



## The more knowledge about heterotic loci is a pre-requisite for enhancing grain yield potential in distant crosses

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### Abstract

Overcoming reproductive barrier is one of key indicators for exploiting heterosis in distant crosses. This paper reports the current studies on the genes/QTLs controlling hybrid sterility as well as the heterosis in distant crosses. To avoid hybrid sterility problem in distant crosses of rice, the use of wide compatibility gene and development of partial hybrid rice were adopted consecutively. Though these efforts made, rice scientists were still concerned about hybrid sterility occurrence, which hamper the exploitation of strong grain yield heterosis in rice. But a better understanding of the genetic factors that govern hybrid sterility and heterosis could facilitate the introgression of useful genes/QTLs in rice. In this review, 57 inter-subspecific genes/QTLs and 18 interspecific genes/QTLs were reported to cause hybrid sterility in distant crosses. On other hand, a total of 33 stable Heterotic loci (HLs) were also found to be associated with yield-related traits. The cross-check observation showed 11 genes/QTLs to be implicated in distant hybrid sterility irrespective of the crosses made. Surprisingly, the marker RM236 was identified to be closed simultaneously to the chromosome region affecting hybrid sterility and heterosis. However, many other stable heterotic loci with positive effect on yield-related traits were isolated in rice. Therefore, we propose the pyramiding of these heterotic loci (HL) via marker assisted selection (MAS) into one adaptable rice variety as an efficient approach to develop new rice variety with higher grain yield potential.

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## Introduction

Rice (*Oryza sativa* L.) is an important cereal crop in the world. It is a staple food for more than half of the world's population (Marathi *et al.*, 2012). The demand of rice grain is constantly growing so that a priority issue of the world rice breeders includes the development of higher yielding rice variety with low input. The genetic improvement of rice is more important for meeting the relentless increase of the world population and ensuring a sustainable agricultural development. It is obvious that the increase of the world population is main factor of reduction of the available arable land. On other hand, an excessive use of chemical products such fertilizers, insecticides and pesticides could affect the world environmental health. Therefore, scientists have tried to find a genetic approach that can increase yield while preserving the environment and production material. Finally, Heterosis exploitation is considered as one of the major keys to reach this achievement. Heterosis is described as a greatest outstanding genetic tool which played an important role in various breeding program to increase grain crop yield (Virmani, 1994, Brandle *et al.*, 1990). Akhter *et al.*, 2008 mentioned the magnitude of heterosis to be depended on the distinctiveness of the parental lines used. However, the useful heterosis can be positive or negative depended up on the breeding objectives. In general positive heterosis is required for grain yield while negative for earliness of growth period (Brandle *et al.*, 1990). The heterosis was evaluated as mid-parent heterosis (relative heterosis), heterosis over the check rice variety (standard heterosis), and heterosis over the best parent (heterobeltiosis) (Virmani, 1994). Heterosis can be affected negatively by the hybrid sterility problem which remained a crucial factor that always influence grain yield in distant crosses (Heuer, 2003, Koide *et al.*, 2008, Moehring, 2011, Adedze *et al.*, 2012). Heterosis is attributed to genetic and environmental factors and due this complexity, the detection of stable HLs with positive effects on yield related traits could be of great value in heterotic rice breeding program. This review suggests a thoroughly distinction in the genetic functions of different HLs and proposes the

pyramiding of useful ones into one adaptable variety as pragmatic solution for exploiting distant heterosis in rice.

### *Reproductive barrier and hybrid sterility*

The cultivated rice species constitutes a potential genetic reservoir for breeding higher yielding varieties. For exploiting grain yield heterosis in rice, scientists have crossed different inbred lines to produces F<sub>1</sub> hybrids that can yield more than the parents. It was demonstrated that the genetically different parental lines could produce F<sub>1</sub> hybrids with higher heterosis (Virmani, 1994, Jagoz, 2011). However, a phenomenon known as reproductive barrier constitutes a bottleneck for assessing heterosis in more distant crosses. This reproductive barrier not hampered the crossability of parent parental lines but cause sterility of their derivatives F<sub>1</sub> hybrids (Hiroko *et al.*, 1962). Inter-subspecific hybrid sterility was early identified in the crosses between *O. sativa* ssp *indica* and *japonica* (Oka, 1964). Sterility genes were reported to cause hybrid sterility in heterozygous combination and render difficult the utilization of strong heterosis between the two subspecies of rice (Koubo *et al.*, 2008, Hu *et al.*, 2006, Moehring, 2011). A large number of *S*-loci have been identified to be involved in the inter-subspecific hybrid sterility through the genetic analysis in rice (Table3), and all these loci function in the heterozygous state. The *S<sub>5</sub>* was reported as the first and principal gene responsible for sterility problem between *japonica* and *indica*. Furthermore, several studies were conducted to explain the genetic mechanism and key indicators of hybrid sterility manifestation in rice Long *et al.*, (2008) indicated two-gene/three-component interaction model at heterozygote complex locus *Sa* to be responsible for the hybrid sterility between *indica* and *japonica* crosses. The phenomenon such as male and female gamete abortions, and reduced affinity between the gametes were further identified as the main causes of inter-subspecific hybrid sterility occurrence between *indica* and *japonica* (Ouyang *et al.*, 2009). The genetic mechanism that governs the inter-subspecific hybrid sterility was elucidated to be the

