Theor Appl Genet (1987) 74:21–30

Isozymes and classification of Asian rice varieties*

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Received December 7, 1986; Accepted January 9, 1987
Communicated by G. S. Khush

Summary. Enzyme variation detected by starch gel electrophoresis was used to investigate the genetic structure of *Oryza sativa* L. species. Fifteen polymorphic loci coding for 8 enzymes were surveyed among 1688 traditional rices from Asia. Multivariate analysis of the data resulted in identification of six varietal groups, with two major ones, groups I and VI, two minor ones, groups II and V, and two satellite ones, groups III and IV. Group I is found throughout tropical Asia; it encompasses most Aman rices in Bangladesh, the Tjereh rices in Indonesia and the Hsien rices in China. Group VI is found mostly in temperate regions and in high elevation areas in the tropics; it encompasses most upland rices from Southeast Asia, the Bulu rices from Indonesia and the Keng rices from China. Groups II, III, IV and V share common differences from groups I and VI which suggest an alternative evolutionary history. Groups II and V are found in the Indian subcontinent from Iran to Burma. Well-known components of these are Aus rices from Bangladesh for group II and Basmati rices from Pakistan and India for group V. Groups III and IV are restricted to some deepwater rices in Bangladesh and Northeast India. Based on analogy with other classifications, Group I might be considered as the "Indica" type and Group VI as the "Japonica" type. Such terms, however, have a depreciated meaning due to discrepancies among various classifications.

Key words: Rice – Isozymes – Varietal classification – Asia

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Introduction

The intraspecific variation in *Oryza sativa* is remarkably extensive and subspecific classification has always been a matter of importance for rice breeders and geneticists.

The pioneering work of Kato et al. (1928) has shown the existence of two main varietal types, designated as Indica and Japonica. The differentiation involved morphological and serological characters as well as intervarietal hybrid fertility. This classification confirmed the empirical distinction the Chinese people had recognized since ancient times between the two types of rice called Hsien (or Sen; Indica) and Keng (Japonica). Although Terao and Mizushima (1942) considered, based on intervarietal hybrid sterility, that it was an oversimplification, the Indica-Japonica opposition has been a constant feature of all the varietal classifications proposed later. A third type was distinguished by Matsuo (1952) on a morphological basis with his classification in three types A, B and C, later referred to as Japonica, Javanica and Indica, respectively, based on their geographical distribution (Morinaga 1954). However, Oka (1958) demonstrated that the Javanica and Japonica morphological types could be considered as the tropical and temperate components of a single Japonica group. Oka and his collaborators have since then accumulated much knowledge on the Indica-Japonica differentiation and its evolutionary significance (see Oka 1983 for a review; Morishima and Oka 1981). Recently, Cheng et al. (1984) have used partly different characters and have shown the validity for all rices of Asia of the Hsien-Keng (or Indica-Japonica) classification originally based on Chinese varieties.

The Indica, Japonica and Javanica terms, referring to the three morphological types, are currently being used by most rice scientists (Chang and Bardenas 1965; Chang 1976) due to more direct observation of the characters involved in their definition.

Biochemical methods of investigation, especially isozyme studies, have provided valuable tools for rice geneticists. Electrophoretically identifiable isozymes have often been utilized for the classification of varieties within *O. sativa*. Chu (1967), Shahi et al. (1969), Pai et al. (1973) and Fu and Pai (1979) showed the existence of peroxidase alleles specific to the Indica and Japonica groups, as defined by Oka (1958).

Table 1. Composition of the varietal sample

Origin	No. of varieties	Parameter diversified (types represented)
Iran	34	Grain type (Sadri-Binam-Gharib-Champa)
Afghanistan	17	
Pakistan	47	15 morphoagronomic groups[a]; altitude
India		Varieties recommended in 1957[b] obtained by pure line selection from native cultivars
Jammu and Kashmir	9	Altitude
Punjab	7	Cycle
Maharashtra & Gujarat	16	Cycle
Karnataka	5	Season (Kharif-Rabi); water regime
Kerala	18	Season
Uttar Pradesh	28	Season
Madhya Pradesh	5	Season (Kharif-Zaid)
Andhra Pradesh	31	Season (Abi-Tabi); water regime
Tamil Nadu	29	Season (Swarnavari-Samba-Navarai)
Bihar	10	Season (Aus-Aman)
Orissa	157	Season (Aus-Sarad); intermediate wild-cultivated rices[c]
West Bengal	26	Season (Aus-Aman)
Sikkim	4	Altitude
Assam	14	Season (Aus-Sali-Asra-Aman-Boro)
NEFA	6	Altitude; cycle
Manipur	7	Cycle
Tripura	6	Cycle
(Unknown origin)	3	
Assam Rice Collection	18	
Nepal	41	Temperature (Tropical-Temperate)
Bhutan	34	Altitude; cycle; water regime
Bangladesh	74	Season (Aus-Aman-Boro); water regime (Upland to floating)
Sri Lanka	34	Season (Maha-Yala); water regime
Burma	89	Grain type (Ngasein-Medon-Emata-Letywezin-Byat); season (Kaukyin-Kauklat-Kaukkyi-Mayin); water regime
Laos	37	Water regime (upland-lowland)
Thailand	224	Altitude; water regime (upland to floating)
Vietnam	59	Season (5th month–10 month); water regime
Kampuchea	13	
Malaysia	48	Cycle; water regime
Indonesia	130	Morphology (Bulu-Gundil-Tjereh); water regime
Philippines	51	Water regime
China, mainland	185	Ecotype (Keng-Hsien)
China, Taiwan	78	Water regime
Korea	32	
Japan	61	Water regime
Total	1,688	

