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Detection of segregation distortions in an *indica-japonica* rice cross using a high-resolution molecular map

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Abstract We have constructed a high-resolution rice genetic map containing 1383 DNA markers covering 1575 cM on the 12 linkage groups of rice using 186 F_2 progeny from a cross between a *japonica* variety, 'Nipponbare', and an *indica* variety, 'Kasalath'. Using this high-resolution molecular linkage map, we detected segregation distortion in a single wide cross of rice. The frequencies of genotypes for 1181 markers with more than 176 genotype data were plotted along this map to detect segregation distortion. Several types of distorted segregation were observed on 6 of the chromosomes. We could detect 11 major segregation distortions at ten positions on chromosomes 1, 3, 6, 8, 9, and 10. The strongest segregation distortion was at 107.2 cM on chromosome 3 and may be the gametophyte gene 2 (*ga-2*). The 'Kasalath' genotype at this position was transmitted to the progeny with about a 95% probability through the pollen gamete. At least 8 out of the 11 segregation distortions detected here are new. The use of the high-resolution molecular linkage map for improving our understanding of the genetic nature and cause of these segregation distortions is discussed.

Key words Gametophyte gene · Genetic map · Hybrid sterility gene · Rice · Segregation distortion

Introduction

Deviation from the expected Mendelian segregation ratio has often been observed in the offspring of intra- and inter-species hybrids. This phenomenon has attracted considerable attention as an evolutionary force that can cause an increase in the population frequency of the heterozygous allele or heteromorphic chromosome (Sandler and Novitski 1957; Charlesworth 1988). The segregation distortion of Mendelian inheritance is caused by genetically linked segregation distorting factors. Segregation distortion can arise either from competition among gametes or from abortion of the gamete or zygote (Lyttle 1991).

One cause of segregation distortion is a hybrid sterility gene that causes the abortion of a gamete or zygote. A gametophyte gene which is a gene that is expressed in a haploid gamete and which is involved in gametophytic competition, is also known to cause segregation distortion. A large number of different genes are transcribed during postmeiosis of the microspore and pollen development in angiosperms (Mascarenhas 1992). Genetic differences among pollen would result in gametophytic competition and gametophytic selection leading to nonrandom fertilization. One of the well-studied systems that causes gamete loss is the segregation distorter system in the fruitfly *Drosophila melanogaster* (Lyttle 1991). This system consists of at least two major loci near the centromere of the second chromosome, the segregation distorter gene and the responder locus. The abortion of a gamete or zygote in hybrid progeny may be induced by several allelic interactions. The best way to elucidate all the causal factors that result in dysfunction of hybrid progeny is to analyze the proportions of genotypes of the surviving progeny over the whole genome.

In rice, 11 gametophyte genes and 20 hybrid sterility genes have been detected, and these are listed in the reports of the Committee on Gene Symbolization, Nomenclature and Linkage Groups of Rice Genetic Cooperative (Kinoshita 1991; Kinoshita 1993). These segregation distorting genes have been detected through the use of different crosses, and several segregation distortions may be expected in a single wide cross. The detection of segregation distortion in a single cross and

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the elucidation of each factor will be required in order to understnad the mechanisms underlying such factors. The use of molecular markers in the high-resolution map permits us to characterize genotypes of surviving progenies over the whole chromosome and to detect major segregation distortion with high accuracy.

The aim of the study described here was to estimate the number, position, and strength of major segregation distortion in a cross between the *japonica* variety 'Nipponbare' and *indica* variety 'Kasalath' using a high-resolution rice genetic map, so that genes may be mapped to determine what the causes of these segregation distortions are. We could observe several types of segregation distortion in seven regions of 6 chromosomes and detected 11 segregation distortions at ten positions on these chromosomes. This is the first study to map all of the major segregation distortions in a single cross with high accuracy and to show the possible elucidation of these multiple segregation distortions for further studies.