cryptic chromosomal aberrations and allelic interaction effects (Koubo *et al.*, 2011). Hereafter, novel genes with major or minor sterility effects were further found to cause inter-subspecific hybrid sterility in rice (Table 3) and the lack of the corresponding wide compatibility genes for all these sterility genes sustain sterility problem in rice.

On other hand, crossability and interspecific hybrid sterility was first reported between *O. sativa* and *O. glaberrima* by Hiroko *et al.*, in (1962). The sterility gene *S<sub>1</sub>* was stated to induce abortion of both male and female gametes possessing its allelic alternative (Koide *et al.*, 2008). The occurrence of interspecific hybrid sterility between *O. sativa* and *O. glaberrima* was mainly attributed to an arrest of pollen development at the microspore stage (Bimpong *et al.*, 2011). Likewise, heterozygous alleles at sterility loci have been demonstrated as the genetic makeup that induces sterility problem at interspecific crosses level. For example, *O. glaberrima*-specific alleles were indicated to cause interspecific hybrid sterility while interacting with *O. sativa*-specific alleles at *S<sub>1</sub>*-locus (Bimpong *et al.*, 2011). One-locus allelic interaction model was described by Zhao *et al.*, (2012) as principal cause of interspecific hybrid sterility in rice. This indicated that the mechanism of sterility occurrence in rice is complicated and complex genetic phenomenon. A series of interspecific sterility loci have been reported such as *S<sub>19</sub>*, *S<sub>20</sub>*, *S<sub>21</sub>*, *S<sub>29</sub>* (*t*), *S<sub>36</sub>* (*t*) from *O. glaberrima* (Doi *et al.*, 1998, 1999, Heuer *et al.*, 2003, Hu *et al.*, 2006, Sano, 1983, 1986, Taguchi *et al.*, 1999, Koide *et al.*, 2008, Li *et al.*, 2011). The pollen killers *S<sub>22</sub>*, *S<sub>27</sub>*, *S<sub>28</sub>* were also mapped in *O. glumaepatula* (Sano, 1994, Sobrizal *et al.*, 2000, 2001, 2002), and *S<sub>44</sub>* (*t*) in *O. longistaminata* (Zhao *et al.*, 2012). The list of the interspecific sterility genes cited in this review is not exhaustive (Table4). We have showed almost 57 interspecific sterility loci between *indica* and *japonica* and 18 interspecific sterility loci between the cultivated and wild rice species (Table 3 and 4). And 11 out the 75 sterility genes were found to cause the sterility of intraspecific and interspecific F<sub>1</sub> hybrids.

Making crosses between genetically different parental lines is the preliminary step for the heterosis exploitation in rice. This cross often results in the accumulation of different specific alleles at different loci, which can affect positively or negatively the hosted rice variety. For this reason, heterosis and hybrid sterility were found to be associated with heterozygous loci in the hybrid (Moehring *et al.*, 2011). Therefore, the rice breeders may face two situations when making distance crosses: how to exploit distant crosses positively while minimizing its related drawback.

#### *Consecutive solutions for the distant heterosis exploitation in crops*

The detection and use of wide compatibility gene *S<sub>5</sub><sup>n</sup>* were described as a great success to overcome the sterility effects of *S<sub>5</sub>* between the two subspecies of rice (Ikehashi and Araki, 1986, Qiu *et al.*, 2005). But this discovering not allow to avoiding definitely the hybrid sterility problem between these two subspecies of rice. The rice scientists of China have developed a new approach for reducing the hybrid sterility problem between *indica* and *japonica*. This approach consisted to develop hybrid rice carrying partially the genomic genes of *indica* in the genetic background of *japonica* or inversely. Cheng *et al.*, (2007) have exploited distant heterosis between *indica* and *japonica* by developing a super higher yielding hybrid Xieyou 9308 that carried 12.5% of *japonica* genetic components, which came from its male parent R9308. Furthermore, Ma and Lu in (2007), and Liu in (2012) have released respectively inter-subspecies hybrids Yongyou6 and Yongyou12, which were derived from *japonica* CMS lines and restorer lines carrying up to 49% of *indica* genes in China. At the same time, Wang *et al.*, (2012) have explored the level of distant heterosis and fertility between the two subspecies of rice by test crossing the *indica* cultivars and chromosome segment substitution lines (CSSL) carrying fragments of *japonica* genes in the genetic background of *indica*. Some intraspecific crosses studies have reported strong heterosis between the parents with an intermediate genetic distance (Luo *et al.*, 1999, Krishnamurthy *et al.*, 2013). All these

reports confirmed the development of the partial hybrid rice as an approach to the sterility problem between these two subspecies of rice. Nowadays, the

most successful inter-subspecies hybrid cultivars developed in China are partial inter-subspecific hybrids with less or more *japonica* genes.

