Theor Appl Genet (2001) 103:855–861

A. Rouamba · M. Sandmeier · A. Sarr · A. Ricroch

Allozyme variation within and among populations of onion (*Allium cepa* L.) from West Africa

Received: 24 August 1995 / Accepted: 26 February 2001

Abstract Local germplasm of onion (*Allium cepa* L.) in West Africa is threatened by extinction. Sixteen populations of onion collected in five countries in West Africa were investigated for isozyme polymorphism using four polymorphic enzyme systems (ADH, MDH, 6-PGDH and PGI) among nine enzyme systems assayed. This is the first report on the genetic diversity of local landraces of onion. The inheritance of two dimeric enzyme systems PGI and MDH was demonstrated using F_2 progeny arrays. The PGI system revealed a single locus with three alleles, and the MDH system revealed three loci with four alleles. Four polymorphic systems revealed nine alleles (*adh-a1* and *a2*, *mdh-c1* and *c2*, *6-pgdh-a1* and *a2*, and *pgi-a1*, *a2* and *a3*) in the 16 local populations observed. The mean number of alleles per polymorphic locus was 2.25, and 67% of the alleles were present in all populations. Allele *6-pgdh-a2* was present in only two landraces (from Niger and Nigeria); it is considered to be a rare allele (frequency approximately 2%). Among the 16 populations, within-population diversity was greater (90%) than between-population diversity (10%). Genetic distance analyses showed an aggregate of all populations except for two, which originated from Nigeria, an English-speaking country.

Keywords *Allium cepa* L. · Isozyme diversity · Inheritance · Germplasm

Communicated by A.L. Kahler

A. Rouamba
Institut d'Etudes et de Recherches Agricoles (IN.E.R.A),
03 BP 7192, Ouagadougou 03, Burkina-Faso

M. Sandmeier · A. Sarr · A. Ricroch (✉)
Universite Paris-Sud XI, CNRS UPRES-A 8079,
Laboratoire Ecologie, Systématique, Evolution, Bât. 362,
91405 Orsay cedex, France

Present address:
A. Ricroch,
Institut National Agronomique Paris-Grignon (INA P-G),
16 rue Claude-Bernard, 75231 Paris cedex 05, France

Introduction

Onion (*Allium cepa* L.) is among the most important crops in West Africa. It ranks after tomato both for production volume and trade. Nevertheless, production of this staple food does not cover West Africa's needs except in Niger where onion is the major vegetable crop. A better understanding of the available genetic variation in onions would lead to qualitative and quantitative improvements in seed quality and production.

Landraces may be valuable sources of genetic variation for the production of modern varieties combining high yield (under minimum agronomic culture), earliness, good storability and quality, including tolerance to several pests and diseases. Farmers grow local landraces adapted to their agricultural practices, environment and consumption criteria. However, local landraces are threatened by increased use of a highly inbred local variety ('Violet de Galmi'), which is widely cultivated in the soudano-sahelian zone, and by other genetically uniform varieties, which have a satisfactory yield but with a low bulb-storage ability (Rouamba et al. 1995).

Samples of onions from 16 populations representing local landraces were collected from five West African countries (Benin, Burkina-Faso, Mali, Niger and Nigeria), to examine the genetic variation within and among the populations (Rouamba et al. 1993). This is the first report on the genetic diversity of local populations of onion using isozymes. Although isozymes have been used for breeding-system analyses or genetic-diversity measurements for many plant species (Brown 1978), there is a paucity of isozyme polymorphism in *A. cepa* (Peffley et al. 1985; Peffley and Orozco-Castillo 1987; Loaiza-Figueroa and Weeden 1990; Cryder et al. 1991; Van der Valk et al. 1991; Shigio et al. 1996). In this study, we report the genetic diversity of nine isozyme systems and present the results of the genetic inheritance analyses of both phosphoglucoisomerase (PGI, EC 5.3.1.9) and malate dehydrogenase (MDH, EC 1.1.1.37) enzyme systems.

Materials and methods

Plant material

Sixteen local cultivated populations of the biennial onion were sampled from Benin, Burkina-Faso, Mali, Niger and Nigeria, and subjected to isozyme analysis (Table 1). The method of collecting onion germplasm in West Africa was described previously (Rouamba et al. 1993). Additionally, five parental lines (P_1, P_2, P_3, P_4 and P_5), and four of their F_1 hybrids ($P_1 \times P_2$, $P_1 \times P_3$, $P_2 \times P_3$, and $P_4 \times P_5$) were obtained from private seed companies. F_1 hybrids were identified using the MDH system. In each instance a single F_1 plant was selected from Burkina-Faso (6BF6) with the genotype designated C1C2C′1C′2 for the MDH locus. The F_1 plant was self-fertilized to produce F_2 progeny, which were used to assess the inheritance of observed isozyme patterns of two systems: malate dehydrogenase (MDH, EC1.1.1.37) and phosphoglucoisomerase (PGI, EC5.3.1.9).

