Influence of the *Oryza sativa* genotype on the fertility and quantitative traits of F_1 hybrids between the two cultivated rice species *O. sativa* L. and *O. glaberrima* Steud.

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Crosses were carried out between the two cultivated rice species, using a constant *Oryza glaberrima* parent and 14 *O. sativa* cultivars, including 11 traditional African ones. The F_1 hybrids were studied for quantitative traits and their fertility. Analyses of the quantitative traits revealed the intermediate position of F_1s with respect to the parental lines and the high heritability of several characters, including the secondary branching within the panicle. All F_1 hybrids showed complete seed sterility and only by an examination of the pollen could the different combinations be discriminated. The hybrids obtained from two *O. sativa* cultivars introgressed from the wild species *O. longistaminata* were particularly sterile.

Key words: rice, *Oryza sativa, Oryza glaberrima*, interspecific hybridization, sterility, quantitative inheritance.

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Des croisements ont été réalisés entre les deux espèces de riz cultivé, en utilisant un parent *Oryza glaberrima* constant et 14 cultivars d'*O. sativa*, dont 11 traditionnels africains. Les hybrides F_1 ont été étudiés pour leur fertilité et des caractères quantitatifs. L'analyse de ces derniers a montré la position intermédiaire des F_1s par rapport aux lignées parentales et l'héritabilité élevée de plusieurs caractères dont la densité de ramifications secondaires sur la panicule. Tous les hybrides F_1 ont présenté une fertilité paniculaire nulle, et seule l'observation du pollen a permis de discriminer les différentes combinaisons. Les hybrides issus de deux cultivars d'*O. sativa* introgressés par l'espèce sauvage *O. longistaminata* se sont montrés particulièrement stériles.

Mots clés : riz, *Oryza sativa, Oryza glaberrima*, hybridation interspécifique, stérilité, génétique quantitative.

Introduction

The cultivation of *Oryza sativa* has spread widely in sub-Saharian Africa, since the introduction of this Asian species several centuries ago. Its spread in West Africa has been partly at the expense of the indigenous cultivated rice species, *O. glaberrima*, which is of lower agronomic value. The low variability of *O. glaberrima* (Second 1982; Miezan and Ghesquière 1986) means that the success of a breeding program centered on this species alone is unlikely. As noted by Bouharmont *et al.* (1985), *O. glaberrima* has more promise as a component of *O. sativa* breeding programs.

These two species belong to the same AA genomic group (Morinaga 1964). Cytological and cytogenical studies have been conducted by several authors, with Bouharmont (1962), Bouharmont *et al.* (1985), and Chu *et al.* (1969) attempting to explain the high sterility of their interspecific hybrids, while a genetic model ("sporogametophytic interaction") to account for it was proposed by Sano *et al.* (1979) and Sano (1983, 1986). This sterility is an important barrier to the use of *O. glaberrima*, but it was demonstrated that the restoration of fertility is possible after several backcross generations (Yabuno 1977; Sano 1986).

The transmission of quantitative traits between the two species was studied by Sano *et al.* (1980). Although other observations were made on morphological traits of F_1 hybrids (Morishima *et al.* 1962; Seetharaman 1962), few results are available for evaluating the effect of the choice of the *O. sativa* parent on the characteristics of F_1 hybrids.

This paper aims to study the influence of the *O. sativa* genotype on the characteristics (fertility and quantitative characters) of F_1 hybrids obtained from crosses between a constant *O. glaberrima* parent and 14 *O. sativa* cultivars, including 11 traditional African ones.

Materials and methods

Plant material

The *O. glaberrima* cultivar CG1-3 was crossed with 11 traditional African cultivars and also with 3 Asian varieties used by Oka (1958) as test strains. Fertilities were also observed for some F_1 hybrids obtained from another *O. glaberrima* cultivar, WO25. Table 1 shows the parental lines. They were obtained from the ORSTOM[2] collection, except for 108, 521, 563, and WO25, which were provided by the National Institute of Genetics (Japan). The purity of parental lines was ensured by successive generations of controlled self-fertilization. The classification of these *O. sativa* genotypes into the *indica* and *japonica* subspecies was based on isozyme studies (Second 1982; Ghesquière and Second 1985; de Kochko 1987). These studies revealed that the genotypes of BS20 and 2LS102 are introgressed from the wild species *O. longistaminata*. The isozyme data also enabled checks to be made at an early stage on the legitimacy of the presumed F_1 hybrids.

