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The high level of wide-compatibility of variety ‘Dular’ has a complex genetic basis

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Abstract Wide-compatibility varieties (WCVs) are a special class of rice germplasm that is able to produce fertile hybrids when crossed to both indica and japonica rice varieties. WCVs may differ greatly in their spectrum and level of compatibility. The objective of this study was to determine the genetic basis of wide-compatibility conferred by ‘Dular’, a landrace variety from India that has demonstrated a high level of wide-compatibility in previous studies with a broad range of indica and japonica varieties. A three-way cross (‘Balilla/Dular//Nanjing 11’) was made and the resulting F_1 population evaluated in the field for spikelet fertility. A total of 235 plants from this population was assayed individually for restriction fragment length polymorphisms (RFLPs) at 159 marker loci covering the entire rice genome at regular intervals. Quantitative trait locus (QTL) analysis identified 5 loci, located on chromosomes 1, 3, 5, 6 and 8, as having significant effects on hybrid fertility, which jointly explained 55.5% of the fertility variation in this population. The QTL on chromosome 5 (f_5) showed the largest effect on hybrid fertility, followed by those on chromosomes 6 (f_6), 3 (f_3) and 1 (f_1), with the one on chromosome 8 (f_8) having the smallest effect. Genotypes each composed of an allele from ‘Dular’ and an allele from ‘Nanjing 11’ at four (f_3 , f_5 , f_6 and f_8) of the five QTLs contributed to the increase of fertility in the population. In contrast, the genotype composed of alleles from ‘Balilla’ and ‘Nanjing 11’ at the fifth locus (f_1) was in the direction of increasing fertility. Analysis of variance using marker genotypes at the five QTLs as the groups

detected two interactions involving four of the five loci, a 2-locus interaction between f_5 and f_8 and a 3-locus interaction among f_3 , f_5 and f_6 . The level of hybrid fertility is the result of complex interactions among these loci. The implication of the present findings in the utilization of the wide-compatibility of ‘Dular’ in rice breeding programs is also discussed.

Key words *Oryza sativa* L. · Indica-japonica cross · Hybrid sterility · Molecular marker · Genetic analysis · Epistasis

Introduction

Wide-compatibility varieties (WCVs) are a special class of rice germplasm that is able to produce fertile hybrids when crossed to both indica and japonica rice (Ikehashi and Araki 1984), while hybrids between indica and japonica varieties usually show partial sterility (Kato et al. 1928). The discovery of WCVs has brought hope for breaking the fertility barrier between indica and japonica subspecies and provided a possibility for exploiting the very strong heterosis demonstrated in crosses between the two subspecies.

A number of WCVs have been identified in the last decade (Pan et al. 1990), and several of them have been subjected to genetic analyses (Ikehashi and Araki 1986; Liu et al. 1992; Zheng et al. 1992; Liu et al. 1997). The results of compatibility tests, by evaluating the fertility of the hybrids between the WCVs and a number of indica and japonica testers, have demonstrated that WCVs vary greatly in the compatible spectrum as well as in the level of compatibility (Pan et al. 1990; Liu et al. 1996). Some WCVs have both a wide spectrum and a high level of compatibility, which may be very useful as WCV germplasms, while others have either a narrower spectrum or lower compatibility and thus may have limited use in breeding programs.

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It has been repeatedly reported that 'Dular', a landrace variety from India, has both a wide compatible spectrum and a high level of compatibility as it produces highly fertile hybrids when crossed to a wide range of indica and japonica varieties (Pan et al. 1990; Liu et al. 1996; Zhang et al. 1997). However, a problem associated with this variety is that it possesses a number of undesirable characteristics, such as a tall and thin plant type and poor yielding, which has made breeders reluctant to use it as a parent in breeding programs. Thus, understanding the genetic basis of wide-compatibility is a prerequisite in order to facilitate the utilization of the wide-compatibility gene(s) in this variety.

