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Isozymic variability of traditional rice (*Oryza sativa* L.) in Africa

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Summary. Eight hundred and thirtyone traditional varieties of rice, *Oryza sativa* L., were collected in Africa and analysed for their isozymic variability on 15 enzymatic systems, representing 37 presumed loci. There appears to be a correlation between the type of rice growing and the two groups Indica and Japonica. The degree of genetic diversity is nearly equal in African rice and the Asian one. Alleles due to introgression or mutational events were identified. The results suggest that the evolution of *O. sativa* is continuous in Africa by means of inter-subspecific or inter-specific crosses.

Introduction

Although its origin is not African, the Asian cultivated species *Oryza sativa* L. is now very widely distributed over this continent. It is the only cultivated rice species in East Africa and is gradually replacing *Oryza glaberrima* Steud., the native cultivated species, in West Africa.

Very little work has been done on this material as it has been considered a reflection of the situation encountered in Asia. Nevertheless, considering the time since its introduction and the special conditions existing in this new environment, it would be interesting to consider these traditional varieties as tools for plant breeders. It is then necessary to evaluate the genetic potential of this crop present on this continent.

Isozyme electrophoresis has been chosen because it allows the study of a great number of genetic markers, independantly of the environmental conditions, on a large collection of cultivars. This technique has been widely employed for rice (Pai et al. 1973; Fu and Pai 1979; Nakagahra 1977; Glazsmann 1982; Second 1982, 1984).

In the present work, 831 traditional cultivars originating from 12 African countries were analysed for 15 enzymatic systems representing 37 presumed loci. The phenol reaction that permits a good estimation between the two types Indica and Japonica (Oka 1958) was observed, as well as the allelic association at four loci which defines "ancestral" and intermediate types between Indica and Japonica as described by Second (1982).

Materials and methods

Vegetal material

All samples analysed are from the Orstom collection conserved in the Ivory Coast. Table 1 summarizes the number and origins of the varieties. Twelve countries from all over the continent are represented but not equally because of the number of varieties available in the collection. All types of rice growing methods and ecological environments are also represented.

The plants were grown in the greenhouse or in the field. According to the enzymatic system, the white or green part of a young leaf or flag leaf was used for the extraction.

Electrophoresis

The list of the enzymatic systems analysed by starch electrophoresis is shown in Table 2. For 13 systems, the extraction, migration and staining was made as described in Second and Trouslot (1980). The endopeptidase (EP) was studied by a technique adapted from Cardy et al. (1982); for shikimate dehydrogenase (SDH) the staining procedure was adapted from Weeden and Gottlieb (cited by Tanksley and Rick 1980).

Phenol reaction

The grain is soaked in 2% phenol solution for 48 h and then dried. The change of color of the hull is observed by comparison with a grain soaked in distilled water for the

Table 1. Origin of the analysed varieties and collecting institutes. IRAT: Institut de Recherche en Agronomie Tropicale, (Montpellier) France; IDESSA: Institut des Savanes, (Bouaké) Ivory Coast; FOFIFA: Foibe Fikaromana Fambolena, (Antananarivo) Madagascar; IRRI: International Rice Research Institute, (Los Baños) Philippines; IITA: International Institute of Tropical Agriculture, (Ibadan) Nigeria

Country	No. of samples	Collecting institute	Rice fields type
Ivory Coast	188	ORSTOM	Upland
Guinea Conakry	240	ORSTOM IRAT IDESSA	Irrigated Upland
Madagascar	228	ORSTOM IRRI FOFIFA	Irrigated Upland
Tanzania	90	ORSTOM IRAT	Irrigated Upland
Zambia	17	ORSTOM IRAT	Irrigated
Guinea Bissau	21	ORSTOM IRAT	Irrigated Upland
Cameroon (North) Tchad (South) Nigeria	24	ORSTOM IRAT IITA	Irrigated (Upland)
Burkina Faso Mali Niger	23	ORSTOM IRAT	Irrigated

same length of time. No change of color is noted as a negative reaction; a darkening of the hull is considered as a positive reaction (Oka 1958).

Allelic association at four loci

Second (1982) mentioned a relation between allelic associations at the four loci EST.E, PGI.A, B, and CAT.A and the percent of sterile pollen of the F1 hybrids studied by Oka (1958). Three associations are called "ancestral" on the basis of the high level of pollen sterility in the F1 of crosses between varieties showing these associations. All other associations correspond to theoretical hybridization between ancestral ones. If a score is given to the present alleles, -1 is given to ancestral Japonica and $+1$ to ancestral Indica. According to the allelic classification given by Second (1984), the same three associations have the greatest ancestral allele score that can be obtained.