Materials and methods

Plant material

'Kasalath' (an *indica* variety) was crossed on to 'Nipponbare' (a *japonica* variety). The F_1 was self-pollinated to produce F_2 seed. More than 90% fertility was observed in these F_1 plants. A total of 186 F_2 plants were used to develop a restriction fragment length polymorphism (RFLP) linkage map of rice (Kurata et al. 1994).

Linkage analysis and detection of segregation distortion

The construction of a linkage map has been described previously (Kurata et al. 1994). There was a total number of 250 355 genotypes for the 1383 markers. These were used to construct the linkage map covering 12 chromosomes with 1575 cM in Kosambi map unit functions with MAPMAKER 3.0b computer software (Lander et al. 1987).

The chi-square test has often been used to detect deviation from expected Mendelian inheritance ratios. In this study, however, we characterized the direction of distorted segregation by plotting the frequencies of each genotype of the markers along the high-resolution genetic linkage map. Continuously scored genotypes can be analyzed as quantitative trait loci (QTL) likelihood maps of surviving progenies. To reduce noise that is raised by an insufficient number of evaluated progeny, we selected 1174 markers with data on more than 176 genotypes to detect segregation distortion in this cross. The average number of progeny used for scoring the frequencies of genotypes was 183.2 per marker. The range of the expected frequency at the 0.99 probability level for the average number of progeny is $25 \pm 9.5\%$ and $50 \pm 13.5\%$ for the homozygote and heterozygote, respectively; at the 0.95 probability level, the range is $25 \pm 7.2\%$ and $50 \pm 10.2\%$ for the homozygote and heterozygote, respectively. Distorted segregation was considered to have been observed when the frequency of any genotype was beyond the respective range.

Results

The rice genetic map was constructed using 186 F_2 plants derived from a cross of 'Nipponbare' and 'Kasalath' as described previously (Kurata et al. 1994). The frequency for individual marker genotypes with data from more than 176 F_2 plants was plotted for 1181 markers along the genetic linkage map (Fig. 1). As the segregation of adjacently linked markers is very similar to each other, three continuous curves of the 'Nipponbare' homozygote, 'Kasalath' homozygote, and the heterozygote have been obtained for each chromosome. These curves can be analyzed as QTL likelihood maps of surviving progeny over the whole chromosome, and segregation distortion can be mapped at the peak position. Since the whole 1575 cM genome was covered with 1174 markers, the factor causing segregation distortion would be expected to be resolved to the nearest 1.3 cM, on average, on this map. Significant segregation distortions were observed at seven regions on the genome (chromosomes 1, 3, 6, 8, 9, and 10).

