

QTL-Based Analysis of Heterosis for Grain Shape Traits in Rice (*Oryza sativa* L.)

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ABSTRACT

To analyze the genetic basis for an enhanced level of heterosis in an intersubspecific rice hybrid, the heterozygotes and homozygotes at each locus should be compared. A set of BC₁F₁, i.e., *indica/japonica*/*japonica* and *indica/japonica*/*indica*, were produced and analyzed with simple sequence repeat (SSR) markers to specifically compare the effect of heterozygotes and homozygotes at each QTL locus for grain shape. Rice grain shape traits have shown an extremely wide diversity. In this review, we discuss QTL-based analysis of heterosis for grain shape traits. In the comparison of marker genotypes of *AA*, *Aa* and *aa*, QTLs were detected either between *AA* and *Aa* or between *Aa* and *aa*, and there is no case in which *Aa* was superior to *AA* and *aa*. In both analyses, each positive effect was contributed from either one of the parents. We concluded that the high level of heterosis in the current *indica/japonica* hybrids was manifested by a cumulative partial dominance effect of the heterozygotes at many loci and not by overdominance. Then, the set of QTL data for positive effects are considered to be systematically utilized in breeding of parental lines by using molecular markers.

Keywords: grain, heterosis, *indica/japonica* hybrid, QTL, rice

Abbreviations: QTL, quantitative trait locus; SSR, simple sequence repeat; WCG, wide compatibility gene

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INTRODUCTION

The term “heterosis” can be defined as the biological phenomenon in which an F₁ hybrid of two genetically different parents shows increased vigor which is greater than the average of both parents.

In rice, Jones (1926) first reported heterosis in which some F₁ hybrids had more culms and higher yield than their parents. In the last decade the high level of heterosis in intersubspecific hybrids has been utilized in hybrid rice breeding (Yuan 1998; Peng *et al.* 1999).

Yield-contributing traits such as grain weight, number of panicles per plant and number of grain per panicle are considerably important traits for rice breeding. Their phenotypic variations are usually continuous instead of discrete and conditioned by allelic variation at several genetic loci. Such characters have been referred to as quantitative traits, and the individual loci controlling a quantitative trait as quantitative trait locus (QTL) (Tanksley 1993).

Advance in molecular markers has greatly facilitated the investigation of the genetic basis of complex quantitative traits. Recently, microsatellites or SSRs have become useful markers for genome analysis, because they are co-dominant with a high level of allelic diversity, and easily

and economically assayed by PCR (McCouch *et al.* 1997). Many QTLs associated with rice grain shape traits were identified until now.

In this article, we briefly review the current status of our knowledge of heterosis especially for grain shape traits in rice, and discuss the prospects of using this information obtained from QTL-based analysis for rice breeding.

EXPLANATION FOR GENETIC BASIS OF HETEROSIS

The genetic basis of heterosis has been explained by two leading hypotheses, namely the dominance hypothesis (Davenport 1908) and the overdominance hypothesis (East 1908; Shull 1908). The dominance hypothesis states that dominant alleles from either parent complement deleterious recessive alleles from the other parent in the heterozygous F₁. The overdominance hypothesis asserts that the heterozygote for a gene is superior to the two homozygotes for the same gene. In addition to the two hypotheses, less widely embraced hypothesis suggests that heterosis may be caused by epistasis between alleles at different loci. The genetic basis of heterosis has been debated for many years and is still not resolved.

EXPLOITATION OF HETEROSIS IN RICE

Cultivated rice (*Oryza sativa* L.) is classified into three varietal groups, *indica*, *japonica*, and *javanica*. The degree of heterosis in different hybrid rice varieties depends greatly on genetic distance between parents, and has the following general trend: *indica/japonica* > *indica/javanica* > *japonica/javanica* > *indica/indica* > *japonica/japonica*. *Indica/japonica* hybrids possess the highest yield potential in both sink and source (Yuan 1994). Accordingly, exploitation of pronounced heterosis in *indica/japonica* hybrids is greatly promising, however, it has been limited by their hybrid sterility. Now, it is widely confirmed that the sterility of *indica/japonica* hybrids is due to gamete abortion caused by an allelic interaction at a particular locus (*S*-locus), where *indica* and *japonica* have *Sⁱ* and *S^j* allele, respectively, and some *javanicas* have a neutral allele, *Sⁿ* (wide compatibility gene (WCG)). The *Sⁱ/S^j* genotype shows gamete abortion, but *Sⁿ/Sⁱ* and *Sⁿ/S^j* do not (Ikehashi *et al.* 1994). Practically, incorporating WCG into parental lines made it possible to develop fertile *indica/japonica* hybrids.

