. Phenotype of zebra leaf might be related to light oxidative damage in strong light conditions (Chai et al., 2010). Soo-Cheul Yoo et al (2009) reported a lethal mutant of tobacco leaf zebra *zn* (zebra-necrosis), which the phenotype is yellow and green zebra stripes occurring in the leaf sheaths cultured in high and low alternating temperatures before the leaves grown up. The gene encodes an unknown functional thylakoid-binding protein, which might be paly important roles in the accumulation process of the thylakoid protein complexes from dark to light conditions (Li et al., 2010). And Soo-Cheul Yoo et al also found that white leaf stripe mutant genes *st1* (*Strip1*) encodes the small subunit of ribonucleotide reductase, which involves chloroplast formation during the leaf growth and development. The leaves of mutant *st1* appears white stripes under

the continued temperatures of 20°C or 30°C, while cultured at alternative changes of 20°C and 30°C daily, the leaves will turn color normal (Soo-Cheul et al., 2009). Xu et al (2010) found that a temperature-sensitive white stripe mutant of rice was allelic to white stripes *st1*, but the white-striped phenotype of a temperature-sensitive white stripe mutant appears after the second leaf growing, while the white stripes of *st1* appears after the 4th or 5th leaf growing.

We have identified a temperature-sensitive white stripe leaf mutant with the background of japonica Nipponbare from the EMS mutant library constructed in our lab. Genetic analysis showed that the mutant trait was controlled by a pair of recessive nuclear genes. In this study, the chlorophyll content, chlorophyll fluorescence parameters and various agronomic traits were measured and analyzed. Genetic mapping was carried out by using separating mapping population derive from the cross of PeiAi 64s and mutant *st10*. Finally, the target gene was mapped on the short arm of chromosome 3 framed between the markers of STR19 and STR24 in the range 150 kb, which laid basis for gene cloning and in-depth study of the functions.

1 Results

1.1 Phenotypic and genetic analysis

White stipe leaves of the mutant appeared in the 2 or 3 leaf stage as shown in Figure 1. The whole leaf of some plants happened in whiteness or even the whole plant become whitening. As the plant grew white stripe in the leaves become narrow, some white stripes in the leaf disappeared and leaves stayed with light color and pale vein compering to the wild type. Leaf color of mutant was sensitive to the change of the temperature; white stripe will be moreobvious in high-temperature than in low-temperature. As shown in Figure 1A, the phenomenon of white panicle occurred in the high temperature while the color of panicle was normal in low temperature. During the September 2010, Hangzhou, consecutive hot weather happed, panicle of mutant whitened, the contents of chlorophyll a and chlorophyll b reduced, in which content of chlorophyll a was 88% content of Nipponbare while the content of chlorophyll b was 92% of the

content of Nipponbare. The numbers of tillers little change between the wild-type and the mutant, whereas plant height of the mutant was significantly shorter, stems became thinner, Kilo-seed weight decreased by 10%, spike length and tiller number did not significantly change any more (Table 1). We employed 9311 as paternal parent and mutant *st10* as maternal parent as well as Peiai 64s as maternal parent and mutant *st10* paternal parent, respectively, to make crosses, the F₁ plants exhibited normal phenotype, the phenotypic separation of F₂ individuals in the population occurred, of which the normal phenotype of plants to mutant phenotype was close to 3 to 1, the Chi test results ($\chi^2=0.139 < \chi^2_{0.05}=3.84$; $\chi^2=0.769 < \chi^2_{0.05}=3.84$) (Table 2) indicated that the mutant trait would be controlled by a pair of single recessive nuclear gene.

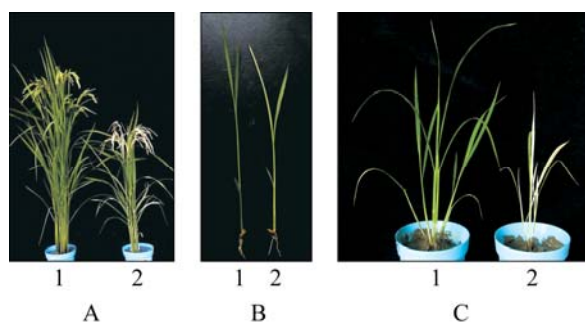


Figure 1 Phenotypes of wild-type *Nipponbare*, and the *st10* mutant at different growing stages

