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Simultaneous improvement for four quality traits of Zhenshan 97, an elite parent of hybrid rice, by molecular marker-assisted selection

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Abstract "Zhenshan 97" is the female parent of a number of widely used hybrids for rice production in China. However, this line is of poor quality because of a high amylose content (AC), a hard gel consistency (GC) and a low gelatinization temperature (GT), together with a chalky endosperm. It had been determined that the three traits for cooking and eating quality, AC, GC and GT, are controlled by the *Waxy* locus and/or the tightly linked genomic region. In this study we improved the eating and cooking quality of Zhenshan 97 by introgressing the *Waxy* gene region from Minghui 63 (wx-MH), a restorer line, that has medium AC, soft GC and high GT. The wx-MH fragment was transferred to Zhenshan 97B by three backcrosses and one selfing, then from Zhenshan 97B to Zhenshan 97A by a cross and a backcross. Molecular marker-assisted selection was applied in the series to select for individuals carrying wx-MH, to identify recombination between the *Waxy* and flanking markers, and also to recover the genetic background of the recurrent parent. According to the marker genotypes, the improved versions of Zhenshan 97B and Zhenshan 97A, or Zhenshan 97B(wx-MH) and Zhenshan 97A(wx-MH), were the same as the originals except for the *Waxy* region of less than 6.1 cM in length. The selected lines and their hybrids with Minghui 63, or Shanyou 63(wx-MH), showed a reduced AC and an increased GC and GT, coupled with a reduced grain opacity. Field examinations of agronomic performance revealed that Zhenshan 97B(wx-MH) and Shanyou 63(wx-MH) were essentially the same as the originals except for a significant decrease in grain weight. The simultaneous improvement of AC, GA, GT and opacity, indicated that the *Waxy* region had major effects on the four quality traits. The improved versions of Zhenshan 97 A and B should be immediately useful in hybrid rice production.

Keywords Rice quality · Amylose content · Gel consistency · Gelatinization temperature · Opacity · Marker-assisted selection

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Introduction

The quality of the rice grain represents a major problem in rice production in many rice-producing areas of the world, and is particularly the case in hybrid rice production in China. Currently, there is a strong emphasis in China on improving the quality of hybrid rice varieties, especially the quality of indica hybrids. The most serious problems lie in the eating and cooking quality, appearance and, to some extent, in milling quality. It is known that the eating and cooking quality of rice is largely determined by three characters specifying the physical and chemical properties of the starch in the endosperm, i.e. the amylose content (AC) (Webb 1980; Juliano 1985; Unnevehr et al. 1992), gel consistency (GC) (Cagampang et al. 1973) and gelatinization temperature (GT) (Little et al. 1958). The chalkiness, or opacity, of the endosperm of the grains is another important characteristic for grain quality, as it not only affects the appearance of the grains, but also affects the resistance to grain breakage.

Shanyou 63, a hybrid between the male-sterile line Zhenshan 97A and the restorer line Minghui 63, is the most-widely used hybrid in rice production in China, thanks to its high yield and wide adaptability. The area planted to this hybrid reached a total of 6.7 million ha per year, accounting for approximately 25% of rice production in China, during its peak period in the late 1980s and early 1990s (Lin and Min 1991). In recent years, however, the planting area of this hybrid has been declining, partly because of its increasing susceptibility to certain diseases such as bacterial blight caused by *Xathomonas oryzae* pv *oryzae* and fungal blast caused by *Pyri-*

cularia grisea. Chen et al. (2000) reported the improvement of bacterial blight resistance of this hybrid by introgression of *Xa21*, a gene with a broad spectrum of resistance to bacterial blight, into Minghui 63 using molecular marker-assisted selection (MAS). It was shown that the improved version of Minghui 63 or Minghui 63(*Xa21*) had a fragment of less than 3.8 cM in length surrounding the *Xa21* locus from the donor parent, with the rest of the genome coming from the recurrent parent, which greatly enhanced the bacterial blight resistance of the hybrid.

