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GENETIC DIVERSITY OF INDIGENOUS RICE IN AFRICA

G. BEZANCON*, J. BOZZA**, G. KOFFI** and G. SECOND**

Office de la Recherche Scientifique et Technique Outre-Mer, Abidjan, Ivory Coast

Introduction

This paper describes studies by IRAT and ORSTOM on the distribution and variability of indigenous rice in Africa, especially the annual species, *O.glaberrima* and *O.breviligulata*, and the perennial, rhizome-forming species, *O.longistaminata*.

Six of the twenty identified species of the genus *Oryza* are of African origin. These are: *O.breviligulata, O. brachyantha, O.eichingeri, O.glaberrima, O.longistaminata,* and *O.punctata*. The chromosome number, genome groupings and geographical distribution of the 20 species of the genus are shown in Table 1.

Oka and Chang (1963) did much of the early collection and assessment of African rice. They considered that the yield potential of the indigenous rices was less than that of *O.sativa* but that *O.glaberrima*, a cultivated species, was more tolerant to adverse conditions such as deep water, drought, blast and diopsids, which commonly occurred in its native habitat (Chang, 1976).

Approximately one thousand samples of *O.glaberrima* and related species have been collected by IRAT and ORSTOM in Mali, Senegal, The Gambia and other West African countries (Figure 1), and these have been grown in the Ivory Coast. The general characteristics of the species collected are:

O.glaberrima: Cultivated type, self-fertile with some cross-pollination; shedding occurs in intermediate types of *O.glaberrima* - *O.breviligulata*.

O.breviligulata: Wild type, mainly self-fertile with some cross-pollination; shedding with a strong dormancy; completes its cycle before cultivated rice; occurs among

**Institut de Recherches Agronomiques Tropicales, B.P. 635, Bouaké, Ivory Coast

TABLE 1

Oryza species: Chromosome numbers, genome groups and geographical distribution (after Chang, 1976)

Oryza species (x = 12)	2n	Genome	Distribution
O. alta	48	CCDD	Central and South America
O. australiensis	24	EE	Australia
O. barthii (*O. breviligulata*)	24	A A^g	West Africa
O. brachyantha	24	FF	West and Central Africa
O. eichingeri	24, 48	CC,BBCC	East and Central Africa
O. glaberrima	24	A^g A^g	West Africa
O. grandiglumis	48	CCDD	South America
O. granulata	24	-	South and Southeast Asia
O. latifolia	48	CCDD	Central and South America
O. longiglumis	48	-	New Guinea
O. longistaminata (*O. barthii*)	24	A^l A^l	Africa
O. meyeriana	24	-	Southeast Asia, Southern China
O. minuta	48	BBCC	Southeast Asia, New Guinea
O. nivara (*O. fatua*, *O. rufipogon*)	24	AA	South and Southeast Asia, South China, Australia
O. officinalis	24	CC	South and Southeast Asia, South China, New Guinea
O. punctata	48, 24	BBCC,BB(?)	Africa
O. ridleyi	48	-	Southeast Asia
O. rufipogon (*O. perennis*, *O. fatua*, *O. perennis* subsp. *balunga*, *O. perennis* subsp. *cubensis*)	24	A^{cu},A^{cu}	South and Southeast Asia, South China
O. sativa	24	AA	Asia
O. schlechteri	-	-	New Guinea

crops and at the edges of rice fields, sometimes in clusters with *O. longistaminata*.

O. longistaminata: Wild type; perennial via rhizomes; mainly cross-pollinated; shedding; suppression of: occurs in homogeneous populations.

O. breviligulata and *O. longistaminata* are species closely related to *O. glaberrima* and may be crossed with *O. glaberrima* and *O. sativa*.

Variability

Methodology

Intra- and inter-region variability of recent collections was examined at various levels to determine the centre of origin (i.e. centre of maximum variability) and the extent of diversity of the species. The reproductive barriers between various indigenous species were examined at autopolyploid and allopolyploid levels.