**Table 1.** Yield-related traits HLLs reported in at least two times in rice.

Traits	HLLs	Chr	Markers	Parents combinations	Generation	References
Spikelet number per panicle	hsp11/ qGY11-2	11	RM224	O. rufipogon Griff X Guichao 2	BC4F1and ILs	Li <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Filled grains per panicle	hgp9a	9	RM342B/ G103b-RZ698	Lemont X Teqing and O. rufipogon Griff X Guichao 2	RILs and ILs	Luo <i>et al.</i> (2001) Luo <i>et al.</i> (2011)
Filled grains per panicle	hgp9c	9	OSR12/ RG451-RZ404	Lemont X Teqing and O. rufipogon Griff X Guichao 2	RILs and ILs	Luo <i>et al.</i> (2001) Luo <i>et al.</i> (2011)
Filled grains per panicle	hgp10/ gp10	10	RM222	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Grain Weight	hgw6a/ gw6b	6	RM204	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Grain Weight	hgw10/ gw10	10	RM222/G89- G1084	Lemont X Teqing, Zhenshan 97 X Minghui 63, and O. rufipogon Griff X Guichao 2	RILs,F2 and ILs	Luo <i>et al.</i> (2001, 2011) Hua <i>et al.</i> (2002)
Grain Weight	hgw11/ gw11b	11	RM21	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Panicles per plant	hpp6a/ tp6a	6	RM133	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Panicles per plant	hpp6b/ tp6b	6	RM217	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Panicles per plant	hpp6c/tp6c	6	RM253	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Panicles per plant	hpp11/tp11	11	RM21	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Yield per plant	hyp2b	2	RM71/ RG437-RZ476	Lemont X Teqing and O. rufipogon Griff X Guichao 2	RILs and ILs	Li <i>et al.</i> (2001) Luo <i>et al.</i> (2011)

HLLs= Heterotic loci, Chr = chromosome.

**Table 1.** Yield-related traits HLLs reported in at least two times in rice (ctd).

Traits	HLLs	Chr	Markers	Parents combinations	Generation	References
Yield per plant	hyp9a/ yd9b	9	RM219	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Yield per plant	hyp9b/ yd9a	9	RM342B	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Yield per plant	hyp9c	9	OSR29/ RG451-RZ404	Lemont X Teqing and O. rufipogon Griff X Guichao 2	RILs and ILs	Li <i>et al.</i> (2001) Luo <i>et al.</i> (2011)
Yield per plant	hyp12b/yd12	12	RM17	Zhenshan 97 X Minghui 63 and O. rufipogon Griff X Guichao 2	F2 and ILs	Hua <i>et al.</i> (2002) Luo <i>et al.</i> (2011)
Yield per plant	hyp2a/ qGY2-1	2	RM236	O. rufipogon Griff X Guichao 2	BC4F1and ILs	Li <i>et al.</i> (2002) Luo <i>et al.</i> (2011)

HLLs= Heterotic loci, Chr = chromosome.

On other hand, up to date, no wide compatibility gene has been reported to overcome reproductive barrier between the different species of rice. However, the African rice researchers have developed the first interspecific rice variety (Nerica) between *O.sativa* and *O.glaberrima* via embryo rescue and anther culture techniques (WARDA, 2000). Nerica rice that contained about 87.4% of *O. sativa* average proportion and 6.3% of *O. glaberrima* genome

(Semagn *et al.*, 2007) have proved the possibility to produce fertile inbred lines with *O. glaberrima* genes in the genetic background of *O. sativa*. Furthermore, the recombinant inbred line (RILs), introgression lines (ILs), and chromosome substituted segment lines (CSSLs) were developed for transferring *O. glaberrima* genomic genes into *O. sativa* genetic background (Aluko *et al.*, 2003, Semagn *et al.*, 2007, Efisue *et al.*, 2009a and 2009b, He *et al.*, 2010,

Bimpong *et al.*, 2010, Ndjiondjop *et al.*, 2012, Adedze *et al.*, 2012). In 2009, Ikeda *et al.*, have crossed NERICA rice and *O. sativa* cultivars and found heterosis for panicle length and number of panicles per plant between the *O. sativa* and *O. glaberrima*. In addition, Adedze *et al.*, (2012) also reported heterosis for yield components in partial interspecific hybrid between the two cultivated species of rice. These

statements show that the development of the partial hybrid still constituted an approach to minimize sterility in relatively distant crosses. In this review, we show the technical route for the development of the introgression lines and partial interspecific hybrids (Fig.1). In spite of these efforts and achievements made, hybrid sterility affects grain formation in relatively distant crosses (Adedze *et al.*, 2012).

