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Wild pearl millet population (*Pennisetum glaucum, Poaceae*) integrity in agricultural Sahelian areas. An example from Keita (Niger)

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Abstract: Morphometric and isozymic analyses of adjacent cultivated and spontaneous populations of pearl millet in Niger revealed in the field a unique continuous distribution of phenotypes ranging from the most cultivated one to a typical cultivated × wild hybrid. The natural population was subdivided into a major wild group and a hybrid wild × cultivated group. Cultivated millet displayed an equilibrium state between recombined domesticated and wild genes. The natural population, in spite of a high rate of immigration by pollen from cultivated plants, retained its structure by apparently reproducing itself exclusively from the major wild group.

Pearl millet, *Pennisetum glaucum* (L.) R. BR., an allogamous diploid grass ranks as the fifth cereal in the world in order of economic importance after wheat, rice, maize, and sorghum. It is also of biological interest and allows the observation of coexistence between a domesticated plant and its wild ancestor, both of the same level of ploidy.

Many spontaneous pearl millet populations are scattered throughout Sahelian Africa from Mauritania and Senegal to Sudan, and their morphological structures differ according to the presence or absence of cultivated millets in their environment (TOSTAIN & al. 1986, TOSTAIN 1992). The Sahelian belt is divided into two parts: an agricultural zone, where in many regions cultivated pearl millet grows sympatrically with spontaneous millet, and a pastoral zone, north of the agricultural zone, where no cultivation is possible and only spontaneous forms are found. Throughout the pastoral zone, spontaneous millet shows a typical morphotype totally different from cultivated millet, characterized essentially by reduced plant height, small spikes, sessile and deciduous involucres with only one small seed hidden in bracts. This can be called the wild type because it shows no trace of domestication. In the agricultural zone, spontaneous millet populations show a very diverse continuous array or morphotypes including many types intermediate between the wild and cultivated millets.

BRUNKEN (1977) considerably simplified pearl millet taxonomy by gathering all cultivated and spontaneous pearl millets into a single biological species but chose nevertheless to keep three subspecies: *P. glaucum* subsp. *monodii* as the wild type, *P. glaucum* subsp. *glaucum* for the cultivated millet, and *P. glaucum* subsp. *stenostachyum* for all the intermediate forms. This infraspecific subdivision has so far been corroborated by isozymic analyses and hybridization observations. TOSTAIN (1992) showed a fundamental isozymic divergence between cultivated millet and wild millets, irrespective of whether they originate from the agricultural or pastoral zone. AMOUKOU & MARCHAIS (1993) noted general post-zygotic sterility in cultivated × wild crosses, but not in wild × wild or cultivated × cultivated crosses. This picture is simple in the case of wild accessions from the pastoral zone. In the case of wild plants from the agricultural zone, the plants used were chosen true to type by the experimenters within very diverse spontaneous populations. This choice raises the question of where the limit between wild and intermediate forms lies in a spontaneous population. Is a wild plant merely a tail of distribution arbitrarily truncated in a normal distribution? Does the coexistence of cultivated and spontaneous populations lead to the blending of the three subspecies?

A preliminary answer has been afforded in a study of two wild samples collected within spontaneous populations of the agricultural zone of Senegal and Niger. The observed offspring evidently consisted of a major wild type group identical with the parental types and of an intermediate group (MARCHAIS & TOSTAIN 1992). But the absence of genetic information on the adjacent fields precluded precise identification of the origin of the intermediate group.

The genotypical structure of adjacent cultivated fields and spontaneous populations was studied at Keita (Niger) to evaluate in each population the possible existence of BRUNKEN's subdivisions, their respective sizes, and their genetic origins.

Material and methods

The chosen locality was Keita (14° 46′ N, 5° 50′ E), 600 km from Niamey, the capital of Niger (Fig. 1). A wadi meanders in pearl millet fields, flanked on each border by a strip of spontaneous millets about 5 m broad. During the monsoon season, water runs in the wadi only a few hours after each rainstorm.