The study reported in this paper was undertaken to characterize the genetic basis of wide-compatibility in 'Dular' using a large number of molecular markers representing the entire rice genome. The specific objectives of this study were (1) to determine the number and genomic locations of loci governing wide-compatibility in this variety, (2) to characterize the effects and the modes of gene actions involved in wide-compatibility and (3) to formulate a strategy for utilizing the high level of wide-compatibility of this variety in rice breeding programs.

Materials and methods

Experimental materials and planting

Three varieties of the Asian cultivated rice (*Oryza sativa* L.) were used in this study: 'Balilla', 'Dular' and 'Nanjing 11'. 'Balilla' is a japonica variety from Italy, 'Dular' is an indica variety from India and 'Nanjing 11' is an indica variety developed by the Agricultural Academy of Jiangsu Province, China. A cross was made between 'Balilla' and 'Dular' in the summer of 1995 in Wuhan. The resulting F₁ plants were crossed to 'Nanjing 11' in the winter of 1995–1996 in Hainan (South China Sea) Island.

The resulting 298 seeds from this three-parent cross ('Balilla/Dular//Nanjing 11') were planted during the 1996 rice growing season at the Experimental Farm of Huazhong Agricultural University, Wuhan. At the tillering stage, two tillers from each plant was peeled off and transplanted to different hills so that each plant was replicated three times in the field. Such tiller peeling is a common practice in rice propagating and does not have any adverse effect on fertility. One replicate was used for DNA extraction, and the other two were used for fertility evaluation.

Spikelet fertility of each plant was scored on the basis of four to five panicles. The population also segregated for the pigment chromogen controlled by the *C* gene locus closely linked to the *S₅* locus on chromosome 6 (Ikehashi and Araki 1986). Phenotypes at the *C* locus were also scored and used as a genetic marker in map construction and gene mapping.

Restriction fragment length polymorphism (RFLP) assay

Total cellular DNA was isolated essentially following the protocol of Murray and Thompson (1980). Restriction digestion, electrophoresis, blotting and hybridization were conducted according to the procedures described by Liu et al. (1997). For surveying the parental

polymorphism, the DNA samples from the three parents were digested using six restriction enzymes (*Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV and *Hind*III) and hybridized with a total of 400 RFLP probes mainly from the Cornell and Japanese Rice Genome Research Program (RGP) maps (Causse et al. 1994; Kurata et al. 1994). A set of well-spaced polymorphic markers was used to assay a large sample of true hybrid plants from this three-parent cross population.

Data processing and statistical analysis

A molecular marker linkage map was constructed using MAPMAKER/EXP 3.0 with a LOD threshold of 3.0 (Lincoln et al. 1992a). The whole genome was searched for the presence of loci governing hybrid fertility using MAPMAKER/QTL 1.0 at LOD threshold 3.0 (Lincoln et al. 1992b). Analysis of variance using marker genotypes as the groups was conducted using the statistical package STATISTICA (StatSoft 1995).

Results

Fertility segregation in the population

The fertility distribution of the 281 truly hybrid plants, as determined by the RFLP analysis of multiple loci, is given in Fig. 1. The distribution was continuous but not normal, indicating a complex genetic basis.

The linkage map

A map, including 159 RFLP loci and one morphological marker locus, was constructed on the basis of 235 of the 281 true hybrid plants using MAPMAKER/EXP 3.0 at LOD 3.0 (map not shown). The total length of the map was 1674 cM, with an average distance of 10.9 cM between adjacent loci. The markers had a good coverage of all 12 chromosomes in both the Cornell and RGP maps (Causse et al. 1994; Kurata et al. 1994). The order of the appearance of the marker loci agreed well with those in the two maps.

