

Sterility genes in interspecific hybrids of *Oryza glaberrima* and *Oryza sativa*

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(Accepted : January, 2010)

The African rice *O. glaberrima* is first choice of useful gene mining in AA genome species because of its resistance to biotic and abiotic stress. The introduction of these characters to *O. sativa* is difficult due to reproductive barriers leading to spikelet sterility. However, fertility can be restored by backcrossing which has resulted in improvement of rice due to transfer of many agronomical traits.

Key words : Gene sterility, Interspecific crosses, Reproductive isolation, Barriers

It is an accepted concept that biological species are groups of interbreeding populations that are reproductively isolated (Mayr, 1942). To understand the origin of species, the genetics of the reproductive barriers between closely related species have been studied extensively (Dobzhansky, 1951; Stebbins, 1958; Coyne, 1992; Coyne and Orr, 1998). Reproductive isolation is the main mechanism acting at various stages in the life history of an organism that is through differential fitness of the gametophyte or zygote via different genes (Dobzhansky, 1951).

O. glaberrima is endemic in inland delta of Niger river in West Africa (Carpenter, 1978) whereas *O. sativa* is of Tropical Asian origin. *O. glaberrima* is supposed to be the first choice of useful gene mining in AA genome species of genus *Oryza* and is a valuable source of genes for *O. sativa* improvement (Jones *et al.*, 1997b). However, experiments dealing with interspecific hybrids between *O. sativa* and *O. glaberrima* suggest that the reproductive barrier is the main obstruction (Morinaga and Kuriyama, 1957; Morishima *et al.*, 1962; Morishima *et al.*, 1963; Chu *et al.*, 1969; Jones *et al.*, 1997a; Sano *et al.*, 1979; Sano, 1983; Tao *et al.*, 1997) causing 100% spikelet sterility in F₁ plants (Sano, 1990). Numerous barriers like segregation distortion, gametophytic abortion and sterility loci located on all chromosomes hinders these interspecific crosses. Since some embryo sacs are fertile, fertility can be restored by back crossing (BC) to the recurrent parent and subsequent selection of fertile progenies in successive selfing generations (Jones *et al.*, 1997a; Heuer *et al.*, 2003). A list of sterility genes is presented in Table 1.

Tao *et al.* (2002) found that a near-isogenic line WAB450-6, derived from interspecific hybrid of *O. sativa*

and *O. glaberrima*, induced frequent abortion of pollen grains but gave completely fertile spikelets when hybridized with its recurrent parent. Similarly Heuer and Miezan (2003) studied that the hybrids between *Oryza glaberrima* with *Oryza sativa* cultivars are partially female fertile and the fertility can be restored by back crossing to a recurrent male parent. They selected a segregating BC₂F₃ population of semi-sterile *O. glaberrima* x *O. sativa indica* hybrid progenies and analyzed it with PCR markers located on the rice chromosome 6. The analyses revealed that semi-sterile plants were heterozygous for a marker (OSR25) located in the waxy promoter (on chromosome 6S), whereas fertile progenies were homozygous for the *O. glaberrima* allele. Though the adjacent markers showed no linkage to spikelet sterility but the semi-sterility of hybrid progenies was maintained upto F₄ progeny, suggesting the existence of a pollen killer in this plant material. Further monitoring of reproductive plant development showed that spikelet sterility was due to an arrest of pollen development at the microspore stage. Hu *et al.* (2004) backcrossed these semi-sterile individuals and showed a clear-cut bimodal distribution for pollen fertility indicating a single gene controlling sterility. This sterility gene was linked with the SSR marker RM7033 on chromosome 2. Since there was no sterility gene previously reported from *O. glaberrima* on chromosome 2, suggested that this gene was a new pollen killer and was tentatively designated as S29(t).

A strong heterosis expressed in hybrids between *Oryza sativa* spp. *indica* and *O. sativa* ssp. *japonica* was observed by Song *et al.* (2005). He studied that the wide-compatibility varieties are able to produce fertile hybrids due to spikelet fertility but the extent to which male and female gamete abortions influence hybrid

Table 1 : List of sterility genes in rice

Sterility gene	Chromosome	Type	Reference
S ₁	6	Gamete sterility	Sano <i>et al.</i> (1979)
S ₂	2	Spikelet sterility	Oryzabase (2006)
S ₃	1	Pollen sterility	Sano (1983)
S ₄	-	Gamete abortion	Sano (1985)
S ₅	6	Hybrid sterility	Ikehashi and Araki (1988)
S ₆	6	Hybrid sterility	Sano (1989)
S ₇	7	Gamete abortion	Oryzabase (2006)
S ₈	6	Gamete abortion	Wan <i>et al.</i> (1993)
S ₉	7	Gamete abortion	Wan <i>et al.</i> (1996)
S ₁₀	6	Gamete abortion	Sano <i>et al.</i> (1994)
S ₁₁	11	Hybrid sterility	Oryzabase (2006)
S ₁₂	-	Hybrid sterility	Oryzabase (2006)
S ₁₃	1	Hybrid sterility	Oryzabase (2006)
S ₁₄	-	Hybrid sterility	Oryzabase (2006)
S ₁₅	12	Female abortion	Wan <i>et al.</i> (1996)
S ₁₆	1	Female abortion	Wan and Ikehashi (1995)
S ₁₇	12	Spikelet sterility	Wan <i>et al.</i> (1998)
S ₁₈	10	Pollen sterility	Oryzabase (2006)
S ₁₉	3	Pollen sterility	Taguchi <i>et al.</i> (1999)
S ₂₀	7	Pollen sterility	Doi <i>et al.</i> (1999)
S ₂₁	7	Pollen sterility	Doi <i>et al.</i> (1999)
S ₂₂	2	Pollen sterility	Sobrizal <i>et al.</i> (2000a)
S ₂₃	7	Pollen sterility	Sobrizal <i>et al.</i> (2000b)
S ₂₄	5	Pollen sterility	Kubo <i>et al.</i> (2000)
S ₂₅	12	Hybrid sterility	Kubo <i>et al.</i> (2002)
S ₂₆	6	Hybrid sterility	Kubo <i>et al.</i> (2002)
S ₂₇	8	Hybrid sterility	Sobrizal <i>et al.</i> (2002)
S ₂₈	4	Pollen sterility	Oryzabase (2006)
S ₂₉	2	Pollen sterility	Hu <i>et al.</i> (2004)
S ₃₀	5	Gamete abortion	Oryzabase (2006)
S ₃₁	5	Hybrid sterility	Zhao <i>et al.</i> (2006)
S ₃₂	2	Embryo sac sterility	Li <i>et al.</i> (2006)
S ₃₃	1	Pollen and spikelet semi sterility	Ren <i>et al.</i> (2006)
S ₃₄	3	Embryo sac sterility	Zhang <i>et al.</i> (2006)