Cultivation and experimental design

The seeds were dehulled, disinfected in a solution of sodium hypo-

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TABLE 1. Varieties used in crossing design

Species	Name	Origin	Enzymatic structure*
O. sativa	ES70-6	Tanzania	*O. sativa* ssp. *japonica*
	YS138-3	Guinea	*O. sativa* ssp. *japonica*
	YS252-1	Guinea	*O. sativa* ssp. *japonica*
	YS45-1	Guinea	*O. sativa* ssp. *japonica*
	521	Japan	*O. sativa* ssp. *japonica*
	563	Japan	*O. sativa* ssp. *japonica*
	BS117	Guinea-Bissau	*O. sativa* ssp. *indica*
	BS125	Guinea-Bissau	*O. sativa* ssp. *indica*
	ES44	Tanzania	*O. sativa* ssp. *indica*
	ES79	Tanzania	*O. sativa* ssp. *indica*
	SS404	Senegal	*O. sativa* ssp. *indica*
	108	Taiwan	*O. sativa* ssp. *indica*
	BS20	Guinea-Bissau	Introgressed *O. sativa* ssp. *indica*
	2LS102	Mali	Introgressed *O. sativa* ssp. *indica*
O. glaberrima	CG1-3	Casamance (Senegal)	
	WO25	Guinea-Bissau	

*See text.

chlorite, rinsed in water, and then sown in Petri dishes. Some hybrid seeds did not germinate, without any particular genotype effect.

After 10 days, seedlings were planted out in 2-L pots. Plants were cultivated in a glasshouse, in constant-irrigation conditions. The first three panicles of each plant were bagged to avoid cross-pollination.

A randomized block design with an unequal number of repetitions per genotype (Table 2) was used in this study.

The varieties BS125, ES44, and ES79 were photosensitive and did not flower. Hence, these genotypes were excluded from the quantitative characters analysis.

Quantitative traits

The number of tillers was counted at 3, 4, 6, and 8 weeks (i.e., T3, T4, T6, and T8). The heading time (HEAD) was the number of days from sowing to heading of the first panicle. Other vegetative characters were scored at heading date: stem diameter (DIA, mean of the three oldest tillers, measured at the first internode level), length (LGF) and width (WIDF) of the flag leaf, ligule length (LIGU), and plant height (HGT). The panicle characteristics were estimated from the mean of the first three panicles: length (LGP), number of primary (BR1) and secondary branches (BR2), number of grains (NGR), and number of spikelet insertions (NSI). The following calculated variables were included in the analyses: LFG/WIDF, T8 − T4, BR1/LGP, BR2/BR1, BR1/LGP, BR2/LGP, and NSI/BR1.

Fertility

The estimation of pollen fertility was based on pollen stainability. Using Alexander's method (1969), three classes of pollen grains were discerned: normal, partially filled with cytoplasm (i.e., intermediate), and empty. For each plant, about 400 grains were scored.

Statistical analyses

For each set including CG1-3, one *O. sativa* genotype, and the related F_1 hybrids, a one-way analysis of variance was done for each trait. Where significant effects were revealed, means were compared by using Newman and Keuls's test. For these analyses, the classes were randomly reduced to equal effectives.

Multivariate analyses were carried out on the quantitative traits and fertility data. These included principal-component analysis and hierarchical ascending classification (euclidian distance and variance aggregation criterion). In principal-component analysis, calculations are performed using active data that determine a system of synthetic coordinates. Supplementary data can then be positioned in this system.

The broad-sense heritability was estimated as the coefficient of intraclass correlation of F_1 hybrids: $h^2 = V_{gh}/(V_e + V_{gh})$, with V_{gh} and V_e, respectively, being the estimates of the factor variance, i.e., genetic variance, and of the error variance.

All calculations were performed on a Goupil-G4 microcomputer, using the statistical software NDMS (ORSTOM).