Another major reason for the decrease in the planting area of this hybrid is the relatively poor cooking and eating quality as well as its appearance, which is increasingly discriminated against by the consumers. The male parent Minghui 63 has a combination of medium AC/soft GC/high GT, together with a translucent endosperm, which represents good quality. The female parent Zhenshan 97 has high AC, hard GC and low GT, together with a chalky endosperm, which is a combination of very poor quality (Tan et al. 1999, 2000). Because of genetic dominance of the unfavored characteristics of the quality traits, the average values of the F_2 seeds born by the hybrids are of poor quality for all the traits, except AC, which appeared to be somewhat intermediate. Moreover, the segregation in the F_2 seeds causes non-uniformity of the quality traits among the grains, which is also not favored by the consumers. In addition to Shanyou 63, Zhenshan 97A is also the female parent for a number of hybrids widely used for rice production in China. Thus, improving the eating and cooking quality of Zhenshan 97 may have a wide range of benefits in rice-improvement programs.

It was shown that AC, GC and GT co-segregate in both F_2 and recombinant inbred line (RIL) populations derived from the Zhenshan 97/Minghui 63 cross, and are controlled by the *Waxy* locus or a genomic region tightly linked to this locus (Tan et al. 1999). Thus, it should be feasible to improve the cooking and eating quality by simultaneously modifying all three traits. Results from a previous study also showed that chalkiness, or opacity, of the grains is controlled by six QTLs (quantitative trait loci) located on five of the 12 chromosomes (Tan et al. 2000)

The reported study was undertaken to improve the cooking and eating quality of Zhenshan 97 by modifying the *Waxy* gene region that controls AC, GC and GT, using Minghui 63 as the donor. It was also intended to assess the effects of this genomic region on the quality traits under near-isogenic conditions.

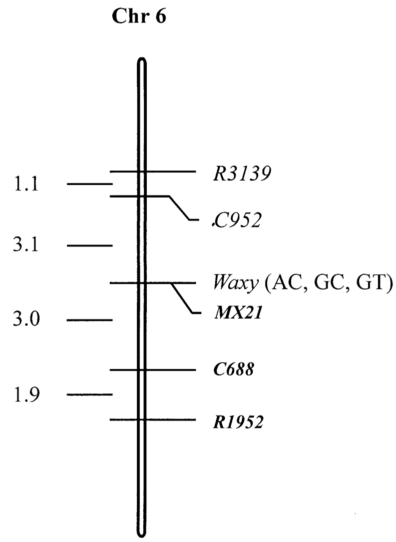

Fig. 1 The local linkage map of the *Waxy* genomic region on rice chromosome 6 (adapted from Tan et al. 1999)

Materials and methods

Genetic materials

Three rice lines were used as the parents in this study. (1) Minghui 63, the restorer line for a number of elite hybrids widely grown in China, was used as the donor of the *Waxy* gene region. This line possessed a combination of medium AC/soft GC/high GT, which represented a relatively good quality. We designate the genomic region controlling these three traits as wx-MH. (2) Zhenshan 97B, the maintainer line for a number of elite hybrids, was used as the recurrent parent. This line had the combination of high AC/hard GC/low GT, representing a poor quality. We designate this genomic region as wx-ZS that is allelic to wx-MH. (3) Zhenshan 97A, the male-sterile counterpart of Zhenshan 97B.

Measuring the quality traits

The experiments for measuring AC, GC and GT were conducted following the same procedures as described previously by Tan et al. (1999). GC is measured by the length of the gel; the longer gel is considered to be softer than the shorter gel. The GT of a grain is usually measured by the alkaline spreading value (ASV); a larger ASV represents more spreading in alkali, indicating that a lower GT and a smaller ASV indicates a higher GT. The percentage of grains with opacity was measured as the number of grains with opacity, counted by visual assessment, in 100 milled-head rice grains selected randomly from each sample.