GRAIN SHAPE TRAITS IN RICE

Domestication has greatly increased the diversity of grain shape traits accompanied by many other changes, as consequences of physiologic response and adaptation to various environments and human needs. Large seeds tended to be selected by human during the early domestication, as evidenced by the fact that most cultivated species have larger seeds than their wild relatives (Harlan 1992). It was reported that a recessive mutation leading to larger grain size may have been part of the domestication syndrome in rice (Li *et al.* 2004). The information of grain shape traits is meaningful for us not only as a component of grain yield, but also evidence on crop evolution studies.

Rice grain shape traits have shown an extremely wide diversity. Hulled and dehulled grains of rice have greater variations in size and shape than those of other cereals. For example, among 80,000 varieties preserved by the IRRI (1986) the variation in length, width and weight of hulled

grains ranges as follows: grain length 4.1-13.7 mm, grain width 1.9-4.1 mm, and 1000-grain weight 8-57 mg, with maximum/minimum ratios of 2-7 (Sato 1997).

GENES INVOLVED IN REGULATION OF GRAIN SHAPE TRAITS IN RICE

To understand molecular mechanism of the control of seed length, dwarf mutant, *dwarf11* (*d11*), that bears seeds of reduced length, was analyzed. The *D11* gene was isolated by a map-based cloning method, and found to encode a novel cytochrome P450 (CYP724B1), which showed homology to enzymes involved in brassinosteroid biosynthesis (Tanabe *et al.* 2005).

The *GS3* locus, a QTL with major effect on grain size was consistently detected around the centromeric region of chromosome 3 in many studies across different genetic backgrounds and environments. The *GS3* gene encoded a putative transmembrane protein (Fan *et al.* 2006).

The cloning and characterization of a QTL for grain width and weight, *GW2*, on the short arm of chromosome 2, was reported. *GW2* encoded a RING protein with E3 ubiquitin ligase activity. Reduction or loss of function of *GW2* increased cell numbers, resulting in a larger spikelet hull, and it accelerated the grain milk filling rate, resulting in enhanced grain width and weight (Song *et al.* 2007).

ANALYSIS OF HETEROSIS FOR GRAIN SHAPE TRAITS BY SINGLE LOCUS COMPARISON

We will take an example to specifically compare the effect of heterozygotes and homozygotes at each QTL locus for grain shape trait in an *indica/japonica* hybrid in rice. A set of BC₁F₁, i.e., *indica/japonica/japonica* and *indica/japonica/indica*, were produced, using IR36 as the *indica* parent and Nekken 2 (NK2) as the *japonica* parent. The two parents, IR36 and NK2, showed highly significant differences in grain shape traits (Fig. 1A, 1B). NK2 has the WCG to show normal spikelet fertility in crosses to *indica* cultivars (Abdelkhalik *et al.* 2005). A common set of SSR markers was applied for both populations for single locus com-