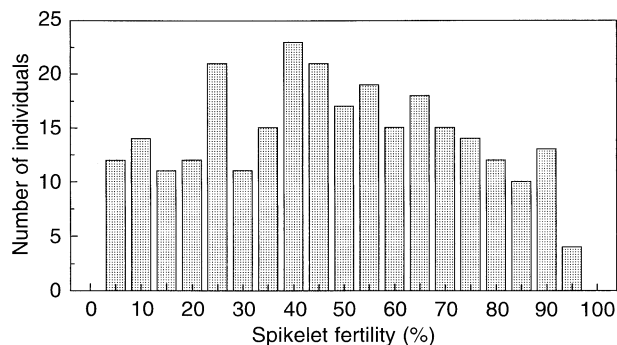


Fig. 1 Distribution of spikelet fertility in the F₁ population of 'Balilla/Dular//Nanjing 11'

Quantitative trait loci (QTLs) controlling hybrid fertility

The search of the entire genome using MAPMAKER/QTL 1.0 at LOD 3.0 resolved five QTLs governing hybrid fertility (Fig. 2). The QTL located in the 3.4-cM interval between R830 and R3166 near the distal end on the short arm (Singh et al. 1996) of chromosome 5 exhibited the largest effect (Table 1), followed by the one located in the 6.4-cM interval between R2349 and the C gene locus on chromosome 6. The effects of the remaining three QTLs, located on chromosomes 1, 3 and 8, respectively, were much smaller. These five QTLs jointly explained 55.5% of the fertility variation in this population as determined by a multiple QTL analysis (Lincoln et al. 1992).

For ease of description, we will designate these QTLs according to their chromosome serial numbers and refer to the QTLs identified on chromosomes 1, 3, 5, 6 and 8 as *f1*, *f3*, *f5*, *f6* and *f8*, respectively. We will also refer to the genotype composed of an allele from 'Dular' and an allele from 'Nanjing 11' as genotype 1 of each locus, and the genotype with an allele from 'Balilla' and an allele from 'Nanjing 11' as genotype 2.

It is also clear from Table 1 that, at the *f1* locus, the allele from 'Dular' had a negative effect on hybrid fertility; genotype 1 showed significantly lower fertility

than genotype 2 of this locus. In contrast, genotype 1 at the other 4 loci exhibited significantly higher fertility than genotype 2 of the respective locus.

Modes of gene actions

An analysis of variance using marker genotypes at the 5 loci as the groups revealed complex relations among the 5 loci in determining hybrid fertility in this cross (Table 2). Locus *f1* (marked by RG532), at which genotype 1 showed a negative effect on fertility, was statistically independent of the other 4 loci, whereas two interactions were detected among the remaining 4 loci.

The first significant interaction occurred between *f5* (marked by R830) and *f8* (RG333). This interaction was characterized by the very different patterns of fertility changes displayed by the two genotypes at the *f5* locus in combinations with the two genotypes at the *f8* locus (Fig. 3). A fertility difference of approximately 18% was detected between genotypes 1 and 2 at the *f8* locus when the *f5* locus was genotype 2, but the difference was much smaller when the *f5* locus was genotype 1. At both loci, genotype 1 showed higher fertility than genotype 2, the 2-locus combination with 'Dular' alleles at both loci displaying the highest fertility (Fig. 3).

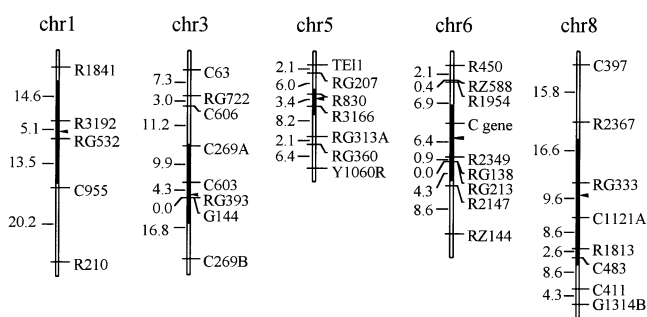


Fig. 2 Distribution of QTLs controlling hybrid fertility in the genome based on the F_1 population of 'Balilla/Dular//Nanjing 11' resolved by MAPMAKER/QTL. The arrow on each chromosomal region indicates the position of the LOD peak, and the black bar represents the 1-LOD supporting interval for each QTL

