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Enzyme diversity in pearl millet (*Pennisetum glaucum*)

2. Africa and India

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Summary. The survey of enzyme polymorphism in West African pearl millet cultivars reported by Tostain et al. 1987 has been extended to include populations from other regions of Africa and from India. The eight enzyme systems studied included: alcohol dehydrogenase, β-esterase, catalase, phosphoglucoisomerase, phosphoglucomutase, 6-phosphogluconate dehydrogenase, glutamate oxaloacetate transaminase, and malate dehydrogenase. One-hundred-ninety-nine populations of millet were analyzed, including 74 populations studied earlier. No new enzyme diversity was observed. Intrapopulation diversity ranged from 70%–90% of the total diversity, depending on their regions of origin. Four principal groups were distinguished in the following decreasing order of diversity: early-maturing cultivars from West and East Africa, late – maturing cultivars from West and East Africa, cultivars from India, and cultivars from southern Africa. The early-maturing cultivars were distributed between two principal focal points from East Africa in the East to Mali in the West. In the center were found millets from Niger which were most diverse. Indian and southern African cultivars were distinct, with the former appearing relatively similar to those of Niger, and the latter somewhat similar to late-maturing cultivars from West Africa, a diverse group that included late-maturing cultivars from East Africa. Based on the results obtained, an evolutionary hypothesis proposed here includes: multiple domestications in the Sahel, creation of early-maturing cultivars and their migration eastwards to India plus a southwards migration to Sudanian zone, and creation of late-maturing cultivars and their migration simultaneously westwards, eastwards, and southwards to southern Africa.

Key words: Isoenzymes – Evolution – Domestication – Biological structure – Genetic distances

Introduction

Tostain et al. (1987) observed that West African early- and late-maturing cultivars of pearl millet (*Pennisetum glaucum* (L.) R. Br.) formed two distinct enzymic groups, which enabled them to put forward an hypothesis on the evolution of pearl millet in West Africa. The current article surveys enzyme polymorphism in millets from other parts of Africa and India, with the objective of confirming and completing the proposed hypothesis of evolution.

Information on pearl millet diversity is available in the literature. Upadhyay and Murty (1970), in a study dealing with both botanical characters neutral to natural selection and environmentally dependent physiological characters, observed that Indian millets were distinct from and less diverse than African millets. Portères (1976), who considered only botanical characters, found that African millets clustered essentially into three groups according to geographical origin: West (subdivided into two subgroups), East, and South, with the Indian millets close to the South Africa group. In addition, he noticed an association between morphological groups in millet and the main agrarian civilizations: paleo-nigritic, nilo-cushitic, and bantu, but provided no interpretation in terms of the evolution of the crop. Brunken et al. (1977) identified maximum morphological diversity in millets from West Africa and concluded that millet domestication occurred most probably in the West African Sahel.

Materials and methods

A collection of 199 samples of millet from West Africa (106), East Africa (32), southern Africa (30), and India (31) were stud-

Table 1. Origin and maturity period of the samples analysed for enzyme characters

Region*	Country or state	No. of samples	
		Early	Late**
West Africa	Mauritania	5	0
	Senegal	10	5
	Mali	9	6
	Burkina Faso	2	8
	Niger	15	0
	Nigeria	0	8
	Guinea	1	4
	Sierra Leone	0	6
	Ivory Coast	0	5
	Ghana	5	7
	Togo	3	4
	Benin	1	2
Total		106	
East Africa	Chad	3	3
	Cameroon	2	6
	Central African Republik	0	5
	Sudan	3	3
	Somalia	3	0
	Uganda	4	0
Total		32	
Southern Africa	Kenya	2	2
	Tanzania	0	4
	Malawi	4	0
	Zambia	1	2
	Mozambique	0	4
	Zimbabwe	5	0
	Botswana	3	0
	South Africa	2	1
Total		30	
India	Rajasthan	4	1
	Uttar Pradesh	8	0
	Gujerat	6	0
	Madhya Pradesh	3	0
	Maharastra	1	2
	Andra Pradesh	1	1
	Tamil Nadu	0	2
	Rayalasecna	2	0
Total		31	

* These regional groupings were defined by the analyses
** Early = early-maturing; late = late-maturing

ied. Information presented in Table 1 indicates that the collection studied covers most of the geographic diversity and maturity variation. To the 74 West African populations studied by Tostain et al. (1987), cultivars from Mauritania (5 accessions), Nigeria (8), Guinea (5), Mali (2), Niger (2), Senegal (3), Ghana (12), Cameroon (1), Central African Republic (1) and Sierra Leone (6) were added. The West African samples were obtained from the ORSTOM collection. Those from Ghana were supplied by W. Schiprack. Other accessions were provided by ICRISAT. Growing periods were determined in field trials at the ICRISAT Sahelian Center in Niger during the 1985 rainy season.