**Table 2.** yield-related traits HLLs reported in two different environments.

Traits	HLLs	Chr	Linked Markers	Parents combinations	Environments	References
Spikelet number per panicle	<i>qSp1</i>	1	C112	Asominori X IR24	2	Xin <i>et al</i> (2011)
Spikelet number per panicle	<i>qSp3a</i>	3	C515	Asominori X IR24	2	Xin <i>et al</i> (2011)
Spikelet number per panicle	<i>qSp3b</i>	3	X249	Asominori X IR24	2	Xin <i>et al</i> (2011)
Spikelet number per panicle	<i>qSp10</i>	10	R1877	Asominori X IR24	2	Xin <i>et al</i> (2011)
Spikelet number per panicle	<i>qSp11a</i>	11	C1350	Asominori X IR24	2	Xin <i>et al</i> (2011)
Filled grain number per panicle	<i>qGp3b</i>	3	X249	Asominori X IR24	2	Xin <i>et al</i> (2011)
Filled grain number per panicle	<i>qGp10</i>	10	X37	Asominori X IR24	2	Xin <i>et al</i> (2011)
Percent seed set	<i>qSsp6</i>	6	X27	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw1b</i>	1	X92	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw3a</i>	3	R19	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw5</i>	5	X387	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw6a</i>	6	X209	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw8a</i>	8	C1121	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw8b</i>	8	X56	Asominori X IR24	2	Xin <i>et al</i> (2011)
1000-grain weight	<i>qGw12</i>	12	C901	Asominori X IR24	2	Xin <i>et al</i> (2011)
Panicle number per plant (PP)	<i>qPp7</i>	7	X338	Asominori X IR24	2	Xin <i>et al</i> (2011)

HLLs = Heterotic loci, Chr = chromosome.

Since heterozygous loci were stated to display heterosis and sterility in hybrid, it is understandable that the partial hybrids may accumulate two different types of heterozygote loci. Some heterozygote loci may operate for heterosis expression while others for sterility occurrence. Keeping this in mind, researchers have tried to detect heterotic loci and conclusive results are obtained from many crops.

#### Heterotic QTLs loci identification in crop

Several heterotic loci reported in previous studies could enhance the crops productivity via genes introgression. In maize, numerous heterotic loci were detected by using the recombinant inbred lines population (Tang *et al.*, 2007), near-isogenic lines (Frascaroli *et al.*, 2012) and introgression lines (Feng *et al.*, 2012), respectively. In sorghum bicolor, Ben-Israel *et al.*, (2012) have mapped heterotic trait loci when performing intraspecific crosses. In cotton, Guo *et al.*, (2013) described heterotic loci for the

agronomic traits by using the chromosome segment introgression lines. Various studies have related heterosis to either additive effects or the dominance and overdominance effects at a single locus level (Li *et al.*, 2001, Luo *et al.*, 2001, Hua *et al.*, 2002, Li *et al.*, 2008, Garcia *et al.*, 2008, Luo *et al.*, 2009, Zhou *et al.*, 2012). For example, Garcia *et al.*, (2008) have attributed the heterosis in maize mainly to the dominant gene action whereas the heterosis in rice was assigned to the additive epistatic effects. More than 150 heterotic loci were revealed in rice (Luo *et al.*, 2001, Luo *et al.*, 2011, Xin *et al.*, 2011, Wang *et al.*, 2013). Among them, some HLLs were identified in intraspecific crosses (Luo *et al.*, 2011) while others were detected in interspecific crosses (Luo *et al.*, 2001, Xin *et al.*, 2011). In case of intraspecific crosses, most of HLLs related in this paper was found between *indica* and *japonica*. In 2001, Luo and Li were the first to identify HLLs between the *japonica* variety Lemont and *indica* variety Teqing, which were further