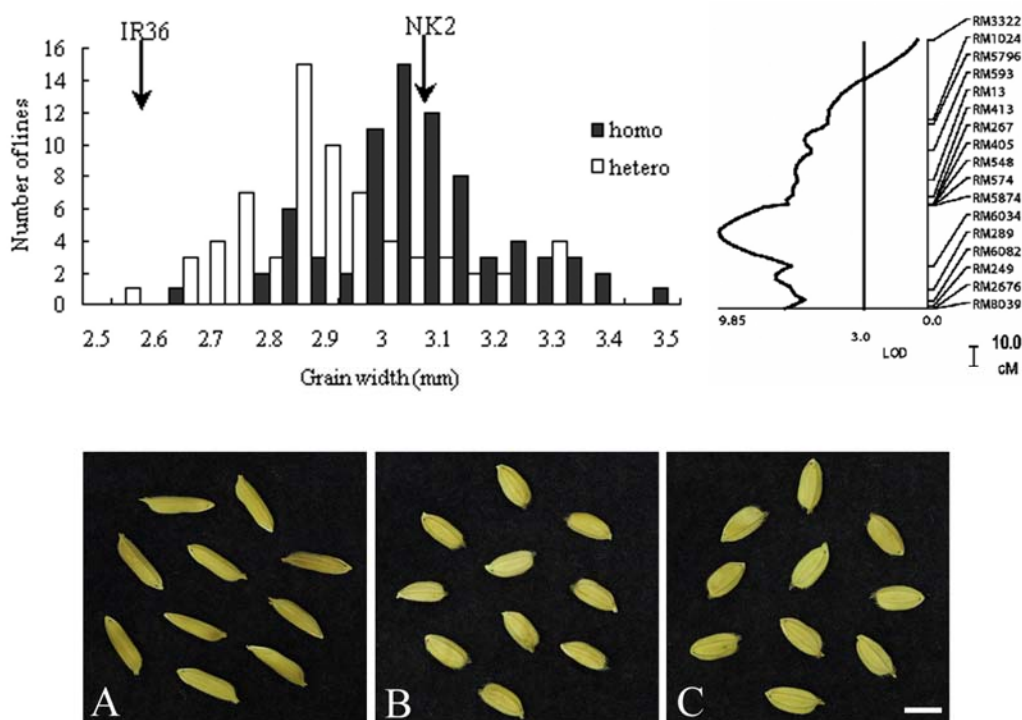


Fig. 1 Frequency distribution of grain width at *qWJ-5* on chromosome 5. Top right linkage map of chromosome 5 shows location of a QTL for grain width. The marker (RM5874) genotype in IR36/NK2/NK2 shows that NK2-homozygous genotype (shaded bars) is of higher value than the heterozygous genotype (unshaded bars). In another population, IR36/NK2/IR36, the QTL for grain width was not detected. The two parents, IR36 (A) and NK2 (B) showed highly significant differences in grain shape traits. (C) Largest grain in IR36/NK2/NK2. Bar = 5 mm.

parison. As a result, a total of ten QTLs were found: two QTLs for grain weight in IR36/NK2//IR36, five QTLs for grain width in IR36/NK2//IR36 and IR36/NK2//NK2, and three QTLs for grain thickness in IR36/NK2//NK2. Here we could estimate the relative effect of heterozygotes and homozygotes, because QTLs were based on the difference between heterozygotes (*Aa*) and homozygotes (*AA* or *aa*). When a heterozygote (*Aa*) was superior to homozygotes (*AA* or *aa*) in one of the backcross populations, it was necessary to compare the effect in another population to see whether the *Aa* was also superior to the other homozygote in the same QTL. If a heterozygote is superior to the corresponding homozygotes in the two populations, this will be an evidence for overdominance. Although the heterozygotes showed superiority to one of homozygotes (*AA* or *aa*), in no case the heterozygotes simultaneously showed a higher level of phenotypic value than both of homozygotes. Thus, there was no evidence for overdominance. One case of comparative distributions of homozygotes and heterozygotes is shown in Fig. 1. At the QTL of grain width qWIJ-5 (neighboring marker RM5874), the *japonica*-homozygote was superior to the heterozygote in IR36/NK2//NK2, whereas no difference between the two genotypes was detected in IR36/NK2//IR36.

The examination of genotypic effect at each QTL in our study revealed that positive effects were contributed either by *indica* or *japonica* parents. In the F_1 genotype, the cumulative partial dominance effects of such heterozygotes are considered to give better performance than the parents.

CONCLUDING REMARKS

QTL analysis is based on statistical verification of the relationship between marker genotype and the traits evaluated.

The parents showing large differences for the traits are employed to detect QTLs. Furthermore, wild species have been utilized to exploit potentially novel useful alleles. In spite of the overall undesirable characteristics of the wild phenotype, progenitor of Asian cultivated rice, *O. rufipogon*-derived allele made a contribution to desirable agronomic effect including grain shape traits (Thomson *et al.* 2003; Lee *et al.* 2005). Several QTLs which had not been detected in the QTL studies between *Oryza* cultivars were reported, indicating their great worth as potentially useful breeding materials.