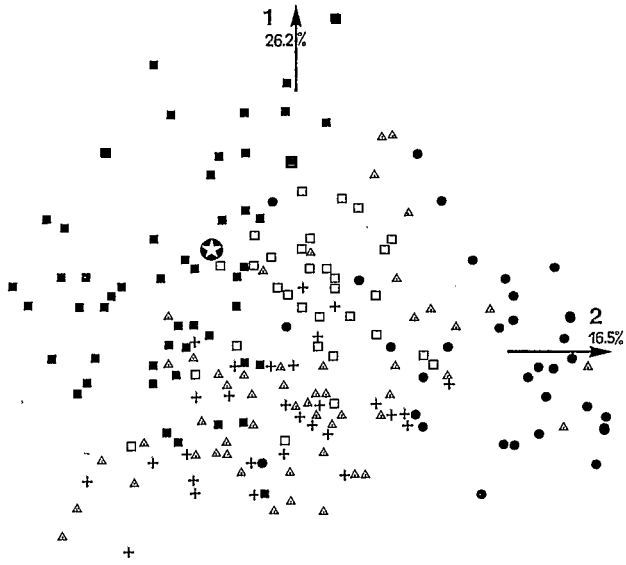

Fig. 1. Principal component analysis of 199 samples of *Pennisetum glaucum*. Projection on the plane (1, 2). ■ = West Africa early-maturing cultivars; △ = West Africa late-maturing cultivars; □ = East Africa; ● = Southern Africa; + = India; ✪ = point of maximum diversity

Data were recorded and analyzed following the methods used by Tostain et al. (1987). Each sample was described by 46 allelic frequencies belonging to 12 genes that control the structure of 8 enzymes: β-esterase (EST), alcohol dehydrogenase (ADH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), glutamate oxaloacetate transaminase (GOT), catalase (CAT), malate dehydrogenase (MDH), and 6-phosphogluconate dehydrogenase (PGD). Discriminant analyses were carried out using the STAT-ITCF computer program.

Principal component analyses deal with unreduced allelic frequencies (covariance matrix) and the spatial representations obtained correspond to Nei's minimum distances. These distances were used to partition Nei's diversity of a set of populations into intra- and inter-population diversities. The coefficient of differentiation expressed the inter-population diversity relative to the total diversity. Mahalanobis' distances between groups, computed in discriminant analyses, were also applied, since they are less sensitive than Nei's distances to the presence of unusual samples.

Results

The enzymatic groups

Principal component analyses. Principal component analysis of the entire data set displayed on the plane (1, 2), the two West African groups already identified by Tostain et al. 1987 viz, Early West and Late West (Fig. 1). Millets from other regions clustered into separate geographical groups to give a distinct southern African group, with East Africa and Indian groups superimposed on the Late West group.

The composition of the southern African and East Africa groups are shown in Table 1. They were defined a

Table 2. Discriminant analyses of the groups observed by principal component analyses

Initial group	No. of samples	Final groups*						
		Early West	Late West	Early East	Late East	Early South	Late South	India
Early West	51	37	1 Senegal 2 Mali	5 Niger	1 Burkina 3 Senegal	0	0	2 Niger
Late West	55	1 Guinea	38	1 Nigeria	1 Ghana 2 Nigeria 2 Ivory Coast 3 Mali 3 Sierra Leone	1 Ghana 2 Sierra Leone 1 Guinea	0	1 Guinea
Early East	15	1 Uganda 1 Cameroon 1 Chad	0	9	0	0	0	1 Sudan 1 Uganda 1 Somalia
Late East	17	1 Sudan	1 Cameroon	1 Cameroon	14	0	0	0
Early South	17	0	1 Malawi	0	0	10	3 Zimbabwe 1 Malawi	2 Kenya
Late South	13	0	0	1 South Africa 1 Tanzania	0	1 Tanzania	10	0
India	31	0	3	0	0	2	0	26

