GENETIC VARIATIONS OF ORYZA GLABERRIMA THEIR SURVEY AND EVALUATION

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ORIGIN AND DISTRIBUTION : *Oryza glaberrima* Steud. is endemic to West Africa, and is grown according to the traditional cultural practice of the people mainly in the inland of West African countries. It may have evolved from domestication of *O. breviligulata* A. CHEV. et ROEHR., which is also endemic to the same area and has similar botanical characters as of *O. glaberrima* (MORISHISMA *et al.* 1963). The origin from *O. breviligulata* was postulated earlier by PORTERES (1956), though some Indian workers (*e.g.,* RICHHARIA, 1960) considered that *O. perennis* was the ancestral species not only for *O. sativa* but also for *O. glaberrima,* and *O. breviligulata* might be a hybrid derivative from *perennis* and *glaberrima.*

It is said that *O. glaberrima* was created in an ancient tribal state, Garamantes, which existed in southern Sahara some 3,500 years ago ; there were more oases and rivers than at present (VIGNIER, 1939). Egypt then had no rice introduced from Asia. *O. sativa* L., the common rice, may have evolved from the Asian form of *O. perennis* (OKA, 1964). Therefore, two parallel series of evolution can be compared with each other, *perennis* to *sativa* and *breviligulata* to *glaberrima* (MORISHIMA *et al.* 1963).

The *breviligulata-glaberrima* series can be distinguished from the *perennis-sativa* series by certain characteristics, *i.e.,* short and tough ligules, few secondary panicle branches, thick panicle axis, death of the plants at seed maturity (annual habit), and a high sterility of the F_1 hybrids with *sativa* or *perennis.* Nevertheless, all these species have the same number of chromosomes which normally pair in the meiosis of the F_1 hybrids (CHU *et al.,* 1970). In an induced tetraploid F_1 hybrid between a *sativa* and a *glaberrima* strain, partial preferential pairing (estimated to be 57 %) was pointed out (OKA, 1968). Their genomes might be slightly differentiated from each other.

The acreage of *glaberrima* rice is not found in statistical reports. It may be estimated as a half of the total rice field in the inland of West Africa, and a quarter or less in the area closer to the Atlantic coast. The rice fields in West Africa can be classified into five types, *i.e.,* deepwater paddy (silted clay, broadcast), rainfed paddy (clay to sandy loam, broadcast or transplanted), upland field (lateritic, bush-fallow shifting), irrigated field (newly reclaimed, mainly in desert areas), and mangrove swamps (acidic sulphuric soil, newly reclaimed along the coast). Plants of *glaberrima* are found in all these types except for mangrove swamps. However, in many places, *sativa* and *glaberrima* are grown in mixtures (Table 1).

It seems that the people do not mind the species difference in their harvest, and rather prefer *glaberrima* rice in their traditional way of life. In certain upland fields, it was observed that the two species resembled each other in the time of maturity and outward appearance, and could not be easily distinguished without an observation of the ligules. Perhaps, unconscious selection for a certain plant type might have resulted in such resemblance. However, natural hybrids between the two species were not frequent, possibly because the flowering time of *glaberrima* is about one hour earlier than that of *sativa.* In an experimental field at Misima, when the plots of the two species were laid side by side and they started flowering in the same week, the pollen flow (from *sativa* to *glaberrima)* was estimated to be 0.44 percent.

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As *glaberrima* varieties are distributed from upland to deepwater conditions, they range from the upland to deepwater (floating) types in the same manner as *sativa* varieties do. The floating type is said to have a higher internode elongation rate, when submerged, than that of *sativa* floating types (Mr. L. MARCHAIS, personal communication). The upland type is supposed to be more tolerant to unfavorable conditions than that of *sativa.* When tested by the *Mimosa* method, however, *glaberrima* did not show a higher drought resistance than *sativa* (MORISHIMA *et al.,* 1962b).

PORTERES (1956) asserted that on the basis of variations in grain shape and other characters, *glaberrima* varieties were divisible into "indicoides" and "japonicoides" types. Observing the pattern of association of various characters, however, we failed to detect among *glaberrima* varieties such a trend of varietal differentiation as comparable to the Indica-Japonica differentiation of *sativa* varieties (MORISHIMA *et al.,* 1962a). The phenol reaction of spikelets is a character conveniently used for distinguishing between the Indica and Japonica types. Among *glaberrima* varieties, 62 were positive while 20 were negative, but the difference in phenol reaction was not associated with differences in other characters by which the Indica and Japonica types were distinguishable.