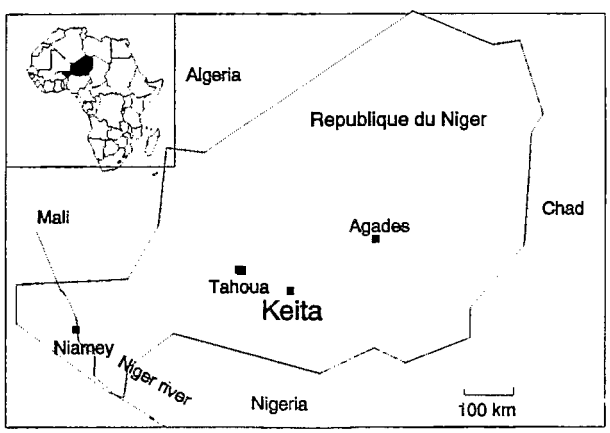

Fig. 1. Geographic position of the village of Keita in Niger, where wild millets grow in sympatry with cultivated millets

In 1988, open pollinated spikes were collected in the wadi spontaneous stand after identification of the maternal plants as either wild or intermediate (the latter are called henceforth chibra in this paper, according to the local designation). In the same way, open pollinated spikes were collected in the adjacent field on cultivated and chibra plants. From this material, 50 wild plant offsprings (designated WILD 88) and 5 cultivated plant offsprings (CROP 88) were grown at the International Crop Research Institute for the Semi Arid Tropics station of Niamey, with a line for each maternal plant. Each line was scored on 10 plants for 7 morphological traits discriminant for the 3 subspecies: main stem length, main spike length, main spike rachis diameter, involucral stalk length, number of spikelets in an involucre, seed length and breadth. In addition, 50 plant offsprings were grown and scored on a chibra plant from the wadi (CHIBRA W) and a chibra plant from the field (CHIBRA F). The latter were included for comparison of the morphological segregations in the previous origins. However, their interest is reduced because farmers never sow chibras seeds and the question in terms of the wadi is mainly to understand how the wild type is maintained.

Preliminary investigations revealed three markers discriminating WILD 88 and CROP 88: a morphological character (foliar limb hairiness) and two isozyme loci (phosphoglucomutase and alcohol dehydrogenase). Foliar limb hairiness is controlled by a two-allele gene: the dominant allele G gives glabrous limb and the gg homozygous recessive genotype gives hairy limb (MARCHAIS & TOSTAIN 1985). Phosphoglucomutase (PGM) and alcohol dehydrogenase (ADH) were analysed according to the methods reported by TOSTAIN & al. (1987). PGM locus A (*Pgm-A*) displayed only 2 alleles F and S. ADH locus A (*Adh-A*) was analysed at pH 6 and displayed only 2 alleles F and S. WILD 88 were scored on 10 plants per maternal plants for the 3 markers; CROP 88 was scored as an average of 50 plants per maternal plants for limb hairiness and 10 plants per maternal plants for isozymes.

At the end of the 1990 rainy season, the same morphological observations as in 1988 (foliar limb hairiness included) were made in situ on 100 plants in the wadi (WADI 90) and 100 plants in the field (FIELD 90), all randomly selected before flowering. These plants were also surveyed for the flowering date distribution of their successive spikes in order to evaluate the degree of reproductive isolation between any observed groups.

Because of incomplete morphological or isozymic data, the number of plants analysed was inferior to the maximum in both years.

The morphological data obtained from the groups in 1988 and 1990 were analysed together by a principal component analysis in order to evaluate the existence of subdivisions within and between families.

Dominant G allele (glabrous limb) frequency was estimated using the DOMT software of RITLAND (1990) which requires the hypothesis that G frequency is the same for ovules and pollen. Consequently, a common G frequency was estimated for the WILD 88 and WADI 90 plants having the wild type phenotype and descending from a wild type maternal plant, which is the case in WILD 88 but only a hypothesis in WADI 90. The method of determining the wild type phenotypes, one of the main questions of this study, is empirical and is presented in the results. A common G frequency was estimated for the CROP 88 and FIELD 90 origins. To test the conformity of 1988 and 1990 G frequencies, the observed phenotypic frequencies were compared to the expected frequencies with a common G frequency assuming panmictic proportions in the bulk of each family. Exceptionally, in the case of CROP 88, the 5 maternal genotypes were evident and the fit could be computed for each maternal spike.

The MLT software of RITLAND (1990) was used to analyse the isozyme data. For each selected group, this software estimates the ovule and pollen allelic frequencies, the most likely maternal genotypes, the fixation index for maternal plants, and the outcrossing rate. By bootstrap methods, the standard deviations are also computed. The maternal genotypes

could not be determined in the WILD 88 origins in the case of one plant offspring. Such plants were analysed together.