[a] From Husain and Akbar 1981
[b] From Richharia 1957
[c] From Oka and Chang 1962

Similar results were obtained by Pai et al. (1975) and Fu and Pai (1979) for acid phosphatase alleles.

When more loci are studied, it becomes possible to determine whether alleles among these loci are associated in multilocus complexes. Such associations indicate restricted recombination between multilocus types and provide a new insight into the species' genetic structure. With only three esterase loci, Nakagahra et al. (1975) and Nakagahra (1977) could build a simple classification which fits well with classifications based on other factors. Second (1982) surveyed 40 presumed loci, 25 of which were polymorphic within *O. sativa*. The varieties clearly tended to cluster into the Indica and Japonica types. With 14 polymorphic loci, Glaszmann et al. (1984) similarly found a strong differentiation of the varieties towards the Indica and Japonica types. They pointed out that the Javanica varieties (Bulu ecotype of Java), the typical upland rices from Africa and America and most upland rices from Southeast Asia belonged to the Japonica group.

Recently, the present author (Glaszmann 1985) identified 6 groups among 120 Asian varieties based on polymorphism at 21 loci. Group I consisted of the typical Indica varieties and group VI consisted of temperate and tropical Japonica rices. Groups II to V were found only along the Himalayas. Although they consist of varieties usually considered as Indica rices, they could be clearly differentiated from group I.

Table 2. Enzymes surveyed; loci identified with their polymorphism indices among 1688 Asian cultivars and correspondence with other locus nomenclatures

Enzyme	Locus	No. of alleles	H[a]	Correspondence to other nomenclatures[b]	
				(a)	(b)
Catalase	Cat-1	3	0.412	Cat-A	Cat
Shikimate dehydrogenase	Sdh-1	4	0.484		
Phosphoglucose isomerase	Pgi-1	2	0.500	Pgi-A	Pgi-1
	Pgi-2	4	0.545	Pgi-B	Pgi-2
Aminopeptidase	Amp-1	5	0.372	Lap-E	Lap
	Amp-2	5*[c]	0.478		Aap
	Amp-3	7*	0.497		
	Amp-4	3	0.051		
Alcohol dehydrogenase	Adh-1	4*	0.090	Adh-A	
Esterase	Est-1	2*	0.170	Est-D	Est-3
	Est-2	3*	0.645	Est-E	Est-4
	Est-4	3*	0.022	Est-B	
	Est-8	2	0.480	Est-Ca	Est-1
Isocitrate dehydrogenase	Icd-1	4*	0.028	Icd-A	
Acid phosphatase	Acp-1	3	0.476	Acp-AMC	

[a] $H = 1 - \Sigma Xi^2$, where Xi is the frequency of ith allele
[b] (a) Second and Trouslot (1980), (b) Glaszmann et al. (1984)
[c] * Including a silent allele

The present paper summarizes results of a survey of 1688 traditional Asian varieties for 15 loci coding for isozymes. It confirms the structure described above and elucidates correspondence between the enzymatic groups and various local ecotypes. The overall enzymatic classification is compared with various anterior classifications.

Materials and methods

Materials

Most varietal samples were provided by IRRI's International Rice Germplasm Center (IRGC).

The records of the germplasm bank provided elements for covering the arrays of local varietal groups and crop environments for 20 Asian countries (Table 1). The accessions represented traditional cultivars or recommended varieties resulting from pure line selection in traditional cultivars.

Sixty-five strains were from the collection of National Institute of Genetics (NIG), Japan, and represented genetic testers used by H. I. Oka for his classification (1958).

164 samples of cultivars grown in North Thailand were provided by J. Dennis, Faculty of Agriculture, Chiangmai University.

A few samples were provided by plant breeders at IRRI.