Markers used for MAS

The MAS system in which wx-MH was introgressed from Minghui 63 to Zhenshan 97B included three markers (see Fig. 1). The primers for the SSR marker waxy, representing the *Waxy* gene used to select for the presence of wx-MH in the process of backcrossing, were designed according to Bligh et al. (1995), with $(CT)_n$ as the targeted SSR sequence. Two RFLP markers, C688 and C952, were used for identifying recombinations between the *Waxy* locus and the flanking markers. Such negative selections would ensure that the introgressed segment surrounding the *Waxy* gene region was shorter than the distance between the two flanking markers (6.1 cM). For background selection, a total of 118 amplified fragment length polymorphism (AFLP) bands were used to recover the genetic background of Zhenshan 97B.

The SSR analysis was carried out essentially according to the procedures described by Wu and Tanksley (1993), except that the reaction volume of PCR was reduced to 10 μl. The experiment procedures for RFLP assay, including DNA isolation, digestion, electrophoresis and Southern-blot hybridization, were done essentially as described previously (Liu et al. 1997). The AFLP assay followed the procedures described by Vos et al. (1995).

The crossing and selection scheme

The wx-MH allele was introgressed into Zhenshan 97B following a recurrent backcrossing procedure, combined with selections using molecular markers. The entire scheme for the selection took three generations of backcrosses and one generation of self-fertilization, essentially as described by Chen et al. (2000, 2001). The selected individuals were designated Zhenshan 97B(wx-MH).

The introgression of wx-MH into Zhenshan 97A was carried out by crossing Zhenshan 97A with the selected Zhenshan 97B(wx-MH) followed by backcrossing, and the homozygous male-sterile lines were designated Zhenshan 97A(wx-MH).

Collection of field data for agronomic traits

The agronomic performance of the original Zhenshan 97B and Zhenshan 97B(wx-MH) was compared at Wuhan in the summer of 2000 and at Hainan (South China Sea) Island in the spring of 2001. A comparison was also made between the original Shanyou 63 (Zhenshan 97A × Minghui 63) and the new crosses of Zhenshan 97A(wx-MH) × Minghui 63, or Shanyou 63 (wx-MH), at Hainan Island in the spring of 2001.

In the Wuhan test, the four lines selected from the BC_3F_2 generation (see the Results sections) were planted with the original Zhenshan 97B. Each of the plots consisted of three rows with 12 plants per row at a planting density of 16.5 cm between plants in a row, and 26.4 cm between rows. Only the ten plants in the middle of the center rows were used for measurement of the agronomic traits.

In the comparison at Hainan, all the materials were tested with three replications following a randomized complete block design. Each plot consisted of five rows with ten plants per row. The distance between plants within a row was 10 cm and the rows were 20-cm apart. The traits measured included heading date, plant height, tillers per plant, number of grains per panicle, weight of 1,000 grains and yield per plant.

Results

Quality of the parents and the hybrid

The measurements for the quality traits of the two parents, Zhenshan 97 and Minghui 63, and the hybrid, Shanyou 63, can be found in Tables 1 and 2. Minghui 63 was of better quality than Zhenshan 97 as reflected by all four traits (Table 1), and the average values of the hybrid appeared to be intermediate (Table 2), consistent with previously reported results (Tan et al. 1999).

MAS

The molecular marker-assisted backcross breeding was conducted following the described MAS system. A cross was made between Zhenshan 97B and Minghui 63, and the F_1 was backcrossed to Zhenshan 97B. In the BC_1F_1, one individual was found to be a recombinant between the waxy marker and C952 in 52 plants containing wx-MH. The plant was subsequently backcrossed to Zhenshan 97B. In BC_2F_1, no recombinant was found between the waxy marker and C688 in 49 plants containing wx-MH. These plants were then backcrossed to Zhenshan 97B by mixing pollen. In BC_3F_1, 45 plants were identified as containing wx-MH. These 45 plants were assayed for their genetic background using AFLP markers with 21 primer pairs (data not shown) to recover the genetic background of Zhenshan 97B. A total of 118 polymorphic bands were detected between the parents. The proportions of recovery of the recurrent parent background ranged from 84.2% to 100%, with an average of 94.2%, which is slightly higher than the expected 93.75% in the BC_3F_1 population. One plant was found to have all the bands from Zhenshan 97B. Six plants with the highest proportions of the Zhenshan 97B backgrounds were assayed with the marker C688 and four plants were found to be recombinants between the waxy marker and C688, including the plant that had all the bands from Zhenshan 97B. Thus a plant carrying a fragment of less than 6.1-cM in length from the donor parent in the targeted region, and also likely having an identical genetic background to Zhenshan 97B, was obtained. This plant was self-pollinated to produce BC_3F_2, from which progenies homozygous for the *waxy* gene region were obtained.