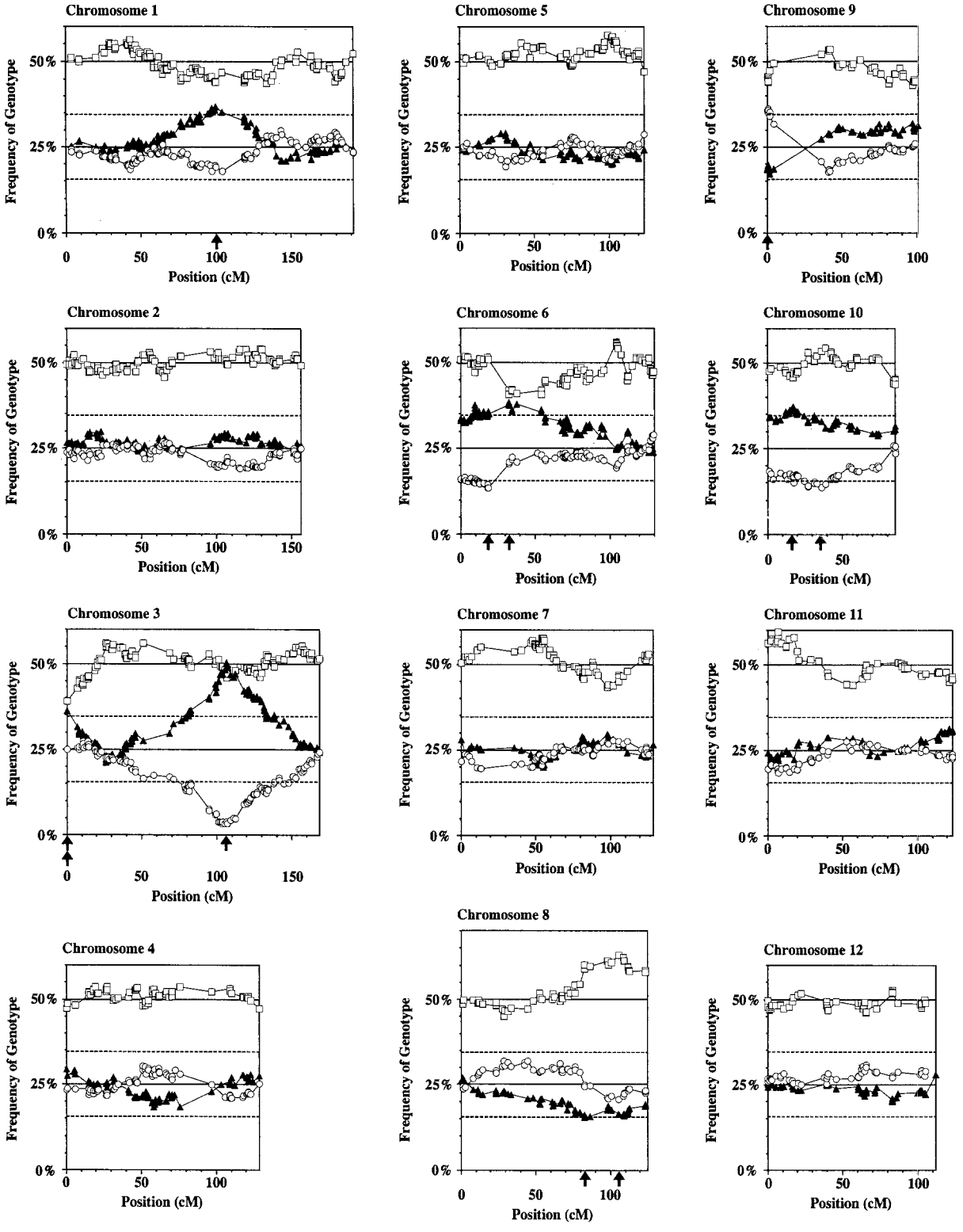
Fig. 1 Frequencies of each allele in F_2 plants from a cross between 'Nipponbare' and 'Kasalath' are plotted along the genetic linkage map. In each chromosome, the left and right ends correspond to the top and bottom ends of the genetic linkage map (Kurata et al. 1994). The frequency of 'Nipponbare' homozygous genotypes (○), 'Kasalath' homozygous genotypes (▲), and heterozygous genotypes (□) are plotted on the marker positions. In a normal segregation, the homozygous genotype accounts for 25% and the heterozygous genotype for 50%. The *dashed lines* show the upper and lower 99% statistical confidence limit of a normal segregation of each homozygote in our cross population (the average number of data for each marker is 183.2). The *arrows* (⬆) at the horizontal axis show the peak positions of the distorted segregation

The most pronounced distortion was observed in the middle of chromosome 3 with 3.2% of the homozygous genotype in 'Nipponbare', 49.5% in 'Kasalath', and 47.3% in the heterozygote. The segregation curves of both homozygous genotypes exceed the normal segregation range with a single peak at the same position, while the heterozygous genotype shows normal segregation. This strong distorted segregation of the markers extends over a large region of chromosome 3, from 50 to 150 cM.

Distorted segregation was also observed for the first time in the middle of chromosome 1. The peaks of the distorted segregation curves for the homozygote genotypes are at the same position, 99.9 cM, where the segregation ratio in 'Kasalath' is 12.0% higher and the ratio in 'Nipponbare' is 6.0% lower than the normal segregation ratio.