In the course of differential development of *indica* and *japonica* groups of rice, one set of genes for positive effects may largely be possessed in a group, while another set of positive genes in another group. Thus, hybrids within a same group may not show clear superiority over the parents as commonly shown in *japonica/japonica* hybrids. On the other hand, if the numbers of contrasting alleles are large in a pair of distantly related parents, then the sum of positive contributions from such parents is considered to be larger. The progeny testing from a cross between *japonica* and *indica* often showed tremendous variation in the traits evaluated, despite small differences in the traits between the parents (Li *et al.* 1997; Redoña and Mackill 1998; Abdelkhalik *et al.* 2005; Wan *et al.* 2006).

Let us now attempt to extend such an understanding into the idea of practical use for rice breeding. Many QTLs associated with rice grain shape traits were identified until now. Tables 1-4 summarize previous QTL studies of grain shape traits, length, width, thickness and weight respectively, between *Oryza* cultivars. Effects of some QTLs were unstable and seem to depend on the materials and the experimental designs employed. However, a great number of universal QTLs were detected, for example, a major QTL

Table 1 QTLs for grain length detected using *Oryza* cultivars.

Chr	QTL	Interval marker	LOD	PVE	R ²	Parents	Population
1	<i>GL</i>	G031003-F16916	2.54	-	11.9	Reiho / Yamadanishiki	<i>japonica / japonica</i> DHL ^{a)}
2	<i>gl2</i>	RM438-RM341	3.71	12.7	-	Domsephid / Gerdeh	<i>indica / indica</i> F ₂ ^{b)}
	-	R1843-RMD1	3.1	6.5	-	Zhenshan 97 / Minghui 63	<i>indica / indica</i> F _{2,3} ^{c)}
	<i>qGL-2</i>	C777-R1989	7.73	5.8	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
	-	CDO1091-RG520	3.42	-	8.0	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
	<i>qGL-2a</i>	C560-C1408	4.0	11.7	-	Nipponbare / Kasalath	<i>japonica / indica</i> BIL ^{f)}
	<i>qGL-2b</i>	G1327-C421	2.9	6.2	-	Nipponbare / Kasalath	<i>japonica / indica</i> BIL ^{f)}
3	<i>gl3</i>	RM251-RM554	6.32	19.3	-	Domsephid / Gerdeh	<i>indica / indica</i> F ₂ ^{b)}
	-	RG393-C1087	41.0	63.8	-	Zhenshan 97 / Minghui 63	<i>indica / indica</i> F _{2,3} ^{c)}
	-	RG393-C1087	33.8	57.6	-	Zhenshan 97 / Minghui 63	<i>indica / indica</i> RIL ^{c)}
	<i>qGL-3a</i>	C80-C1677	27.79	32.2	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
	<i>qGL-3b</i>	XNpb249-C1468	7.3	11.6	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
	-	CDO457-RZ142	4.63	-	10.4	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
	-	RZ452-RZ284	9.95	-	20.9	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
	<i>GS3</i>	GS09-MRG5881	129.2	95.6	-	Minghui 63 / Chuan 7	<i>indica / indica</i> BC ₃ F ₂ ^{g)}
4	-	RZ656-RG449	5.71	-	12.7	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
	-	RG476-RG620	3.77	-	8.6	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
	<i>GL</i>	RM255-RM131	3.47	-	16.4	Reiho / Yamadanishiki	<i>japonica / japonica</i> DHL ^{a)}
5	<i>gl5</i>	RM437-RM289	3.61	13.5	-	Domsephid / Gerdeh	<i>indica / indica</i> F ₂ ^{b)}
	<i>qGL-5</i>	Y1060L-R569	7.85	10.3	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
	<i>qGL-5</i>	R1436-R2289	3.2	8.6	-	Nipponbare / Kasalath	<i>japonica / indica</i> BIL ^{f)}
6	<i>qGL-6</i>	R674-R2549	5.1	15.0	-	Nipponbare / Kasalath	<i>japonica / indica</i> BIL ^{f)}
	<i>GL</i>	RM204-RM276	2.48	13.0	-	Reiho / Yamadanishiki	<i>japonica / japonica</i> DHL ^{a)}
7	<i>gl7</i>	RM481-RM125	3.53	12.4	-	Domsephid / Gerdeh	<i>indica / indica</i> F ₂ ^{b)}
	-	RG128-C1023	3.9	15.4	-	Zhenshan 97 / Minghui 63	<i>indica / indica</i> F _{2,3} ^{c)}
	<i>qGL-7</i>	XNpb379-XNpb268	15.97	19.1	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
	-	RG711-RG650	8.0	-	17.2	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
8	<i>gl8</i>	RM72-RM515	4.58	15.8	-	Domsephid / Gerdeh	<i>indica / indica</i> F ₂ ^{b)}
9	<i>qGL-9</i>	XNpb339-C796C	12.16	10.7	-	Asominori / IR24	<i>japonica / indica</i> RIL ^{d)}
10	-	RZ625-RZ337	3.66	-	8.4	Labelle / Black Gora	<i>japonica* / indica</i> F ₂ ^{e)}
11	-	G44-G257	3.1	7.2	-	Zhenshan 97 / Minghui 63	<i>indica / indica</i> RIL ^{c)}
	<i>GL</i>	B01482- RM332	5.31	-	23.4	Reiho / Yamadanishiki	<i>japonica / japonica</i> DHL ^{a)}
12	<i>qGL-12</i>	C443-R617	2.4	6.6	-	Nipponbare / Kasalath	<i>japonica / indica</i> BIL ^{f)}