Results

Morphological variation pattern. The six origins – WILD 88, WADI 90, CROP 88, FIELD 90, CHIBRA W, and CHIBRA F – scored for the same 7 morphological traits, were analysed in the same principal component analysis. The first axis accounted for 70% of the variation and expressed, as expected, the contrast between wild and domesticated millets (Table 1). The frequency distributions along the first axis inside each origin allowed empirical consideration of three groups: one group, which we designated wild, included the classes numbered from 1 to 7; these pheno-

Table 1. Frequency distributions of individual plants in classes cut along the first axis of a principal component analysis on morphological characters of the different families

Class		WILD 88		WADI 90		CROP 88		FIELD 90		CHIBRA			Empirical group definition
Number	Limit									W	F		
1	− 4.0	1											
2	− 3.6	2											
3	− 3.2	11		2							1		
4	− 2.8	34	67%	6	62%							33%	wild
5	− 2.4	58		17						1	5		
6	− 2.0	23		10						11	4		
7	− 1.6	10		5						5	6		
8	− 1.2	12		9				1		4	1		
9	− 0.8	7		1						10	6		
10	− 0.4	6		3				1		7	2		
11	0.0	10		3				1		6	4		
12	0.4	14	33%	4	38%	1	24%	4	46%	2	6	65%	chibra
13	0.8	13		2		1		10			3		
14	1.2	4		2		4		5		1	5		
15	1.6	4				3		7		1	6		
16	2.0			1		4		7		1			
17	2.4					6		4		1	1		
18	2.8					7		6					
19	3.2					6		5					
20	3.6					4		13					
21	4.0					5		3					
22	4.4					4	76%	6	54%			2%	cultivated
23	4.8					5		3					
24	5.2							2					
25	5.6					1							
26	6.0					2							
Total		209		65		53		78		50	50		

types were not observed in the offspring of the cultivated spikes chosen by us (CROP 88) or by the farmers (FIELD 90). A second group, which we designated cultivated, included the classes numbered from 17 to 26; these phenotypes were not observed in the offspring of the wild spikes chosen by us (WILD 88) or in the spontaneous WADI 90 population. The third group, designated chibra, included all the phenotypes common to the wadi and to the field.

The mean characteristics of these empirical groups allowed a correspondence to be established with BRUNKEN's (1977) subspecies (Table 2). The empirical wild group corresponds to subsp. *monodii*, the cultivated group to subsp. *glaucum*, and the chibra group to subsp. *stenostachyum*. This correspondence is not very precise because of the large ranges of variation indicated by BRUNKEN for each trait.

The open pollinated offspring of the two chibra spikes – CHIBRA W and CHIBRA F – displayed broad-ranging continuous segregation, in full agreement with polygenic segregations observed in wild × cultivated millet crosses (MARCHAIS & TOSTAIN 1985), and in contradiction to BRUNKEN's assertion that chibras do not segregate (BRUNKEN 1977). This contradiction is probably due to the arbitrary limits fixed for the chibra definition. Within the current limits, a chibra mother generates mostly chibra offsprings (65%), many wild offsprings (33%), but very few cultivated offsprings (2%).

As expected, the distribution observed in FIELD 90 practically excludes the presence of chibra spikes in the seed stock used by the farmer, otherwise wild plants should be present.

The empirical limit set in Table 1 for wild plants (below the value − 1.2) finds some significance in the detailed distribution for the offspring of each individual WILD 88 spike shown in Table 3. The spikes have been arranged in that way that a gap is apparent at the level of the classes numbered 13 and 14 between the aforesaid wild and chibra groups. This gap produces a minimum in the total WILD 88 distribution. The discrimination is not absolute. Six plants are at the borderline and can be included in either of the two groups. The two groups observed in the offspring of WILD 88, generated only by wild mothers, suggested the following hypothesis: the wild group descended from the previous generation wild

Table 2. Means (standard errors in parentheses) for the morphological traits of the three groups identified in the wadi and the field compared with the ranges of variation of BRUNKEN's three pearl millet subspecies