The ends of chromosomes 3 and 9 showed a different type of distorted segregation from that shown by chromosomes 1 and 3. Segregation of the homozygous genotype in 'Kasalath' is 10% higher while that of the heterozygous one is 10% lower than normal segregation at 0 cM on chromosome 3. At 0 cM on chromosome 9, segregation of the 'Nipponbare' homozygous genotype is 10% higher and that of the 'Kasalath' genotype 6% lower than normal segregation. There is no previous report of the presence gametophytic genes or hybrid sterility genes at the ends of these two chromosomes.

The observed segregation patterns on chromosomes 6, 8, and 10 are complicated. The peaks of the distorted



segregation curves are not clear, and the peaks for the homozygotes and the heterozygote are not at the same position on these chromosomes. The variation in the peak positions among the segregation curves for the homozygote genotypes and heterozygote ones is caused by multiple segregation distortions in these regions. The lowest frequency for 'Nipponbare' on chromosome 6 is 13.4% at 18.5 cM, at which position the 'Kasalath' genotype is 10% higher than normal and the heterozygous genotype is within the normal range. On the other hand, the highest frequency for 'Kasalath' on chromosome 6 is 38.5% at 32.6 cM; at this position the

frequency of the heterozygous genotype is the lowest on this chromosome. The lowest frequency for 'Kasalath' on chromosome 8 is 15.5% at 82.9 cM, where 'Nipponbare' segregation is normal and segregation of the heterozygous genotype is 10% higher than normal. Segregation of the heterozygote on chromosome 8 shows the highest frequency, 63.0%, at 105.6 cM, a position at which both homozygous genotypes have lower segregation frequencies than normal. On chromosome 10, 'Kasalath' homozygote has the highest ratio of 37.1% at 17.1 cM, while the the lowest one is of 'Nipponbare', 13.6% at 36.3 cM. Six different segregation distortions were seen to exist on chromosomes 6, 8, and 10 as different peak positions of the segregation curves.

In summary, several different types of distorted segregation curves were observed in seven regions, with ten different peak positions, in this cross. The peak positions and the corresponding marker names at the site at which the strongest distorted segregation was observed are listed (Table 1). Four peak positions on chromosomes 1, 3, and 9 are distant from each other. The close peak positions of the distorted segregation curves were observed on chromosomes 6, 8, and 10. For the 'Nipponbare' homozygote, allelic segregation of more than 25% was observed on chromosome 9 and for the 'Kasalath' homozygote such segregation was observed on chromosomes 1, 3, 6, and 10. Distorted segregation for the heterozygote was observed on chromosomes 3, 6, and 8.

Discussion

Skewed segregation ratios of molecular markers have been observed in maize (Gardiner et al. 1993; Chao et al. 1994), rice (McCouch et al. 1988; Causse et al. 1994), *Populus* (Bradshaw and Stettler 1994), common bean (Vallejos et al. 1992), oat (O'Donoughue et al. 1992), barley (Heun et al. 1991). Despite the seeming ubiquity of the observation of the distorted segregation of molecular markers in plant pedigrees, very few studies have pursued the causes of the distorted segregation of these molecular markers. The investigation presented here is the first study to search for distorted segregation in a single cross using molecular markers across the whole of a plant genome.

F_2 progenies were used for this study, consequently we could not determine whether the distorted segregation occurs in the male or female gamete. However, there must be no serious female gamete abortion in this cross, because the seed fertility of the hybrid between 'Nipponbare' and 'Kasalath' was higher than 90%.