Seeds with no insecticide or fungicide treatments were sown directly into soil in greenhouses. Leaves of 6-week-old plants (130–150 mg per plant) were used for electrophoresis for all enzyme systems except alcohol dehydrogenase (ADH, EC1.1.1.1). ADH was assayed using root extracts of the same individuals. Twenty three to forty eight individuals of each local population were studied for each system. The inheritance of PGI and MDH isozyme patterns were analyzed using parents, F_1 hybrids, and F_2 progeny. Twenty three to 48 individuals of the parental lines and F_1 hybrids arrays were analyzed. For the F_2 progeny 32 and 65 individuals were studied for inheritance of the PGI and MDH enzyme systems, respectively.

Electrophoresis

A total of nine enzyme systems were assayed for the study: alcohol dehydrogenase (ADH, EC1.1.1.1), catalase (CAT, EC1.11.1.6), malate dehydrogenase (MDH, EC1.1.1.37), 6-phosphoglucodehydrogenase (6-PGDH, EC1.1.1.43), glutamic-oxalo-acetic-transaminase (AAT-GOT, EC2.6.1.1), phosphoglucomutase (PGM, EC2.7.5.1), phosphoglucoisomerase (PGI, EC5.3.1.9), acid phosphatase (ACP, EC3.1.3.2) and leucine-aminopeptidase (LAP, EC3.4.11.1).

Enzyme extraction and starch-gel electrophoresis techniques were those of Vallejos and Tanksley (1983) and Schields et al. (1983). Fresh leaf samples were macerated in 150–200 µl of extraction buffer at 5°C. The macerated material was centrifuged at 10000 tr/min for 10 min. Staining conditions were conducted according to Peffley et al. (1985) and Ricroch (1990).

A modification of the extraction and separation conditions described by Schields et al (1983) was used to characterize the PGI system. The extraction buffer consisted of TRIS-HCl (0.1 M), KCl (10 mM), $MgCl_2$ (1 mM), mercapto-ethanol (14 mM), EDTA (1 mM), ascorbic acid (0.1 M) and PVP soluble 40 T (0.2 g/ml). Fresh samples were dipped into liquid nitrogen for 1 min. Two extraction buffers were used to compare isozyme expression for the MDH enzyme system. The best results were obtained when the extraction buffer consisted of TRIS-HCl (0.1 M) and glutathion (10 g/l) at pH 8.5. The gel and electrode buffers were histidine/citrate at pH 5.7 and pH 6.5 respectively for the PGI and MDH systems (Trigui et al. 1996).

Statistical procedure

Hardy-Weinberg analyses of 32 F_2 individuals were used to determine the inheritance of PGI and MDH polymorphism (Emigh 1980). The dimeric PGI system appears to be encoded by a single dimeric locus (*Pgi-A*) with three alleles designated *pgi-a1*, *pgi-a2* and *pgi-a3*. The letter A designates the cathodal migration of bands (Schields et al. 1983). The dimeric MDH enzyme appears to be encoded by three independent loci (*Mdh-A*, *Mdh-B* and *Mdh-C*) with no interaction with four alleles (*a1*, *b1*, *c1* and *c2*). *Mdh-A* and *Mdh-B* are monomorphic loci. The third locus *Mdh-C* is polymorphic (alleles *c1* and *c2*).

Table 1 Collection sites of 16 local populations of onion in Africa

Population	Collection site	Country (and latitude)
1B	Malenville (granary)	Benin (11°5N)
6BF	Zoula (granary)	Burkina-Faso (12°2N)
18BF	Koudougou (market)	Burkina-Faso (12°2N)
24BF	Ouanrégou (granary)	Burkina-Faso (11°7N)
26BF	Tougan (granary)	Burkina-Faso (13°4N)
31BF	Kongounsi (granary)	Burkina-Faso (13°3N)
8 M	Ningeri (market)	Mali (14°5N)
2NI	Soumarana (granary)	Niger (13°3N)
6NI	Sabanguida (granary)	Niger (13°6N)
7NI	Eroufa (granary)	Niger (13°6N)
8NI	Galmi (granary)	Niger (13°6N)
9NI	Tonfafi (granary)	Niger (14°2N)
11NI	Dabaga (field)	Niger (17°2N)
14NI	Ayorou (granary)	Niger (14°5)
1NA	Yibiya (field)	Nigeria (12°4N)
2NA	Yibiya (field)	Nigeria (12°4N)

The panmictic balance per population for all polymorphic loci was tested using the sign test (Sokal and Rohlf 1969). The sign test counts the number of positive and negative signs among the differences between expected and observed values of mean heterozygosity. We tested the hypothesis that the *n* plus and minus signs are sampled in equal proportions, as might be expected if there were no true differences between the two paired samples. We calculate the expected probability of sampling one minus sign in a sample of the 16 populations assuming p=0.5.