* For misclassified samples, the country of origin is shown

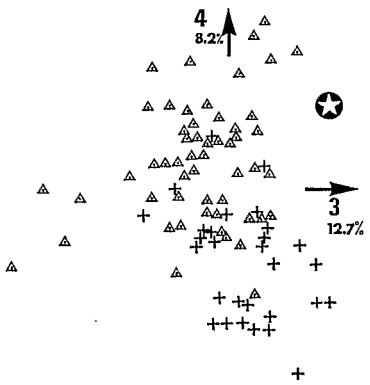

Fig. 2. Principal component analysis of the complete file. Projection on the plane (3, 4). + = India; △ = Late-maturing cultivars from West Africa; ✪ = Point of maximum diversity

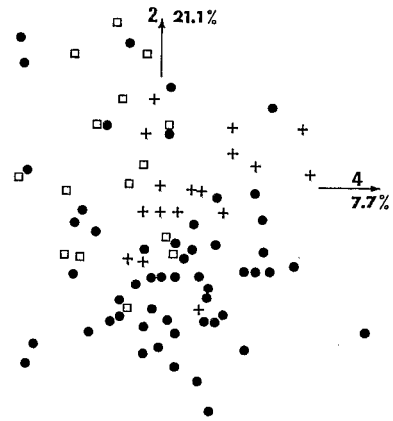

Fig. 3. Principal component analysis of West and East African pearl millets. Projection on the plane (2, 4). ● = West Africa late-maturing cultivars; □ = East Africa early-maturing cultivars; + = East Africa late-maturing cultivars

posteriori according to the data analyses. Samples from Cameroon, the Central African Republic, Uganda, and Somalia grouped with those from Chad and the Sudan, whereas Kenya cultivars clustered with accessions from southern Africa. Within the groups, no apparent clustering of samples according to their country of origin was observed. On the plane (3, 4) of the same analysis, the Indian group appeared well separated from the Late West group (Fig. 2).

In an analysis restricted to samples from West and East Africa, a fairly clear separation between the early-maturing and late-maturing cultivars from East Africa was apparent (Fig. 3). In the Early West group, three subgroups corresponding to accessions from Mali, Niger, and Togo were observed. Samples from Mauritania and Senegal fell between the Mali and Niger subgroups and the Ghanaian cultivars clustered with the Togo group. Within the Late West group, the clustering had the form of a fruit with a stone: a central kernel rich in diversity comprising samples from Mali, Burkina Faso, and Nigeria, surrounded by cultivars from the coastal countries, which were lower in diversity and the more so farther west. Samples from the far west, Sierra Leone, Guinea, and Senegal displayed a strong disper-

Table 3. Classification by discriminant analysis of early- and late-maturing cultivars from each region according to the enzyme types for West African early- and late-maturing cultivars

Initial groups	Final group*							
	West Africa		East Africa		Southern Africa		India	
	EW	LW	EW	LW	EW	LW	EW	LW
Early cultivars	48	3	8	7	1	16	13	12
Late cultivars	3	52	4	13	0	13	2	4

* EW = enzyme type of West African early maturing cultivars; LW = enzyme type of West African late maturing cultivars

Table 4. Genetic parameters of the enzyme groups

Group	Nei's diversity	Coeff. of differentiation	Distances*							
			Early West	Niger	Late West	Early West	Late East	Early South	Late South	India
Early West	2.99±0.05	0.168	–	–	0.177	0.144	0.217	0.468	0.584	0.213
Niger	2.91±0.10	0.098	–	–	0.141	0.110	0.195	0.437	0.598	0.146
Late West	2.53±0.04	0.214	1.90	1.96	–	0.072	0.095	0.195	0.319	0.105
Early East	2.76±0.11	0.155	2.11	1.89	2.05	–	0.081	0.199	0.292	0.118
Late East	2.50±0.09	0.114	2.43	2.58	1.83	2.37	–	0.309	0.435	0.245
Early South	2.27±0.11	0.210	2.63	2.69	2.08	2.44	2.88	–	0.055	0.248
Late South	1.88±0.10	0.329	2.84	3.18	2.44	2.66	3.18	1.78	–	0.381
India	2.37±0.06	0.167	2.32	2.12	2.17	2.51	2.80	2.47	2.87	–

* Above the diagonal are shown Nei's minimum distances and below the diagonal the Mahalanobis distances computed by the discriminant analysis

sion which extended into the Late East group. The Early East group was distinct from the Early West group, but located in the prolongation of the Mali-Niger axis.