confirmed by Luo *et al.*, in 2011 (Table1). Meanwhile, Xin *et al.*, (2011) also have reported many stable HLs between *Japonica* variety Asominori and *indica* variety IR24 in two different environments (Table2). In case of interspecific crosses, several HLs with yield-related traits were identified between the Chinese common wild rice (*Oryza rufipogon* Griff) and the cultivated rice guichao2 (Li *et al.*, 2001, Luo *et al.*, 2001, Hua *et al.*, 2002, Luo *et al.*, 2011). In 2002, Hua *et al.*, have reported single-locus heterotic effect in rice by using recombinant inbred lines while the QTL *qGY2-1* has been confirmed to be an overdominant heterotic locus in the heterozygote state in rice (Luo, 2006). Heterotic locus *qGY2-1/hyp2* was mapped in rice at 102.9-kb of chromosome region by using NILs population (Luo, 2006, He *et al.*, 2006). On other hand, locus *qGY11-2/hsp11* was located between markers RM224 and RM3577 by using chromosome fragment substitution analysis (Luo *et al.*, 2009, 2011). Furthermore, Xue *et al.*, (2008) showed that the near isogenic line heterozygous for *Ghd7* has produced higher number of spikelets than that of the two homozygous parents. Two years ago, the genetic basis of heterosis expression in hybrid rice Shanyou 63 was explained. It is observed that the overdominance/ pseudo-overdominance was an important contributor to heterosis of yield, number of grains per panicle, and grain weight while dominance  $\times$  dominance interaction was related to heterosis of tillers per plant (Zhou *et al.*, 2012). In heterotic loci exploitation, more attention must be accorded to some recessive loci which operate as heterotic loci, but cause the hybrid weakness, sterility, and a large variation in heading date (Xin *et al.*, 2011). HLs such as QTLs *qGp5'*, *qSsp2b* and *qGw1b* were reported to express negative effects in ILs analysis, but positive effects in heterosis analysis (Xin *et al.*, 2011). The hybrid breakdown locus *hbd2* reported by Matsubara *et al.*, (2007) is located in the similar position of the HL *qSsp2b* identified by Xin *et al.*, (2011). The QTL *qSsp2b* is not mentioned in the tables of HLs due its identification in only one environment. In general, the 33 heterotic loci with relatively stable effects were specified in this review. We highlighted all the

sterility genes/QTLs and HLs along with their linked markers to render feasible their exploitation in breeding program. Surprisingly, the marker RM236 appeared among the linked markers of the sterility genes/QTLs and those of HLs (Li *et al.*, 2007, Luo *et al.*, 2011, Xu *et al.*, 2014). The chromosome region linked to this marker may be either a complex locus that involved in heterosis and sterility expressions or may genes with different genetic functions. *Sa* locus that cause *indica-japonica* hybrid male sterility was already reported as complex locus in rice (Long *et al.*, 2008).

In the relatively distant crosses, little information was provided about the use of heterotic loci for improving grain yield. For instance, high heterosis was reported for several agronomic traits between two cultivated species *O.sativa* and *O.glaberrima*, however, sterility problem still constitute a principal bottleneck for developing interspecific hybrid with high grain yield heterosis. This may be due to the two different reasons: firstly the lack of the information about the identified interspecific heterotic loci in rice; secondly, each HL may express positively between its hosted parental lines. In case of specificity, preliminary work need to be done for detecting HLs with positive effect on yield traits between each distantly related varieties and undertake their pyramiding in one variety for exploiting their genetic effect. Since HLs could behave differently depend on the environments, it also needs to access their genetic stability before being used in rice breeding.

#### Perspectives

Distant cross breeding is regarded as one the key determinants to make progress in grain yield increase. However hybrid sterility becomes a frequent problem against this achievement. The detection of wide compatibility gene and the development of partial hybrid have constituted the efforts made against the sterility problem in rice. But, unfortunately, all these approaches have not allowed overcoming completely the existing reproductive barrier in rice. The current review provides information for exploiting the useful genes of the

distant related rice varieties via the detection and pyramiding of heterotic loci, which could open new avenues to overcome sterility problem in rice. Near isogenic lines is considered as the principal genetic population to detect the genetic effects of different heterozygote loci in distant crosses. The technical route of the development of near isogenic lines (Fig.2)

is showed in this review. However, more knowledge about the genetic effects of each heterozygous locus could help to find loci that involved in heterosis expression. Knowledge about the genomic locations of the sterility and heterotic loci would be a pre-requisite to expedite the incorporation of heterotic loci in rice.