Allele frequencies for polymorphic loci were estimated in each of the 16 populations. The mean allelic frequency was calculated by pooling all populations. Allele-frequency estimates were obtained using BIOSYS software (Swofford and Selander 1981) for the assessment of genetic diversity or population structure. Within-population diversity was assessed by determining the average allele frequency per locus, the proportion of polymorphic loci, the mean heterozygosity, and Nei's diversity index (Nei 1967). Diversity between populations was determined using Wright's index (Wright 1967). Nei's index and Wright's F statistics index were used as a measure of genetic differentiation of populations for the polymorphic loci. The fixation index given by the G_{st} value $(H_t\text{-}H_s/H_t)$, defined as the between-population variability relative to the total variability, measures the amount of genetic variation in all populations combined that is attributable to genetic differentiation among local populations. The relationship among populations was determined using Nei's genetic distances (Nei 1978).

Results

Inheritance of PGI and MDH isozymes

Six phenotypic patterns of the PGI enzyme system are presented in Fig. 1. Three single-band isozyme patterns were observed in zones 1, 3 and 6, and represented the homozygous parents, P_1, P_2 and P_3, respectively. Three bands characterized the heterozygous hybrids HF_1 ($P_1 \times P_2$), ($P_1 \times P_3$) and ($P_2 \times P_3$). The intense staining of the intermediate band (zones 2, 4 and 5) corresponds to the interaction of two alleles. The PGI enzyme system is hypothesized to be encoded by a single locus with three alleles. We expected 25% of individuals with a one-band genotype (A2A2), 25% of individuals with a one-band genotype (A3A3), 50% of individuals with a three band

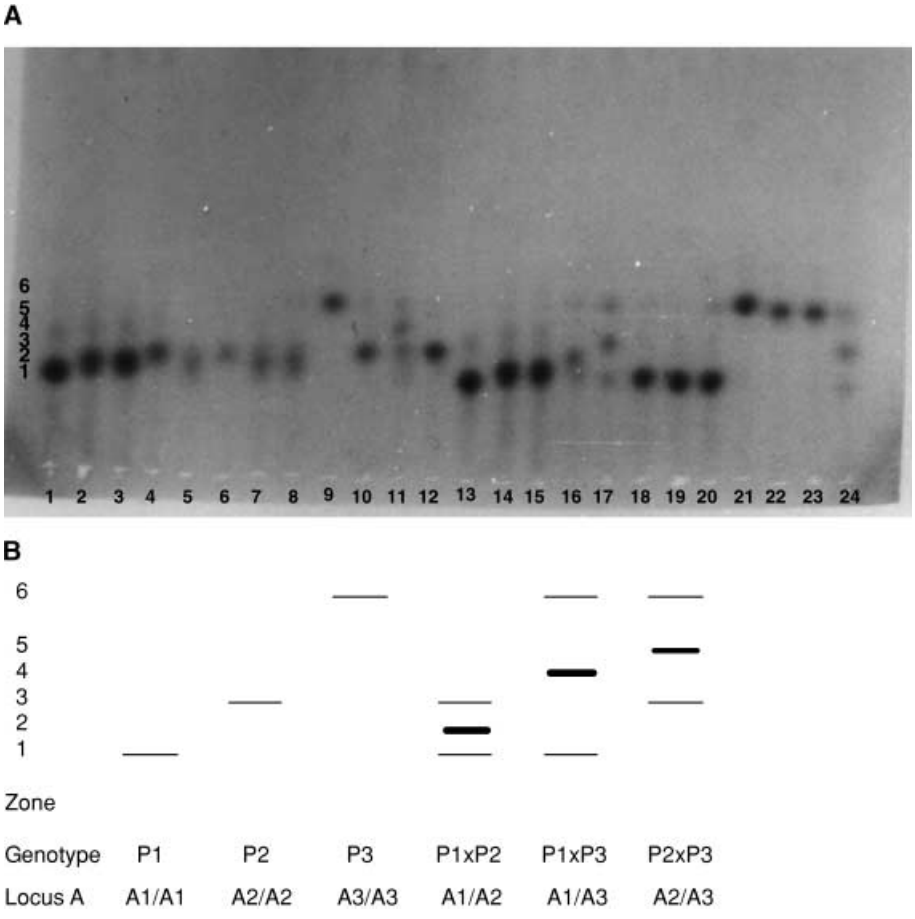

Fig. 1 Electrophoretic gel of the PGI enzyme system (**A**). Ten individuals of parent P_1 are shown in *lanes 1 to 4*, *13 to 15*, and *18 to 20*; two individuals of parent P_2 corresponded to *lanes 10 and 12*, and four individuals of the parent P_3 are shown in *lane 9* and *21 to 23*. Five individuals of hybrid F_1 ($P_1 \times P_2$) are shown in lanes *5 to 8* and *16*; two individuals of hybrid F_1 ($P_1 \times P_3$) are shown in lanes *17 and 24*, and a single individual of the hybrid F_1 ($P_2 \times P_3$) corresponded to *lane 11*. Schematic representation of the six PGI phenotypes observed in three parental lines and their F_1 hybrids (**B**)