Group	Plant height cm	Spike length cm	Spike rachis diameter 1/10 mm	Involucre stalk length 1/10 mm	Number of spikelets/ involucre	Seed length 1/10 mm	Seed breadth 1/10 mm
Wild	112 (27.6)	13.3 (3.0)	12.7 (3.2)	1.1 (1.0)	1.0 (0.18)	24.5 (2.4)	12.1 (1.4)
monodii	< 300	2.5–20	5–15	< 2.5	mostly 1	20–30	10–15
Chibra	167 (28.1)	25.9 (5.6)	24.3 (5.4)	6.0 (3.2)	1.7 (0.49)	30.6 (3.0)	17.1 (2.6)
stenostachyum	often > 300	5–150	15–60	2–15	mostly 2	20–45	10–22
Cultivated	213 (24.4)	51.4 (10.6)	64.8 (13.5)	29.1 (16.9)	2.1 (0.37)	33.5 (2.6)	23.9 (2.6)
glaucum	often > 300	4–200	50–130	11–250	1–9	20–55	16–32

Table 3. Detailed morphological frequency distribution along the first axis of the principal component analysis for each maternal plant of the WILD 88 group and for the whole of WILD 88 and WADI 90 origins

Class		WILD 88 individual spike number																				WILD 88		WADI 90
n°	Limit	58	57	64	66	0	97	55	4	1	54	85	70	61	53	86	6	63	68	56	93	Bulk	Total	
1	− 3.8	1																					1	
2	− 3.6																							
3	− 3.4									1												1	2	
4	− 3.2			1	1																	1	3	1
5	− 3.0			1				1	1				1						2			2	8	1
6	− 2.8	1	1		2	1		1	1				1	1	2	1						3	15	3
7	− 2.6	2	2				1	3	1	1		1	1		3				2			2	19	3
8	− 2.4	1	1	2	4	2	1	2	2	2		2	1	1	1	1	3		1			7	34	8
9	− 2.2			4	1	1	3	2			1				1	1	1	2	1		1	5	24	9
10	− 2.0		1			1	1			1		1	3						1	1	1	2	13	5
11	− 1.8	2								1			1		1			1		1		3	10	5
12	− 1.6			1										2	1	1	1	1				1	8	2
13	− 1.4																		1	1			2	3
14	− 1.2																				2	2	4	4
15	− 1.0										2	1	1	1	1	1	1						8	5
16	− 0.8										1	1					1						3	
17	− 0.6								1	1	1		1										4	1
18	− 0.4										1							1	1		1		4	3
19	− 0.2									1										1			2	
20	0.0									1	1	1		1				1					5	1
21	0.2										1					1	2					1	5	2
22	0.4																				1	2	3	2
23	0.6							1	1	1		1		1		3		1		1		1	11	2
24	0.8					3	1		1		1	1						1			1		9	1
25	1.0				1				1		1					1							4	1
26	1.2																			1		1	2	
27	1.4																			1	1		2	2
28	1.6					1												1			1		3	
29	1.8																					1	1	
30	2.0																							
31	2.2																							1

group by endogamic reproduction. and the chibra group was fathered by pollen from cultivated plants. This hypothesis was tested with the markers (see next section).

The splitting of CROP 88 and FIELD 90 into a cultivated and a chibra group is not supported by an evident discontinuity (see Table 1) and the hypothesis here is that the two parts. although of agronomic significance. constitute a single reproductive community. This hypothesis was also tested.

Tests of homogeneity between empirical groups within each origin. The wild and chibra groups within WILD 88 differed significantly according to the gla-

brous – hairy limb segregations (Table 4). These groups differed also in WADI 90, to a lesser degree, probably because of the small sample size. In CROP 88 also, the small sample sizes prevented a statistical test but the chibra and cultivated segregations seemed similar. In FIELD 90 both groups were statistically very homogeneous.

The tests of homogeneity with PGM and ADH markers were performed by classifying first the offspring genotypes according to the most likely maternal genotypes, as estimated by RITLAND's MLT software dealing with the complete offspring of each maternal plant, for pooled groups (Table 5). In the case of ADH, the maternal genotype of offsprings composed of only one plant could not be estimated; these genotypes were pooled. After this preliminary classification, it was easy to sum in each group the plants pollinated by an F or S pollen. The genotypes FS from an FS mother were of course ignored. The test of homogeneity was applied to the F and S alleles counted in the pollen. The result was clear: wild and chibra groups of WILD 88 were fathered by pollen with statistically different *Pgm-A* and *Adh-A* allele frequencies. Conversely, no difference in their *Pgm-A* and *Adh-A* allelic patterns was observed between cultivated and chibra groups of CROP 88.