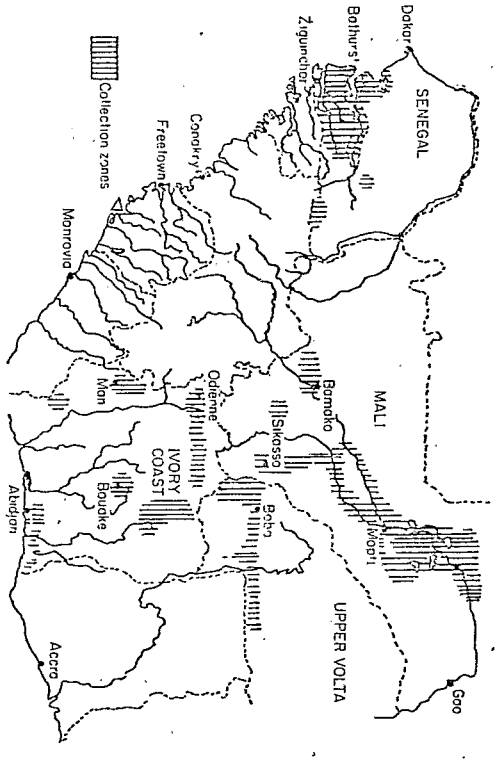

Fig. 1. Rice collection sites in West Africa, 1974-76.

Initially, the collections were grown under the same conditions and observed from early growth stage to maturity in order to define the characteristic profile of each and to assess the phenotypic variability among them. The characters were later subjected to numerical taxonomy in order to group similar samples, show the extent of genetic heterogeneity within the groups, and to demonstrate the rela-

tionships among the groups. The clustering of similar samples allowed homogeneous samples to be combined and further work was done with a smaller number of populations.

Variability was also examined by isozyme separation by electrophoresis on starch gels. The enzymes studied for *O.glaberrima, O.breviligulata, O.longistaminata* and *O.sativa* were esterases, peroxidases, acid phosphatases, malate dehydrogenases and leucine aminopeptidases. These studies gave information on variability of loci, comparative variability of populations and on the geographic distribution of the variability.

Ecology of Indigenous Rices

Genome A, which defines the *sativa* complex of *Oryza* is represented in Africa by *O.longistaminata, O.breviligulata (O.barthii), O.glaberrima* and now, *O.sativa*, the last having been introduced relatively recently. These species are compatible when crossed but there are many reproductive barriers. The distribution of the major indigenous *Oryza* species in Africa is shown in Figure 2.

O.longistaminata was found by us in diverse habitats, all of which received abundant sunshine. These included the salt lagoons of the Casamance delta, the deep waters of the

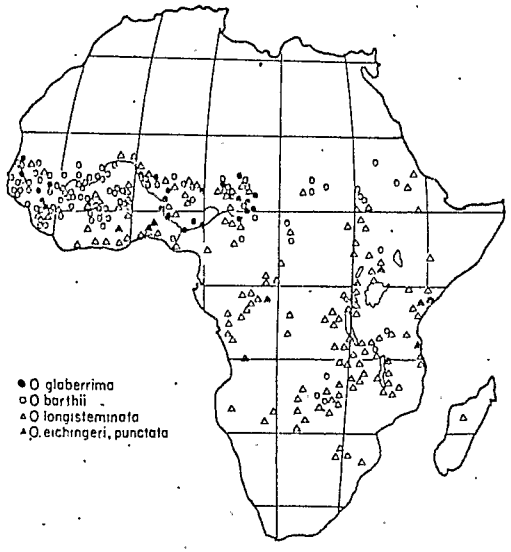

Fig. 2. Known distribution of four indigenous rice species in Africa.

Niger inland delta in Mali and the dry, sandy rice fields of Senegal. It occurred in both running and stagnant water, dry river beds and pools. It was also found in the forest zone in Cameroon.

O.breviligulata occurred in the savanna in low-lying areas subject to flooding, especially those with enriched soil due to their use as watering holes. The species produced many large seeds and strongly-bearded spikelets. A weedy type was found in cultivated rice fields in the central Niger delta.

O.longistaminata and *O.breviligulata* sometimes occurred together around water holes. In the central Niger delta, *O.breviligulata* was a weed in cultivated rice fields, but *O.longistaminata* became dominant once the field was abandoned. The former annual species had a competitive advantage in disturbed and enriched habitats.

O.glaberrima was widespread in Casamance, Senegal, where it occurred mainly as early-maturing types; floating and late types were found in Central Niger delta. It was found infrequently in The Gambia, Upper Volta and Ivory Coast.