genotype (A2A3) in the F_2 segregation of locus A. We observed nine individuals (A2A2), ten individuals (A3A3), and 13 individuals (A2A3) among 32 individuals, respectively. Differences between expected and observed frequencies were not significant at the level of 5% (χ^2=1.19; *df* 2).

Three MDH phenotypes are presented in Fig. 2. Parents showed three or four bands while F_1 hybrids showed five bands. Parent P_4 showed four bands (zones 1, 2, 4 and 5), and parent P_5 showed three bands (zones 1, 2 and 3). Hybrid F_1 (P4×P5) showed five bands corresponding to zones 1, 2, 3, 4 and 5, respectively. To explain the zymogram patterns observed we offer the following hypothesis: bands are encoded by three different loci (A, B and C), one of them being duplicated (C′). Concerning the cross presented in Fig. 2, we may infer that the loci A and B are monomorphic, loci C and C′ presenting two alleles each. Thus, the five zones can be interpreted in the following way. Zone 1 revealed a single band designated A1. Zone 2 corresponded to the juxtaposition of two alleles, a single allele b1 of the monomorphic locus Mdh-B and the allele 1 of the locus Mdh-C. Zone 3 corresponded to the superposition of the allele 1 of the locus Mdh-C′ (a presumed duplicated locus) and the interaction of the alleles 1 and 2 of the locus Mdh-C. Zone 4 corresponded to the allele 2 of the locus Mdh-C and the interaction of the alleles 1 and 2 of the duplicated locus Mdh-C′. Zone 5 corresponded to allele 2 of the duplicated locus Mdh-C′. We expected 25% of individuals with three bands (C1C1C′1C′1), 25% of individuals with four bands (C2C2C′2C′2), and 50% of individuals with five bands (C1C2C′1C′2) in the F_2 progeny. We observed 15 individuals (C1C1C′1C′1), 16 individuals (C2C2C′2C′2), and 34 individuals (C1C2C′1C′2) among the 65 between expected, respectively, individuals examined. Differences and observed frequencies were not significant at the 5% level (χ^2=0.11; *df* 2). Therefore the MDH enzyme system appears to be encoded by three loci with four alleles.

Isozyme banding patterns of other enzyme systems

Three isozyme phenotypes were observed for each of the enzyme systems ADH and 6-PGDH, respectively. The ADH isozyme patterns suggested a single polymorphic locus with two alleles *adh-a1* and *adh-a2*. The isozyme band patterns of 6-PGDH suggested a single polymorphic locus with two alleles 6-*pgdh-a1* and *6-pgdh-a2*. A single band was observed for each of the enzyme systems PGM, CAT, ACP, LAP and AAT-GOT. These single-band enzyme systems were assumed to each represent a monomorphic locus with a single dominant allele.