PVE, Percentage of phenotypic variance explained

R², coefficient of determination

* tropical *japonica*

a) Yoshida *et al.* 2002; b) Rabiei *et al.* 2004; c) Tan *et al.* 2000; d) Wan *et al.* 2006; e) Redoña and Mackill 1998; f) Li *et al.* 2003; g) Fan *et al.* 2006

Table 2 QTLs for grain width detected using *Oryza* cultivars.

Chr	QTL	Interval marker	LOD	PVE	R ²	Parents	Population
1	<i>qWLJ-1</i>	RM84-RM259	2.52	7.6	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	-	C161-R753	3.8	13.7	-	Zhenshan 97 / Minghui 63	<i>indica</i> / <i>indica</i> F _{2,3} ^{c)}
2	<i>gb2</i>	RM279-RM555	7.08	16.2	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	<i>qWII-2</i>	RM213-RM166	3.43	10.7	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	<i>qWLJ-2</i>	RM233A-RM8	3.69	11.0	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	-	RG139-CDO686	4.01	-	9.1	Labelle / Black Gora	<i>japonica</i> * / <i>indica</i> F ₂ ^{e)}
3	<i>qGW-2</i>	G275-C560	6.2	15.4	-	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
	<i>gb3</i>	RM7-RM251	15.02	34.1	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	-	RZ448-RZ403	3.5	-	7.9	Labelle / Black Gora	<i>japonica</i> * / <i>indica</i> F ₂ ^{e)}
	<i>qGW-3</i>	G332-C80	5.0	12.7	-	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
	<i>GS3</i>	GS09-MRG5881	8.9	19.8	-	Minghui 63 / Chuan 7	<i>indica</i> / <i>indica</i> BC ₃ F ₂ ^{g)}
4	<i>GWh</i>	T082023-RM241	3.49	-	16.0	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
5	<i>gb5</i>	RM437-RM289	6.2	14.9	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	<i>qWLJ-5</i>	RM13-RM289	9.47	26.1	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	-	RG360-C734a	20.6	55.2	-	Zhenshan 97 / Minghui 63	<i>indica</i> / <i>indica</i> F _{2,3} ^{c)}
	-	RG360-C734a	16.5	44.0	-	Zhenshan 97 / Minghui 63	<i>indica</i> / <i>indica</i> RIL ^{c)}
6	<i>qGW-5a</i>	R830-R3166	11.0	32.5	-	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
	<i>GWh</i>	RM31-M031078	6.31	-	27.1	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	<i>gb6</i>	RM527-RM3	4.43	10.5	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	-	RG424-C962	2.6	10.4	-	Zhenshan 97 / Minghui 63	<i>indica</i> / <i>indica</i> F _{2,3} ^{c)}
7	-	RZ667-RG424	2.5	4.6	-	Zhenshan 97 / Minghui 63	<i>indica</i> / <i>indica</i> RIL ^{c)}
	<i>gb7</i>	RM481-RM125	4.21	10.1	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	<i>qWLJ-7</i>	RM125-RM11	2.57	8.0	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	-	RG711-RG650	10.54	-	22.0	Labelle / Black Gora	<i>japonica</i> * / <i>indica</i> F ₂ ^{e)}
8	<i>gb8</i>	RM256-RM230	8.48	20.0	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}
	-	RZ143-RG333	3.24	-	7.5	Labelle / Black Gora	<i>japonica</i> * / <i>indica</i> F ₂ ^{e)}
9	<i>gb9</i>	RM434-RM201	3.79	9.5	-	Domsephid / Gerdeh	<i>indica</i> / <i>indica</i> F ₂ ^{b)}