Enzyme Variability

Enzymatic variability among *Oryza* spp. has been reported earlier by several workers (Chu, 1967; Chu and Oka, 1967; Shahi *et al.*, 1969). In this work, enzymatic variability was studied for 500 lines of *O.glaberrima* and 300 lines of *O.breviligulata*, from 280 and 105 different populations respectively from Malian and Senegambian centres and a few from Upper Volta and Ivory Coast. The variability of *O. sativa* was examined in 95 lines obtained from Ivory Coast, Mali, Senegal, and INRA, Montpellier, France (japonica types).

Five enzymatic families were examined in extracts from young or mature leaves: esterases, peroxidases, leucine aminopeptidases, acid phosphatases and malate dehydrogenases. The results have been published in more detail elsewhere (Bezancon *et al.*, 1977a, 1977b) and the interested reader is referred to this publication for detailed figures.

Esterases. The zymograms had a wide variety of enzyme forms which differed in their migration speed and their differential affinity for the α and β forms of the substrate. The analysis of the zymograms for species is given in Table 2.

The variability of *O.breviligulata* included that of *O. glaberrima*. There were many cases of coincidence among the three autogamous species but in no instance did the African and Asian lines match perfectly. *O.breviligulata* was richer individually in forms of esterases than *O.sativa*,

TABLE 2

Analysis of esterase zymograms

Species	*O.breviligulata*	*O.glaberrima*	*O.sativa*
Character			
No. visible bands			
Max.	12	10	9
Min.	9	9	7
No. variable bands (combinations)	5	2	7
Avg. no. different types on same band (presence/absence/different positions)	1.64	1.18	2.18

with *O.glaberrima* lying between the two. There was most variability in *O.sativa*, due to the loss of certain bands. Homogeneity in *O.glaberrima* is connected with this individual richness in forms of esterases, more than *O.sativa*.

Peroxidases. The conclusions were the same as for esterases, in that the variability of *O.breviligulata* was higher than that of *O.glaberrima*, which it included completely, and the Asian and African forms were not identical.

Malate dehydrogenase. Four of the 5 species studied had a single five band zymogram. *O.longistaminata*, however, had ten different zymograms with four to nine bands each.

Acid phosphatases. No variability was found in the two annual African species, which have, in common with *O.sativa*, the most frequent zymogram of the *japonica* types (Pai *et al.*, 1975). However, *O.longistaminata* was of a more variable type. The banding pattern is shown in Figure 3 as an example of the type of result obtained.

Leucine amino-peptidase. The variability of *O.sativa* included that of *O.glaberrima* and *O.breviligulata*.

Geographical Distribution of Enzyme Variability

The samples analysed have been classified in relation to the area of collection. The geographical distribution of the esterase variability in *O.breviligulata* (B) and *O.glaberrima* (G) is given in Table 3. Mali in the table is the part of Mali separate from the inland Niger delta and Northern Senegal is along the Senegal river near Richard Toll. Three types of esterases (A, B, C) were common to the two species, they are the most frequent types in *O.breviligulata*. Most of the samples of *O.breviligulata* represented the weedy form of the species. Different zymograms of A, B and C have been found in the wild populations of *O.breviligulata* in which they occurred frequently. Further analysis of wild populations of *O. breviligulata* should make it possible to determine whether this species can be divided into wild and weedy populations on the basis of enzyme variability. The B and C esterase types are clearly differentiated by area, on a similar pattern for both species. In each area the percentages of different types were similar for both species.

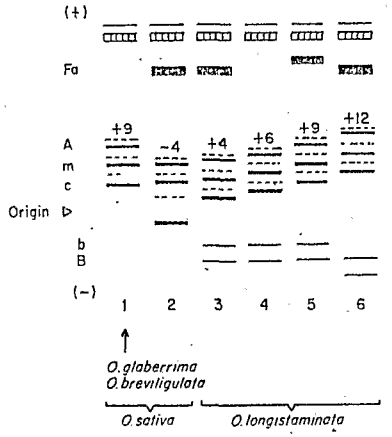

Fig. 3. Band variability observed for acid phosphatases of different rice species. (Not all the zymograms of *O.longistaminata* have been shown.)

More detailed analysis showed that the "floating" population (late, with a high number of internodes) have only the A and C types, whereas the "erect" populations (early, with fewer internodes) have the A and B types. The geographical separation of the B and C types are therefore explained by the fact that floating rice is mainly found in the Niger delta in Mali while the erect types are also grown in non-flooded areas.