TABLE 2. Number of plants per genotype

	Parent	Hybrid with: CG1-3 as female	CG1-3 as male	WO25 as female
ES70-6	6	6	6	9
YS138-3	4	8	—	—
YS252-1	4	5	—	—
YS45-1	7	7	7	—
521	4	5	4	—
563	4	—	6	—
BS117	5	7	—	4
BS125	6	6	—	—
ES44	5	7	5	—
ES79	5	5	—	—
SS404	4	—	3	7
108	4	2	6	—
BS20	4	5	4	8
2LS102	4	8	—	—
CG1-3	7	—	—	—

Results

Quantitative traits

Univariate analyses

(i) Differences between parents

The *O. glaberrima* CG1-3 cultivar differed from most of the *O. sativa* cultivars (Table 3), not only in the taxonomic character of ligule length (short) but also in tillering (greater in number), stem diameter, size of the flag leaf, and secondary branching of the panicle (reduced). This last trait is considered by Sano *et al.* (1980) to be a diagnostic character to separate the two species.

The difference in the tillering of CG1-3 compared with the *O. sativa* cultivars (except 2LS102) largely arose in the first weeks, the tillering speed of most cultivars being approximately equal subsequently.

TABLE 3. Mean values of *O. glaberrima* and *O. sativa* parents for quantitative traits

Trait	CG1-3 (*O. glaberrima*)	ES70-6	YS138-3	YS252-1	YS45-1	521	563	BS117	SS404	108	BS20	2LS102
T3	3.6	1.3	2.2	1.0	1.4	1.0	1.5	2.0	2.0	1.0	1.0	3.0
T4	5.1	2.5	3.8	3.3	2.6	1.8	3.5	3.8	4.0	2.0	3.5	7.5
T6	8.4	7.5	8.5	4.2	7.8	6.0	7.8	7.4	9.0	7.0	10.5	15.5
T8	10.5	7.5	9.0	4.2	7.8	6.8	10.0	7.8	10.3	8.0	10.7	15.7
HEAD (days)	56.3	68.8	72.8	85.5	82.7	51.5	55.0	61.8	94.7	81.5	64.5	61.0
LGF (mm)	339	443	355	360	418	345	402	313	601	224	470	397
WIDF (mm)	18.6	19.3	15.2	16.8	18.1	12.7	12.7	12.6	11.3	12.5	14.2	9.5
LGF/WIDF	18.1	22.6	23.1	21.4	22.0	27.2	31.8	24.8	53.7	17.8	33.0	41.6
HGT (cm)	82.8	101.5	105.6	76.0	77.9	55.2	59.2	100.0	129.8	110.5	76.3	96.4
LIGU (mm)	3.3	16.8	18.5	11.7	14.6	11.5	16.5	17.6	18.7	13.2	14.8	13.2
DIA (mm)	7.8	10.1	10.0	12.4	13.4	5.7	6.6	9.3	12.5	13.5	8.8	11.1
LGP (mm)	25.0	25.8	18.6	18.5	21.3	18.9	18.0	23.0	25.2	21.9	26.8	22.4
BR1	10.0	9.1	8.1	7.7	10.0	5.3	9.1	10.6	10.4	10.1	10.2	7.8
BR2	3.9	21.5	8.1	6.0	8.1	11.0	7.3	17.2	18.1	12.6	32.1	4.5
BR2/BR1	0.4	2.4	1.0	0.8	0.9	2.1	0.8	1.6	1.8	1.2	3.1	0.5
NSI	83.8	121.3	78.3	66.5	84.5	63.9	72.6	109.1	108.8	86.7	143.4	59.9

NOTE: Values of *O. sativa* parents that do not differ at $p < 5\%$ from those of CG1-3 are indicated by underscoring.

(ii) Comparisons between hybrids and parents

The relationships between the F_1s and each of the parents are given in Table 4.

Most of the hybrids were plants of normal vigour. They showed ligule lengths intermediate between those of the parents and a very split panicle with strongly awned spikelets.