Table 1 QTLs controlling hybrid fertility in the 'Balilla/Dular//Nanjing 11' population resolved by QTL analysis using MAPMAKER/QTL 1.0

Flanking markers	Locus designation	Chromosome location	LOD score	Variance explained (%)	Effect ^a
RG532-R3129	<i>f1</i>	1	3.49	6.8	-12.9
RG393-C603	<i>f3</i>	3	4.55	8.7	14.5
R830-R3166	<i>f5</i>	5	15.76	26.6	25.3
C gene-R2349	<i>f6</i>	6	9.06	17.1	20.5
C1121A-RG333	<i>f8</i>	8	3.07	6.6	12.6
Total				55.5	

^a Effect of the genotype having the 'Dular' allele on spikelet fertility (%)

Table 2 Results from an analysis of variance using marker genotypes as groups at 5 marker loci. Only significant interaction terms are listed in the table

Effect	df	MS effect	F	P
<i>f1</i> (RG352)	1	0.384	14.6	0.0002
<i>f3</i> (RG393)	1	0.405	15.4	0.0001
<i>f5</i> (R830)	1	2.151	81.9	0.0000
<i>f6</i> (R2349)	1	1.438	54.7	0.0000
<i>f8</i> (RG333)	1	0.447	17.0	0.0001
<i>f3</i> × <i>f6</i> *	1	0.287	10.9	0.0011
<i>f5</i> × <i>f6</i> *	1	0.158	6.0	0.0151
<i>f5</i> × <i>f8</i>	1	0.209	7.9	0.0053
<i>f3</i> × <i>f5</i> × <i>f6</i>	1	0.221	8.4	0.0041
Error	202	0.026		

* These two 2-locus interactions are nested in the three-way interaction *f3* × *f5* × *f6*, hence they cannot be interpreted independently

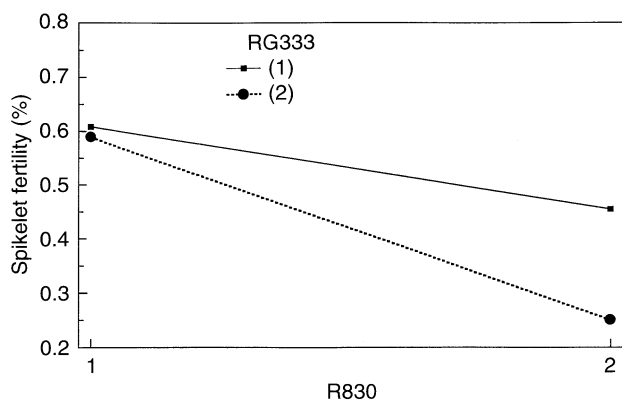


Fig. 3 Schematic representation of the interaction between two QTLs conditioning hybrid fertility marked by R830 (*f5*) and RG333 (*f8*). Genotype 1 of each locus is composed of an allele from ‘Dular’ and an allele from ‘Nanjing 11’, and genotype 2 of each locus consists of alleles from ‘Balilla’ and ‘Nanjing 11’

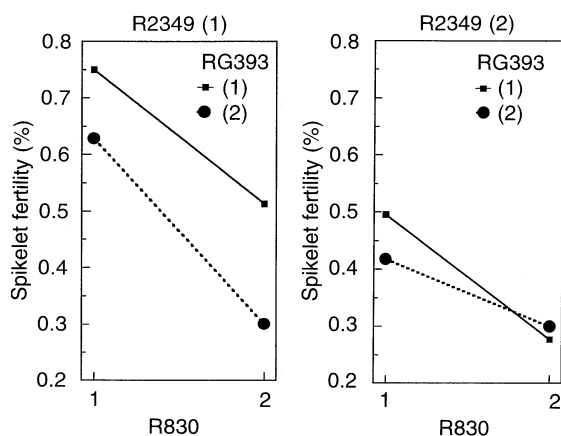


Fig. 4 Schematic representation of the interaction among three QTLs conditioning hybrid fertility marked by R830 (*f5*), R2349 (*f6*) and RG393 (*f3*). See Fig. 3 for designations of the genotypes of each locus