Between-group comparison of marker gene frequencies. As a consequence of the tests of homogeneity, the three marker gene frequencies were estimated separately for the wild and chibra parts of WILD 88 and WADI 90, but together for all plants of CROP 88 and FIELD 90. With the limb hairiness gene, a frequency of the glabrous allele, G, common to all plants of 1988 and 1990 was estimated and tested for its fit to each year's data.

Table 4. Test of homogeneity within each origin between the morphological groups for foliar limb hairiness segregations

Origin	Maternal genotype	Offspring phenotype	Group			Total	Probability of homogeneity
			wild	chibra	cultivated		
WILD 88	bulk	glabrous	109	42		151	
		hairy	30	28		58	
		total	139	70		209	0.01
WADI 90	bulk	glabrous	26	10		36	
		hairy	14	15		29	
		total	40	25		65	0.08
CROP 88	gg	glabrous		2	11	13	
		hairy		7	22	29	not
		total		9	33	42	computed
	Gg	glabrous		4	4	8	
		hairy		0	3	3	not
		total		4	7	11	computed
FIELD 90	bulk	glabrous		14	14	28	
		hairy		22	28	50	
		total		36	42	78	1

Table 5. Tests of homogeneity within each origin between the morphological groups for allele frequencies on pollen side

Origin	Maternal genotype	Offspring genotype	Group			Total	Probability of homogeneity
			wild	chibra	cultivated		
A. Phosphoglucomutase							
WILD 88	FF	FF	90	38			
		FS	8	18			
	FS	FF	3	1			
		FS	0	2			
		SS	0	1			
	Sum of F pollen		93	39			
	Sum of S pollen		8	19		159	0.00
CROP 88	FS	FF		0	6		
		FS		3	3		
		SS		2	6		
	SS	FS		4	10		
		SS		3	13		
	Sum of F pollen			4	16		
	Sum of S pollen			5	19	44	1
B. Alcohol dehydrogenase							
WILD 88	FF	FF	8	17			
		FS	6	0			
	FS	FF	3	4			
		FS	5	5			
		SS	5	0			
	SS	FS	9	6			
		SS	13	1			
	bulk	FF	7	9			
		FS	18	9			
		SS	6	2			
	Sum of F pollen		27	36			
	Sum of S pollen		30	3		96	0.00
CROP 88	FF	FF		6	17		
		FS		1	6		
	FS	FF		1	7		
		FS		0	2		
		SS		1	0		
	SS	FS		3	7		
		SS		1	0		
	Sum of F pollen			10	31		
	Sum of S pollen			3	6	50	1

The cultivated origins CROP 88 and FIELD 90 exhibited a low frequency of the glabrous allele (0.20) which fits well with the 5 CROP 88 maternal genotypes, the 5 very homogeneous CROP 88 individual segregations, and the bulk segregation

of FIELD 90 (Table 6). Thus the frequency of the G allele did not seem to have changed between 1988 and 1990. The glabrous limbs were more frequent in the wild part of the wadi origins CROP 88 and WADI 90, where the G frequency reached 0.50. The homogeneity of G frequencies between 1988 and 1990 can be accepted in the wadi with a probability of 0.15.

The hypothesis that the chibra parts in the wadi are a product of wild × field crosses can be accepted with a probability of 1 for WILD 88 and of 0.15 for WADI 90.

The *Pgm-A* and *Adh-A* allele F frequencies estimated with 1988 data gave a clear picture: In the wild part of WILD 88, the ovule and pollen frequencies were very similar, whereas in the chibra part the pollen frequencies were very similar to the CROP 88 frequencies and statistically different from wild part frequencies (Table 7). In CROP 88, the ovule frequencies are given without standard errors because there were only 5 maternal plants.

The estimates of F and t fitted non-inbred parents and a 100% outcrossing rate, but the standard errors were high, thus preventing precise analysis of a possible departure from the panmixia model.