In most cases, the F_1 hybrids manifested characters that were intermediate between those of their parents. However, some rare cases of transgression were observed. Heterosis (F_1 > parents) was the most frequently seen for the character height (hybrids with ES70-6, BS117, YS45-1, YS138-3, YS252-1). In rare cases, F_1s were smaller sized than their parents; thus hybrids with BS20 showed depressed tillering. This hybrid was the only one showing a reduced vigour.

Only a few examples of differences between reciprocal hybrids were observed: these included flag-leaf length for hybrids involving 521, number and density of secondary branches for those with YS45-1 and BS20.

Multivariate analyses

A principal-component analysis was carried out on F_1 hybrids, parents being treated as supplementary data.

As shown in Table 5, the first four axes described 75.5% of the total variability. Axis 1 represents panicle characteristics (number of spikelets, secondary branching). The number of primary branches was not represented on this axis, but on the third. The heading date, height, and particularly the tillering contribute to axis 2. Axis 4 is correlated to the flag-leaf length.

Figure 1 shows the mean point of each genotype on the plane defined by axes 1 and 2. All F_1 coordinates fall within the range occupied by the parental ones. This confirms the lack of transgression noted in the univariate analyses.

All parental and hybrid genotypes (excluding those involving BS125, ES44, and ES79) were then classified by hierarchical ascendant classification, using their coordinates on the axes 1–4 of the principal-component analysis as variables. For 9 of the 11 cases, F_1s were classified in the same group as their *O. sativa* genitor (Fig. 2). This indicates that a high proportion of *O. sativa* characteristics is passed to CG1-3.

This can be seen more clearly in Table 6, which gives the results of the quantitative analysis of characters. The broad-sense heritability is important for synthetic variables from axes 1, 2, and 4. The parent–offspring regression is significant for the two first axes, indicating there is an additive transmission of characters such as tillering or number of spikelets per panicle.

Fertility

Classification of the hybrids on the basis of their fertilities was only possible through an examination of pollen fertility since all F_1 hybrids showed no seed fertility. Table 7 presents the results of pollen fertility of both parents and F_1s.

The level of normal pollen is in all cases very low, and this explains why no seed fertility is observed. No difference is observed between reciprocal crosses, except those between CG1-3 and ES44.

A principal-component analysis of F_1s with CG1-3 was performed using the three descriptive variables of the pollen. Axis 1 separates those hybrids bearing empty pollen from those with intermediately filled pollen, while axis 2 is correlated with level of normal pollen. This illustrates a quasilinear relationship ($y = 1 - x$) between the proportions of empty and intermediate pollen and an absence of correlation between the proportions of normal and intermediate pollen.

Figure 3 shows the three main groups obtained by the hierarchical ascendant classification using factorial coordinates. The hybrid CG1-3/ES44 is separated by its higher level of normal pollen (3%). F_1 hybrids with BS20 and 2LS102 are characterized by a high rate of empty pollen (>80%). It is of interest that similar data were obtained for the hybrid WO25/BS20. Other F_1s appear to be relatively homogenous.

Discussion

The level of pollen fertility of F_1s between CG1-3 and all *O. sativa* parents is comparable with the observations of Morishima *et al.* (1962), Chu *et al.* (1969), and Yabuno (1977) on other F_1 hybrids between *O. glaberrima* and *O. sativa*. Like the last author, we found no seed fertility. We did not find any combination that showed the exceptional high level (64%) noted by Bouharmont *et al.* (1985).

Morishima *et al.* (1962) reported that the highest F_1 fer-

TABLE 4. Distribution of mean values of F_1 hybrids with respect to parental values

Trait	No. of F_1 hybrids						
	<G and <S	<G	<S	=G and =S	>G	>S	>G and >S
T3	2	9					
T4		4	1	6			
T6		2	2	8			
T8	1	5	1	4			
HEAD	1	1	6	1	5		1
LGF	1		1	8			2
WIDF		6		3		8	
LGF/WIDF	1		7	2	1		2
HGT		1	1	2		1	5
LIGU			8		11		
DIA			5	1	8		2
LGP		2		2		6	2
BR1	1	1		6		4	
BR2			5	3	6		1
BR2/BR1			5	3	4		2
NSI		2	2	6	1		1