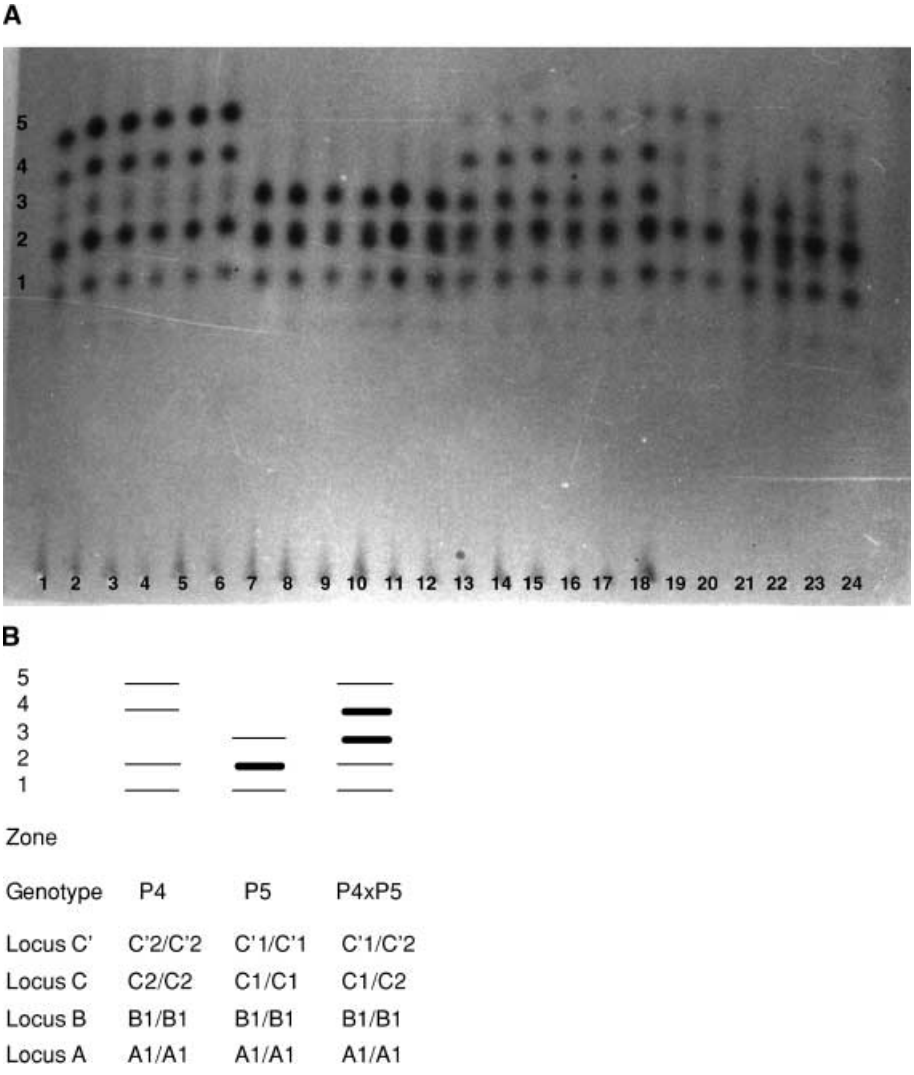

Fig. 2 Electrophoretic gel of the MDH enzyme system (A). In *lanes 1 to 6* and *19 to 20*, parent P_4 showed four bands (*zones 1, 2, 4 and 5*). In *lanes 7 to 12* and *21 to 22*, parent P_5 showed three bands (*zones 1, 2 and 3*). In *lanes 13 to 18* and *23 to 24*, hybrids F_1 ($P_4 \times P_5$) showed five bands corresponding to *zones 1, 2, 3, 4, and 5* respectively. Schematic representation of the three MDH phenotypes observed in two parental lines and the F_1 hybrid (**B**)

Table 2 Allelic variation within 16 local landraces of onion in Africa

Allozyme	Population code																
	1B	6BF	18BF	24BF	26BF	31BF	2NI	6NI	7NI	8NI	9NI	11NI	14NI	1NA	2NA	8M	Mean
adh-a1	0.848	1.000	1.000	1.000	1.000	1.000	0.826	1.000	1.000	0.913	0.837	1.000	0.856	0.478	0.870	0.957	0.925
adh-a2	0.152	0.000	0.000	0.000	0.000	0.000	0.174	0.000	0.000	0.087	0.163	0.000	0.144	0.522	0.130	0.043	0.075
mdh-c1	0.375	0.281	0.427	0.531	0.354	0.281	0.208	0.125	0.302	0.354	0.198	0.333	0.396	0.167	0.542	0.281	0.327
mdh-c2	0.625	0.719	0.573	0.469	0.646	0.719	0.792	0.875	0.698	0.646	0.802	0.667	0.604	0.833	0.458	0.719	0.673
6pgdh-a1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.822	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	0.984
6pgdh-a2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.178	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.016
pgi-a1	0.188	0.250	0.250	0.115	0.344	0.585	0.287	0.266	0.255	0.219	0.240	0.656	0.191	0.000	0.188	0.042	0.255
pgi-a2	0.510	0.406	0.583	0.698	0.396	0.383	0.436	0.383	0.340	0.573	0.354	0.198	0.511	0.844	0.167	0.833	0.476
pgi-a3	0.302	0.344	0.167	0.188	0.260	0.032	0.277	0.351	0.404	0.208	0.406	0.146	0.298	0.156	0.646	0.125	0.269
(M.H.) obs[a]	0.105	0.069	0.085	0.068	0.098	0.074	0.099	0.080	0.067	0.077	0.096	0.071	0.120	0.094	0.115	0.075	
(M.H.) exp[b]	0.113	0.089	0.089	0.081	0.110	0.077	0.107	0.099	0.091	0.101	0.105	0.080	0.113	0.088	0.118	0.065	

[a] (M.H.) obs, mean heterozygosity observed by direct count (all loci considered)
[b] (M.H.) exp, mean heterozygosity expected in Hardy-Weinberg proportion (all loci considered)