- = Not known

sterility are yet not known. His studies were based on F₁ population of 202 true hybrid plants derived from a three-way cross, where a partial regression analysis showed that the pollen and embryo sac fertility contributed almost equally to spikelet fertility. Wang *et al.* (2005) developed a multipoint method of maximum likelihood (ML) to estimate the positions and effects of the segregation distortion loci (SDLs) in two F₂ populations of rice (*Oryza sativa* L.). One of the parents Bhadua was found to be spikelet semi-sterile. After mapping the SDLs and calculating the recombination frequencies, the molecular linkage maps were constructed to detect QTLs underlying spikelet fertility. It was found two major QTLs underlying spikelet fertility were detected on chromosomes 6 and 8,

respectively. Similarly Song *et al.* (2005) did QTL analysis based on a linkage map of 191 polymorphic marker loci and identified two QTLs for pollen fertility, one QTL for embryo sac fertility, and three QTLs for spikelet fertility. It was found that the S5 locus, previously identified as a locus for wide compatibility by spikelet fertility analysis, is a major locus for embryosac fertility, and a QTL on chromosome 5 had a major effect on pollen fertility. The study also detected a QTL on chromosome 8, showing a large effect on spikelet fertility but no effect on either pollen or embryo sac fertility. These two loci coincided with the two major QTLs for spikelet fertility.

Li *et al.* (2006) studied the molecular mechanism of the partial sterility in the *indica/japonica* hybrids. A

spontaneous semi-sterile mutant named as W207-2 was found from a *japonica* rice variety Nipponbare, in which pollen fertility was about 50 per cent and spikelet fertility about 40 per cent and the semi-sterility was controlled by recessive nuclear genes with no cytoplasmic effect. On comparing the two, they found that the spikelet fertility after pollinating with the pollen of W207-2 was 50.45%, and still semi-sterility, however, when pollinated with Nipponbare pollen, the spikelet fertility increased to 85.55%. It implied that the female fertility of W207-2 was normal. By analyzing the F₂ population, the results suggested that the spikelet semi-sterility was mainly caused by pollen semi-sterility.

Ren *et al.* (2006) developed a series of *O. glaberrima* introgression lines in the background of *O. sativa* for genetic analysis of traits specific to the species and also to introduce alien factors controlling hybrid sterility from *O. glaberrima* into *O. sativa* or from *O. sativa* into *O. glaberrima* (Sano, 1990). Large variation in pollen sterility was observed during development. Genotyping with SSR markers showed that the distribution of spikelet fertility was near the same, which means there was a gamete eliminator that caused pollen grain and spikelet semi-sterility, but the role was not fully understood (Sano, 1990). This gamete eliminator was mapped on chromosome 1 as a new gene S33 (t).

Zhang *et al.* (2006) took 59 accessions of *O. glaberrima* and made a backcross population of BC7F1 with 123 individuals. In the mapping population of BC7F1, pollen grain fertility segregated into semi-sterile and normal type of plants and fitted well with the expected monogenic 1:1 ratio. SSR mapping using the population revealed that the semi-sterility locus was located in the region on chromosome 3 and was designated as S34(t).

Genetic and cytological analyses revealed that the semi-sterility was primarily caused by partial abortion of the embryo sac by Li *et al.* (2006). He studied two independent loci responsible for the hybrid sterility located on chromosomes 2 and 5, by the construction of linkage map from the backcross population. The gene on chromosome 5 mapped to the previously reported sterility gene S31(t), while the gene on chromosome 2, a new hybrid sterility gene, was tentatively designated as S32(t). Further analyses showed that wide-compatibility variety Dular had neutral alleles at loci S31(t) and S32(t) that can overcome the sterilities caused by these two genes. These results are useful for map-based cloning of S32(t) and for marker-assisted transferring of the neutral allele in hybrid rice breeding.

Interspecific crosses between *O. glaberrima* and *O. sativa* are generally performed in order to gain access

to the African rice gene pool for the improvement of irrigated rice in West Africa. Thus, to find the accessions where compatible intercrossing can be carried out between *O. glaberrima* and *O. sativa* in spite of sterility genes would help in accessing the African rice germplasm and overcoming the increase food security in Africa. Moreover, many agronomical traits can be transferred to *O. sativa* thereby increasing its tolerance to biotic and abiotic stresses.

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