Discriminant analyses. The groups identified by principal component analyses were confirmed by discriminant analysis (Table 2). Although the Early-Late disjunction was not observed in the southern African group, the a priori groups Early South and Late South were included in the discriminant analysis to give a complete and balanced grouping. The Indian group was treated as a whole because of the low number of late-maturing accessions.

Over 72% of the samples were well-classified and this is high, considering the many groups involved. It corroborates the existence of the enzyme groups identified by the principal component analyses. As expected from the results of Tostain et al. (1987), the 43 additional West African accessions tested in this study grouped according to maturity period.

The misclassified samples provided valuable information on the relationship between groups, in particular, between Early West and Early East, Laste West and Late East, Early South and Late South. The Indian group included samples from Niger, Sudan, Uganda, Somalia, and Kenya reflecting, we believe, a path of migration of the crop. The Late West group appeared dispersed and contained elements common to all other groups.

The Early-Late disjunction was strong in the West and East Africa groups, but weaker in the southern African group. In order to see if this disjunction was universal, a discriminant analysis was applied to the Early West and Late West groups with other samples as additional unknown elements. It can be seen in Table 3 that Late East is a part of Late West, but Early East is different from Early West because it is not linked to the western Early-Late disjunction. Southern African millets are, as a whole, closer to Late West than to Early West. Indian millets do not seem to be affected by the western Early-Late disjunction. Finally, the West Africa Early-Late disjunction does not exist elsewhere.

Inter-group distances. The detailed analysis of inter-group distances showed that, for each group, its closest neighbour is the Late West group (if we consider Early South and Late South as a same group) (Table 4). However, it should be noted that Late West is closer than Late East to Early East. Niger, a component of the Early West group, was included in Table 4 to show that the Indian millets are very distant from the southern African group, but close to Niger and the Late West group.

Table 5. Distribution of Nei's diversity in each group for each gene

Genes	Early West	Early East	Late West	Late East	South	India
Est A	0.82	0.82	0.81	0.81	0.81	0.77
Adh A	0.63	0.71	0.73	0.64	0.50	0.64
Pgm A	0.50	0.38	0.48	0.38	0.15	0.48
Cat A	0.47	0.27	0.10	0.11	0.29	0.16
Pgi A	0.28	0.13	0.27	0.38	0.08	0.04
Pgd A	0.18	0.23	0.13	0.08	0.11	0.05
Mdh A	0.05	0.12	0.01	0.01	0.02	0.02
Mdh C	0.02	0.04	0.00	0.03	0.01	0.14
Pgd B	0.02	0.00	0.00	0.03	0.06	0.06
Got B	0.02	0.06	0.01	0.02	0.04	0.00
Got A	0.02	0.00	0.00	0.01	0.00	0.00
Mdh B	0.00	0.00	0.00	0.00	0.00	0.00

Table 6. Frequencies of discriminant alleles

Genes	Enzymic groups						
	Early West	Late West	Early East	Late East	Early South	Late South	India
Est A							
2	16.2	26.1	16.8	23.5	21.0	30.4	11.7
3	14.8	23.5	14.7	19.6	23.2	19.3	6.3
7	17.8	10.9	18.7	13.6	20.6	7.7	36.8
Adh A							
4	6.1	10.4	15.2	14.6	4.6	2.5	0.3
5	37.3	31.9	29.0	19.0	11.2	14.4	47.0
6	6.2	25.5	14.3	5.3	63.2	67.5	27.0
7	47.2	30.1	39.7	54.5	18.0	15.0	24.8
Pgi A							
3	83.5	84.4	92.8	74.5	93.5	99.7	97.8
Pgm A							
2	51.8	39.6	25.6	25.2	13.7	2.5	39.5
Cat A							
2	38.2	5.0	15.9	6.2	13.8	24.1	8.7

Organization of enzyme diversity

Enzyme diversity was maximum in the Early West group and decreased in the following order: Early East, Late West and East, India, and southern Africa (Table 4).