Strains of *O. glaberrima* and *O. breviligulata* can be divided into two groups isolated by an F_1 weakness barrier (controlled by a set of complementary dominant semi-lethals ; CHU and OKA, 1971). However, the two groups did not seem to differ in other morphological and physiological traits.

YIELDING POTENTIAL : Data evaluating the yielding potential of *glaberrima* varieties are meagre. At the Badeggi Rice Research Station, Northern Nigeria, an experiment of 31 *glaberrima* varieties showed a range of grain yield from 1.2 to 3.5 ton/ha. A variety, Jatau, gave 2.7 ton/ha on the average for several years when 27 kg/ha of nitrogen was applied. Our test of two *glaberrima* varieties in various cultural conditions at Taichung, Taiwan, also showed a considerable yielding potential of the varieties (Table 2). Since no breeding effort by the modern technique has been made, *glaberrima* may be compared only with unimproved varieties of *sativa.* They are productive under such unfavorable cultural conditions as no fertilizer application and no weeding.

The tillering capacity of *glaberrima* varieties does not seem to be inferior to that of *sativa* varieties. The leaf at the time of heading would not differ between the species, though these agronomic characters widely vary in each species among varieties. The number of spikelets per panicle would be smaller in *glaberrima* than in *sativa* as *glaberrima* has only a few secondary panicle branches. Many *glaberrima* varieties retain the characters of their wild progenitor, *e.g.,* easy grain shedding and pronounced seed dormancy (Table 3).

The death of the plants at maturity seems to make a sharp contrast to *sativa* which is essentially a perennial plant. In this respect, *glaberrima* rice may be compared with wheat and barley. Possibly, because of the annual habit, the senescence of leaf and straw proceeds fast with seed ripenning, suggesting a high rate of translocation of nutrients to the grain. In improved *sativa* varieties, about 3/4 of carbohydrate deposited in the grain is due to assimilation after heading. Possibly, *glaberrima* has a lower rate of reliance upon assimilation after heading. However, when grown with an amount of nitrogenous fertilizers, the plants badly lodge at maturity. Therefore, *glaberrima* rice may not be highly responsive to nitrogen unless stiff-strawed variants are selected.

The amylose content of the grain, which showed a wide range among *sativa* varieties, would also vary among *glaberrima* varieties. A strain we have selected had a medium degree of stickiness of boiled rice. Data on the quality characters of *glaberrima* rice are not available.

A BREEDING EXPERIMENT : The grain of most *glaberrima* varieties has red pericarp. Looking for plants with colorless pericarp or white grain, we found three out of about 400 examined, which were from Gambia. Most *glaberrima* varieties are strongly sensitive to photoperiod and their duration depends upon daylength. Search for non-sensitive ones gave 8 out of 84, which were from Guinea. From hybridization of the two exceptional types (17 crosses in total), 37 F_2 plants were selected which were insensitive to photoperiod and had white grain. In a part of the crosses, insensitivity was monogenic recessive (3 : 1), while it was digenic (15 : 1) in the others. Colorless pericarp was monogenic recessive in all crosses.

With the view to obtaining non-lodging plants, their F_3 lines were inter-crossed in 35 random cross-combinations, and their progeny lines were tested for two years. Thirty non-lodging F_3F_2 plants were selected from about 1,100, but their F_3 lines showed that selection was unsuccessful. Their grain yield was 301 g/m^2 on the average as compared with 447 g/m^2 of an improved *sativa* variety (T65) in an adjacent plot. Then, the bulked seed was irradiated with 20 kR gamma-rays, and about 10,000 M_2 plants (by one-kernel-from-one-panicle method, from about 1,000 M_1 plants) were tested, and 21 non-lodging plants were selected. But their M_3 lines all lodged again ; we had to give up our trial to select non-lodging *glaberrima* strains.

In order to obtain different types of mutants, the bulked seed was treated with EMS (0.5 %, 5 hours at 27°C after 2 hours presoaking), and about 7,000 M_2 plants (from about 1,000 M_1 plants, by one-kernel-from-one-panicle method) were examined for morphological mutants. The results gave a spectrum of various mutants, which may be used as markers for genic analysis (Table 4).

One of them, the glutinous (waxy) mutant, may be worthy noted. It was detected by iodine test of M_2 seeds on M_1 panicles (1/3,780 = 0.026 %). Its segregation in heterozygous M_2 panicles (83 : 25) proved that it was controlled by a recessive gene. On the other hand, iodine tests of more than 400 strains collected from various West African countries gave no glutinous one ; no report of glutinous *glaberrima* rice may be found in the literature. The induced mutant, which seems to be a new type, will be tested for chemical characters of starch, as to whether or not the gene locus is the same as that of *sativa,* and for its agronomic characters.