Results

Electrophoretic patterns

Except for the endopeptidase and the shikimate dehydrogenase, all the zymograms and the interpretations of the genetic determinism are given in Second and Trouslot (1980).

The endopeptidase shows three zymograms (Fig. 1a), the interpretation calls for a single gene with three alleles.

The shikimate dehydrogenase presents three patterns (Fig. 1b) – one gene with three allelic forms may explain this result.

Table 2. Enzymatic systems analysed

| Enzyme	Abbreviation	Reference
Oxydo-reductase:		
Peroxidase	POX	Second and Trouslot (1980)
Catalase	CAT	Second and Trouslot (1980)
Alcohol dehydrogenase	ADH	Second and Trouslot (1980)
Glutamate dehydrogenase	GDH	Second and Trouslot (1980)
Malate dehydrogenase	MDH	Second and Trouslot (1980)
Isocitrate dehydrogenase	ICD	Second and Trouslot (1980)
Phosphogluconate dehydrogenase	PGD	Second and Trouslot (1980)
Shikimate dehydrogenase	SDH	Weeden and Gottlieb
Transferase:		
Glutamateoxaloacetate transaminase	GOT	Second and Trouslot (1980)
Phosphoglucomutase	PGM	Second and Trouslot (1980)
Isomerase:		
Phosphoglucose isomerase	PGI	Second and Trouslot (1980)
Hydrolase:		
Esterase	EST	Second and Trouslot (1980)
Leucine aminopeptidase	LAP	Second and Trouslot (1980)
Acid phosphatase	ACP	Second and Trouslot (1980)
Endopeptidase	EP	Cardy et al. (1982)
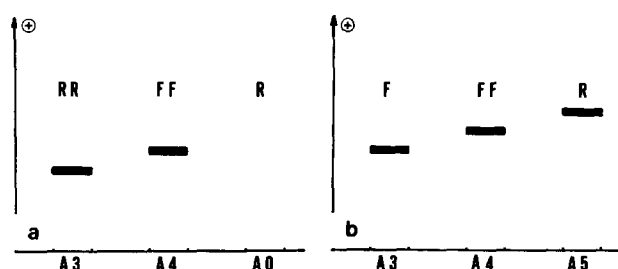
Fig. 1. a Endopeptidase zymograms. R = rare; RR = very rare; FF = very frequent. b Shikimate dehydrogenase zymograms. F = frequent; FF = very frequent; R = rare

Table 3. Phenol reaction frequencies of *O. sativa* in Africa. RCI: Ivory Coast; GUI: Guinea; MAD: Madagascar; TAN: Tanzania; ZAM: Zambia; GBI: Guinea Bissau; CTN: Cameroon, Tchad, Nigeria; BMN: Burkina Faso, Mali, Niger

	RCI	GUI	MAD	TAN	ZAM	GBI	CTN	BMN
Positive reaction	0	0.83	0.54	0.89	0.94	0.67	0.92	1
Negative reaction	1	0.17	0.46	0.11	0.06	0.33	0.08	0

Table 4. Relationship between the phenol reaction and the alleles at the ACP.Amc locus. Number of varieties showing a type of reaction and the allele they possess

	Phenol −	Phenol +
ACP.Amc +9	345	4
ACP.Amc −4	9	473

Phenol reaction

Table 3 summarizes the results obtained. In the Ivory Coast all the varieties analysed are phenol negative; in this country upland rice is the only one way of traditional culture. In Guinea, where the majority of rice fields are of the aquatic type (Bezancon et al. 1983), the vast majority are phenol positive cultivars (83%). In Madagascar, the cultivation of rice is very diversified (de Kochko 1985) and the two types of reaction are nearly equal. In Tanzania, the majority of the phenol negative varieties originate from the islands (Zanzibar and Pemba), however, throughout the entire country there is a predominance of samples showing a positive reaction. Zambia is entirely represented by phenol positive varieties. Guinea Bissau, where various types of rice culture are practised, contains mainly phenol positive cultivars (67%) but the proportion of phenol negative ones is numerically important (33%). Sahelian countries, where only irrigated culture is done, show a high percentage of phenol positive reaction.

Except for the Ivory Coast, traditional varieties of *O. sativa* are mainly phenol positive, i.e. they are predominantly of the Indica type.