Technique

The plants were germinated in plastic dishes at ambient temperature under natural light. Crude extracts of water soluble proteins were prepared from the plumule and coleoptile of the seedlings 4 to 6 days after germination by homogenization in a little distilled water. Imbibed filter paper wicks were then inserted into a starch gel and subjected to horizontal electrophoresis at 4 °C. Eight enzymes were separated at pH 8.0 as described by Second (1982); catalase (CAT), shikimate dehydrogenase (SDH), phosphoglucose isomerase (PGI), aminopeptidase (AMP), alcohol dehydrogenase (ADH), esterase (EST), isocitrate dehydrogenase (ICD), and acid phosphatase (ACP). They permitted surveying 15 polymorphic loci (Table 2).

For a given variety, two to five plants were individually analyzed. When heterogeneity was detected within a variety, the most frequent genotype was used for data analysis.

Data analysis

The data were subjected to a Factor Analysis of Correspondences (FAC) as already described in Glaszmann et al. (1984). This analysis identifies several independent axes which account for the largest part of the whole variation, and provides coordinates of the varieties along these axes.

Groups were identified from the distribution of the dots representing the varieties on the planes defined by the most important axes. They correspond to areas with a high concentration of dots surrounded by zones of low density of dots.

Variation within and between the groups was quantified using Nei's (1975) diversity index and genetic distance.

Results

Allelic variation

A large amount of variation was observed and many electrophoretic variants were identified. Table 2 sum-

marizes the observations and their interpretation. Correspondence with nomenclatures used previously is given.

The number of alleles per locus ranges from 2 to 7 and averages 3.6. The diversity indices are high and denote existence of several frequent alleles for loci Cat-1, Sdh-1, Pgi-1, Pgi-2, Amp-1, Amp-2, Amp-3, Est-2, Est-8 and Acp-1. The polymorphism is reduced to the presence of one or several rare alleles besides a very frequent one for loci Amp-4, Adh-1, Est-1, Est-4 and Icd-1.

Genetic structure of the species

Factor analysis of correspondences. The data constituted by the matrix (1688 varieties × 15 loci) were subjected to FAC.

Axes 1, 2, 3 and 4 account for 82.1%, 7.6%, 4.4% and 2.9% of the whole diversity, respectively.

Six clusters were identified from a synthesis of the distribution of the varieties on planes (1,2) and (3,4) and designated groups I to VI (Fig. 1). Groups I, II, III, IV, V and VI appear clearly on plane (1,2) whereas groups II, IV, V and (I + III + VI) appear on plane (3,4). The 120 varieties previously found to cluster into six groups (Glaszmann 1985) scatter in a similar way, which suggests the identity of the two classifications. The distribution of the varieties is: 900 varieties (53.3%) in group I, 123 (7.3%) in group II, 6 (0.4%) in group III, 11 (0.7%) in group IV, 106 (6.3%) in group V, 451 (26.7%) in group VI and 90 (5.3%) varieties not classifiable. Groups III and IV contain a very small number of varieties and one may question whether they would still appear after a more extensive varietal sampling.