The statistic k is used to denote the proportion of the allele with the factor causing segregation distortion. Thus, k can vary from 0.5 (Mendelian segregation) to 1.0 (complete segregation distortion with only one gamete genotype transmitted to the progeny). The frequencies of each genotype in the F_2 can be expressed by the statistic k in the case of a single segregation distortion. The expected frequency at the position of the factor is $(1/2)\ k$ for the homozygote. For another homozygote, the expected frequency is $(1/2)\ (1-k)$. For the heterozygote, the expected frequency is 1/2. The frequency of the heterozygote in the F_2 does not deviate 1/2 for a single segregation distortion. When significant distorted segregation is observed in the heterozygote, we can expect that distorted segregation occurs in both the male and female. If we hypothesize two genes are involved in major distorted segregation, one gene in the male with statistic k_1 and one in the female with the statistic k_2, the frequencies of each genotype in the F_2 can be predicted. When both genes come from the same parent, k_1k_2 and $(1-k_1)(1-k_2)$ are homozygote and $(k_1+k_2-2k_1k_2)$ is heterozygote. We define the gene statistic constant as follows: both k_1 and k_2 have values between 0.5 and 1.0. Then the frequency of the heterozygote, $(k_1+k_2-2k_1k_2)$, is less than 0.5. When deviation for the segregation of the heterozygote is less than 0.5, distorted segregation exists in both the male and female, and both distorted segregations tend to transmit the same genotype. When the genes in the male and female tend to transmit the opposite genotype, $k_1(1-k_2)$ and $(1-k_1)k_2$ are homozygote and $(k_1+k_2-2k_1k_2)$ are heterozygote in the F_2. Since both k_1 and k_2 are between 0.5 and 1.0, the heterozygote

Table 1 Locations of markers showing the peak of the distorted segregation curves

Chromosome	Position[1]	Marker name	Nipponbare homozygote (deviation[b])	Kasalath homozygote (deviation[b])	Heterozygote (deviation[b])
1	99.9 cM	R1928	19.0% (−6.0%)	37.0% (+12.0%)	44.0% (−6.0%)
3	0.0 cM	L375	24.9% (−0.1%)	36.2% (+11.2%)	39.0% (−11.0%)
3	107.2 cM	C198	3.2% (−21.8%)	49.7% (+24.7%)	47.0% (−3.0%)
6	18.5 cM	L1092	13.4% (−11.6%)	35.8% (+10.8%)	50.8% (+0.8%)
6	32.6 cM	R2349	20.9% (−4.1%)	38.5% (+13.5%)	40.7% (−9.3%)
8	82.9 cM	R2736	24.3% (−0.7%)	15.5% (−9.5%)	60.2% (+10.2%)
8	105.6 cM	R2367	20.7% (−4.3%)	16.3% (−8.7%)	63.0% (+13.0%)
9	0.0 cM	C152	35.5% (+10.5%)	18.8% (−6.2%)	45.7% (−4.3%)
10	17.1 cM	G1125	17.2% (−7.8%)	37.1% (+12.1%)	45.7% (−4.3%)
10	36.3 cM	Y1053R	13.6% (−11.4%)	33.0% (+8.0%)	53.4% (+3.4%)

[a] Position indicates the map location of the marker at the distorted peak in the high-resolution genetic map (Kurata et al. 1994)
[b] Deviation from the normal Mendelian segregation ratio

frequency, $(1-k_1-k_2+2k_1k_2)$, is greater than 0.5. When deviation for segregation of the heterozygote is greater than 0.5, distorted segregation exists in both the male and female and the distorted segregation tend to transmit the opposite genotype.

Significant segregation distortions were observed on 6 chromosomes. Assuming the distorted region of the segregation ratio of the heterozygote genotype has two genes, we can predict at least 11 major distorted segregations at ten positions in this cross. Each distorted segregation is discussed below in relation to our present knowledge of gametophyte genes and hybrid sterility genes.

Distorted segregation of the markers was observed in the middle of chromosome 1 (Fig. 1, Table 1). The shapes of the segregation curves are simple, and the peak positions of the homozygous segregation curves are the same. The segregation ratio for heterozygous is 1/2; the segregation distortion in this region is at 99.9 cM. The statistic k for the distortion with transmission to the 'Kasalath' gamete is between 0.62 and 0.74. Two gametophyte genes and one male sterility gene have been reported on chromosome 1 (Nakagahra 1981; Maekawa and Kita 1985; Suh et al. 1990). These genes are located between the extra glume gene mapped at around 0 cM and the Dee-geo-woo-gen semidwarf gene mapped at around 50 cM on chromosome 1 (Fig. 1) (Kinoshita 1993; Ogi et al. 1993; Saito et al. 1991; Kurata et al. 1994). The segregation distortion at 99.9 cM on chromosome 1 has not previously been reported.