In terms of the overall enzyme variability, *O.glaberrima* has maximum variability in the Niger delta area where both erect and floating types are grown. The variability of *O.breviligulata* occurs outside the Niger delta, mainly in the wild forms which are found in river beds disturbed by cattle in the savanna zone.

Zymograms of autogamous species are those most frequently found in *O.longistaminata*. However, for the highly variable enzyme (esterase) *O.longistaminata* does not include the autogamous species' variability.

TABLE 3

Percentages of A, B, and C esterase types of O.breviligulata (b) and O.glaberrima (g) from different regions

	Area species							
	Sene-Gambia		Northern Senegal	SE Senegal	Mali		Inland Niger delta	
Esterase type	b	g	b	g	b	g	b	g
A	67	80	7	45	27	27	28	28
B	33	20	-	48	73	62	7	4
C	-	-	93	8	-	10	65	68

Population Variability

The variability within populations was examined. Samples from individual populations were heterogeneous for esterases and peroxidases. Therefore one population could contain all the variability possible within the species. There was a trend towards homogeneity in the populations compared with interpopulation variability. Heterogeneity was higher for *O.breviligulata* than *O.glaberrima*. However, individual plants and their progeny were homogeneous in their enzymatic patterns.

Enzymatic variation in *O.longistaminata* from Mali and Senegal was compared to that of *O.perennis*, a related Asian species. There was much greater variation in *O. longistaminata* than in *O.perennis, O.breviligulata* or *O. glaberrima* for esterases, peroxidases, malate dehydrogenase and acid phosphatases.

The high enzymatic variability of the allogamous groups of *O.longistaminata* compared to the autogamous Asian and African rices is associated with the greater tolerance of the species to environmental stress. For example, seeds vary in their heat sensitivity, providing sufficient variation within the population to allow some seeds to develop at extreme temperatures which are unsuitable for the autogamous species.

The adaptability of *O.longistaminata* to its environment is both spatial and temporal, in that it can also adapt to various pressures which appear during its evolution. The theory of fitness in a structured environment (Levins, 1965) explains this heterozygosis in a heterogeneous environment. An allele may be dominant in a population while at the same time allowing a great deal of variation around the optimum.

There are reproductive barriers between the autogamous and the allogamous types of *O.longistaminata*. These allow *O.breviligulata* to invade certain habitats that have been

invaded and enriched by animals and at the same time maintain occasional interchanges with *O.longistaminata*.

These reproductive barriers may be regarded as filters of genetic flow selected at an adjusted level by the species (Pernes *et al.*, 1975). The homozygosity of the autogamous groups makes them retain out of the total variability only those variations strictly suited to their habitat. Hence the convergence of the variability of the African and Asian autogamous groups. The convergence increases during domestication when the species acquire stricter autogamy, which is linked to a man-controlled environment. The acquired autogamy and domestication also result in reduced enzyme variability.

The simplification of zymograms is more marked as one moves towards more developed cultivated types. Thus *O. sativa* has lost some bands relative to *O.glaberrima*. The differentiation of ecotypes may cause the loss of certain isozymes. It is also possible that there is a relationship between the adaptability of a line and the number of enzymes it contains.

The genetic pool of *Oryza* genome A in Africa can be considered to be of two types according to the definitions of Pernes *et al.* (1975). These are:

a) *Reservoir compartment: O.longistaminata:* The perennial habit and self-incompatability which are linked with vegetative reproduction allow it to carry a heavy genetic load (alleles that are silent or have little adaptation in the present environment). High heterozygosis preserves many other variants besides the best adapted dominant allele which is often retained in the autogamous section. This variability enables it to survive in an area in which there are some slow environmental variations but it develops best in an area free of abrupt changes.

b) *Colonization compartment:* The acquired autogamy leads to a lower variability suited to a particular environment. The reduced genetic load gives a high reproductive potential which enables them to spread rapidly in a scattered migrant habitat with differentiation into ecotypes. Many recessive alleles are fixed, which results in poorer enzyme resources, enzymatic degeneration and reproductive barriers caused by the formation of pairs of complementary lethal genes.

In Africa, a "filter of gene flow" has apparently developed which has preserved high heterozygosity in the allogamous pool, allowing substantial storage of allelic variability. It also operates by restriction of *O.longistaminata* from the localized ecological site of *O.breviligulata*.