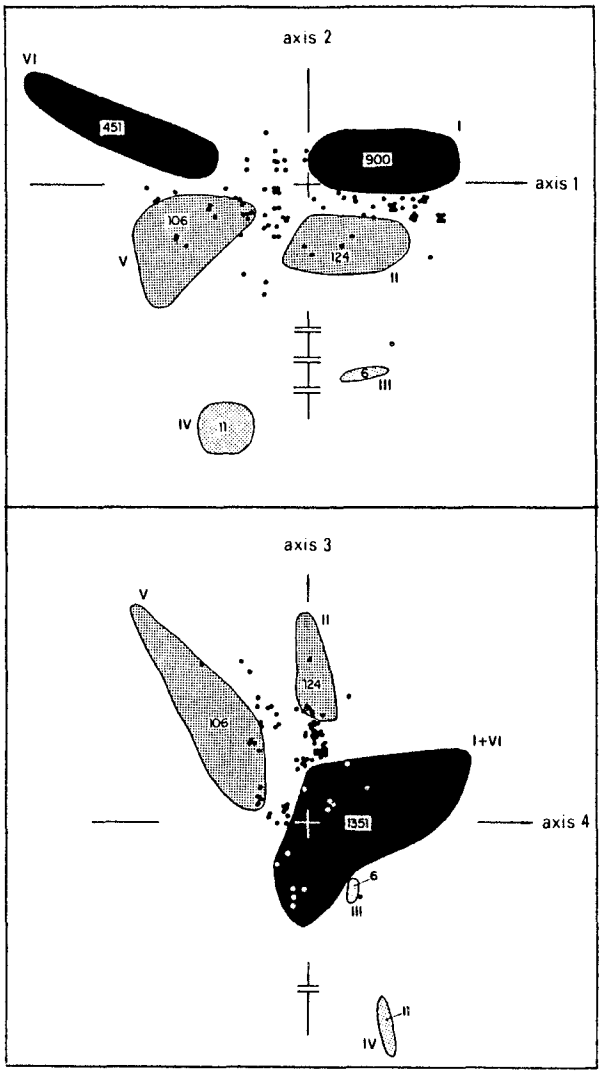

Fig. 1. Six varietal groups on planes (1, 2) and (3, 4) of a Factor Analysis of Correspondences of isozyme variation at 15 loci among 1688 rice varieties. Sizes of the groups are indicated. Isolated dots represent 90 varieties with intermediate positions or unstable classification

The enzymatic groups

Nature and geographic distribution. Table 3 shows the correspondence between the enzymatic groups and local ecotypes, and Fig. 2 shows the geographical distribution of all the groups in Asia.

Group I is present in whole tropical Asia. It is dominant in the south of Indian subcontinent; in Bangladesh, it comprises most varieties of the Aman ecotype; in continental Southeast Asia, it contains all the lowland varieties; in Indonesia, it corresponds to the Tjereh ecotype; in China, it corresponds to the Hsien ecotype.

Group II is observed exclusively in South and West Asia. It is rare in South India and Sri Lanka, whereas it is very frequent along the Himalayas, from Iran to Assam hills. Its varieties have a short cycle and can be grown in various hydric conditions, from irrigated, as in Pakistan, to strictly upland, as in Bangladesh. Some present a high flood tolerance (FR 13A) and some present heat tolerance (N22). In Bangladesh and the surrounding Indian regions, group II clearly corresponds to Aus ecotype, and also includes some Boro rices.

Group III is found only in Bangladesh and in the Manipur State of India. It consists of particular rices, of short cycle, photoperiod insensitive and adapted to deep water conditions.

Group IV corresponds to the Rayada rices of Bangladesh. These are very particular rices, sown in November–December and harvested up to 12 months later, cold tolerant in early stages, photoperiod sensitive, able to stand 12 days flooding and to adjust their elongation up to a 6 m depth.

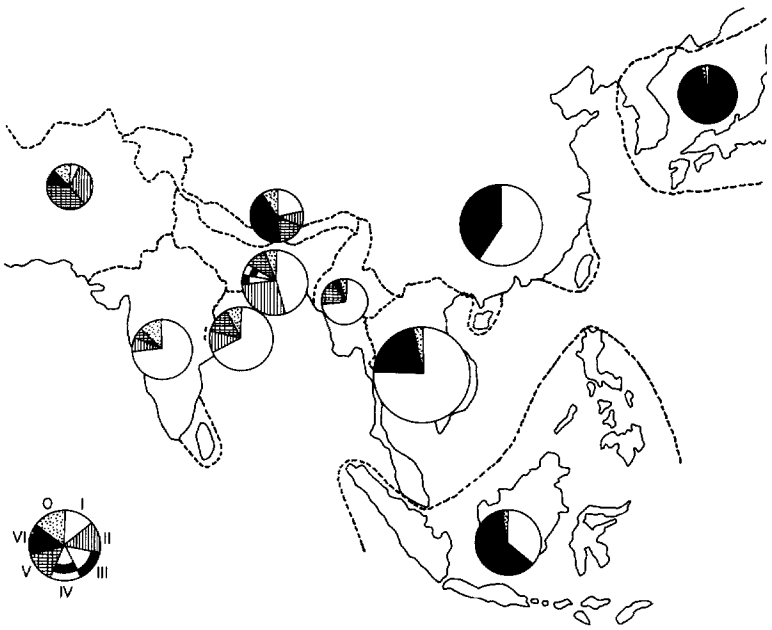

Fig. 2. Distribution of 1688 Asian rice varieties in 6 varietal groups based on isozyme variation at 15 loci. Groups are designated I to VI; class 0 corresponds to unclassified varieties

Table 3. Distribution of well-known varietal types in six groups based on isozyme polymorphism in Asian domestic rice

Origin	Type	Enzymatic groups						Intermediates
		I	II	III	IV	V	VI	
Bangladesh	Deepwater	10	1	5	11	–	–	–
	T. Aman	28	–	–	–	2	–	–
	Aus	2	32	–	–	–	–	1
	Boro	2	6	–	–	–	–	–
Thailand, Laos	Lowland	168	–	–	–	–	–	–
	Upland	12	–	–	–	–	64	–
Java, Bali	Tjereh	10	–	–	–	–	–	–
	Gundil	4	–	–	–	–	10	–
	Bulu	–	–	–	–	–	24	–
China	Hsien	84	–	–	–	–	–	–
	Keng	–	–	–	–	–	26	–
Korea, Japan		2	–	–	–	–	89	2

Group V spreads from Iran to Burma. It consists of very diverse varieties, many of which are considered as high quality rices, such as the Sadri rices from Iran, the Basmati rices from Pakistan, India and Nepal and some rices from Burma which also have a very high cooking elongation.