Table 1 The measurements of the quality traits of the four selected lines of Zhenshan 97B compared to the parental varieties

Variety/line	Amylose content (%)	Gel consistency (mm)	Gelatinization temperature (ASV)[b]	Opacity (%)
Wuhan				
Zh-6	15.8	52.0	2	35.6
Zh-8	16.8	47.9	2	54.0
Zh-17	16.1	56.1	2	49.3
Zh-22	15.6	51.7	2	40.7
Zhenshan 97B	27.8	29.5	6	82.0
Minghui 63	16.9	53.8	2	9.3
$LSD_{0.05}$[a]	1.11	4.21		8.23
$LSD_{0.01}$	1.61	6.21		12.38
Hainan				
Zh-6	16.3	57.6	1	28.8
Zh-8	16.3	54.0	1	40.8
Zh-17	15.3	53.2	1	33.3
Zh-22	15.6	52.3	1	25.5
Zhenshan 97B	27.9	28.1	6	85.3
$LSD_{0.05}$[a]	1.29	3.84		4.05
$LSD_{0.01}$	1.88	5.59		5.97

[a] $LSD_{0.05}$ and $LSD_{0.01}$ mean the least significant differences at 0.05 and 0.01 probability levels, respectively

[b] The ASV difference of Zhenshan 97 with Minghui 63 and the selected lines is qualitative

Table 2 The measurements of the quality traits of hybrids between the four selected lines and Minghui 63 (Hainan 2001)

Hybrid	Amylose content (%)[a]	Gel consistency (mm)[a]	Gelatinization temperature (ASV)	Opacity (%)[a]
Zh-6/Minghui 63	16.6 ± 1.1[b]	54.2 ± 3.8[b]	1	10.0 ± 2.2[d]
Zh-8/Minghui 63	16.6 ± 0.9[b]	52.3 ± 2.6[b]	1	7.8 ± 2.1[d]
Zh-17/Minghui 63	17.1 ± 1.7[b]	55.2 ± 4.1[c]	1	13.0 ± 4.3[d]
Zh-22/Minghui 63	16.1 ± 0.9[b]	54.7 ± 2.4[b]	1	15.0 ± 2.2[d]
Shanyou 63	23.5 ± 5.9	35.3 ± 12.5	4.8	39.5 ± 5.1

[a] Data presented as average ± SD
[b] The variance of the measurement was significantly different from Shanyou 63 at the 0.01 probability level
[c] The variance of the measurement was significantly different from Shanyou 63 at the 0.05 probability level
[d] The variance of the measurement was not significantly different from Shanyou 63

Table 3 Comparison of the agronomic traits between original Zhenshan 97B and the four selected lines of Zhenshan 97B(wx-MH) (Hainan 2001)

Variety/ line	Days to heading	Plant height (cm)	Panicle length (cm)	Tillers/ plant	Grains/ panicle	Grain weight (g/1,000)	Spikelet fertility (%)	Yield/plant (g)
Zh-6	94.0	63.9	19.3	10.1	73.7	25.5	71.8	19.8
Zh-8	95.0	63.1	18.9	8.6	80.5	24.6	71.8	16.3
Zh-17	94.0	62.1	18.3	8.8	75.6	25.5	70.5	15.4
Zh-22	96.7	66.0	18.8	8.2	84.4	25.0	68.7	14.3
Zhenshan97B	93.0	59.7	18.5	9.0	87.2	27.3	72.5	20.7
$LSD_{0.05}$[a]	0.79	6.06	0.62	2.28	14.10	0.74	4.61	5.45
$LSD_{0.01}$	1.01	8.82	0.90	3.32	20.52	1.08	6.71	7.93