**Table 3.** Intersubspecific sterility genes reported in rice.

Locus	Chr.	Linked markers	References	Locus	Chr.	Linked markers	References	Locus	Chr.	Linked markers	References
<i>S5</i>	6	cloned	Chen <i>et al.</i> (2008)	<i>S21</i>	7	R1245, C213	Doi <i>et al.</i> (1999)	<i>ft</i>	1	RG532, R3129	Wang <i>et al.</i> (1998)
<i>S7</i>	7	Est-9, Rc	Yanagihara <i>et al.</i> (1992)	<i>S22</i>	2	S910	Sobrizal <i>et al.</i> (2000)	<i>f3</i>	3	RG393, C603	Wang <i>et al.</i> (1998)
<i>S8</i>	6	Cat-1, Pox-5	Wan <i>et al.</i> (1993)	<i>S23</i>	7	C1340	Sobrizal <i>et al.</i> (2000)	<i>f8</i>	8	C1121A, RG333	Wang <i>et al.</i> (1998)
<i>S9</i>	4	RM5586, RM5749	Zhao <i>et al.</i> (2006)	<i>S24</i>	5	R830, R3166	Koubo <i>et al.</i> (2000)	<i>qSS-6a(S5)</i>	6	R2171	Wang <i>et al.</i> (2005)
<i>S10</i>	6	OSR19	Zhu <i>et al.</i> (2005)	<i>S25</i>	12	G193	Koubo <i>et al.</i> (2001)	<i>qSS-8a</i>	8	XNpb278	Wang <i>et al.</i> (2005)
<i>S11</i>	-	-	Sawamura <i>et al.</i> (1996)	<i>S27</i>	8	G2132	Sobrizal <i>et al.</i> (2001)	<i>qSS-2</i>	2	RM263	Wang <i>et al.</i> (2005)
<i>S13</i>	-	-	Taneichi <i>et al.</i> (2005)	<i>S28</i>	4	XNpb237	Sobrizal <i>et al.</i> (2002)	<i>qSS-6b(S5)</i>	6	RM539	Wang <i>et al.</i> (2005)
<i>S14</i>	-	-	Harino <i>et al.</i> (2008)	<i>S33</i>	3	RM15621, RM15627	Yokoo <i>et al.</i> (1984)	<i>qSS-8b</i>	8	RM6863	Wang <i>et al.</i> (2005)
<i>S15</i>	12	Sdh-1, Pox-2	Wan <i>et al.</i> (1996)	<i>S34</i>	11	RM167, RM552	Yokoo <i>et al.</i> (1984)	<i>qSPTF1</i>	1	RM128, RM9	Yan <i>et al.</i> (2003)
<i>S16</i>	1	Est-5	Wan <i>et al.</i> (1995)	<i>Sa</i>	1	cloned	Long <i>et al.</i> (2008)				
<i>S17</i>	12	Sdh-1	Wan <i>et al.</i> (1998)	<i>Sb</i>	5	A8, A14	Li <i>et al.</i> (2006)				
<i>S18</i>	11	Pgd-1, RM536	Singh <i>et al.</i> (2006)	<i>Sc</i>	3	P24-49, P24-95	Yang <i>et al.</i> (2004)				
<i>S29</i>	2	RM425	Zhu <i>et al.</i> (2005)	<i>Sd</i>	1	PSM93, PSM74	Li <i>et al.</i> (2008)				
<i>S30</i>	7	RM11	Zhu <i>et al.</i> (2005)	<i>Se</i>	12	PSM180, PSM182	Zhu <i>et al.</i> (2008)				
<i>S31</i>	5	RM5579, RM13	Zhao <i>et al.</i> (2007)	<i>Sf</i>	-	-	Zhang <i>et al.</i> (1994)				
<i>S32</i>	2	RM236, L2165	Li <i>et al.</i> (2007)	<i>f5</i>	5	WFRM3, WPRO-1	Wang <i>et al.</i> (2006)				
<i>S1</i>	6	-	Sano <i>et al.</i> (1990)	<i>pf12</i>	12	RM19, RM247	Song <i>et al.</i> (2005)				
<i>S2</i>	6	-	Sano <i>et al.</i> (1983)	<i>qHPS-3</i>	3	RM16	Chen <i>et al.</i> (2006)				
<i>S3</i>	9	-	Sano <i>et al.</i> (1983)	<i>qHPS-5</i>	5	RM440	Chen <i>et al.</i> (2006)				
<i>S4</i>	-	-	Sano <i>et al.</i> (1985)	<i>qHPS-7</i>	7	R1789	Chen <i>et al.</i> (2006)				
<i>S6</i>	6	RM3183, C133A	Koide <i>et al.</i> (2008)	<i>qPLL7</i>	7	RM234, RM172	Yan <i>et al.</i> (2003)				
<i>S12</i>	2	-	Sano <i>et al.</i> (1994)	<i>qPLL9</i>	8	OSR28, RM107	Yan <i>et al.</i> (2003)				
<i>S19</i>	3	R1468	Taguchi <i>et al.</i> (1999)	<i>S26</i>	6	L688	Koubo <i>et al.</i> (2001)				
<i>S20</i>	7	C1057, R2401	Doi <i>et al.</i> (1999)	<i>spf8</i>	8	H4698-1, H3878-1	Song <i>et al.</i> (2005)				

Chr = Chromosome

The gray colored sections represented the genes observed to be involved in intra and interspecific sterility.