Group VI is dominant in temperate areas and in high elevation areas in Southeast Asia and South Asia. It includes the Bulu rices from Java and Bali, most upland rices from Southeast Asia, the Keng rices from China and the traditional rices from Japan and Korea.

Gene diversity and intergroup differentiation. Table 4 gives the diversity indices within the groups, the genetic distances between the groups and the frequencies of unclassified varieties which can be explained by recombination between two groups. The former parameter quantifies the extent of variation still present in the groups. The later two permit evaluation of the extents of differentiation between any two of the groups and their comparison. All these parameters have a limited significance, however, for groups III and IV, because of their very small size.

Several comments are noteworthy in the scope of this paper:

1. As far as our sample of loci is concerned, the most polymorphic groups are groups I and V, followed by groups II and VI, then group IV and lastly group III.

Table 4. Probability of identity of two randomly chosen alleles within the groups (Ix, diagonal), genetic distance between the groups (Dxy, Nei 1975, below diagonal) and frequencies of intermediates[a] between the groups (Int., above diagonal)

Ix / Dxy	Int.	I	II	V	VI	III	IV
I		0.792	0.054	0.066	0.014	0.046	0.045
II		0.273	0.881	0.139	0.046	0.000	0.000
V		0.470	0.361	0.796	0.058	0.036	0.000
VI		0.504	0.546	0.149	0.872	0.057	0.022
III		0.454	0.258	0.579	0.997	0.970	0.000
IV		0.522	0.584	0.303	0.361	0.423	0.941

[a] Unclassifiable genotypes which can be produced by recombination among varieties of two distinct groups are considered as intermediates between these groups.

$$\text{Frequency of intermediates} = \frac{N}{(Nx + Ny + N)}$$

where N is the number of intermediates and Nx and Ny are the sizes of groups x and y

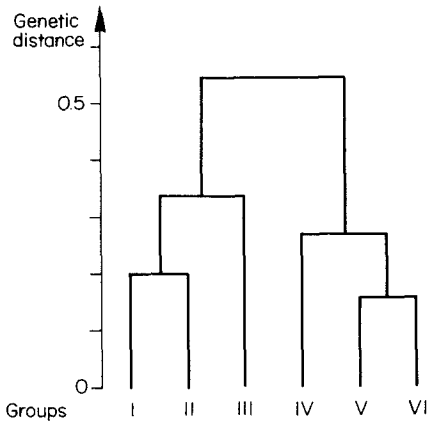

Fig. 3. Dendrogram constructed from the genetic distances (Nei 1975) among 6 groups of rice varieties, as estimated from 15 isozyme loci

The diversity of groups I and V suggests possible further subgrouping.

2. The dendrogram of Fig. 3 built from Table 4 shows two main clusters, one consisting of groups I, II and III, the other of groups IV, V and VI. This illustrates predominance of axis 1 in the FAC.

3. The differentiation along axis 1 is much stronger between groups I and VI, with a genetic distance of 0.504 and 1.4% of intermediates, than between groups II and V, with a genetic distance of 0.361 and 13.9% of intermediates.

Correspondence with anterior classifications

Classification by Oka (1958). In 1958, Oka classified 147 varieties into two main types, named "Continental" and "Insular" and later referred to as Indica and Japonica. The main discriminating characters were awn length, phenol reaction of the grain, $KClO_3$ resistance, low temperature resistance and drought resistance. One hundred and seven of these varieties were included in our sample. Table 5 gives the correspondence between the two classifications. Group I and group VI are clearly identifiable to Indica and Japonica in the sense of Oka. Little information arises regarding groups II, III, IV and V since they were little or not represented.

Classification of Jacquot and Arnaud (1979). Jacquot and Arnaud (1979) investigated the position of upland varieties in relation to the three classical morphological types Japonica (A), Javanica (B) and Indica (C) first identified by Matsuo (1952). Some of the varieties were also studied for isozymes (Glaszmann et al. 1984). Data for 46 quantitative characters used by Jacquot and Arnaud were subjected to a Principal Component Analysis (PCA). Axes 1, 2 and 3 accounted for 33.3%, 14.2% and 11.2% of the whole variation. Figure 4 shows the distribution of the varieties on the plane formed by axis 1 and a combination of axes 2 and 3, where the coordinate of a variety is given by:

$$C = \frac{\text{coordinate on axis 2} + \text{coordinate on axis 3}}{\sqrt{2}}$$

The enzymatic classification of the varieties is indicated by different symbols.