The two sections form two largely independent entities that are nevertheless connected, and they represent the

overall pool of variability of native African types.

By studying populations where the two species exist side by side it will be possible not only to sample their respective variability but also to gain a better understanding of possible introgressions. However, to collect maximum allelic variability, it is preferable to use the large populations of *O. longistaminata* which retain maximum heterozygosity.

From the wild pools one may repeat the process of domestication to obtain transgressions for new ecological areas that can be cultivated. It also may be possible to introduce new characters into cultivated varieties, such as self-incompatibility.

Study of Variability by Factor Analysis of Correspondences

Correspondence analysis was used to study variability within *O. glaberrima* and *O. breviligulata*, since no *a priori* hypothesis is introduced on the characters or the samples, and it enables them to be projected simultaneously on two planes. The dispersion of these projections on the most discriminant planes makes it possible to assess and compare the variability of each group of individuals.

A total of 858 individuals were examined, collected in the inland Niger delta, central, southern and south-eastern Mali, eastern Senegal and Casamance.

Forty-nine characters were observed at various growth stages and thirty-two of these were retained for the analysis. Two different sets of planes I-II and I-III were used for interpretation (Figures 4 and 5).

Results

The following variability in agronomic characters was observed:

Plant height	69-235 cm (avg. 148 cm)
No. shoots	4-100 (20-48 with 2 modes)
No. panicles at flowering	4-75 per plant (23-28 with 2 modes)
Avg. no. nodes per stalk	4-14 (4.8-10 with 2 modes)
Avg. panicle length	13-34 cm (avg. 25.3 cm)
Length of cycle, planting to maturity	90-210 days (avg. short cycle, 120 days; photoperiod-sensitive types during short days, 140 days)
Lodging	307 lodged; 551 not-lodged
Shedding	482 shedding; 476 non-shedding

In general, the observations of two modes corresponded to erect and floating ecotypes.

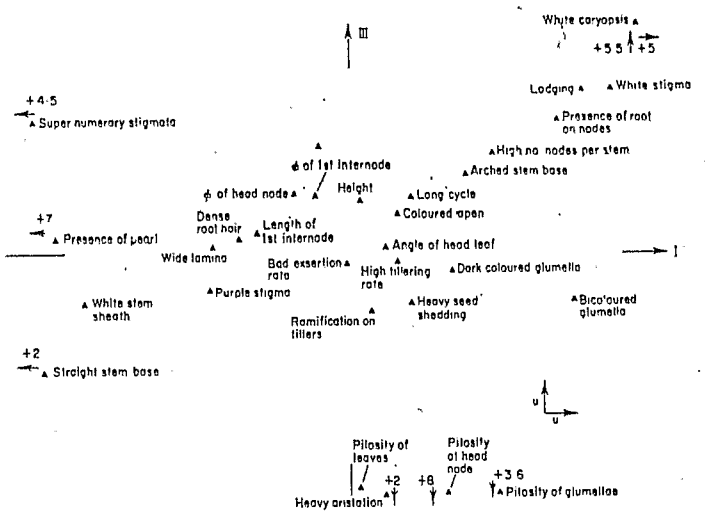

Fig. 4. Characters used in factor analysis by correspondences and their projection on axes I-III.

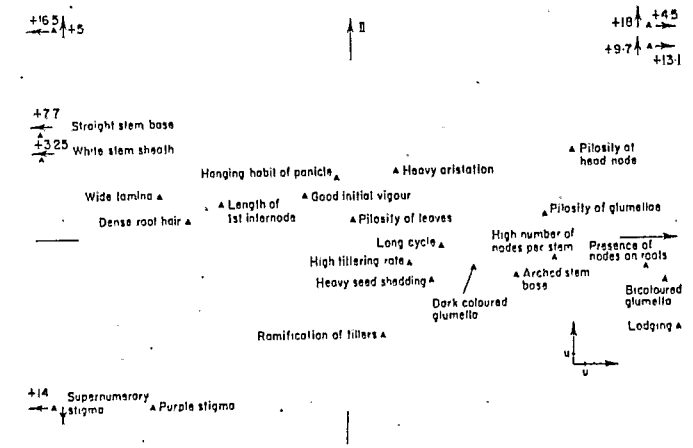

Fig. 5. Characters used in factor analysis by correspondences and their projection on axes I-II.