Note: A: Phenotypes of wild type and the mutant at heading stage; B: Phenotypes of wild type and the mutant at 3-leaf stage; C: Phenotypes of wild type and the mutant at tillering stage

1.2 Temperature gradient experiments

In order to clarify the critical temperature of mutant in the temperature-sensitive change, the experiment of mutant *st10* and wild-type *Nipponbare* were treated to be growing with the same growth conditions except the temperatures at 24°C, 28°C and 32°C, respectively. The phenotype of the mutant was more obvious at 32°C than at 24°C or 28°C. The chlorophyll of mutant and wild-type was not significantly differences in temperature treatments at 24°C or 28°C. The leaf color of mutant was turning clear whiteness at 32°C and chlorophyll content was also decreasing of which content of chlorophyll a was decreasing by 17%, as well as decrease of chlorophyll b by 11%. The chlorophyll content under the three temperature conditions at three-leaf stage were shown in Figure 2.

1.3 Analysis of green fluorescence

To further analyze mutant photosynthetic potential, we also measured the chlorophyll fluorescence parameters of *Nipponbare* and the mutant. The photochemical efficiency of PS II refers to the number of the transmitting electron or the time of electronic charge separation occurs in reaction center while PS II absorbs a photon, which usually presented with chlorophyll fluorescence parameters F_o' , F_m , F_v/F_m (Shen et al., 2009). F_o' , F_v/F_m' , F_m' are the three parameters under the conditions of light reaction, presenting the status of light reaction of sample.

As indicated in figure 3, under the light reaction conditions, three parameters of mutant were smaller

Table 1 Phenotypic characteristic of the mutant *st10* and the wild-type *Nipponbare*

Materials	PH/cm	EL/cm	ETP	TKW/g	Chla (mg/g)	Chlb (mg/g)	Chla/Chlb	CCar (mg/g)
<i>st10</i>	78.0±1.5	20.0±0.5	14±1.8	21.2±0.2	3.36±0.04	1.02±0.005	3.28±0.05	0.82±0.14
<i>Nipponbare</i>	94.5±2.8	20.4±0.9	15±1.5	23.5±0.2	3.41±0.11	1.11±0.03	3.08±0.03	0.82±0.14

Table 2 Genetic analysis of mutant *st10*

Cross	F ₁ phenotype	F ₂ population			× ² (3:1)
		Wild-type phenotype	Mutant type phenotype	Total	
<i>st10/9311</i>	Wild type	356	114	470	0.139
<i>PA64s/st10</i>	Wild type	407	124	531	0.769

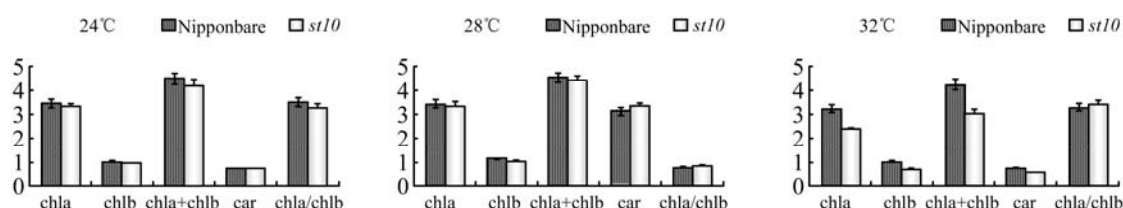


Figure 2 Pigment content of *st10* at the treatments of different temperatures

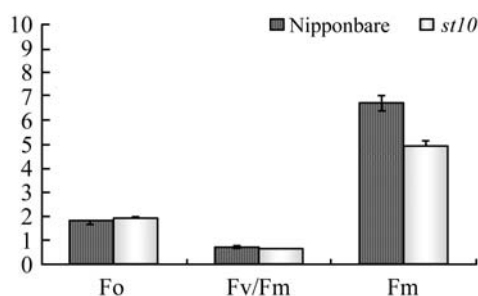


Figure 3 Chlorophyll fluorescent parameters of mutant and wild type under the conditions of light reaction