The markers in the region of less than 10 cM on chromosome 3 show distorted segregation (Fig. 1, Table 1). The peak positions of the segregation curves are at 0 cM on this chromosome. Since the frequency of the heterozygote genotype at the peak position is low, 2 segregation distortions are expected to be influenced by both the female and male genotype. The k statistic in the female and the male must favor transmission to the 'Kasalath' genotype. There are no reports of either a gametophyte gene or a sterility gene in this region, and so these segregation distortions have not been reported until now.

The most pronounced distorted segregation of markers in this cross was observed in the middle of chromosome 3 (Fig. 1, Table 1). The shapes of the segregation curves are simple, and the peaks of the homozygous segregation curves are at the same position. The frequency for the heterozygote is 1/2. The segregation distorting factor for this region is a single factor at 107.2 cM. The k statistic for this distorted segregation with favorable transmission to the 'Kasalath' gametes is between 0.94 and 0.99. On the basis of work with *japonica* marker lines and 'Kasalath', Nakagahra (1972) reported that the gametophyte gene-2 (*ga-2*) in the middle of chromosome 3 is a prominent distorter gene. The distorted segregation at 107.2 cM detected in this study probably reflects the location of *ga-2* at this position.

The segregation curves in the region between 0 cM and 50 cM on chromosome 6 are complicated (Fig. 1, Table 1). We observed two different peak positions for the distorted segregation frequencies of homozygote genotypes at 18.5 cM and 32.6 cM and distorted heterozygote segregation frequencies. At least 2 distorted segregations were expected to be influenced by both the female and male genotype in this region. Both segregation distortions favor transmission to the 'Kasalath' genotype. There are many reports of gametophytic genes and hybrid sterility genes in this region using different cross combinations (Ikehashi and Araki 1986; Iwata et al. 1964; Mori et al. 1973; Nakagahra 1986; Nakagahra et al. 1974; Oka 1957, 1974; Oka and Doida 1962; Sano 1990). We could not assign these segregation distortions observed on chromosome 6 to specific genes.

On chromosome 8 we observed two different peak positions for distorted segregation curves of homozygote genotypes at 82.9 cM and 105.6 cM and distorted segregation of the heterozygote (Fig. 1, Table 1). We expect both the male and female gametes in this region to be involved in these distorted segregation curves. One distorted segregation favors transmission to the 'Kasalath' genotype and another distorted segregation favors transmission to the 'Nipponbare' genotype. No gametophyte genes or hybrid sterility genes have been reported before this in this region.

The markers in the distal region of chromosome 9 show distorted segregation (Fig. 1, Table 1). The peak positions of segregation curves are at the end of the chromosome. The segregation ratio of the heterozygote is 1/2. The segregation distortion of the markers in this region must be caused by a single factor. The k statistic indicates that the transmission of the 'Nipponbare' gamete is favored with values between 0.62 and 0.71. There are no previous reports of gametophytic genes or hybrid sterility genes on the end of chromosome 9.

We observed two distorted segregation peaks for homozygote genotypes at 17.1 cM and 36.3 cM on chromosome 10 (Fig. 1, Table 1). Since there was no significant deviation of the segregation ratio of the heterozygote genotype, these distorted segregations might act on either the male or the female gamete. There are no previous reports on distorted segregation involving chromosome 10.

Eleven different segregation distortions were detected on 6 chromosomes using 1174 molecular markers in 186 F_2 progenies from a cross between *japonica* and *indica* cultivars. To our knowledge, no previous investigation has ever attempted to detect segregation distortions over all the chromosomes in a single cross. Further studies are necessary to elucidate the nature of these distorted segregations. Reciprocal backcross experiments will verify whether the segregation distortion involves the male or female parent. Since 11 segregation distortions have been found in this single cross, many more are likely to exist in rice. Near-isogenic lines are being developed to enable the full mechanism behind distorted segregation to be understood. Interactions

among different segregation distortions could not be considered in this analysis, however, step-by-step progress in gene characterization will reveal the types of mechanism involved in distorted segregations.

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