[a] The $LSD_{0.05}$ and $LSD_{0.01}$ mean the least significant differences at 0.05 and 0.01 probability levels, respectively

Table 4 Comparison of the main agronomic traits between original Shanyou 63 and the four hybrids from the selected lines (Hainan 2001)

Hybrid	Days to heading	Plant height (cm)	Panicle length (cm)	Tillers/ plant	Grains/ panicle	Grain weight (g/1,000)	Spikelet fertility (%)	Yield/plant (g)
Zh-6/Minghui 63	102.0	76.0	22.3	11.3	81.7	27.6	68.8	23.5
Zh-8/Minghui 63	101.0	77.5	21.9	10.5	80.3	27.4	69.0	21.6
Zh-17/Minghui 63	102.0	76.9	22.1	10.9	77.9	27.6	66.2	22.1
Zh-22/Minghui 63	104.0	78.3	22.3	10.9	74.6	27.2	66.4	21.3
Shanyou 63	103.0	78.8	22.5	10.6	76.1	28.4	67.4	21.7
$LSD_{0.05}$[a]	0.88	2.6	0.9	2.4	18.9	0.7	2.5	8.3
$LSD_{0.01}$	1.18	3. 9	0.2	3.6	28.8	1.0	9.8	11.1

[a] The $LSD_{0.05}$ and $LSD_{0.01}$ mean the least significant differences at 0.05 and 0.01 probability levels, respectively

Four individuals were selected as the improved version of Zhenshan 97B, or Zhenshan 97B(wx-MH), based on their grain quality and appearance in the field, to propagate the BC_3F_3.

The plant having the genetic background most similar to Zhenshan 97B (118 AFLP bands) obtained in the BC_3F_1 was backcrossed to Zhenshan 97A at the time when the BC_3F_1 was self-pollinated to produce the BC_3F_2. The progeny plants containing wx-MH were then crossed with plants that were homozygous for wx-MH from the BC_3F_2 population. Individuals homozygous for wx-MH resulting from crosses with the four selected BC_3F_2 plants mentioned above were kept as improved versions of Zhenshan 97A, or Zhenshan 97A(wx-MH). These four selected lines of Zhenshan 97A(wx-MH) were subsequently crossed with Minghui 63 to produce the Shanyou 63(wx-MH) hybrids.

Comparison of the quality traits

The quality traits of four selected lines of Zhenshan 97B(wx-MH) and the original Zhenshan 97B were measured using seeds harvested from Wuhan in the summer of 2000 and Hainan in the spring of 2001. Analyzing the quality traits of the seeds from both the Wuhan and Hainan harvests (Table 1) showed that, compared with original Zhenshan 97B, all four lines of Zhenshan 97B(wx-

WH) exhibited a greatly decreased AC, in combination with a greatly increased GC and GT; all the measurements were approximately identical to Minghui 63. Interestingly, the improved lines also exhibited a concomitant large reduction in grain opacity. A similar comparison of the quality traits was also made between the original Zhenshan 97A and the four lines of Zhenshan 97A(wx-MH), and changes of all the four traits (AC, GT, GC and opacity) were also observed (data not shown).

The quality traits of the improved hybrids, Shanyou 63(wx-MH) developed from the four selected lines, were also compared against the original Shanyou 63 (Table 2). As expected, all four new hybrids showed, on average, a decreased AC accompanied by an increased GC and GT in both the Hainan and Wuhan tests. Reduction in the opacity of the new hybrids was also observed compared with the original hybrid. It should also be noted that, as expected, all the traits were much more uniform in the new hybrids than the original hybrids, as indicated by the standard deviations of the traits. The improvement of the uniformity was statistically significant in AC and GC, but not for opacity in all the four new hybrids. Such uniformity is highly desirable for good grain quality.