The 7,000 M_2 plants were cut at maturity to search for those ratooning from the stubble. Though it was in late October (1976), 20 regenerating plants were selected and transplanted into a greenhouse. However, all of them died in the greenhouse ; the search for perennial mutants was unsuccessful.

HYBRIDIZATION BETWEEN *GLABERRIMA* AND *SATIVA* : There is no particular crossing barrier between the two cultivated species. The F_1 plants are almost completely pollen-sterile, but 10 to 45 percent of embryosacs are normal anatomically, and backcrosses can be made (CHU *et al.,* 1969). Therefore, genes can be transferred from one to the other species if the sterility barrier occurring in backross generations is overcome.

From B_8F_3 lines which had been obtained by selecting in each backross generation plants showing a medium degree of pollen sterility, we have selected isogenic F_1-sterile lines (self-fertile) with the genetic background of either *sativa* or of *glaberrima* parent. The isogenic lines showed an about 50 percent pollen sterility when crossed with *sativa* or *glaberrima* parent (according to their genetic background) irrespective of the direction of crosses, but the F_2 plants were almost completely fertile (Table 5).

To account for this particular behavior of F_1 sterility, underlying genes may be assumed as follows : The *sativa* parent has A_1/A_1 while its isogenic F_1-sterile line has A_1^s/A_1^s introduced from the *glaberrima* parent. When an A^s gene is present in the sporophytic tissue of the F_1 plants (A_1/A_1^s), gametes (both pollen and embryosac) carrying A_1 degenerate during the course of development. The same model may be adopted to the isogenic F_1-sterile lines with *glaberrima* background. An evidence supporting this hypothesis was obtained from a line which had a gene for pigmentation of leaf sheath and apiculus in close linkage with A_1^s. Its semi-sterile F_1 plants with the *sativa* parent (colorless) were colored indicating the dominance of the pigmentation gene, and all the F_2 plants which were fertile (59 in total) were colored (no segregation). In contrast, the F_2 plants with its colorless sib-lines showed a 3 colored : 1 colorless segregation. It may be asserted that the F_1 sterility is due to a sporo-gametophytic interaction of particular genes.

On the basis of this hypothesis, the parental genotypes are A_1/A_1 A_2^s/A_2^s for *sativa* and A_1^s/A_1^s A_2/A_2 for *glaberrima.* Then, the F_1 plants between the isogenic F_1-sterile line with *sativa* background and that with *glaberrima* background should have the same genotype, A_1^s/A_1^s A_2^s/A_2^s, and should be fertile. However, they showed a high sterility. Further, exceptions to the above-mentioned genetic behavior of sterility were pointed out, which are now under observation. This indicates that there are other sterility genes in addition to those with sporo-gametophytic effects as worked out from the recurrent backcrossing experiment.

Expectedly, various genic substitutions are involved in species hybrids. Even among varieties of *sativa,* there were found a number of sets of duplicate genes causing gametophytic F_1 sterility (OKA 1957 ; 1974), similar ones causing sporophytic sterility in F_2 and later generations (OKA and DOIDA, 1962), and cytoplasmic male sterility with restorer genes (SHINJYO, 1969). It is not an easy task to completely work out the genic substitutions controlling the sterility of species hybrids.

Further, the plants derived from the early generations of backcrossing were observed for characters distinguishing the two species. Though the plants were heterozygous and character values were largely intermediate between the parental values, the data suggested that recombinations took place. Observations of homozygous progeny lines are under way.

Because of the F_1 sterility, it is difficult to obtain F_2 seeds, but it is not impossible if a large enough number of F_1 plants are grown in a good condition in isolation from other rice plants. From such an experiment (108 x W039) conducted at Taichung, 27 F_2 plants were raised. Their F_7 lines which restored self-fertility were tested at Misima. Out of 18 lines tested, one had short ligules, another was completely annual, and two had few secondary panicle branches, but many others had the traits of *sativa* parent. One of them showed a high F_1 pollen-fertility when test-crossed with the *glaberrima* parent. An observation of character correlations among the lines proved that genes could be recombined in the species hybrid, though the occurence of a few significant correlations suggested a trend to recombination restriction (Table 6).