Heterosis is complex genetic phenomenon based on dominance and overdominance models. Detection and pyramiding of heterotic loci could be considered as accurate genetic tools for exploiting considerable yield heterosis in rice (Fig.3). Recently, *O.glaberrima*

was state as rich genetic reservoir for improving genetically *O.sativa* (Sarla *et al.*, 2005) and heterosis for yield and yield components was also reported in the partial interspecific hybrid rice between two cultivated rice species *O.sativa* and *O.glaberrima*

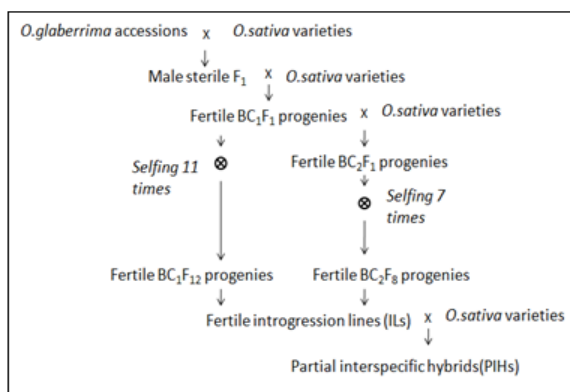
(Adedze *et al.*, 2012). But, hybrid sterility hampered heterosis exploitation for grain yield between them. From this review, it can be imperative to detected HLs between *O.sativa* and *O.glaberrima* varieties, which can be use to improve grain yield heterosis between these two species of rice. We suggest the pyramiding of the interspecific heterotic loci as pragmatic genetic method to improve the grain yield

heterosis in distant hybrid rice breeding. The consideration of the genetic markers closed to these HLs could lead to their genetic mapping and cloning, which would be meaningful in the distant rice breeding program. The detection of the heterosis loci become one the promising ways to exploit distant heterosis while minimizing the hybrid sterility in rice.

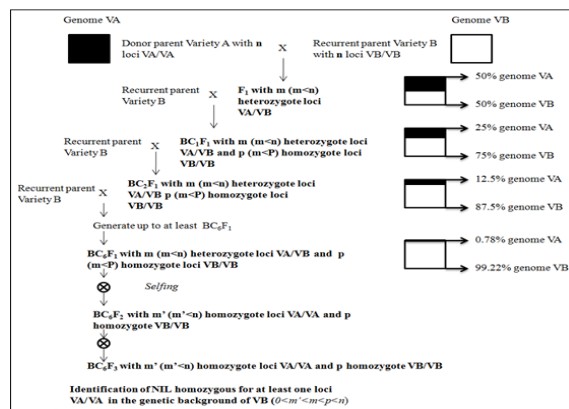
**Table 4.** Interspecific sterility genes detected in rice.

Locus	Chr.	Linked markers	Interspecific Crosses	References
<i>qSS-3</i>	3	RM132	<i>O.sativa</i> X <i>O.glaberrima</i>	Li <i>et al.</i> (2011)
<i>qSS-6a</i>	6	RM190	<i>O.sativa</i> X <i>O.glaberrima</i>	Li <i>et al.</i> (2011)
<i>qSS-7</i>	7	RM5752	<i>O.sativa</i> X <i>O.glaberrima</i>	Li <i>et al.</i> (2011)
S36(t)	2	RM208- RM482	<i>O.sativa</i> X <i>O.glaberrima</i>	Li <i>et al.</i> (2011)
<i>S1/ qSS6</i>	6	RM586	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S44(t)</i>	6	RM5814 -RM20695	<i>O.sativa</i> X <i>O. longistaminata</i>	Zhao <i>et al.</i> (2012)
<i>S19/ qSS3</i>	3	RM22	<i>O.sativa</i> X <i>O.glaberrima</i>	Taguchi <i>et al.</i> (1999)
<i>S20/ qSS7a</i>	7	RM295	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S21/ qSS7b</i>	7	RM3589	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S29(t)/ qSS2</i>	2	RM236	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S37(t)/ qSS1</i>	1	RM562	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S38(t)/ qSS4</i>	4	RM518	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S39(t)/ qSS12</i>	12	RM5568	<i>O.sativa</i> X <i>O.glaberrima</i>	Xu <i>et al.</i> (2014)
<i>S22</i>	2	S910	<i>O.sativa</i> X <i>O. glumaepatula</i>	Sobrizal <i>et al.</i> (2000)
<i>S28</i>	4	XNpb237	<i>O.sativa</i> X <i>O. glumaepatula</i>	Sobrizal <i>et al.</i> (2002)
<i>S27</i>	8	G2132	<i>O.sativa</i> X <i>O. glumaepatula</i>	Sobrizal <i>et al.</i> (2001)
<i>S4</i>	4	-	<i>O.sativa</i> X <i>O.glaberrima</i>	Sano <i>et al.</i> (1985)
<i>S6</i>	6	-	<i>O.sativa</i> X <i>O.rufipogon</i>	Sano <i>et al.</i> (1992)

Chr = Chromosome, The gray colored sections represented the genes observed to be involved in intra and interspecific sterility.