As identified by Jacquot and Arnaud, it is possible to roughly distinguish the three morphological types Japonica, Javanica and Indica. Varieties of enzymatic groups I and II fall into the Indica type. Varieties of enzymatic group VI cluster into the Japonica and Javanica types (Table 5). Varieties 'H4', 'Century Patna 231', 'IR5', 'IR8' and 'Taichung Native 1' occupy positions somewhat ambiguous. This comes from its long and slender grain for 'Century Patna 231' and their short stature for 'IR5', 'IR8', and 'Taichung Native 1'.

'Basmati 370', the only variety of enzymatic group V, has an Indica morphology.

IRRI-IBPGR classification. As that by Jacquot and Arnaud, the IRRI-IBPGR classification is mostly based on morphology (IBPGR-IRRI Rice Advisory Committee 1980) and distinguishes the three plant types first described by Matsuo (1952) plus a "hybrid" type. Figure 5 permits comparison of this classification and that by Jacquot and Arnaud. There is a clear discrepancy for many varieties which were identified as Javanica by Jacquot and Arnaud and are described as Indica in the IRRI-IBPGR scheme. Most of them are upland

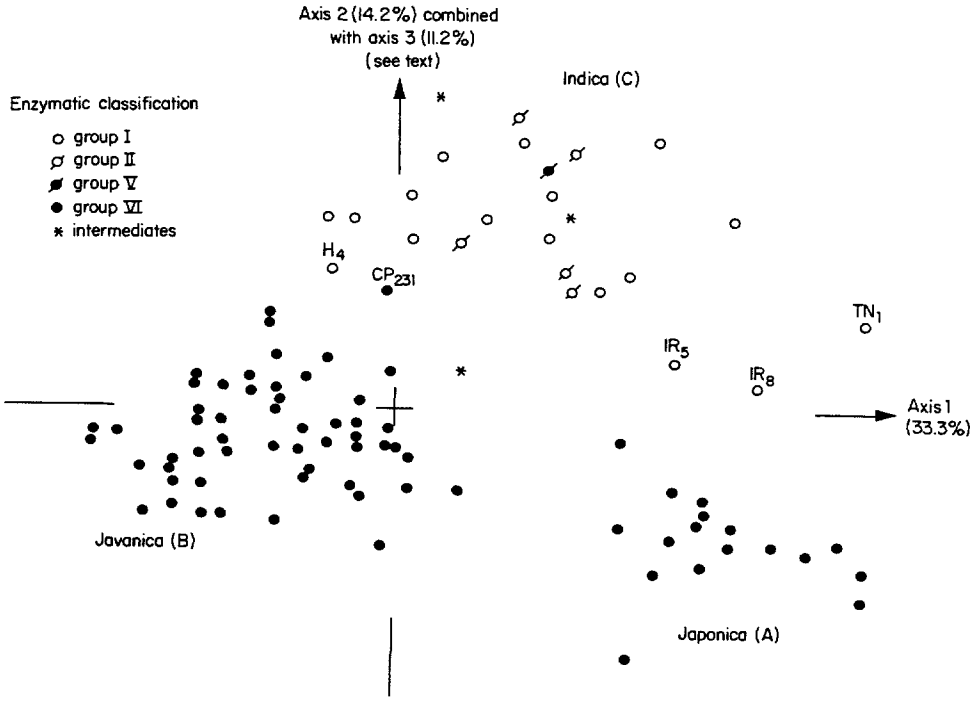

Fig. 4. Identification of 3 morphological types from the Principal Component Analysis of variation for 46 morphological characters among 97 varieties (from Jacquot and Arnaud 1979); enzymatic classification of the varieties is indicated