A hybridization breeding experiment was conducted by Mr. B. D. A. BECK at the Badeggi Rice Research Station (personal communication) aiming at incorporation of vegetative vigor and flood resistance of *glaberrima* into *sativa* varieties. The F_6 lines made available through his courtesy, 28 in total number, were also tested at Misima. All the lines showed characters of *sativa* and a high F_1 sterility with *glaberrima* parent when test-crossed, except that one had short ligules, two had few secondary panicle branches, and one appeared to be annual. In this type of experiments, as the early generation plants are highly sterile and are easily contaminated by alien pollen, it is difficult to observe the pattern of character recombination. Yet, it may be asserted that the characters of *sativa* predominate in the hybrid progeny.

The populations of *O. glaberrima* in West African contain a large amount of genetic variations (MORISHIMA and OKA, 1970). Some are hybrid swarms with its wild form, *O. breviligulata,* and introgression would constantly create new variants. Further, in some deepwater fields observed in Mali and Niger, *O. perennis* subsp. *barthii* and *O. sativa* grow together forming a sympatric population of four *Oryza* species (OKA and CHANG, 1964) ; *barthii* is isolated from other species by a partial crossing barrier (death of young F_1 zygotes owing to complementary dominant lethals ; CHU and OKA, 1970a). Nevertheless, introgression takes place across this and other reproductive barriers to increase the genetic variability within populations (CHU and OKA, 1970b). Observations of the genetic variations may bring to light various new genes.

CONCLUSION : It seems that *glaberrima* rice is grown by the people in West Africa as a component of their traditional life. The situation may be compared with that of classical wheat species like *Triticum dicoccum* which is still grown in Near East and Ethiopia. The importance of genetic diversity in crop species as the breeding material is now increasingly acknowledged. Presumably, it may also become acknowledged that genetic diversity plays a role in maintaining the stability of agroecosystems. Rice experiments conducted in Africa have been concentrated on *O. sativa* in the past. It is now hoped to look more closely into the breeding potentiality of *O. glaberrima* and its genes which deserve incorpolation into *sativa* varieties. Conservations of germplasms of *O. glaberrima* and other African crop species should be put in practice as those would be rapidly diminishing with the modernization of agriculture.

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Table 1 – Mixing of *sativa* and *glaberrima* in different types of rice fields in West Africa (No. of fields observed)

Type	Pure *sativa*	Mostly *sativa*	Half-to-half mixture	Mostly *glaberrima*	Pure *glaberrima*
Upland		2	2	4	5
Rainfed lowland	4	10	1	1	
Deepwater		1	1	5	1

After OKA and CHANG (1964)

Table 2 – Grain yield of *sativa* and *glaberrima* varieties under different growing conditions (g/m^2, mean for 1960 and 1961, at Taichung, Taiwan).

Variety (type, origin)	Transplanted				Broadcast				Mean ± σ
	FW	OW	FO	OO	FW	OW	FO	OO	
sativa :									
124 (Indica, Taiwan)	282	263	176	154	230	185	126	105	190 ± 98.4
647 (Japonica, Celebes)	204	196	146	100	218	301	82	82	166 ± 77.6
T65 (Japonica, Taiwan)	344	241	175	96	139	96	5	7	138 ± 115.1
glaberrima :									
W028 (Pubescent)	253	216	158	113	238	253	131	101	183 ± 64.2
W039 (Glabrous)	212	169	168	92	156	197	50	61	138 ± 62.0

FW : Fertilized, weeded, OW : No fertilizer, weeded, FO : Fertilized, no weeding, OO : No fertilizer, no weeding.
T65 is an improved variety. After MORISHIMA *et al.* (1962a).

Table 3 – Distributions of character values as compared between *O. sativa* (Sa) and *O. glaberrima* (G1).