Table 3 Measures of heterozygosity for the four polymorphic loci assayed

Enzyme locus	Allele	Measures of heterozygosity			
		H_s[a]	H_t[b]	H_a/H_t	G_{st}[c]
Mdh-C	*c1*	0.009	0.011	0.805	0.19
	c2	0.009	0.011	0.805	0.19
	Total	0.017	0.022	0.805	0.19
Adh-A	*a1*	0.014	0.015	0.930	0.07
	a2	0.014	0.015	0.930	0.07
	Total	0.029	0.031	0.930	0.07
6-pgdh-A	*a1*	0.002	0.002	0.924	0.07
	a2	0.002	0.002	0.924	0.07
	Total	0.003	0.004	0.924	0.07
Pgi-A	*a1*	0.023	0.025	0.931	0.06
	a2	0.031	0.033	0.933	0.06
	a3	0.016	0.018	0.898	0.10
	Total	0.070	0.076	0.924	0.07

[a] H_s, within-population heterozygosity
[b] H_t, total heterozygosity
[c] G_{st}, relative differentiation between populations

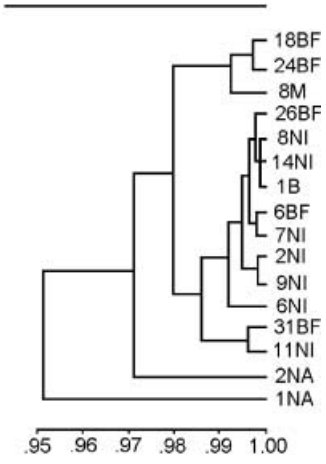

Fig. 3 Dendrogram based on the Nei's genetic distance of 16 local populations of onion in West Africa

Table 4 Mean heterozygosity values for four enzyme loci among all onion populations studied

Enzyme locus	Allele	F_{is}[a]	F_{it}[b]	F_{st}[c]
Mdh-C	*c1*	–0.005	0.055	0.060
	c2	–0.005	0.055	0.060
	Mean	–0.005	0.055	0.060
Adh-A	*a1*	–0.037	0.163	0.193
	a2	–0.037	0.163	0.193
	Mean	–0.037	0.163	0.193
6-pgdh-A	*a1*	0.226	0.329	0.133
	a2	0.226	0.329	0.133
	Mean	0.226	0.329	0.133
Pgi-A	*a1*	0.124	0.246	0.140
	a2	0.137	0.261	0.143
	a3	0.188	0.271	0.101
	Mean	0.150	0.260	0.129
Over all loci	2.250	0.072	0.178	0.114

[a] F_{is}, within-population fixation index
[b] F_{it}, within-population deficiency of heterozygotes
[c] F_{st}, fixation index

Within-population and between-population diversity

Nine alleles were observed for the four polymorphic loci: two alleles each for *Adh-A*, *Mdh-C*, and *6-pgdh-A* and three alleles for *Pgi-A* (Table 2). Among the populations studied, the mean number of alleles per locus was 2.25 for the four polymorphic loci. In addition, 66.6% of alleles were present in all populations. Allele *adh-a2* was absent in all populations that originated from Burkina-Faso. Allele *6-pgdh-a2* was a rare allele with an average frequency of 0.016. This allele was present in only two populations (6NI and 2NA) that originated from South of Niger and North of Nigeria, respectively (Table 1). The dendrogram based on Nei's distance showed that population 6NI was closer to population 2NA than to the other populations from Niger (Fig. 3).

Population heterozygosity (H_s), defined as the expected average heterozygosity among populations, varied from 0.004 (*6-pgdh-A*) to 0.071 (*Pgi-A*) with an average over the four loci of 0.030 (Table 3). Total heterozygosity (H_t) ranged between 0.004 to 0.076, from *6-pgdhA* and *Pgi-A*, respectively, with an average over the four loci of 0.033. The within-population variability relative to the total variability given by the H_s/H_t value varied from 0.805 (Mdh-C) to 0.930 (Adh-A) with an average over the four loci of 0.906. G_{st} varied from 0.070 (*Adh-A*) to 0.195 (*Mdh-C*) with an average over the four loci of 0.094.

The within-population fixation index (F_{is}), which is equivalent to population heterozygosity (H_s), varied across loci from positive to negative values (Table 4). Allele frequencies varied between populations as indicated by the greater value of the fixation index (F_{st}), defined as the lack of heterozygotes between populations, compared to the value of the fixation index within-population (F_{is}) for each polymorphic locus. The average values of F_{st} and F_{it} were low (0.114 and 0.178 respectively). The lack of heterozygotes within-populations (F_{it}) was greater for *Pgi-A* and *6-pgdh-A* (0.260 and 0.329, respectively) than for *Mdh-C* and *Adh-A* (0.055 and 0.163, respectively). The sign test counts 13 nega-

tive signs among the differences between expected and observed values of mean heterozygosity per population (Table 2). These differences were significant at the 5% level.