Dispersion of the characters

O.glaberrima is much more variable than *O.breviligulata* whose variability is contained completely within that of *O.glaberrima* (Figure 6). Most of the *O.breviligulata* samples appear to be weedy forms which are very similar to the cultivated species. However, some characters, such as aristation, and leaf pilosity are discriminatory.

The characters of roots on nodes, number of nodes, lodging, seed shedding, coloured stem sheath and ramified stems describe the floating habit, whereas the converse forms describe the erect type. Floating-late and erect-early types were observed in all regions surveyed.

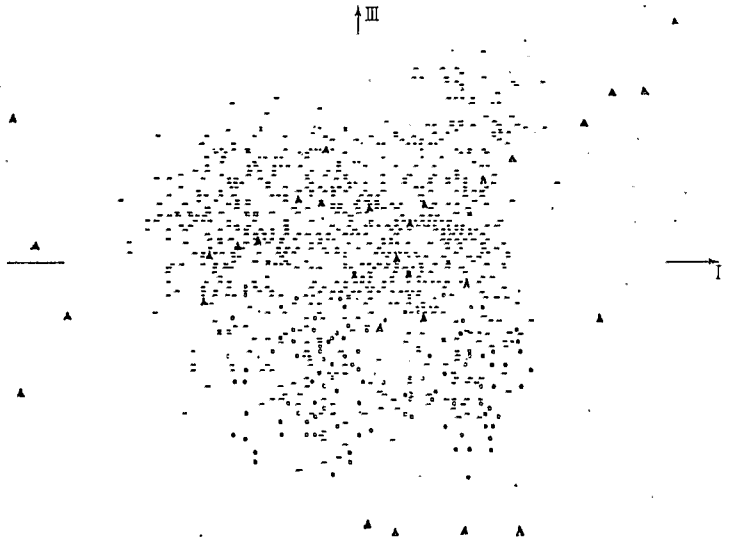

Fig. 6. Comparison of samples of *O.glaberrima* (-) and *O.breviligulata* (o), with character sites (Δ) plotted on axes I-III.

Characters that are unsuitable for cropping such as lodging, arched stem bases, ramified stems and seed-shedding were present on many floating types collected from the inland Niger delta. Converse characters were common in samples from Casamance where there exists a long tradition of rice cultivation with more advanced cultural practices.

An analysis by regions (diagrams not presented) showed that east Senegal has the least variability for *O. glaberrima*. The inland Niger delta where all the inter-

mediate forms between wild and cultivated types occur, has the maximum variability for this species. In the central area of Senegal there is a wide range of cultivated types, ranging from non-flooded to floating types (Figure 7). In each region, *O.breviligulata* covered only a small portion of the variability of *O.glaberrima*. In the plane I-II, the specific characters of *O.breviligulata* were much less discriminant than in the plane I-III, giving a variability for the wild species comparable to that of the cultivated. In a region by region analysis, this is not so apparent. The widest range of variability of the delta area is on axis II, whereas the dispersion of the southern and central area is at its highest on axis I. Rice in Casamance is most affected by domestication.

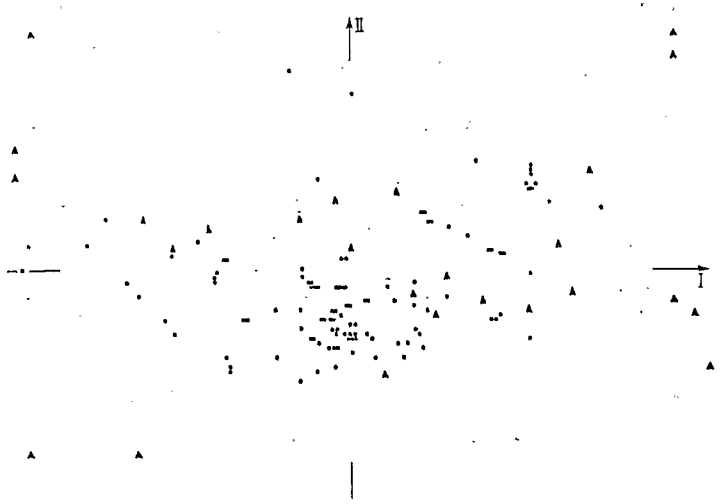

Fig. 7. Variability of *O.glaberrima* (o) and *O.breviligulata* (-) samples from central Mali, with character sites (Δ) plotted on axes I-II.