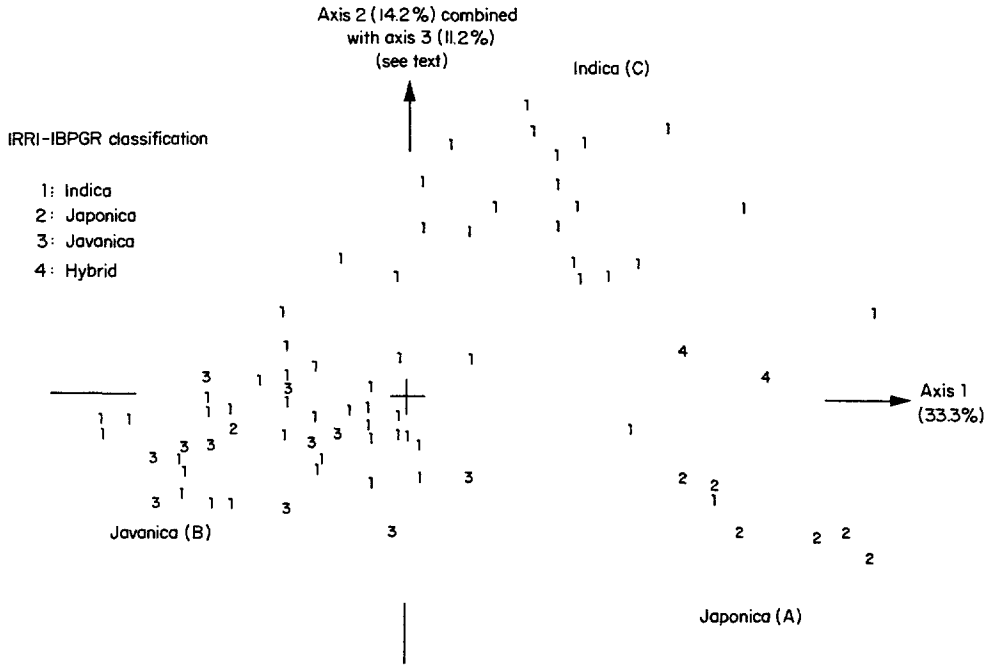

Fig. 5. Distribution of 77 varieties on a plane which discriminates the Japonica, Javanica and Indica morphological types (from Jacquot and Arnaud 1979); their classification in the IRRI-IBPGR scheme is indicated

Table 5. Correspondance between the enzymatic classification and anterior classifications of Asian cultivated rice

Author	Enzymatic group						Intermediates
	I	II	III	IV	V	VI	
Oka (1958)							
Indica	57	1	–	–	1	1	–
Japonica	–	–	–	–	–	46	–
Adapted from (see Fig. 4) Jacquot and Arnaud (1979)							
Indica	13	5	–	–	1	–	1
Javanica	–	–	–	–	–	53	1
Japonica	–	–	–	–	–	17	–
Intermediates	4	–	–	–	–	1	1
IRRI-IBPGR (1) W Asia + S Asia + Burma							
Indica	337	102	6	11	90	34	60
Javanica	3	4	–	–	–	3	3
Japonica	–	4	–	–	–	3	2
Intermediates	3	–	–	–	2	3	–
(2) SE Asia excluding Burma							
Indica	170	2	–	–	1	79	2
Javanica	3	–	–	–	–	35	–
Japonica	–	–	–	–	–	3	1
Intermediates	2	–	–	–	–	14	1
(3) E Asia							
Indica	78	–	–	–	–	8	1
Javanica	–	–	–	–	–	–	–
Japonica	12	–	–	–	–	62	–
Intermediates	2	–	–	–	–	–	–
Cheng et al. (pers. commun.)							
Hsien	84[a]	71	6	–	1	–	16[b]
Hsien-cline	–	22	–	–	7	–	2[b]
Keng-cline	–	2	–	11	14	–	–
Keng	–	–	–	–	49	26[a]	3[c]

[a] These varieties were not analyzed by G. S. Cheng and his colleagues, but had been sent to IRGC as typical Hsien and Keng varieties

[b] Intermediate between groups I and II

[c] Intermediate between groups V and VI

rices which have rather thin grains or which have glabrous grains, whereas the definition of the Javanica type in the IRRI-IBPGR scheme involves broad and thick grains with long hairs (Chang and Bardenas 1965).

Table 5 gives the correspondence between the enzymatic classification and the IRRI-IBPGR classification. There is a clear concordance in East Asia where group I and group VI roughly correspond to Indica and Japonica. In Southeast Asia, excluding Burma, most Javanica and Japonica varieties belong to group VI. However, many varieties described as Indica also belong to group VI; most of them are upland rices. In the western part of Asia, most varieties are classified as Indica, although all enzymatic groups are represented. Thus, there is agreement between the two classifications when the variation is restricted to tropical Indica versus temperate Japonica. However, there is no concordance when variation is more complex, such as in the hilly areas of Southeast Asia or in the Indian subcontinent.

Classification by Cheng et al. (1984, pers commun.)

Cheng and his colleagues recently showed that the traditional classification of rices in China into the Hsien (Indica) and Keng (Japonica) types could be success-

fully extended to all Asian rices. The main characters taken into account were shape of the grain, phenol reaction, glume hairiness, leaf pubescence, interval between first and second nodes of panicle axis and glume color at heading. As a test to their classification, these authors analyzed cultivars which did not belong to enzymatic groups I or VI. A significant number of them appeared as intermediates; they were further classified as Hsien-cline or Keng-cline. Correspondence between the enzymatic groups and Hsien, Hsien-cline, Keng-cline and Keng types is given in Table 5.