Comparison of field and wadi heading dates. Plants from WADI 90 and FIELD 90 were also surveyed for the heading dates of their successive spikes. In FIELD 90, the chibra and cultivated parts expressed similar heading date pattern (Table 8). In WADI 90, the chibra part flowered in synchrony with FIELD 90 but the wild part started to flower slightly later than FIELD 90 and continued to flower for almost one month after FIELD 90. Hence, about 40% of wild spikes flowered in

Table 6. Foliar limb hairiness: estimation of the frequency of the dominant glabrous allele G in the field, all groups pooled (first part) and in the wadi for the wild group only (second part). The third part tests whether the chibra groups in the wadi can be hybrids between the wild group and the field millets. The expected frequencies assuming allele G frequencies common to 1988 and 1990 are reported in parentheses

Origin	Maternal genotype	Offspring	
		glabrous	hairy
Field: Allele G common frequency = 0.20 standard error = 0.05			
CROP 88	gg	15 (9.8)	34 (39.2)
	gg	8 (9.6)	40 (38.4)
	gg	7 (9.6)	41 (38.4)
	gg	10 (9.2)	36 (36.8)
	Gg	28 (27)	17 (18)
FIELD 90	bulk	32 (29.5)	50 (52.5)
Wild groups in the wadi: Allele G common frequency = 0.50 standard error = 0.04			
WILD 88 (wild group)	bulk	109 (104)	30 (35)
WADI 90 (wild group)	bulk	26 (30)	14 (10)
Test of the hypothesis: the chibra groups in the wadi are wild × field hybrids			
WILD 88 (chibra group)	bulk	42 (42)	28 (28)
WADI 90 (chibra group)	bulk	10 (15)	15 (10)

Table 7. Estimation of Pgm and Adh F allele frequencies in the ovules and pollens of the different groups identified. Multilocus estimations of the maternal fixation index F and the outcrossing rate are also shown. Standard errors are reported in parentheses

Group	Pgm-A (F) frequency		Adh-A (F) frequency		Multilocus	
	ovule	pollen	ovule	pollen	index F	t
CROP 88	0.2	0.45 (0.125)	0.7	0.82 (0.06)	0.011	1.04 (0.27)
WILD 88						
Wild group	0.97 (0.022)	0.90 (0.045)	0.50 (0.094)	0.49 (0.064)	0.11 (0.27)	0.88 (0.13)
Chibra group		0.65 (0.06)		0.88 (0.05)		

Table 8. Percentage distribution of individual spike heading dates in the morphological groups observed in situ in 1990

	Heading date													Sample size
	August						September						October	
	5	10	15	20	25	31	5	10	15	20	25	30	5	
WADI 90														
Wild	0	0	3	7	7	5	41	3	3	3	11	14	3	165
Chibra	0	10	2	9	18	8	45	5	1	1	1	0	0	103
FIELD 90														
Chibra	9	10	0	14	8	46	12	1	0	0	0	0	0	51
Cultivated	2	9	0	13	10	47	15	4	0	0	0	0	0	53

the absence of non-wild flowers. The range of variation for heading date is, indeed, a feature of domestication. A cultivated plant produces few spikes in a short time interval, whereas a wild plant may continue to produce new spikes over several weeks, if the environment is favourable.

Discussion

Multivariate analysis of morphological traits discriminating cultivated and wild millets and the three diagnostic genes lead to conclusions similar for 1988 and 1990 that differ between wadi and field.

As to the wadi millets, the offspring of wild plants in 1988 and the natural population in 1990 clearly showed a subdivision between an endogamous major group and a minor group descending from crosses between the aforesaid wild group and the millets growing in the neighbouring field. The presence of backcross genotypes between these two groups cannot be totally excluded but does not seem to be frequent. In this natural population, BRUNKEN's subspecies have some biological significance, which is paradoxical in the presence of a high fertilization rate of wild plants by field millets: 33% in WILD 88 and 38% in WADI 90. This situation may

reflect an equilibrium if the chibra plants in the wadi leave no offspring each year because of some natural elimination.