The second highly significant interaction was detected among the 3 loci, *f3* (RG393), *f5* (R830) and *f6* (R2349); the fertility level of the genotypes at 1 locus was dependent upon the genotypes of the other 2 loci (Fig. 4). Again the highest fertility was observed in the multilocus combination containing ‘Dular’ alleles at all 3 loci, although the combination showing the lowest fertility was not necessarily the one carrying non-‘Dular’ alleles at all 3 loci (Fig. 4).

Fertility of various multilocus genotypes

The fertility for each of the 32 five-locus combinations is given in Table 3. The highest fertility occurred in the multilocus combinations with genotype 2 at the *f1* locus and genotype 1 at *f3*, *f5* and *f6* (2111), irrespective

Table 3 Fertility for each of the 5-locus combinations

RG532 (<i>f1</i>)	RG393 (<i>f3</i>)	R830 (<i>f5</i>)	R2349 (<i>f6</i>)	RG333 (<i>f8</i>)	Spikelet fertility (%)
1 ^a	1	1	1	1	75.4
1	1	1	1	2	57.7
2	1	1	1	1	79.4
2	1	1	1	2	80.5
1	2	1	1	1	64.0
1	2	1	1	2	58.7
2	2	1	1	1	71.3
2	2	1	1	2	59.3
1	1	1	2	1	43.6
1	1	1	2	2	52.6
2	1	1	2	1	46.5
2	1	1	2	2	52.6
1	2	1	2	1	37.1
1	2	1	2	2	32.5
2	2	1	2	1	47.6
2	2	1	2	2	46.1
1	1	2	1	1	60.4
1	1	2	1	2	41.3
2	1	2	1	1	57.5
2	1	2	1	2	53.5
1	2	2	1	1	31.3
1	2	2	1	2	15.0
2	2	2	1	1	47.1
2	2	2	1	2	21.1
1	1	2	2	1	25.1
1	1	2	2	2	19.5
2	1	2	2	1	40.0
2	1	2	2	2	21.7
1	2	2	2	1	32.2
1	2	2	2	2	13.3
2	2	2	2	1	52.6
2	2	2	2	2	28.5

^aGenotype 1 of each locus was composed of an allele from ‘Dular’ and an allele from ‘Nanjing 11’; genotype 2 of each locus consisted of an allele from ‘Balilla’ and an allele from ‘Nanjing 11’

of the genotype at the *f8* locus (fertility 80.5% when the *f8* locus was genotype 1, and 79.4% when *f8* was genotype 2). There were also 2 other multilocus combinations that gave normal or nearly normal fertility (75.4% for the 5-locus combination with genotype 1 at all 5 loci, i.e. 11111, and 71.3% for combination 22111). Fertility for the remaining 28 combinations was much lower (<65%).

Discussion

Several models have been suggested in studies with respect to the genetic basis of wide-compatibility. The most well-known is the allelic interaction model proposed by Ikehashi and Araki (1986). According to this model, there are three alleles at the S_5 locus: a neutral allele, S_5^0 ; an indica allele, S_5^i ; and a japonica allele, S_5^j . A zygote formed of the S_5^0 allele with either of the other two alleles, i.e. $S_5^0S_5^i$ and $S_5^0S_5^j$, would be fully fertile,

while a zygote genotypically $S_5^i S_5^j$ would be partly sterile. Ikehashi and Araki (1986) also determined, using morphological markers, that the S_5 locus is located on chromosome 6.