The correlation between the phenol reaction and the alleles at the ACP.Amc locus has been pointed out by Shahi et al. (1969), Fu and Pai (1979). Inouye and Hagiwara (1980) for Asian rices. The present situation is quite similar as is shown by the association of the alleles ACP.Amc +9 and −4 and the negative and positive reaction, respectively (Table 4).

Allelic association at four loci

Of the 24 possible associations (3*2*2*2), considering the most frequent alleles at each locus, only 12 were observed (Table 5). Among these associations only two, called intermediate, show indiscriminantly the two types of phenol reaction.

As shown in Table 6, it appears that a large majority are of the "hybrid" and intermediate forms (87%); ancestral associations of Indica and Japonica are rare (5 and 8%, respectively). In Asia, ancestral associations are much more frequent (39 and 21%, respectively, Second 1982).

The situation of each country is quite different. The Ivory Coast contains a great proportion of "hybrid" Japonica associations and only some Indica forms (hybrid or ancestral), what is in good agreement with the phenol reaction. Guinea is much more diversified, each association found in Africa is represented. Nearly half of the varieties from Madagascar have only 2 associations (3 and 6); ancestral Indica associations are very rare (< 1%), some associations are absent (5, 7, 9, 12).

Rice varieties from Tanzania are distributed in nearly all the associations found in the whole continent. Only one, number 6, is absent. Ancestral Indica associations are numerous (31%).

In Sahelian regions, Japonica associations, ancestral and hybrid, are very rare or absent. This result is also in good agrement with the phenol reaction.

Only a very few varieties have a phenol reaction inverse of the expected one (< 2%).

Allelic distribution

Of the 37 loci studied, 77 alleles were identified, some of which are very rare (POX.C0-C3-C4-C5; POX.D2; LAP.E0; GOT.A2; GOT.B0; GOT.C2; PGI.B3–B4; ICD.A2; ADH.A2; MDH.A0; EP.A3). Among them, some had never previously been observed in Asia in *O. sativa* (POX.C0-C4-C5; LAP.E0; MDH.A0) (Second 1984; Glazsmann et al. 1984; Glazsmann pers. commun). Each of these three alleles was found in only one variety.

With the exception of the Ivory Coast, nearly all the standard alleles of *O. sativa* are present everywhere in Africa (Table 7). The Ivory Coast lacks many of the

Table 5. Allelic associations at the four loci EST.E, PGI.A–B, and CAT.A

Association No.	Association name	Allele				Allele score	Phenol reaction
		EST.E	CAT.A	PGI.A	PGI.B		
1	Ancestral Japonica	0	2	2	1	−4	−
2	Hybrid Japonica	1	2	2	1	−2	−
3	Hybrid Japonica	0	1	2	1	−2	−
4	Intermediate	1	1	2	1	0	− or +
5	Intermediate	2	1	2	1	0	+ or −
6	Hybrid Indica	0	1	1	1	0	+
7	Hybrid Indica	1	1	2	2	+2	+
8	Hybrid Indica	1	1	1	1	+2	+
9	Hybrid Indica	2	1	2	2	+2	+
10	Hybrid Indica	2	1	1	1	+2	+
11	Ancestral Indica	1	1	1	2	+4	+
12	Ancestral Indica	2	1	1	2	+4	+

Table 6. Distribution of the genetic structures defined by the four loci EST.E, CAT.A, PGI.A and B in Africa. Other structures have the rare alleles at the PGI.B locus or the phenol reaction is not the one expected

Allelic association	RCI	GUI	MAD	TAN	ZAM	GBI	CTN	BMN	TOT
1	21	1	13	7	−	−	−	−	42
2	45	14	2	1	−	1	−	−	63
3	102	12	56	2	−	2	2	−	176
4	19	17	36	5	3	3	8	3	94
5	−	44	−	11	−	2	1	6	64
6	−	20	60	−	1	1	1	2	85
7	−	1	−	10	1	−	−	−	12
8	−	18	30	14	4	2	−	2	70
9	−	3	−	1	−	1	3	−	8
10	−	77	29	11	−	6	8	8	139
11	−	2	1	19	6	−	−	−	28
12	−	26	−	9	1	1	1	−	38
Others	1	5	1	−	1	2	−	2	12
Total	188	240	228	90	17	21	24	23	831

Indica ancestral alleles. Zambia seems not to contain some ancestral Japonica alleles (EST.D0; CAT.A2; PAC.Amc +9 . . .) but this might be due to the sample size (17).