Most varieties of groups I, II and III are classified as Hsien or Hsien-cline, whereas most varieties of groups IV, V and VI are classified as Keng or Keng-cline. The Hsien-Keng differentiation appears clearly related to the differentiation along axis 1 of the FAC on isozyme data.

Discussion and conclusions

The relevance of isozymes for rice classification purposes has already been discussed (Glaszmann 1986). The methodology rests upon the identification of multiallelic associations across independent genes, which indicate existence of varietal types separated by restricted recombination.

The resulting classification exhibits high concordance with anterior schemes based on other types of characters. In addition, it highlights a new aspect of the genetic structure of rice germplasm. Two main geographic areas can be distinguished on the basis of genetic variation. (1) In East and Southeast Asia, excluding Burma, the variation is reduced to the group I-group VI binarity. (2) In West and South Asia, including Burma, the diversity is much higher and the genetic structure is much more complex; all groups are encountered, as well as many unclassifiable varieties; group I is almost absent from Western South Asia and West Asia and group VI is restricted to high elevations.

The ensemble made of groups II, III, IV and V and their peripheral varieties may constitute an alternative gene pool beside groups I and VI for the following reasons:

1. They have a similar geographic distribution.
2. They share some special alleles, which participate in their differentiation along axis 2 of the FAC.
3. Enzymatic variation is continuous, unlike that between group I and group VI.
4. The concordance between the various classifications is much less clear when only these varieties are considered.
5. They exhibit a particular behavior regarding sterility in crosses with groups I or VI. The partial fertility of Aus varieties (group II) with Tjereh or Aman varieties (group I) as well as with Bulu and Japanese varieties (group VI) has been well documented (Morinaga 1968). Similarly, varieties such as 'Basmati 370' and 'Pankhari 203' (group V) are known to show low fertility with 'Peta', 'Sigadis', and 'Taichung Native 1' (group I) as well as with 'Rodjolele' and 'Boegi Imba' (group VI) (Engle et al. 1969). Some cytoplasm-nucleus interactions reinforce this observation, such as male sterility due to combination of 'Chinsurah Boro II' (group II) cytoplasm with 'Wu 10' (group VI) nucleus and of 'Taichung Native 1' (group I) cytoplasm with 'Pankhari 203' (group V) nucleus (Virmani et al. 1981).

These observations and the comparison between the classifications can be summarized as follows:

Group I corresponds to the Indica type in the sense of Oka; it is comprised of tropical lowland varieties, and characterized by the so-called "Indica" (C) morphology; it still exhibits a large amount of enzymatic variation, which suggests possible further subgroupings.

Group VI corresponds to the Japonica type in the sense of Oka; it is distributed mostly in the temperate regions, in the hilly areas of East and Southeast Asia and along the Himalayas; it comprises the so-called "Japonica" (A) and "Javanica" (B) morphological types.

Some varieties differ from the typical Indica and Japonica types; they are present mostly in the Indian subcontinent, where they represent more than a third of all the varieties, and especially along the Himalayan foothills. They show a differentiation analogous to the Indica-Japonica differentiation but its extent is much smaller. One may assume that this ensemble has arisen from alternative evolutionary processes.

The above summary privileges the scheme of Oka (1958) for its remarkable correspondence with the enzymatic classification. This scheme, however, when it is considered for use, has the fault of involving terms such as "Indica" and "Japonica". These terms together with "Javanica" and "Sinica" originate from the same semantic process involving geographic considerations. They have been used in various schemes with various definitions and have become highly ambiguous. The most illustrative example is that of "Sinica", used by Chang (1976) to replace "Japonica" because of the immediate Chinese origin of the Japanese varieties, while used by Nakagahra (1977) to designate "Indica" varieties from China. Even when various classifications broadly correspond to each other, there remain many discrepancies. Many varieties exhibit a "Javanica" morphology in a given scheme, are described as "Indica" in another scheme and belong to the "Japonica" type in the sense of Oka. Such examples throw confusion among rice scientists.

Cheng et al. (1984) advocate international use of "Hsien" and "Keng" to designate the two main types in the species. Adoption of a new terminology appears very opportune and might indeed facilitate communication among rice researchers.

Among other characters, isozymes permit early and fast assessment of the nature of a variety. They constitute a tool particularly adapted to international

research by being independent from the environment. Expansion of their use can only be recommended.

Acknowledgements. The author is grateful to the staff of the International Rice Germplasm Center, headed by Dr. T. T. Chang, for kindly supplying most seed samples, to Mr. M. Arnaud who performed the multivariate analyses and to Mr. M. Jacquot and Dr. D. V. Seshu for reading the manuscript.

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