

FRUIT AND STONE VARIABILITY IN THREE ARGAN (*ARGANIA SPINOSA* (L.) SKEELS) POPULATIONS

Fouzia Bani-Aameur & Abderrahim Ferradous

Laboratoire de Recherche sur la Variabilité Génétique, Université Ibn Zohr, Faculté des Sciences, Département de Biologie, BP: 28/S 80 000 Agadir, Morocco; Phone: (212) 48 22 09 57; Fax: (212) 48 22 01 00, e-mail: baniaameur@hotmail.com

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ABSTRACT

Little is known about morphological variability of argan (*Argania spinosa* (L.) Skeels), a multipurpose tree endemic to Morocco. During three following years, 11 fruit and stone characters (fruit color, fruit and stone weight, length, width and width / length ratio, flesh weight, and stone chambers number) were observed on 30 mature fruits collected from 30 trees within each of three populations in the major area of distribution of the specie, southwest of Morocco. The study established a high level of morphological variability. However, inter-population (between population) contribution to total variance was lower than intra-population (tree/population or its interaction with year). The most discriminant criterion between populations were the least variable characters. Three clusters grouping the morphotypes were not related to geographical distribution, showing a lack of between population diversity. Values of repeatability (an estimate of broad sense heritability) varied between 52% and 8%. These were as high as 45% for characters of economic importance (i.e. fruit and stone weight), thus exhibiting variability to capture in an argan breeding program.

Key words: *Argania spinosa*, diversity, fruit, phenotypic variation, heritability

INTRODUCTION

Genetic diversity estimates differences between individual types within a population as the types are determined by the observed traits (GREGORIUS 1987). As it is, there are two categories of species: the generalists and the specialists (VAN DIJK, 1984). Generalist species show high flexibility surviving within varying environments due to ecological changes. Whereas specialist species are formed of a number of populations of specialised types confined to well determined habitats.

Argan (*Argania spinosa* (L.) Skeels), a multipurpose perennial tree endemic to Morocco is mainly located in the south west region, even though relict populations of small sizes are observed north at Oued Grou, north-east at Bni Snassen and south at Goulimine (EHRIG 1974; PRENDERGAST & WALKER 1992). It happens in a wide array of environments where soils are ranging from heavy clay to sandy dune soils, altitudes from sea level to 1500 m, temperatures from 3.8 °C isotherm to 50 °C and annual rainfall between 440 mm and 120 mm (EMBERGER 1925; BOUDY 1950; BOUDY 1952, METRO, 1970; EHRIG 1974).

Argan has recently received increased attention, because of national and international focus on non-timber producing trees for environment preservation and rural communities well being. Its principal interest

are the fruits collected from the wild which are a major source of income for autochthonous populations through the oil extracted from the nut, the flesh used as animal feed and the shell used as fuel (BOUDY 1952; EHRIG 1974; MAURIN 1992). To enhance argan fruit biology database we initiated, within three populations, investigations concerning typology (BANI-AAMEUR, FERRADOUS & DUPUIS 1999) and phenology (FERRADOUS, BANI-AAMEUR & DUPUIS 1996). Site, season, and their interactions were significant effects on morphometric traits of argan fruit and stone. Although individual trees within and between populations showed morphological differences, it is not determined yet if the observed differences are due to genetic changes, ecotypic diversity or to plastic response to different local environments. The objective of this paper is to complement previous work thus characterising the amount and pattern of variability of eleven fruit and stone characters in three argan populations under natural environments.

MATERIALS AND METHODS

Thirty random adult argan trees were sampled once within each of three populations located at Ait Melloul, Argana and Ait Baha, three different sites in argan main area of distribution (Fig. 1). Ait Melloul is located 12.5 km from the Atlantic ocean at 35 m altitude in the Souss plain; Argana 60 km from the Atlantic ocean at 620 m