Discussion

Inheritance of PGI and MDH isozymes

Inheritance analyses using F_2 progeny suggest that the dimeric PGI enzyme is encoded by a single locus (*Pgi-A*) with three alleles designated *pgi-a1*, *pgi-a2*, and *pgi-a3*.

The dimeric MDH enzyme appears to be encoded by three independent loci (*Mdh-A*, *Mdh-B* and *Mdh-C*) with no interaction with four alleles (*a1*, *b1*, *c1* and *c2*) (Fig. 2). Our results did not agree with those described earlier (Peffley et al. 1985; Peffley and Orozco-Castillo 1987). *Mdh-A* and *Mdh-B* are monomorphic, the third locus *Mdh-C* is polymorphic (alleles *C1*, and *C2*). Also there appears to be a duplicated MDH locus designated *Mdh-C′* (alleles *c′1*, and *c'2*).

Allozyme variation

Four of the nine enzyme systems ADH, MDH, 6-PGDH and PGI, were polymorphic in our study. Peffley and Orozco-Castillo (1987) have assayed allozyme variation within and among 188 cultivars of onion using four systems; only one system was found to be polymorphic (*adh-a1* and *adh-a2*) due to the narrow genetic diversity of the inbred varieties studied. These two alleles were also present in the populations we examined. Shigio et al. (1996) examined a small sampling within *Allium* species (including seven *A. cepa* varieties of onion) using the PGI enzyme system. Among the three alleles found in populations of our study two corresponded to those observed in *A. cepa* (onion). The third allele was present only in *Allium oschaninii* (a putative common ancestor of onion) and could be considered as a progenitor allele. These results suggest that the evolutionary history of onion in West Africa is probably based on a single-genotype introduction of onion coming from Central Asia where *A. cepa* (onion) was cultivated from *A. oschaninii*.

Geographical differentiation

The low average value of F_{st} (0.114) indicates that no strong divergence has occurred between populations. The dendrogram based on Nei's genetic identity shows no relationship between allele frequency and the geographical origin of collected populations, except for the two populations from Nigeria (Fig. 3). These two populations from an English-speaking country (1NA and 2NA) remained distinct although they have been collected in an area close to Niger (French-speaking country). No commercial exchange of seeds and bulbs occurred between French-speaking and English-speaking farmers, while within and between French-speaking countries transfers of seeds and bulbs occurred allowing mixing of isolated onion populations (Rouamba et al. 1993). Before colonization local tribes exchanged plant material.

Allozyme frequencies did not differ among populations of the cultivated species. We had assumed that population differentiation would be evident on a continental scale (Africa). Indeed in pearl millet, allele frequencies change predictably from East to West Africa (Leblanc 1983; Tostain, Riandey and Marchais 1987; Sandmeier et al. 1989; Tostain and Marchais 1989). Geographical patterns of genetic diversity among local populations of rice are associated with historical exchanges between ethnic groups speaking the same language and sharing the same (agri)cultural practices (Pernès 1983).

Genetic variability

Thirteen populations among the 16 examined revealed a paucity of heterozygotes (F_{it}=0.178), as the test of sign confirmed (Table 3). Wright's F values suggested subdivision of local populations. There are several possible causes. First, although onion is predominantly allogamous, autogamy even at a low rate occurs in the populations sampled. Unpublished data confirmed results obtained by Schweisguth (1976). Second, since farmers produced seeds from a very small quantity of bulbs as progenitors, genetic drift may have been a factor (Rouamba et al 1993). Within-population diversity (90.6%) was greater than between-population diversity (9.4%). In pearl millet, Pilate-André (1992) found a similar pattern (75% and 25% for the within-population and between-population diversity, respectively). The mean diversity among the 16 populations studied (G_{st}=0.09) was similar to the genetic diversity found in predominantly outcrossing species (0.07) such as onion (Loveless and Hamrick 1984).

In summary, this study provides useful information on allozyme variability which leads to a better understanding of the genetics of the widely cultivated onion. The results suggest that in order to increase the genetic diversity of onion landraces, it will be necessary to initiate similar studies on a continental scale over Africa.

Acknowledgments We are grateful to Dr. E.P. Lacey and Dr. E.B. Peffley for scientific support and to Dr. F. Lamy, Mrs. E. Samain and M. Mariam for software assistance. The authors wish to acknowledge Mr. Boussac and Mr. Feyt from the "Clause" and "Agrocinq" seed companies for providing seeds of onion F_1 hybrids. This work was supported by a grant from the Ministry of Research of Burkina-Faso. Orsay University, and the Centre National pour la Recherche Scientifique (CNRS) in France financially supported this work.