Practical Application of Variability

The aims of an improvement programme involving indigenous rices are to use *O.glaberrima* in association with *O.sativa* and to improve *O.glaberrima* itself, relative to *O.sativa*.

In using *O.glaberrima* in association with *O.sativa*, the beneficial characters of either parent could be incorporated with appropriate back-crossing to avoid loss of desirable characters. Alternatively, a new species could

be created by tetraploidy. *O.glaberrima* is favoured by some West African farmers because of its adaptation to the area and also because of its cooking qualities. Hence, varietal improvement of this species alone, as has been done for *O.sativa*, might be useful.

In hybridization between *O.sativa* and *O.glaberrima*, a high proportion of sterility among the progeny occur. Jacquot (pers. comm.) reported high sterility in F_1 populations irrespective of the direction of crossing. In F_2, fertility varied and in F_4, it varied within the lines, but breeding for fertility was positive. Diallel crosses should enable compatible and incompatible genome structures to be identified.

Conclusion

Extensive investigations in Mali and Sene-Gambia during 1974-1976 showed that:

1. There are two forms of *O.breviligulata*, a relatively rare wild type, and a frequently-encountered weedy type. Homologous variation was observed in weedy *O.breviligulata* and *O.glaberrima* in terms of their geographical distribution and their division into two ecotypes, erect and floating.
2. The enzymatic variability was higher in *O.breviligulata* than in *O.glaberrima* and it included the latter.
3. The allogamous species *O.longistaminata* showed high enzymatic variability. Autogamous African and Asian species showed a lower and converging variability.
4. There is a maximum genetic variability in *O.longistaminata*, which is a large and polymorphous population. Some populations of this species should be collected, sampled with precision and exploited as much as possible.
5. The variability of the African autogamous species, *O.breviligulata* (wild and weedy types), *O.glaberrima* and *O.sativa* is geographically scattered. Sampling should be done throughout their areas of distribution. In particular, *O.glaberrima* should be collected where it has resisted introduction of *O.sativa*. The wild form of *O.breviligulata* should be collected outside the areas of cultivation of *O.glaberrima*.

It is considered that the range of genetic diversity in indigenous African rices and the ability of these species to withstand stresses commonly encountered in their environment offer considerable potential for their use in varietal improvement programmes for both *O.sativa* and *O. glaberrima*.

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COLLECTION AND CONSERVATION OF EXISTING RICE SPECIES AND VARIETIES OF AFRICA

S.D. SHARMA and W.M. STEELE

International Institute of Tropical Agriculture, PMB 5320, Ibadan, Nigeria

African rice, *O. glaberrima*, was domesticated in parts of West Africa about 3,500 years ago (Portères, 1956). Its origin was independent of Asian rice and it was domesticated from a different wild progenitor, *O. barthii* (syn. *O. breviligulata*). Today, intergrades between these two species are found and are known as weed forms of *O. barthii* (Bezancon *et al.*, 1977a, 1977b) or as '*stapfii*' forms (Chang, 1976). They are basically hybrids of different degrees and are not a species. In addition to these species endemic to Africa, are other indigenous species, the most closely related of which is *O. longistaminata*, a perennial rhizomatous species of wider distribution (Fig.1).

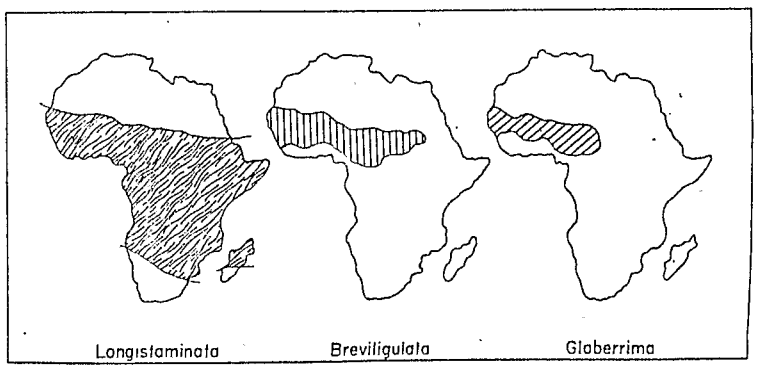

Fig. 1. Distribution of *O. longistaminata*, *O. breviligulata* and *O. glaberrima* in Africa.