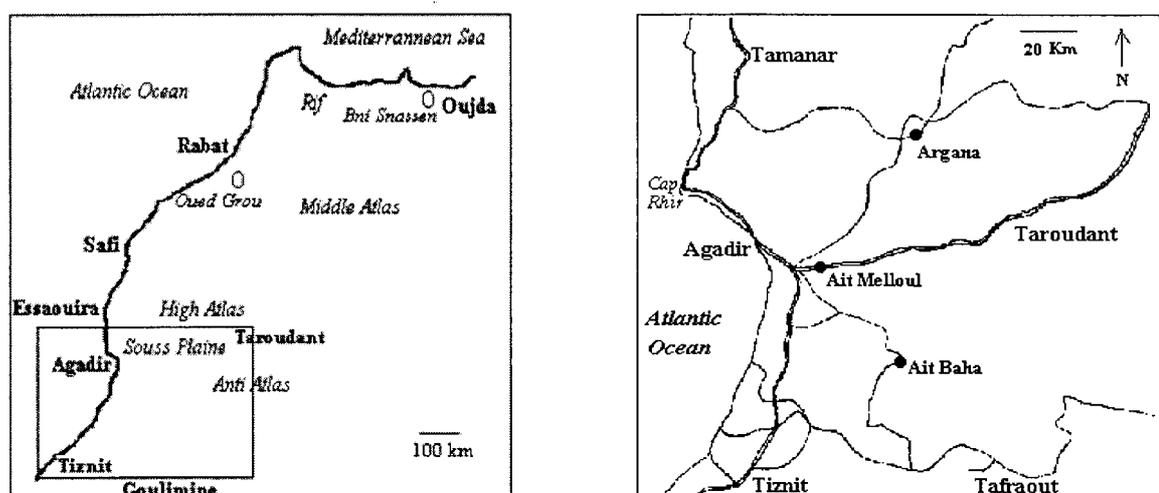


Figure 1. The geographical location of Ait Melloul, Argana and Ait Baha populations. Note that the three populations are included within argan main area of distribution south west of Morocco as contrasted to relict population of Bni Snassen, Oued Grou or Goulimine.

Table 1. Expected mean squares for analysis of variance of argan fruit and stone characters.

Source of variation	Degrees of freedom	Mean square	Expected mean squares
Year	2	MS_y	$\sigma^2 + 30\sigma_{y \times tlp}^2 + 2700\sigma_y^2$
Population	2	MS_p	$\sigma^2 + 90\sigma_{tlp}^2 + 2700\sigma_p^2$
Year \times population	4	MS_c	$\sigma^2 + 30\sigma_{y \times tlp}^2 + 900\sigma_{y \times p}^2$
Tree / population	87	MS_{tlp}	$\sigma^2 + 90\sigma_{tlp}^2$
Year \times tree / population	174	MS_{ni}	$\sigma^2 + 30\sigma_{y \times tlp}^2$
Year \times tree / population \times fruit (error)	7830	MS_{nie}	σ^2

Repeatability: $H^2 = \sigma_{tlp}^2 / (\sigma^2 + \sigma_{tlp}^2 + \sigma_{y \times tlp}^2)$

altitude on the southern slopes of High Atlas mountains and Ait Baha located farther south, 50 km from the Atlantic ocean at 550 m altitude on the northern slopes of Anti Atlas mountains in the southwest of Morocco. Climate of this region is of arid Mediterranean type. Rainfall is scarce and very variable (0 to 300 mm in annual average), taking place mainly during the cold period, while summer season is dry (FERRADOUS, BANI-AAMEUR & DUPUIS 1996). Still there are differences between the sites, Ait Melloul being warm arid under oceanic influence, Argana cold arid and Ait Baha warm arid pre-Saharan (EMBERGER 1955; FERRADOUS, BANI-AAMEUR & DUPUIS 1996). Their soils are brown calcic at Ait Melloul, red fersialitic at Argana and brown containing stones and gravels at Ait Baha. More detailed ecological information about observation sites is available in FERRADOUS, BANI-AAMEUR & DUPUIS

(1996).

For three seasons (1990–1992), 30 mature fruits were collected from the sampled trees at each site. An array of four ripe fruit colors (FC) was established and coded 1 to 4 from the lightest to the darkest: 1 = light yellow, 2 = yellow, 3 = red and 4 = dark red. Weight (g), length and width (mm) of the fruit (FE, FL, FW) and the stone (SE, SL, SW) were measured. The width / length ratio was calculated for the fruit (FR), and the stone (SR). Flesh weight (FS) was deduced subtracting stone weight from fruit weight. Counts of stone chambers (CN) were made.