Diversity in the Early West group was significantly higher than in the Early East group, but in the latter it was equal to that observed in samples from Mali. For each region, the Late group was always less diverse than the Early one.

The coefficient of differentiation showed that for regions where millet is a major crop (the Early West, Early East, and India groups), intra-population diversity makes up 80%–90% of the total diversity, whereas in regions where pearl millet is of minor importance (mainly late-maturing cultivars), the intra-population diversity falls below 70% of the total diversity observed. These figures can be accounted for by high levels of allogamy in pearl millet and by genetic drift.

It appears that, together, the Early West and Early East groups contain the total enzyme diversity present in pearl millet and the other groups do not contribute additional new diversity.

It is noted that: (a) the total pearl millet diversity computed according to intra-group diversities and inter-group Nei's distances is 2.709, which is less than the total diversity in the Early West group of 2.99. Furthermore, the inter-group diversity comprises only 6.7% of the total diversity. The group Early West and Early East together have a diversity of 2.95, which is equivalent to that of the Early West group. Early East group is as diverse as Early Mali but is distinct. The combined group Mali and Early East is more diverse than its components and is as diverse as Niger. (b) The genes that are quasi-monomorphic in the Early West group remain so in the other groups. No rare alleles in the West Africa group become frequent elsewhere. The ordering of genes by decreasing diversity is the same in all groups (Table 5). The only novelty is the presence, outside of West Africa, of some new rare allozymes for genes *Mdh C, Adh A, Est A,* and *Got A.* (c) Among the alleles which discriminate groups, in general, the most frequent allele in the Early West group tends towards fixation in the other groups (Table 6). A unique case of frequency inversion was observed with *Adh A6,* whose frequency varied from 0.06 in the Early West to 0.67 in the Late South group. However, a comparison restricted to the Mali and Early East groups shows a frequency inversion for the *Pgm A2* allele (0.76 in Mali and 0.26 in Early East). Therefore we are of the opinion that the axis Mali-Niger-Early East connects different principal focal points of diversity and that the combined group Early West and Early East is the source of all pearl millet diversity.

The occurrence of all the pearl millet enzyme diversity in samples from a unique geographical region, the low inter-regional diversity, the early-late disjunction in West African millets with occurs consistently even in cultivars from the same village, irrespective of ecological zone or country (Tostain et al. 1987), and the disappearance of this early-late disjunction outside of West Africa leads us to believe that the environment has had little effect on the organization of pearl millet enzyme diversity and that these observations are due to migrations, foundations, and genetic drift from a unique gene source.

Discussion

The analysis of enzyme polymorphism in pearl millet has shown that the total enzyme diversity is contained in

early-maturing cultivars grown south of the Sahara between Senegal and the Red Sea, and that this diversity is organized into centers corresponding to Mali, Niger, Ghana, and East Africa. Considering that most of these centers of diversity are in the Sahel, which is the only region where the cross-fertile wild species *Pennisetum violaceum* is currently found, it would seem that the cultivation of pearl millet occurred at multiple sites across the Sahelian belt and that this domestication first produced early-maturing cultivars.

The strong divergence between Indian and southern African millets and their relative proximity with West African millets, which are the most diverse, implies that Indian and South African millets have independent origins in West Africa. The similarity between samples from India and Niger and the few samples from Niger, Sudan, Uganda, Kenya, and Somalia which group with Indian cultivars, would seem to indicate a path of migration from Niger or the central Sahel to India via the Arabian coast, Iran, and Pakistan.

This hypothesis of pearl millet migration is corroborated by the discovery on the coast of Abu Dhabi of 4,500-year-old sorghum spikelets, from the site of an oasis (Cleuziou and Costantini 1982). Similarly, the discovery in the Indus Valley of large cities from the Harappa civilization, which by 5,000 BP had already developed trade links with Arabia (Jarrige 1977) validates the existence of this migration route. It is justifiable to support this hypothesis with evidence from the domestication of sorghum, since sorghum was most probably brought into cultivation in East Africa (Harlan and Stemler 1976; Ollitrault 1987) during the same period as pearl millet and by the same people. Therefore, it is logical to assume that sorghum and pearl millet migrated together with the same farmers or traders.