In Burkina Faso, Mali, and Niger, the ancestral Japonica alleles are also frequently absent (EST.I2; EST.J1; CAT.A2 . . .).

Some alleles characteristic of African wild species *O. longistaminata* or *O. breviligulata* are found in a few varieties (PGI.B3–B4; GOT.A2; GOT.C2; ADH.A2).

Looking at the allelic frequencies calculated on the basis of the number of varieties analysed, there appears to be a discrepancy according to the origin of the varieties (Table 8). Thus the EST.D0 allele, not very frequent throughout the major part of the continent (f=0.16), is predominant in the Ivory Coast (f=0.71). In the same way, EST.E0 is to be found very frequently only in the Ivory Coast and Madagascar (f=0.66 and 0.57, respectively); in the other regions it is more rare (f< 0.17). This is also the case for POX.B4 which is the

Table 7. Alleles present in Africa. ?: when the EST.F2 band is present it is often difficult to determine the nature of the EST.H band. * other(s) rare allele(s)

Locus	RCI	GUI	MAD	TAN	ZAM	GBI	CTN	BMN
EST.Ca	2	1–2	1–2	1–2	1–2	1–2	1–2	1–2
EST.B	1	0–1	0–1	0–1	0–1	0–1	1	0–1
EST.C	0	0–2	0–2	0–2	0–2	0–2	0–2	0–2
EST.D	0–1	0–1	0–1	0–1	0–1	0–1	0–1	0–1
EST.E	0–1	0–1–2	0–1–2	0–1–2	0–1–2	0–1–2	0–1–2	0–1–2
EST.F	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2
EST.G	0–1	0–1	0–1	0–1	0–1	0–1	0–1	0–1
EST.H	?–1	?–1	?–1	?–1	?–1	?–1	?–1	?–1
EST.I	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0
EST.J	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1–2
POX.A	1	1	1	1	1	1	1	1
POX.B	3	3–4	3–4	3–4	3–4	3–4	3–4	3–4
POX.C	1–2	1–2–3	1–3–*	1–2	1	1–2	1–2	1–2
POX.D	1	1–2	1	1	1	1	1	1
POX.E	2	2	2	2	2	2	2	2
LAP.E.	1–3	0–1–2–3	1–2	1–2–3	1–2–3	1–2	1–2–3	1–2–3
GOT.A	1–2	1–2	1	1	1	1	1	1
GOT.B	0–1	0–1	0–1	1	1	1	1	1
GOT.C	1	1–2	1	1	1	1–2	1	1
PGI.A	2	1–2	1–2	1–2	1–2	1–2	1–2	1–2
PGI.B	1	1–2–*	1–2	1–2	1–2–*	1–2–*	1–2	1–2
PGD.A	1–3	1–2–3	1–2–3	1–2–3	1–3	1–2–3	1–2–3	1–2–3
PGD.B	1	1	1	1	1	1	1	1
PGM.A	1	1	1	1	1	1	1	1
CAT.A	1–2	1–2	1–2	1–2	1	1–2	1	1
ICD.A	1–2	1	1	1	1	1	1	1
ADH.A	1–2	1–2	1	1	1	1–2	1	1
MDH.A	1	1	0–1	1	1	1	1	1
MDH.B	1	1	1	1	1	1	1	1
MDH.C	1	1	1	1	1	1	1	1
GDH.A	1	1	1	1	1	1	1	1
GDH.B	1	1	1	1	1	1	1	1
SDH.A	3–4	3–4–5	3–4	3–4	3–4	3–4–5	3–4–5	3–4
EP.A	4	0–4	0–3–4	0–4	0–4	0–4	0–4	0–4
ACP.Amc	+9	+9/ −4	+9/ −4	+9/ −4	−4	+9/ −4	+9/ −4	−4
ACP.Fa	0	0/ +	0/ +	0/ +	+	0/ +	0/ +	0/ +
ACP.E	1	1	1	1	1	1	1	1

most common allele in general (f=0.65) except in the Ivory Coast, where it is absent, and in Madagascar, where it is rare (f=0.04).

PGI.B2 was found frequently in Tanzania and Zambia, but only one variety from Madagascar shows this allele.

Genetic diversity

Genetic diversity has been calculated using the heterozygosity index of Nei (1975) on 37 loci in association with other parameters of diversity, number of alleles per locus, number of polymorphic loci, etc. (Table 9).