Analysis of variance was performed on these eleven variables, on a three random factors design using a sample of 30 fruits per tree, 30 trees per population repeated over three seasons. Season and population were orthogonal factors whereas the factor tree was

hierarchical to the factor population because the trees were not repeated between sites. To draw a general conclusion among the three argan stands, population was considered as a random effect. (STEEL & TORRIE 1960). The portion of variance that can be attributed to each factor was estimated from the expected mean squares in the analysis of variance (Table 1). Considering year as a special environment, a repeatability value (an estimate of broad sense heritability) was calculated using the formula $R = \sigma^2_{vp} / (\sigma^2 + \sigma^2_{vp} + \sigma^2_{y \times vp})$ where σ^2_{vp} is the variance of a tree within a population, σ^2 is the error term variance, and $\sigma^2_{y \times vp}$ the interaction year \times tree within a population variance (KEMPTHORNE 1973).

To describe the pattern of argan population diversity, different multivariate analysis methods were applied to tree means (BERNSTEIN, GARBIN & TENG 1988). From the concordance of trends estimated by these different methods, it was expected to infer complementary and significant aspects of argan populations evolutionary process. Differences among populations was investigated using discriminant function analysis (DFA). It allowed to calculate the discriminant structure of the data showing the multivariate relationship among characters. Divergence among populations were investigated using Mahalanobis D^2 method. A

hierarchical comparative cluster analysis (Average Linkage Method) based on Euclidean distances between trees tested the pattern of structure of the three populations. Finally principal component analysis which has the advantage to be indiscriminant, had to reveal groups if they existed, whereas the determination of the origin of the tree is not required before analysis. STATISTIX, STATITCF, and NTSYS computer programs were used for statistical analysis.

RESULTS

Variability analysis

Effects of individual tree /population, year, the interaction year \times population as well as the interaction year \times tree/population were significant for all characters (Table 2). Population was significant only for FW, FR, SL, FS, and FC. Large variability was observed between trees as it shows from remarkable values of population means, maximums, minimums and coefficients of variation (Table 3). For metric traits, trees at Argana had the highest maximums, Ait Baha the lowest minimums, whereas the rank of population mean depended on the character. Tree/population means varied from simple to quadruple for FS, to triple for FE and SE and to double

Table 2. Variance components and repeatability estimate of argan fruit and stone weight (FE, SE) length (FL, SL), width (FW, SW) and width / length ratio (FR, SR), flesh weight (FS), fruit color (FC) and stone chamber number (CN).

Source of variance	Variance					
	FE	FL	FW	FR	SE	SL
Year σ^2_y	0.072**	2.805**	0.185**	0.001**	0.107**	2.466**
Population σ^2_p	0.041ns	0.891ns	0.206*	0.001**	0.018ns	0.939**
Year \times population $\sigma^2_{y \times p}$	0.315**	4.464**	1.478**	0.001**	0.118**	3.201**
Tree/population σ^2_{vp}	0.638**	16.178**	2.395**	0.008**	0.316**	7.248**
Year \times tree/population $\sigma^2_{y \times vp}$	0.238**	5.046**	1.397**	0.003**	0.120**	2.326**
Year \times tree/population \times fruit (error) σ^2	0.515	12.583	26.456	0.038	0.273	6.175
Repaetability	0.46	0.48	0.08	0.17	0.45	0.46

Source of variation	Variance				
	SW	SR	FS	FC	CN
Year σ^2_y	0.190**	0.001**	0.010**	0.002**	1.5 10^{-3} **
Population σ^2_p	0.027ns	0.001ns	0.019**	0.047**	1.7 10^{-3} ns
Year \times population $\sigma^2_{y \times p}$	0.462**	8.6 10^{-4} **	0.069**	0.007**	2.3 10^{-3} ns
Tre/population σ^2_{vp}	1.652**	0.007**	0.107**	1.610 $^{-3}$ **	0.049**
Year \times tree/population $\sigma^2_{y \times vp}$	0.576**	1.8 10^{-3} **	0.057**	3.8 10^{-3} **	0.015**
Year \times tree/population \times fruit (error) σ^2	1.012	4.5 10^{-3} **	0.251	0.013	0.144
Repeatability	0.51	0.52	0.26	0.09	0.23