Character	class interval (Basic Value)	Sp.	Score 0	1	2	3	4	5	6	7	8	9	10	No. of strains	Mean
Spikelet length	0.4 mm	Sa.	1	4	7	12	13	19	15	4	1	2	2	80	8.05
	(6.2 mm)	Gl.				2	3	24	24	9	4			68	8.44
Spikelet width	0.25 mm)	Sa.	1	9	14	23	14	14	3	1	1			80	3.63
	(1.25 mm)	Gl.			1	4	26	33	3	1				68	3.38
Lth/width ratio	0.25	Sa.	2	6	17	13	12	14	11	3		1	1	80	2.70
	(1.75)	Gl.		1	4	51	12							68	2.52
Apiculus hair length	0.1 mm	Sa.	3		24	19	7	8	7	3	2			73	0.35
	(0 mm)	Gl.	47				1	12	7	1				68	0.17
Awn length	1 cm	Sa.	68	3		2	4	6	1					84	0.73
	(0 cm)	Gl.	56	2	1	3	4							66	0.44
Weight of 100 grains	0.2 gm	Sa.	1	2	9	9	12	19	10	8	7	5	2	84	2.32
	(1.3 gm)	Gl.			1	1	8	13	3	1	2	1		30	2.31
Anther length	0.2 mm	Sa.	4	6	11	9	8	5	4					47	2.38
	(1.8 mm)	Gl.	2	11	5	3								21	2.09
Ligule length	0.4 cm	Sa.			4	24	34	29	3					94	2.09
	(0.2 cm)	Gl.	58	23										81	0.40
Panicle length	2 cm	Sa.	1	1	2	10	16	31	26	10	4	2	2	106	20.0
	(10 cm)	Gl.		1	4	10	14	18	14	3				64	19.1
Rachis no. per panicle	2	Sa.	3	8	33	31	20	6						106	9.9
	(4)	Gl.		2	6	16	19	14	2	4				63	12.4
Spikelet no. per panicile	20	Sa.	1	2	4	18	28	20	15	6	8	2	2	106	110.6
	(20)	Gl.		4	11	18	17	8	3	1	1			63	90.2
Days required for overcoming dormancy (Unhulled seeds)	20 days	Sa.	20	25	29	18	1	2	1	1				97	53.8
	(20 days)	Gl.							17	7	2			26	148.4
$KClO_3$ resist. (Conc. in log)	0.3	Sa.			6	20	31	38	8	3				106	-2.31
	(-3.6)	Gl.	4	2	15	19	16	6	2					64	-2.69
Low temp. resist. (index number)	0.1	Sa.	24	24	10	7	8	6	2	4	2		1	88	0.22
	(0)	Gl.		1		4	1	2	1	7	10	3	3	32	0.68
Damage by drought (Index-no.)	0.5	Sa.	1	2	6	24	25	15	16	27	2			118	2.58
	(0)	Gl.							3	4	22			29	3.83
Floating ability (Index-number)	2	Sa.	2	2	1	1		1	2	1				10	10.2
	(4)	Gl.		1		1	3	3	2	1				11	13.1
Degree of grain shedding (Index)	1	Sa.	42	39	14									95	
	(1)	Gl.	37	36	11	4								88	

After Morishima *et al.* (1962a)

Table 4 – Mutants selected from an M_2 population (7079 plants, EMS treated) of a *glaberrima* strain insensitive to photoperiod and with colorless pericarp.

Type compared with *sativa* mutants	No. of plants	Frequency x 10^{-4}
Dwarf, "Daikoku"	10	14.1
Dwarf, tillering		11.3
Dwarf, others	18	21.4
Chlorosis	13	18.4
Narrow leaf	4	5.6
Broad leaf	1	1.4
Brown discoloration	9	12.7
Rolled leaf	1	1.4
Branching	1	1.4
Brittle culm	2	2.8
Liguleless	12	17.0
Lax panicle	1	1.4
Long empty glume	1	1.4
Double glume	1	1.4
Hairy glume	1	1.4
Awned	1	1.4
Apiculus coloration	1	1.4
Minute grain	2	2.8
Large grain	2	2.8
Round kernel	1	1.4
Long kernel	1	1.4
Glutinous endosperm	1	2.6*
Early heading	3	4.2
Early lodging	1	1.4
Semi-sterile	2	2.8

*Frequency of heterozygotes ; homozygote frequency is its 1/4.

Table 5 – Distributions of pollen fertility in B_8F_1 and B_8F_2 generations of a backcrossing experiment between *sativa* and *glaberrima*.

Generation	Pollen fertility (%) 15	25	35	45	55	65	75	85	95	No. of	No. of
sativa background :											
B_8F_1	1	1	4	8	11	7	2		6	40	13
B_8F_2			1		2	2	2	1	253	261	9
glaberrima background :											
B_8F_1		1	8	12	10	2				33	5
B_8F_2									98	98	4

Table 6 — Correlation of characters among 18 F_7 lines from *sativa* (108) * *glaberrima* (W039).

Character	(1)	(2)	(3)	(4)	(5)	(6)
1) F_1 pollen-fertility with *sativa* (108)						
2) F_1 pollen-fertility with *sativa* (T65)	.50*					
3) F_1 pollen-fertility with *glaberrima* (W039)	-.18	-.26				
4) Ligule length	.00	.59**	.01			
5) No. of secondary panicle branches/primary branch	-.28	.03	-.24	-.20		
6) Regenerating ability of excised stem segment	.09	.34	-.23	.47*	.14	
7) Lemma hair length	.03	.27	-.44	.23	-.08	-.25

*Significant at 5 % level, **at 1 % level.