Table 8. Allelic frequencies at the most polymorphic loci

Allele	RCI	GUI	MAD	TAN	ZAM	GBI	CTN	BMN
EST.Ca1	0	0.68	0.46	0.86	0.94	0.48	0.92	0.65
EST.Ca2	1	0.32	0.54	0.14	0.06	0.52	0.08	0.35
EST.C0	1	0.42	0.68	0.71	0.18	0.62	0.21	0.39
EST.C2	0	0.58	0.32	0.29	0.82	0.38	0.79	0.61
EST.D0	0.71	0.17	0.19	0.12	0	0.10	0.08	0.09
EST.D1	0.29	0.83	0.81	0.88	1	0.90	0.92	0.91
EST.E0	0.66	0.10	0.57	0.10	0.06	0.14	0.13	0.13
EST.E1	0.34	0.27	0.30	0.57	0.82	0.38	0.33	0.22
EST.E2	0	0.63	0.13	0.33	0.12	0.48	0.54	0.65
POX.B3	1	0.43	0.96	0.63	0.12	0.33	0.25	0.22
POX.B4	0	0.57	0.04	0.37	0.88	0.67	0.75	0.78
POX.C1	0.91	0.99	0.97	0.91	1	0.95	0.92	0.96
POX.C2	0.09	0.01	0	0.09	0	0.05	0.08	0.04
OTHERS	0	<0.01	0.03	0	0	0	0	0
LAP.E0	0	<0.01	0	0	0	0	0	0
LAP.E1	1	0.96	0.57	0.86	0.59	0.95	0.58	0.78
LAP.E2	0	0.03	0.43	0.13	0.35	0.05	0.33	0.13
LAP.E3	0	0.01	0	0.01	0.06	0	0.08	0.09
PGI.A1	0	0.57	0.47	0.61	0.76	0.48	0.42	0.43
PGI.A2	1	0.43	0.53	0.39	0.24	0.52	0.58	0.57
PGI.B1	>0.99	0.86	>0.99	0.54	0.47	0.81	0.88	1
PGI.B2	0	0.14	<0.01	0.46	0.47	0.10	0.12	0
OTHERS	<0.01	<0.01	0	0	0.06	0.10	0	0
PGD.A1	0.80	0.58	0.68	0.59	0.82	0.38	0.67	0.65
PGD.A2	0	0.04	0.19	0.02	0	0.10	0.17	0.04
PGD.A3	0.20	0.38	0.13	0.39	0.18	0.52	0.17	0.30
CAT.A1	0.65	0.91	0.93	0.91	1	0.95	1	1
CAT.A2	0.35	0.09	0.07	0.09	0	0.05	0	0
ACP.Amc+9	1	0.17	0.45	0.13	0	0.24	0.08	0
ACP.Amc−4	0	0.83	0.55	0.87	1	0.76	0.92	1
ACP.Fa0	1	0.19	0.45	0.12	0	0.24	0.08	0
ACP.Fa+	0	0.81	0.55	0.88	1	0.76	0.92	1
SDH.A3	<0.01	0.56	0.13	0.24	0.41	0.57	0.38	0.84
SDH.A4	>0.99	0.41	0.87	0.76	0.59	0.38	0.58	0.16
SDH.A5	0	0.03	0	0	0	0.05	0.04	0

The Ivory Coast's genetic diversity occupies a particular situation with an average heterozygosity of $H = 0.05$: this demonstrates a low polymorphism of the traditional varieties. Zambia, with an average heterozygosity of $H = 0.12$, also contains varieties weakly polymorphic. Tanzania, Madagascar and Guinea Bissau have the most diversified varieties with $H = 0.21$–0.20–0.20, respectively. The other countries occupy an intermediate position.

In total, there is an average number of 2.1 alleles per locus. The average heterozygosity is $H = 0.22$, which is similar to the result found by Second (1982) who surveyed 40 presumed loci on a mondial sample with $H = 0.23$.

Among the 37 loci 28 are polymorphic (76%) with 68 alleles.