References

Brown AHD (1978) Isozymes, plant population genetic structure and genetic conservation. Theor Appl Genet 52:145–157

Cryder CM, Corgan JN, Urquhart NS, Clason D (1991) Isozyme analysis of progeny from (*Allium fistulosum*×*Allium cepa*) × *Allium cepa*. Theor Appl Genet 82:337–345

Emigh TH (1980) A comparison of tests for Hardy-Weinberg equilibrium. Biometrics 36:627–642

Hamrick JL, Linhart YB, Mitton JB (1979) Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annu Rev Ecol Syst 10:173–200

Leblanc JM (1983) Enzyme polymorphism of *Pennisetum americanum* in the Ivory Coast. Japan J Genet 58:121–131

Loaiza-Figueira F, Weeden NF (1990) Effects of seed increases procedures on isozyme polymorphism in *Allium*. FAO/IBPGR Int Plant Genet Res Newslett 83/84:1–3

Loveless MD, Hamrick JL (1984) Ecological determinants of genetic structure in plant populations. Annu Rev Ecol Syst 15:65–95

Nei M (1967) Genetic distances between populations. Am Nat 106:283–293

Nei M (1978) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

Peffley EB, Orozco-Castillo C (1987) Polymorphism of isozymes within plant introductions of *Allium cepa* L. Hortscience 22: 956–957

Peffley EB, Corgan JN, Horak KE and Tanksley SD (1985) Electrophoretic analysis of *Allium* alien addition lines. Theor Appl Genet 71:176–184

Pernès J (1983) La génétique de la domestication des céréales. La recherche 14:911–919

Pilate-André S (1992) Etude de l'organisation de la diversité génétique du complexe des mils pénicellaires (*Pennisetum* ssp.) par les marqueurs enzymatiques et par l'analyse moléculaire de la région ADH. Thèse de docteur en sciences de l'Universite Paris-XI

Ricroch A (1990) Evaluation des ressources génétiques de populations locales d'*Allium cepa* L. et analyse de la bulbification en conditions naturelles et contrôlées. Thèse de docteur en sciences de l'Universite Paris-XI

Rouamba A, Ricroch A, Sarr A (1993) Collecting onion germplasm in West Africa. FAO/IBPGR Int Plant Genet Res Newslett 94/95:15–17

Rouamba A, Robert T, Sarr A, Ricroch A (1995) Multivariate analyses for evaluation of agronomic potentiality of onion landraces from West Africa. Genome 39:1128–1132

Sandmeier M, Pilate-André S, Tazi L, Trigui L, Pernès J (1989) Variations de la fréquence allélique du gène ADH dans des populations de mil *Pennesitum typho*. In: 11ème réunion du groupe de biologie et génétique des populations, p 83

Schields CR, Orton TJ, Stuber CW (1983) An outline of general resource needs and procedure for the electrophoretic separation of active enzymes from plant tissue. In: Tanksley SD, Orton TJ (eds) Isozymes in plant genetics and breeding, Part A. Elsevier, Amsterdam, pp 443–468

Schweisguth B (1976) Physiologie de l'oignon, adaptation des cultivars et aptitude à la conservation. Oignon-INVUFLEX 27–32

Shigio M, Tashiro Y, Isshiki S, Miyazaki S (1996) Genetic analysis of phosphoglucoisomerase in cultivated and wild species of section *cepa* in *Allium*. Euphytica 90:195–200

Sokal R, F Rohlf (1969) Biometry. The principles and practices in biological research. Freeman, p 776

Swofford DL and Selander RB (1981) Biosys-1, a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J Hered 72:281–283

Tostain S, Riandey MF, Marchais L (1987) Enzyme diversity in pearl millet *Pennisetum glaucum*. 1. West Africa. Theor Appl Genet 74:188–193

Tostain S, Marchais L (1989) Enzyme diversity in pearl millet *Pennisetum glaucum*. 2. Africa and India. Theor Appl Genet 77:634–640

Trigui N, Sandmeier M, Salanoubat M, Pernes J (1986) Utilisation des données enzymatiques et morphologiques pour l'étude des populations et de la domestication des plantes. I. Séparation et identification génétique d'isozymes chez le mil (*Pennisetum thyphoides*). Agronomie 6:779–788

Vallejos CE, Tanksley SD (1983) Segregation of isozyme markers and cold tolerance in an interspecific backcross of tomato. Theor Appl Genet 66:241–247

Van der Valk, kik C,Vestapen F, Everink JT, de Vries JN (1991) Independent segregation of two isozyme markers and interplant differences in nuclear content in the interspecific backcross (*Allium fistulosum*×*Allium cepa*)×*Allium cepa*. Euphytica 55:151–156

Wright S (1967) The interpretation of population structure by F-statistics with special regard to systems of mapping. Evolution 19:395–420