TABLE 5. Description of the first four axes of the principal-component analysis of quantitative traits: percentage of variation explained, characters involved (coordinate and correlation)

Character	Axis 1 (30.2%)		Axis 2 (23.2%)		Axis 3 (13.1%)		Axis 4 (9.0%)	
	Coordinate	Correlation	Coordinate	Correlation	Coordinate	Correlation	Coordinate	Correlation
T6			0.40	0.84				
T8			0.40	0.85				
HEAD			−0.31	−0.65				
LGF							−0.63	−0.82
HGT			−0.32	−0.68				
LGF/WIDF							−0.48	−0.62
LGP	−0.30	−0.71						
BR1					−0.41	−0.65		
BR2	−0.38	−0.92						
NSI	−0.38	−0.90						
BR2/LGP	−0.35	−0.84						
BR2/BR1	−0.37	−0.88						
NSI/BR1	−0.37	−0.88						

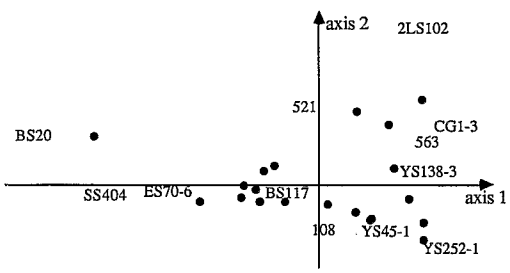

FIG. 1. Representation of the mean points of parental genotypes (indicated by their name) and of F_1 hybrids (points) on the plane defined by the first two axes of the principal-component analysis of quantitative traits.

tilities between *O. glaberrima* and *O. sativa* were observed between *O. glaberrima* and some *O. sativa* ssp. *indica* varieties. In our study also, the most fertile combination involves an *O. sativa* ssp. *indica* variety, i.e., ES44.

As far as we know, there is no explanation of why some *O. sativa* ssp. *indica* varieties have a greater compatibility than other *O. sativa* varieties with *O. glaberrima*. One can presume that part of the answer lies at the cytoplasmic level. Indeed, Yabuno (1977) and Sano (1986) demonstrated the existence of nucleocytoplasmic interactions in hybrids between *O. glaberrima* and *O. sativa*. We observed a difference between CG1-3/ES44 and its reciprocal cross. Bouharmont *et al.* (1985) reported such differences in crosses between *O. sativa* and *O. breviligulata*, the wild ancestor of *O. glaberrima*.

On the basis of the analysis of chloroplastic genome polymorphism, Dally (1988) confirmed the distinction of *O. sativa* ssp. *indica* and *O. sativa* ssp. *japonica* and showed that there was a great similarity between *O. sativa* ssp. *indica* plastotypes and those of the wild species *O. rufipogon*. These findings are in accord with observations of Morishima *et al.* (1962), who reported that the less-sterile interspecific hybrids with *O. glaberrima* involved, in addition to the already men-

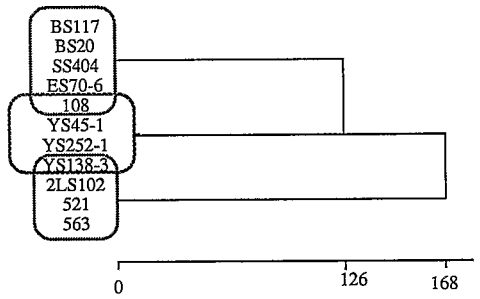

FIG. 2. Classification of *O. sativa* parents and F_1 hybrids using quantitative traits: dendrogram obtained from hierarchical ascendant classification. Overlapping parts show the two varieties classified in different groups from their related F_1s.

TABLE 6. Analysis of synthetic variables obtained from the principal-component analysis of quantitative traits (axes 1–4)

	(1)			(2)	
Axis	V_{gh}	V_e	h^2	r	test
1	3.08	1.50	0.67	0.74	**
2	2.54	1.49	0.63	0.68	*
3	1.36	1.08	0.56	0.36	ns
4	1.06	0.58	0.65	−0.15	ns

NOTE: (1) Estimates of the genetic variance V_{gh}, of the error variance V_e, and of broad-sense heritability, h^2. (2) Parent–offspring regression: Pearson's correlation coefficient r and level of significance. *, Significant at $p < 0.05$; **, significant at $p < 0.01$.