Table 9. Value of genetic diversity for *O. sativa* in Africa. NLA: number of loci analysed; NAO: number of allele observed at each locus; AAL: average number of alleles per locus; AHAL: average heterozygosity for all the loci; NPL: number of polymorphic loci; NAP: number of alleles at the polymorphic loci; AAPL: average number of alleles per polymorphic locus; AHPL: average heterozygosity for the the polymorphic loci

Country	NLA	NAO	AAL	AHAL	NPL	NAP	AAPL	AHPL
RCI	37	54	1.5	0.05	17	34	2	0.12
Guinea	37	71	1.9	0.16	27	62	2.30	0.22
Madaga	37	66	1.8	0.20	23	52	2.26	0.32
Tanza	37	61	1.6	0.19	21	45	2.19	0.34
Zambia	37	56	1.5	0.12	16	35	2.19	0.29
Gu.Bis	37	65	1.8	0.20	24	52	2.17	0.31
Ca.T.Na	37	60	1.6	0.15	19	42	2.21	0.28
BF.M.Nr	37	57	1.5	0.15	16	36	2.25	0.35
Total	37	77	2.1	0.22	28	68	2.43	0.30

Conclusion and discussion

The phenol reaction seems to be a good criterion of classification for traditional African varieties. The relation between this reaction and the type of rice growing method appears to be close: upland varieties are in a large majority phenol negative and irrigated ones are predominantly phenol positive. This reaction is also correlated with the allelic association at the four loci EST.E; PGI.A–B; CAT.A.

The allelic associations at the four loci show a few ancestral forms but a great number of "hybrid" and intermediate ones. The varieties of the Japonica type (ancestral and "hybrid") are found in the tropical humid regions of West Africa, Ivory Coast, Guinea, Guinea Bissau and in the islands of Zanzibar, Pemba and Madagascar. The Indica type varieties are spread all over the continent except in the Ivory Coast where traditional rice culture is exclusively of an upland type. Environmental conditions seem to maintain diversification in the two types of Indica and Japonica, although not in ancestral allelic associations. The collected varieties are representative enough of African traditional rice, overall for the Ivory Coast, Guinea, Madagascar and Tanzania, to discard a sample effect in the frequency distribution of the allelic associations.

The introduction of *O. sativa* into Africa did not involve a loss of genetic diversity; all the standard alleles present in Asia could be identified and new ones descended from introgressions derived from endemic species (*O. longistaminata, O. breviligulata, O. glaberrima*) or from mutational events were observed.

In few regions the coexistence of the two types of Japonica and Indica has caused an intermingling of the genetic materi-al, which can explain the high level of diversity and the abundance of "hybrid" associations. However, environmental conditions seem to maintain the diversification at a continental scale by favoring one type over the other. Such an effect of the environment on the genotype has already been described in Asia (Nagamatsu and Omura 1960; Oka 1964).

Furthermore, natural hybridizations might have a mutational effect. It is in the regions where various types are observed that the rare nul electromorphs are found in intermediate varieties between Indica and Japonica. Such events have been observed in regions of contact between different species or semispecies, where individuals were found carrying rare alleles either alien to parental populations or found much more frequently than in the parental populations (Hunt and Selander 1973; Sage and Selander 1979).

A strong correlation has been demonstrated between the heterozygosity of common alleles and the number of rare alleles in species of *Drosophila* (Koehn and Eanes 1976).

According to the hypothesis of Second (1982) the two types of Indica and Japonica issue from two different centers of domestication and, therefore, they can be considered as two semispecies. Introgression between them could be due to relaxed selective barriers for the incorporation of new alleles (Hunt and Selander 1973) and the minor alleles could be favored in the new genetic environment (Stebbins 1971). The high level of heterozygosity may increase the rate of novel allelic variants (Sage and Selander 1979).

The production of new alleles can be explained by various mechanisms. Intra-cistronic recombination, as it is an important source of genetic variation in populations, might act as a locus-specific mutational process (Watt 1972). Ohno et al. (1969) have suggested that intragenic recombination is a source of an appearance of new electromorphs.

A transposon could act in a new genetic pool and contribute to a change of the genomic organization, including mutational events, especially considering the locus MDH.A. Such a phenomenon would produce a nul allele and no polymorphism was observed at this locus, as intragenic recombination might generate new allelic sequence if a minimum level of variation already exists at the locus in question (Watt 1972). The explanation cannot be an introgression event because the allele A0 was never observed in other rice species.

The evolution of *O. sativa* in Africa is continuous; it results from the introgressions from endemic species, *O. glaberrima, O. breviligulata* and *O. longistaminata* and from cross-hybridization between the two types of Indica and Japonica which may have caused mutations whose expression and conservation is favorised in new genetic environments.

Africa contains a wide genetic reservoir but each country represents a particular situation where the variability is generally much more restricted. From the restrictive parameters of the collection maintained by ORSTOM, the genetic diversity of the continent can be represented.

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