than that of wild-type, the F_v/F_m' of mutant *st10* declined 13% off compared to *Nipponbare*, indicating that the maximum photosynthetic quantum yield of mutant *st10* was slightly lower than that of *Nipponbare* leading to reduce photosynthetic efficiency of PS II of the mutant. Under the dark reaction conditions, the F_0 of mutant increased by 7% than that of wild-type, whereas the F_v/F_m of mutant decreased by 17% off than that of wild-type (Figure 4). Therefore, photosynthetic efficiency of the mutant decreased more obvious under the dark reaction conditions than under the light reaction conditions. The dark-adapted conditions, the amount of maximum fluorescence and minimum fluorescence of the mutant was significantly less than that of the wild type. As the mutant captured less the amount of light energy in the carbon assimilation process of photosynthesis, the amount of CO_2 fixed in primary reaction also decreased, thereby the plant photosynthetic efficiency reduced. The chlorophyll contents of mutant and *Nipponbare* were quite similar in tillering stage, so the photosynthetic electron transferring process can still be normal maintained.

1.4 Primary mapping and fine mapping of *st10* gene

We used published SSR markers evenly distributed in

rice genome to scan the polymorphic SSR markers between the genomes of *Nipponbare* and *PeiAi 64s*. The 64 pairs of SSRs with polymorphisms were obtained for primary mapping in this research. Thirty of randomly selected seedlings with mutant phenotype in the F_2 population were mixed to extract DNA as a mixed DNA pool. The mutant gene was primary mapped on chromosome 3 framed between CHL-8 and RM16 with the genetic distances of 86.0 cM and 91.1 cM, respectively. In order to further fine mapping the target gene, we searched the markers in this region and designed 19 pairs of STS (Sequence Tagged Site) markers, polymorphic analysis showed that 10 of the STS markers between the two parents exhibited significantly polymorphisms (the marker sequence shown in Table 3). By using 2885 individuals of F_2 mapping populations, the mutant gene was finally mapped on chromosome 3 framed between the STR19 and STR24 in the range of physical distance about 150 Kb, 19 exchanging plants in the left flanking occurring, while 3 exchanging plants in the right flanking (Figure 5, Figure 6).

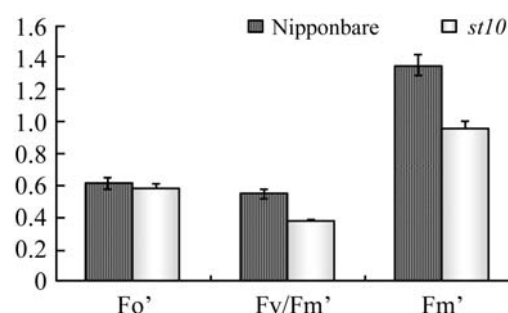


Figure 4 Chlorophyll fluorescent parameters of mutant and wild type under the conditions of dark reaction

Table 3 Markers used for fine mapping of *st10* gene

Makers	Forward primer sequence	Reverse primer sequence	Distance/Mb
CHL-8	GTTTTACCGATGGTTGATG	ATCGTGGATGCCTTTGGAG	18.392
STR6	GCGAGTGTCTTCGTTTGT	GACTTGTTCCACTCCACTCT	22.388
STR12	GGTTACATCTCCTTTTCGTT	CTTTGTTTGCTGCCATCT	22.584
STR14	TTGCCTATTATGGAGTCACC	GCATTCTCTGATTGAAAACC	22.636
STR15	GTCGCCCTCTCCTCCG	CGTCGTTGTAGTGGCTCTGT	22.701
STR16	TCTAAAAGTGGATGACAAGGG	CCACGGCTAATGTTGTTT	22.747
STR17	TTTTCGTTAGCATCACTTG	GCACACATTTCAAGATTCAA	22.864
STR18	TCCCTCTCCTATCTATGTGA	GAACCGATGATGTTGATGC	22.889
STR19	TCCATTGTCAAAGGTAGG	TATTTGGTGAGTGGGATG	22.505
STR20	GCCACTTTCAATCTTATGC	AAATGTGAACCCGGACTA	22.464
STR21	AGGCAGAGGAAGAAGGAG	TTTTTGGTGGACTGGAAG	22.537

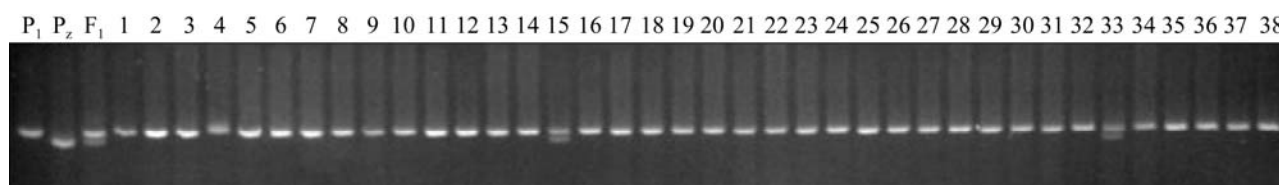


Figure 5 Electrophoretic banding pattern generated by STR6 marker for fine mapping among parts of plants with *st10* phenotype in F₂ population