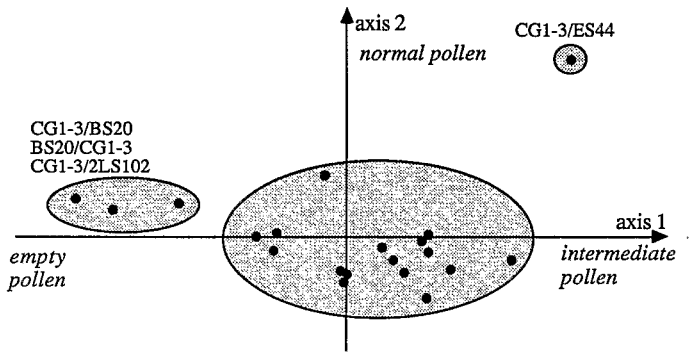

FIG. 3. Representation of F_1 hybrids on the plane defined by the first two axes of the principal-component analysis of pollen data. The interpretation of axes is indicated in italics. The groups obtained from hierarchical ascendant classification are shaded.

tioned *O. sativa* ssp. *indica* varieties and to *O. breviligulata*, some accessions of *O. rufipogon* (called *O. perennis* in the original paper).

Discrimination among F_1 combinations is possible not only through the proportion of normal pollen but also by that of intermediate pollen. If one considers that intermediate pollen reflects a more developed state than does empty pollen, BS20 and 2LS102 are the least compatible with CG1-3 of the 14 tested *O. sativa* varieties. The observation of reduced tillering of hybrids with BS20 supports the unfavourable combination of BS20 with CG1-3. Both BS20 and 2LS102 show isozymic alleles typical of the wild species *O. longistaminata*, so the presence of a genome fragment of this species is a possible explanation of our observations.

TABLE 7. Pollen fertility of parents and F_1 hybrids

	Pollen (%)		
Genotype	Normal	Intermediate	Empty
CG1-3	90	8	2
WO25	92	5	3
ES70-6	95	4	3
YS138-3	98	2	0
YS252-1	97	1	3
YS45-1	93	5	2
521	87	10	3
563	98	1	1
BS117	96	4	1
SS404	90	8	3
108	93	3	4
BS20	91	5	4
2LS102	73	25	1
CG1-3/ES70-6	0.1	27.2	72.7
ES70-6/CG1-3	0.2	25.0	74.8
CG1-3/YS138-3	0.3	39.4	60.3
CG1-3/YS252-1	0.4	37.9	61.7
CG1-3/YS45-1	0.8	39.3	59.9
YS45-1/CG1-3	0.5	43.2	56.3
563/CG1-3	0.8	47.8	51.5
CG1-3/521	0.1	34.1	65.9
521/CG1-3	0.7	39.2	60.1
CG1-3/BS117	1.1	27.2	71.7
CG1-3/BS125	0.3	26.6	73.2
CG1-3/ES44	3.2	41.1	55.7
ES44/CG1-3	0.6	40.3	59.1
CG1-3/ES79	0.1	42.9	57.0
SS404/CG1-3	0.5	36.2	63.3
CG1-3/108	0.0	35.0	65.0
108/CG1-3	0.1	34.8	65.1
CG1-3/BS20	0.0	7.7	92.3
BS20/CG1-3	0.0	11.5	88.5
CG1-3/2LS102	0.3	16.5	83.3
WO25/ES70-6	0.5	39.2	60.3
WO25/SS404	1.0	43.1	55.9
WO25/BS117	1.3	24.8	74.0
WO25/BS20	0.2	14.6	85.2

The analysis of quantitative characters shows that in this study, interspecific hybridizations do not induce abnormal or unstable plants. Overall visual impressions attest to the likeness of all hybrids to the two cultivated species; however, it is evident that the choice of the *O. sativa* parent has a direct influence on the characteristics of the F_1 hybrids. This conclusion, if it is found to apply to a larger sample of *O. glaberrima* varieties, would suggest that plant breeders, especially those in Africa, should use *O. glaberrima* in their programs.

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