PVE, Percentage of phenotypic variance explained

R², coefficient of determination* tropical *japonica*a) Yoshida *et al.* 2002; b) Rabiei *et al.* 2004; c) Tan *et al.* 2000; d) Abdelkhalik *et al.* 2005; e) Redoña and Mackill 1998; f) Li *et al.* 2003; g) Fan *et al.* 2006**Table 3** QTLs for grain thickness detected using *Oryza* cultivars.

Chr	QTL	Interval marker	LOD	PVE	R ²	Parents	Population
2	<i>qTHJ-2</i>	RM233A-RM145	4.08	12.0	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{b)}
	<i>qTHJ-2-2</i>	RM324-RM452	3.70	11.1	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{b)}
	<i>GT</i>	W131132-RM109	2.04	-	9.9	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
3	<i>GS3</i>	GS09-MRG5881	5.3	12.1	-	Minghui 63 / Chuan 7	<i>indica</i> / <i>indica</i> BC ₃ F ₂ ^{c)}
4	<i>GT</i>	T082023-RM241	2.03	-	9.7	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
5	<i>qTHJ-5</i>	RM289-RM249	4.96	14.7	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{b)}
	<i>GT</i>	RM31-M031078	4.36	-	19.6	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}

PVE, Percentage of phenotypic variance explained

R², coefficient of determination* tropical *japonica*a) Yoshida *et al.* 2002; b) Abdelkhalik *et al.* 2005; c) Fan *et al.* 2006

for grain length on the centromeric region of chromosome 3 (Redoña and Mackill 1998; Tan *et al.* 2000; Rabiei *et al.* 2004; Fan *et al.* 2006; Wan *et al.* 2006), a QTL for grain width on chromosome 5 (Tan *et al.* 2000; Li *et al.* 2003; Rabiei *et al.* 2004; Abdelkhalik *et al.* 2005), a QTL for grain thickness on chromosome 2 (Yoshida *et al.* 2002; Abdelkhalik *et al.* 2005), and a QTL for grain weight on chromosome 5 (Lin *et al.* 1996; Li *et al.* 1997; Ishimaru 2003; Abdelkhalik *et al.* 2005). These universal QTLs had a relatively large effect on the phenotype and are supposed to be useful for rice improvement (Tables 1-4). In addition to exploitation of genetic potential in wild relatives, reclassification of known QTLs into those positive from the *indica* group or from *japonica* group will be useful for breeding parental lines in hybrid rice breeding. A positively contributing allele at each QTL may be tagged by a marker allele at each locus in such a classification. It is possible to possess advantageous combinations of QTLs in a single plant by crossing and marker-assisted selection. Further studies using many superior hybrids are expected to enhance well-organized utilizations of heterosis.

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Table 4 QTLs for grain weight detected using *Oryza* cultivars.