Conversely, in 1988 and 1990, no evidence of subdivisions among the diverse array of morphological variants in the field could be found, in spite of great differences in agronomic value. Many plants showed different mixtures of wild and domesticated traits: for instance, long spike associated with shedding spikelets, or a relatively small spike with big seeds. Field millets seemed to form a unique reproductive community isolated from wadi millets. The chibra plants in the field, according to their marker gene frequencies, did not seem to be cultivated × wild hybrid plants. They were probably recombinant genotypes generated by repeated backcrosses between chibra and cultivated plants. Such a stable situation is also observed in many parts of Sahelian Africa, where no spontaneous millet populations exist but where millet fields are, nevertheless, invaded each year by chibras, which play the role of weeds. Several explanations can be advanced. Traditionally, the farmer harvests grains from chibra plants for food but not for sowing. The cultivated spikes, chosen as seed source by the farmer at the time when all types of plants are ripe, were pollinated in part by chibra plants. Furthermore, the taxonomy made by the farmer is probably not very strict. Many long spikes with big grains, for instance, are chosen as seed source in spite of shedding spikelets. It thus seems that farmers further the coexistence of chibra and cultivated plants.

BRUNKEN's subspecies are in any case inadequate to describe the diversity of pearl millet fields, where the distinction between cultivated and chibra plants is not evident. Chibra plants appear to represent a tail of a continuous distribution for agronomic values, strictly dependent on millet culture. This interpretation is in line with the supposition that in the wadi chibras are unadapted and leave no offspring.

The structure of populations reported here suggests only one major subdivision among pearl millets, between wild millets on the one hand, and chibra and cultivated millets on the other. Wild millet is more than a subjective and arbitrary selection of rare, marginal, odd phenotypes from a natural population. It is rather a stable core surrounded by unadapted transient chibras, each year generated by pollen from neighbouring fields.

Different flowering times and differences in population sizes between wild and field millets can partly explain the genetic structure observed. At the time of field flowering, all the fields in the region flowered at the same time. Pollen from fields was overabundant in relation to wild pollen, which may explain the apparent absence of influence of wild millets on field offspring. In terms of the wadi, the many wild tillers flowering after cultivated and chibra plants could ensure true to wild type offspring.

But this does not explain why in the long term wild plants are not eliminated by chibras. It is uncertain whether only genetic mechanisms, like pollen competition advantageous to wild pollen, are frequent and strong enough to account for the real situation (MARCHAIS & TOSTAIN 1985, ROBERT & al. 1991). Chibra polygenic segregations imply that wadi population discontinuity is not accounted for by monogenic heredity, but rather by the elimination of chibra offspring. The monogenic model considered by LAREDO & PERNES (1988) is unrealistic. Ecological mechanisms must also contribute to elimination of non-*monodii* plants. The striking contrast between natural wadi and artificial field environments probably produces

what GRANT (1971) calls an environmental control of hybridization, and perhaps a Wallace effect: chibras are at a disadvantage in the wadi, thus potentially favouring genetic mechanisms limiting hybridization.

Curiously, the problem of coexistence between a domesticated allogamous species and its wild relatives in a situation of sympatry does not seem to have been thoroughly studied, even in the case of maize. Maize is particularly interesting in this regard because it presents many similarities with pearl millet.

An annual allogamous spontaneous plant, the teosinte, grows in Mexico and is experimentally easily crossed with maize, although it is morphologically markedly different from maize (GOODMAN 1988). Although teosinte × maize crosses generate a continuous array of segregants for the discriminant morphological traits, globally controlled by at least 5 major blocks of genes (DOEBLEY & STEC 1991), under natural conditions teosinte exhibits two main forms distinct from maize and ranked in two subspecies: *Zea mays* subsp. *parviglumis*, a wild teosinte spatially isolated from maize fields, and *Zea mays* subsp. *mexicana*, a weed in Mexican maize fields (ILTIS & DOEBLEY 1980). The weedy teosinte is isozymically different from maize and intermediate forms are very rare in the field (DOEBLEY 1990). Some partial isolating mechanisms have been identified: cross incompatibility factors between maize and teosinte (KERMICLE & ALLEN 1990). There are also differences in flowering time: Teosinte and maize start at the same time, but the former flowers 10 days longer (GALINAT 1988). However, these isozymic and hybridization studies seem to have involved groups of plants chosen as true to maize and teosinte types. It does not seem that the complete individual genotypic structure of a maize field invaded by teosinte plants has been surveyed for morphological traits, isozymic genes, flowering dates, and gametophyte factors.

Consequently, the current study raises the unanswered question of the survival of a wild plant in the presence of its domesticated relative but, at least, the fact is here established that wild millets exist and maintain themselves as an endogamic group among cultivated millets. The data presented here could be used comparatively in later years to monitor the evolution of spontaneous millets in the same wadi at Keita.

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