The early-maturing cultivars would have been well-adapted to cross the arid lands of Arabia and Iran. Although the oldest pearl millet seen recorded from India dates back to only 3,200 BP (Allchin 1969), the Abu Dhabi discovery of sorghum indicates that the migration to India started about 5,000 BP and that pearl millet domestication commenced at least by 6,000 BP.

Such an early date for the domestication of pearl millet is plausible because it is known that between 10,000 and 4,000 BP, the Sahara was much wetter than it is today (Servant 1983) and was inhabited by many sedentary human settlements. Pearl millet domestication would have been well advanced by 4,500 BP, when the Sahara became more arid and a radical change in the human populations occurred (Roset 1983).

The origin of southern African millets seems strongly based on West African late-maturing cultivars, which themselves probably descended from a restricted number of early-maturing cultivars (Tostain et al. 1987). All the late-maturing cultivars seem to have originated from a generally diverse core composed of millets from Mali, Burkina Faso, and Nigeria, countries adjacent to Niger. Therefore, as found by the previous study (Tostain et al. 1987), Niger appears to be the source for the migration of late-maturing cultivars, which simultaneously spread along the forest belt westwards towards Senegal and east and southwards through the corridor between Uganda and Kenya to cross the equator. The late-maturing cultivars would have been better adapted than early cultivars to traverse the equatorial zone with its heavy rainfall.

This interpretation of the results of the enzyme analyses is corroborated by linguistic and archaeological facts and again by evidence from the domestication of sorghum. The presence of pearl millet in the savanna zone in northern Ghana is dated to around 3,250 BP (Davies 1968). Linguists describe a migration of Bantu languages starting from Central Africa (Cameroon or Nigeria) around 3,500 BP and spreading throughout southern Africa. Similarly, archaeologists attribute the establishment of the Iron Age culture in southern Africa to its southwards spread from north of the equator (Phillipson 1984). Furthermore, Harlan and Stemler (1976) suggest a migration of the sorghum guinea race, which is well-adapted to environments with heavy rains, from western Africa to southern Africa about 1,000 years after the migration of sorghum to India.

Ollitrault (1987) proposes an alternative theory based on his observations on enzyme diversity in sorghum. West African guinea sorghums are, in fact, composed of two different enzymatic types, one specific to West Africa and the other specific to southern Africa. Ollitrault suggests that the first type was founded by a direct migration from the East African centre of domestication and that the second type is the result of a secondary migration from southern Africa. However, the evolutionary model put forward here would seem to explain quite well this enzyme similarity between southern African sorghums and some West African sorghums. The sorghum migration towards Southern Africa probably started from Central Africa and split into a West branch and an East-South branch on contact with the forest.

Conclusions

This article describes the study of enzyme polymorphism in pearl millet for eight enzymes: EST, ADH, PGI, PGM, CAT, PGD, GOT, and MDH. Six polymorphic proteins, coded by one loci each, were observed: EST A, ADH A, PGI A, PGD A (four dimeric enzymes), PGM A (monomeric enzyme), and CAT A (tetrameric enzyme). Their variability did not appear to be determined by the environment. In spite of the low number of enzyme markers and the small amount of inter-population and inter-group diversity, a clear and coherent picture of pearl millet do-

mestication and evolution was perceived: multiple site domestications in the African Sahel – creation of early-maturing cultivars and their migration to India plus a southward migration into the Sudanian zone – creation of late-maturing cultivars – continuation of the migration, simultaneously, westwards and east and southwards to southern Africa. Harlan's (1971) non-center outline fits quite well with enzyme data. The pearl millet evolutionary outline proposed here for pearl millet shows a remarkable parallelism with those proposed for sorghum and finger millet *Eleusine coracana* (Purseglove 1976).

We are in the process of analyzing a comprehensive collection of *P. violaceum,* as more information on the main sites of domestication is needed to complete the model of evolution and domestication proposed here. It is also important to evaluate the usefulness of currently available information on enzyme diversity in a breeding program.

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