Chr	QTL	Interval marker	LOD	PVE	R ²	Parents	Population
1	<i>QKw1</i>	RG236-RG381	3.46	-	8.1	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>tgwt1</i>	RG173-RG532	3.01	12.6	-	Tesanai 2 / CB	<i>indica</i> / <i>indica</i> F ₂ ^{c)}
2	<i>QKw2a</i>	RG598b-RG139	3.33	-	6.6	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>QKw2b</i>	RG83-RG634	2.59	-	4.1	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>tgwt2</i>	RG171-RG437	4.23	14.8	-	Waiyin 2 / CB	<i>indica</i> / <i>indica</i> F ₂ ^{c)}
	<i>GWt</i>	RM145-RM109	3.92	-	18.0	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	-	C560-G275	3.99	-	16.5	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
3	<i>QKw3a</i>	RG104-RG348	2.88	-	5.1	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>QKw3b</i>	RG445a-CDO109a	6.82	-	11.7	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>QKw3c</i>	RG910a-RG418	3.57	-	7.2	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>GWt</i>	X03617-RM168	2.23	-	10.6	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	<i>GS3</i>	GS09-MRG5881	72.8	83.4	-	Minghui 63 / Chuan 7	<i>indica</i> / <i>indica</i> BC ₃ F ₂ ^{g)}
4	<i>tgwt4</i>	RG143-RG214	2.74	8.5	-	Tesanai 2 / CB	<i>indica</i> / <i>indica</i> F ₂ ^{c)}
	<i>qWEI-4</i>	RM348-RM280	2.77	9.0	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	-	Pericarp-RG476	4.52	-	10.2	Labelle / Black Gora	<i>japonica</i> / <i>indica</i> F ₂ ^{c)}
	<i>GWt</i>	RM255-RM131	2.24	-	11.0	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	<i>GWt</i>	T082023-RM241	2.19	-	10.4	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
5	<i>QKw5</i>	RG182-RG13	5.10	-	16.3	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>tgwt5</i>	RG182-RG13	2.73	14.8	-	Tesanai 2 / CB	<i>indica</i> / <i>indica</i> F ₂ ^{c)}
	<i>qWEI-5</i>	RM249-RM163	2.76	9.0	-	IR36 / Nekken 2	<i>indica</i> / <i>japonica</i> BC ₁ F ₁ ^{d)}
	<i>GWt</i>	RM31-M031078	2.99	-	13.9	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	-	R3166-R1838	2.22	-	10.2	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
6	<i>QKw6</i>	RG424-RG179	3.09	-	6.0	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>tgwt6</i>	C358-C556	3.71	-	14.0	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
8	-	RG333-RZ562	3.35	-	7.7	Labelle / Black Gora	<i>japonica</i> / <i>indica</i> F ₂ ^{c)}
10	<i>QKw10</i>	CDO98-RG752	3.77	-	10.3	Lemont / Teqing	<i>japonica</i> / <i>indica</i> F ₄ ^{b)}
	<i>tgwt10</i>	RG241-RG561	3.52	22.8	-	Waiyin 2 / CB	<i>indica</i> / <i>indica</i> F ₂ ^{c)}
	-	R1629-R2447	2.02	-	10.1	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}
11	<i>GWt</i>	RM332-A071162	2.27	-	10.7	Reiho / Yamadanishiki	<i>japonica</i> / <i>japonica</i> DHL ^{a)}
	-	G257-S2260	3.56	-	12.1	Nipponbare / Kasalath	<i>japonica</i> / <i>indica</i> BIL ^{f)}

PVE, Percentage of phenotypic variance explained

R², coefficient of determination* tropical *japonica*a) Yoshida *et al.* 2002; b) Li *et al.* 1997; c) Lin *et al.* 1996; d) Abdelkhalik *et al.* 2005; e) Redoña and Mackill 1998; f) Ishimaru 2003; g) Fan *et al.* 2006

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JAPANESE ABSTRACT

広親和性遺伝子の利用によりイネ日印交雑における雑種不稔が解決され、高度のヘテロシスがハイブリッド育種に利用されている。強いヘテロシスが現れる日印交雑後代を用いた研究結果から、我々は日印雑種の高度のヘテロシスは、対立遺伝子の相互作用による超優性効果(Aa>AA)ではなく、多くの座でヘテロの遺伝子型の部分優性の効果が累積されることによって現れると結論した。一方、栽培イネの種子は用途により様々な大きさや形が選抜されてきた為、非常に変異に富んでいる。更に、粒形は収量に密接に関連することから、育種上重要な形質でもある。ヘテロシス利用の観点から粒形に關与する QTL について、日本型親とインド型親のどちらが正の効果を示す対立遺伝子をもっているのかという情報を整理すれば、分子マーカーの利用による親系統の育成に有用であると考えられる。この総説では、イネにおけるヘテロシスの利用および粒形質を制御する遺伝的メカニズムについて概説し、イネ育種への利用の可能性について議論する。