Note: P₁: Peiai64s; P₂: *st10*; F₁: Peiai64s/*st10*; 1–38: F₂ plants with *st10* phenotype

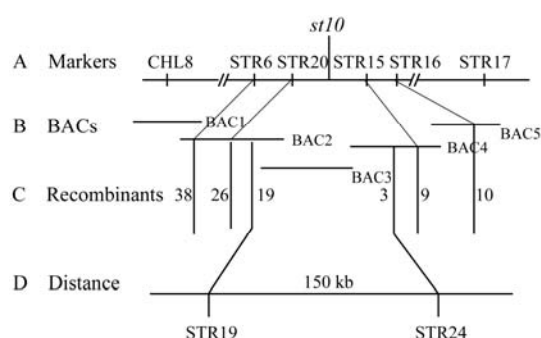


Figure 6 Fine mapping of *st10* on rice chromosome 3

2 Discussions

Temperature-sensitive leaf color mutant is the ideal material to study the biochemical processes and biological origin of chloroplasts in higher plants as well as to clarify the mechanism of leaf color changes, also to in-depth explore the relationship between photosynthesis and temperature response. Liu et al. found a yellow-green leaf mutant of rice, which the leaf color was normal when the temperature was below 23°C, while yellow-green phenotype of leaves occurred once the temperature was higher than 26°C. With the rise of the temperature chlorophyll content of

mutant leaves decreased in trends. At the conditions of low temperatures chlorophyll content of the mutant and wild-type were quite similar, whereas at the conditions of high temperature, the contents of chlorophyll a and chlorophyll b of the mutant was significantly lower than that of the control. Under field conditions, the chlorophyll a content of the mutant in seedling stage decreased by 30% compared with wild-type and the content of chlorophyll b decreased by 50%. The gene was identified as *Cde1(t)*, encoding a glutamyl-tRNA synthetase, that was the key enzyme to catalytic bind glutamic acid and t-RNA, playing an important role in the ALA (5-aminolevulinic acid) synthesis (Liu et al., 2007). Dong et al studies on rice heat-sensitive leaf mutant (*tsc1*) 7436S showed that mutant phenotypes presented three colors of white, light green and green at the temperatures of 23.1°C, 26.1°C and 30.1°C, respectively. However, the seedlings treated at temperature 23.1°C were transferred to the normal temperature of 30.1°C, the mutant phenotype recovered to normal green color. Transmitting electronic microscopic (TEM) analysis showed that thylakoid structure of mutant was abnormal

bubbly-like and grana lamellae structure disappeared compared with the control (Dong et al., 2001). Wu et al found a green turning type albino mutant W25 that the leaf color was completely whitening in temperature conditions of 15°C, 20°C and 25°C, while at 30°C and 35°C, the first or second leaf exhibited light green or normal green (Wu et al., 1996). Meanwhile, temperature-sensitive mutants had been reported in other species, such as in *Arabidopsis* (Markwell et al., 1992), cotton (Alberte et al., 1974), barley (Gálová et al., 2000), soybean (Stockinger et al., 1994), corn (Pasini et al., 2005).

In recent years, it has been many reports on the studies of mutations of uneven color leaves in rice (such as white stripe leaves, zebra leaves, etc.), however, these reports were mostly concentrated on the studies of in the aspects of morphology and physiology of the mutants, it remains to be clarified the formation mechanism of mutant and regulating gene, mechanism of occurrence in the similarities and differences of leaf color uneven or uniform mutation, and influences of the temperature on the mutant phenotype. In this study, the characteristics of temperature-sensitive white stripe mutant *st10* were determined including chlorophyll fluorescence parameters, agronomic traits and chlorophyll, while the mutant gene was fine mapped on chromosome 3 within the range of 150 kb, which might lay fundamentals for exploring the molecular mechanism of leaf color mutation and regulation of temperature on the gene expression related to leaf color mutation in plant.