**Fig. 1.** Technical route for the development of introgression lines and partial interspecific hybrid rice by using two cultivated rice species *O.sativa* and *O.glaberrima* as parental lines (Source: Adedze *et al.* 2012).

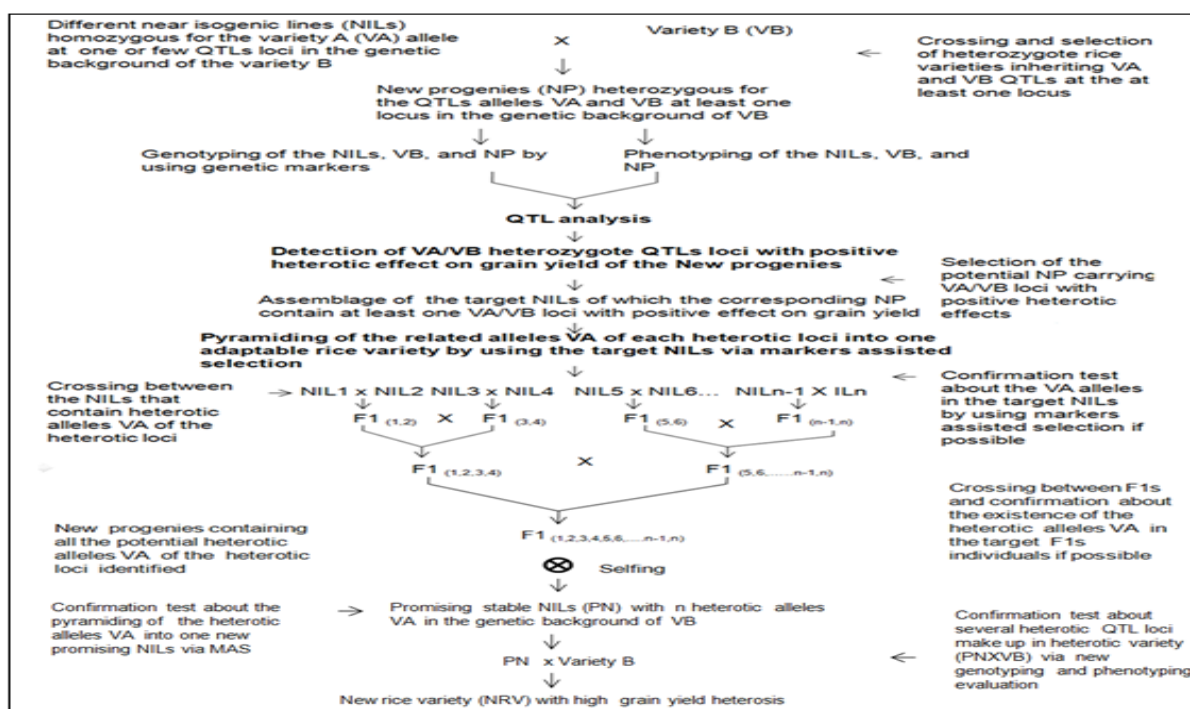


**Fig. 2.** Backcross procedure illustrating the theoretical development of near isogenic lines with one or few homozygote alleles VA/VA in the genetic background of variety B. VA= variety A, VB= variety



B,  $n$  = percentage of homozygote VA/VA and VB/VB loci in the genetic background of variety VA and variety VB, respectively.  $m$  = percentage of heterozygote loci VA/VB in the F<sub>1</sub> hybrids and BC<sub>(1-6)</sub> F<sub>1</sub> progenies,  $m'$  = percentage of homozygote VA/VA

in the genetic background of BC<sub>6</sub>F<sub>2</sub>, BC<sub>6</sub>F<sub>3</sub> and NILs,  $P$  = percentage of homozygote loci VB/VB in the genetic background of BC<sub>(1-6)</sub> F<sub>1</sub>, BC<sub>6</sub>F<sub>2</sub>, BC<sub>6</sub>F<sub>3</sub> and NILs.  $0 < m' < m < p < n$ .



**Fig. 3.** Technical route proposed for identifying and pyramiding heterotic loci in one adaptable rice variety via marker assisted selection. NIL= Near isogenic line, VA= variety A, VB= variety B, NP= new progenies, F<sub>1</sub>= cross progenies between two NILs with heterotic allele VA, PN Promising NILs, NRV= New rice variety, 1, 2, 3, 4, 5, 6,....n-1,n = different heterotic alleles from variety A.

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