Comparison of the agronomic performance

The results of agronomic performance of the four selected lines of Zhenshan 97B(wx-MH) and the original Zhenshan 97B are presented in Table 3. The four selected lines were later by 1–3 days in heading, which was statistically significant. Another significant reduction occurred in grain weight, with the four lines lighter than the original Zhenshan 97B by 2.1 g per 1,000 grains on average. Consequently, a significant reduction was also detected for yield between one of the four lines and the original Zhenshan 97B. The results from the Wuhan planting in the summer of 2000 (data not shown) showed that all the agronomic traits of the four selected lines were not significantly different from the original Zhenshan 97B, except for a decrease in grain weight.

The agronomic performance of the four new hybrids were also compared with the original Shanyou 63 (Table 4). In the Hainan planting, a significant reduction in grain weight (about 1.0 g per 1,000 grains) was detected for all four hybrids. However, unlike the Zhenshan 97B comparison, this reduction did not significantly reduce the yield per plant in any of the hybrids.

Discussion

Using MAS in three generations of backcrossing followed by one generation of selfing, we successfully introduced the wx-MH fragment from Minghui 63 into Zhenshan 97B, which was subsequently transferred to Zhenshan 97A. The improved versions of the male-sterile and maintainer lines, Zhenshan 97A(wx-MH) and Zhenshan 97B(wx-MH), contained a fragment less than 6.1-cM in length of the *Waxy* gene region from the donor parent, with the rest of the genome coming from the original Zhenshan 97. The introduction of this fragment has greatly improved the cooking and eating quality of the lines and the resulting hybrids, with the agronomic performance essentially the same as the original maintainer line and hybrid.

The improvement can be viewed in two ways. First, changes of the means of the three traits in the seeds produced by the hybrids represented an overall improvement of the grain quality. Second, the increased uniformity of the grains with respect to the three traits achieved due to the homozygosity of the *Waxy* region in the hybrid is also highly desirable for quality improvement.

Two concomitant changes also occurred with the transferring of the wx-MH fragment. The first is an accompanied reduction in opacity exhibited by both the selected lines and their hybrids, a change that is highly favorable for quality improvement, as it affects both the intactness and appearance of the milled rice. The second is a reduction in grain weight that was detected in both the selected lines of Zhenshan 97B(wx-MH) and the hybrids. However, reduction in the overall yield was not detected in the hybrids, presumably because of phenotypic plasticity as a result of the strong heterosis (Zhang et al. 1994). These lines should be immediately useful for hybrid production, although further testing is still ongoing.

The data generated in this study also allowed for the evaluation of the effects of the *Waxy* gene region on quality and agronomic performance under near iso-genic conditions. The results clearly confirmed that the Waxy region indeed had major effects on the three traits for cooking and eating quality. It should also be noted that a minor QTL (with a LOD score of 2.5–4.0, explaining 5.0–7.5% of the phenotypic variation) for opacity (white core) (Tan et al. 2000) and another minor QTL (with a LOD score of 2.6–4.7 explaining 5.2–8.6% of the phenotypic variation) for grain weight (Yu et al. 1997) were previously detected as being approximately located in the chromosomal region containing the *Waxy* gene. It still remains to be determined whether the observed concomitant reductions in opacity and grain weight are due to tight linkage between the QTLs and the *Waxy* locus, or pleiotropic effects of the *Waxy* locus. However, it is highly interesting that minor QTLs detected in segregating populations can play a large role in modifying the phenotypes under near-isogenic conditions. The successful transfer of the two QTLs, although unintended in planning the experiment, clearly indicates the real existence and usefulness of QTLs in a breeding program.

Transfer of the *Waxy* region from Minghui 63 has certainly ensured the uniformity of the quality traits in the hybrid, by avoiding genetic segregation of the important quality traits in grains of hybrid rice as the commercial product. However, there is also an important concern with modifying the *Waxy* region of Zhenshan 97 using Minghui 63 as the donor since the introduction of the genetic background from Minghui 63 may decrease the level of heterozygosity, which may reduce the level of heterosis. The present results showed that such a risk can be avoided by thorough cleaning of the genetic background, although further testing is still necessary to ensure that the introduction of such a fragment will not have adverse effects on hybrid performance.

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