3 Materials and Methods

3.1 Materials used in this study

Mutants *st10* used in our laboratory was obtained from the mutagenesis of japonica variety Nipponbare induced with ethyl methane sulphonate (EMS). F₂ segregating population as mapping population was derived from the cross between maternal parent Peiai 64s and paternal parent *st10* mutant constructed.

3.2 Determination of chlorophyll content

Taking flag leaves from the mutant and the control Nipponbare in tillering stage and removing the main vein, cutting small pieces in side length of 2~3 mm. Taking leaf pieces of 0.15~0.2 g soaked in 25 mL in a mixture of acetone and ethanol (95% acetone:

ethanol=2:1) with 4 replicates dark cultured at 26°C for 24 hours. Taking the solution to measure the optical density values of chlorophyll a, chlorophyll b and carotenoids in the UV spectrophotometer (DU640) with three wavelengths of 470 nm, 645 nm and 663 nm. The contents of chlorophyll a, chlorophyll b and carotenoid were calculated following with Arnon's method (Arnon, 1949).

3.3 Temperature gradient experiment

Germinated seeds of the mutant and Nipponbare were placed on media with 0.8% agar and cultured with lighting for 24 hours at three temperatures of 24°C, 28°C and 32°C, respectively. Observing and recording the mutant's phenotype, taking leaves to determine the content of chlorophyll until the mutant phenotype is obviously exhibiting in three leaf stage.

3.4 Determination of chlorophyll fluorescence parameters

Using a portable chlorophyll fluorometer (PAM-2500, Germany) measured values of rice flag leaf under the light reaction conditions as well as the values of F₀, F_m and F_v/F_m under the dark reaction conditions. The experiment was performed at 9:00-10:00 am on July 23, 2010 (in tillering stage) with three replicates, the averaged measure values were used for calculation following with the formula as below:

$$F_v/F_m = (F_m - F_0) / F_m$$

$$[F_v'/F_m' = (F_m' - F_0') / F_m']$$

Determination in light reaction: when the measured leaves being adapted to light, turning on the measuring light to determine steady-state fluorescence of the leaves, and then turning on the saturation pulse light to measure the maximum fluorescence F_m', turning off the actinic light and turning on far-red light to excite PS I making the PS II electron transporters in the status of oxidation prior to measuring the minimum fluorescence F₀' of light-adapted leaves.

Determination in dark reaction: Using the dark-adapted leaf folder to hold rice flag leaf on the position from one third base, closing the folder and staying 20 min in dark environment. Putting the light-emitting diodes into the hole of the leaf folder, turning on the measuring light to obtain F₀ value, then turning the

saturation pulse to obtain F_m values, subsequently turning the action light, 1 min later turning the saturation pulse to measure F_v/F_m (Bo Shen et al., 2009).

3.5 Molecular tagging of mutant *St10*

Map-based cloning approach was employed in this study. We used published SSR markers to scan the genome-wide polymorphic SSR markers between the genomes of Nipponbare and PeiAi 64s. The scanned 64 pair SSRs with polymorphisms was used for primary mapping. Ten STS markers with obvious polymorphisms were developed by using the softwares of Premier 5.0 and DNAMAN of which primers were synthesized by Shanghai Yingwei Jieji Company. Physical locations on chromosome were following the NCBI website of <http://www.ncbi.nlm.nih.gov>. PCR reaction performed as follows: in total of 20 μ L reaction volumes including: DNA template 2 μ L; 10 \times PCR buffer 2 μ L; dNTP (2.5 mmol/L) 2 μ L; Primer F (2.5 μ mol/L) 2 μ L; Primer R (2.5 μ mol/L) 2 μ L; *Taq* polymerase 1 μ L; adding ddH₂O 9 μ L up to 20 μ L. Reaction procedures as follows: 94°C pre-denaturing 4 min, then 40 cycles of 94°C denaturing 40 s, annealing 55°C 40 s, 72°C extending 40 s, finally 72°C extending 10 min, keeping at 15°C ready for use. Amplified products were separated with 4% or 5% agarose gel electrophoresis, stained by ethidium bromide and observed under UV lamp.

Author's contributions

HYH GXZ and YCR are the persons who carried out this experiment; JH, JL, ZYG and LBG participated in some in lab work; and the data analysis and in field work; Ljand OQ conceived the project and designed the experiments as well as wrote and revised manuscript. All authors had read and agreed the final text.

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