In fertility analyses of many indica-japonica hybrids, it has often been observed that there is considerable variation in the fertility level in hybrids from the same WCV crossed to different indica or japonica varieties (Gu et al. 1993, Liu et al. 1996), suggesting the involvement of additional genes that modify hybrid fertility in the presence of the wide-compatibility gene. To evaluate such a possibility, Liu et al. (1997) conducted a genome-wide analysis on the wide-compatibility of the variety '02428' using RFLP markers covering all 12 rice chromosomes. They identified 1 major locus, corresponding to S_5 in chromosomal location, and 2 minor loci on chromosomes 2 and 12, respectively, conditioning wide-compatibility. They also determined that hybrid sterility is essentially the result of allelic interactions within loci.

In the present study, we uncovered a complex genetic basis for the high-level wide-compatibility demonstrated by the variety 'Dular'. Our analysis revealed several distinct features concerning the genetic complexity of the wide-compatibility in this variety. First, the number of loci involved in wide-compatibility (or hybrid sterility) as determined by single-locus analysis is larger than those identified in all previous studies of wide-compatibility. In fact, this number is comparable to those identified for typical quantitative characters such as yield and yield component traits in many previous studies (e.g. Stuber et al. 1992; Lu et al. 1996; Yu et al. 1997).

Second, not all the alleles from the wide-compatibility variety 'Dular' contribute to the increase in fertility. Single-locus analysis showed that alleles from 'Dular' at 4 of the 5 loci contributed to a fertility increase, whereas the 'Dular' allele at the 5th locus decreased hybrid fertility. This situation is also similar to the results from QTL analyses of many quantitative traits in which alleles from the higher parents sometimes contribute to a decrease in performance (e.g. Yu et al. 1997).

The third feature concerns the inter-locus interactions among the loci resolved by QTL analysis. The interactions involved 4 of the 5 loci, including pairwise and a three-way interactions, and indicated a very complex genetic basis for the wide-compatibility of 'Dular'. Thus, the effect of 1 locus on fertility expression is critically dependent on the genotypes of other loci. Such interactions are also similar to those identified for yield and yield component traits reported recently (Li et al. 1997; Yu et al. 1997). Interactions between loci have also been detected to play a role in the genetic basis of hybrid sterility in indica-japonica crosses (Wu et al. 1996; Li et al. 1997), although the modes of interactions may not be as complex as the one identified in the present study.

One issue remaining to be resolved is the relationship of the $f6$ locus on chromosome 6 identified in this study with the previously identified S_5 locus. It is highly likely that they are the same locus based on the well-coincided chromosomal locations determined by molecular marker-based linkage analysis (Liu et al. 1997). However, the allele from 'Dular' at this locus, according to the analysis of the present study, seems to be much less effective in conferring wide-compatibility than the one from var '02428' assessed in our previous study. This suggests the possibility that the allele from 'Dular' may be a different allele of the S_5 locus with a lower level of wide-compatibility than the one detected in '02428'. Whether or not this is the case remains to be determined in future studies.

These results have significant implications in breeding for wide-compatibility varieties. Although the genetic basis is complex, the fact that the highest performing multilocus combinations are the ones with genotypes 1 at the $f3$, $f5$ and $f6$ loci and genotype 2 at $f1$, irrespective of the genotypes at the $f8$ locus, suggests that only 4 loci need to be considered in the breeding programs. This suggests that the strategy for utilizing the wide-compatibility of 'Dular' may involve introducing the 'Dular' alleles at the $f3$, $f5$ and $f6$ loci into the breeding lines leaving behind the 'Dular' allele at the $f1$ locus. This can be accomplished within a few generations with marker-assisted selection techniques using the closely linked markers identified in the present study. Another possibility is to pyramid the 'Dular' allele at the $f5$ locus with the S_5^m allele of '02428', as these two appeared to be the major alleles in their respective systems. However, this possibility has yet to be tested since the effects of the two alleles on wide-compatibility may not be additive.

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