** : significant at $\alpha = 0.01$, * : significant at $\alpha = 0.05$, ns : non-significant.

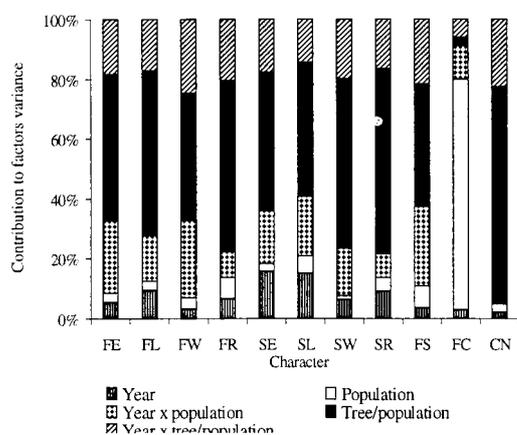


Figure 2. Percent contribution to total variance of sources of variation and their interactions of argan fruit and stone weight, length, width and width / length ratio (FE, FL, FW, FR, SE, SL, SW, SR), flesh weight (FS), fruit color (FC) and stone chamber number(CN).

for the remaining metric traits. These intervals as well as coefficient of variation values illustrate breeding potential to capture for enhancing argan fruit and stone characteristics.

Year variance varied from two to 18 % (Table 2, Fig.2). Population variance, which is confounding a variance due to differences between geographical sites ($\sigma^2_{\text{geographic site}}$) and a variance due to differences between argan population ($\sigma^2_{\text{inter-population}}$), was the lowest except for FC. Population variance was high for FC because the sites were contrasting. Then for all the remaining traits, none of geographic site or population, as a source of variance had a comparatively important effect on stone and fruits variability. Though variances due to differences between years or to the interaction population \times year were greater than the variance due to differences between populations, their effect was not the most important, except for CN (Table 2, Fig.2). Having in mind that population is confounding both of geographic site and tree population effects, the contribution to total factors variance of the sum of variances due to year (σ^2_y) and the interaction year \times population ($\sigma^2_{y \times p}$), could be viewed as an estimate of environment variance.

Individual tree (tree/population) and its interaction with year had much larger variances than year, population or/and their interaction. It formed the dominant source of variation for all characters absorbing from 40 % to 70 % of total factors variance (Table 2, Fig.2). Because each tree was associated to a site where tree specimens were not repeated, σ^2_{tp} component of variance ($\sigma^2_{tp} = \sigma^2_{\text{genotype}} + \sigma^2_{\text{genotype} \times \text{population}}$) was confounding a variance due to differences between tree geno-

Table 3. Mean, maximum (Max.), minimum (Min.) and coefficient de variation (CV%) of argan fruit and stone weight, length, width and width / length ratio (FE, FL, FW, FR, SE, SL, SW, SR), flesh weight (FS), fruit color (FC) and stone chamber number(CN).

Character	Population	Seasons			
		Mean	Max.	Min	CV %
FL (mm)	Ait Melloul	30.2	38.5	21.8	13.1
	Argana	29.0	40.2	22.6	15.2
	Ait Baha	27.2	35.1	21.6	13.8
FW (mm)	Ait Melloul	18.4	20.6	16.6	5.8
	Argana	19.4	23.9	16.6	8.7
	Ait Baha	18.8	21.9	14.7	8.7
FR	Ait Melloul	0.6	0.8	0.5	11.3
	Argana	0.7	0.8	0.5	14.5
	Ait Baha	0.7	0.9	0.5	15.1
FE (g)	Ait Melloul	3.6	5.2	2.3	21.8
	Argana	3.9	5.8	2.9	19.9
	Ait Baha	3.4	5.3	2.0	22.9
FS (g)	Ait Melloul	1.1	1.8	0.6	25.5
	Argana	1.4	2.7	0.9	26.7
	Ait Baha	1.2	2.0	0.8	24.9
SL (mm)	Ait Melloul	23.7	29.6	17.7	12.5
	Argana	22.0	29.4	18.0	12.9
	Ait Baha	21.6	25.3	17.3	11.0
SW (mm)	Ait Melloul	15.0	17.7	12.9	7.5
	Argana	15.1	17.8	12.5	7.7
	Ait Baha	14.5	17.1	10.2	10.5
SR	Ait Melloul	0.6	0.8	0.5	10.5
	Argana	0.7	0.8	0.5	13.1
	Ait Baha	0.7	0.9	0.4	13.9
SE (g)	Ait Melloul	2.5	3.6	1.5	13.7
	Argana	2.5	4.0	1.7	20.4
	Ait Baha	2.2	3.5	1.2	25.3
CN	Ait Melloul	2.2	2.5	1.9	5.8
	Argana	2.3	3.0	2.0	11.4
	Ait Baha	2.2	3.0	1.8	12.1
FC	Ait Melloul	4.0	4.0	4.0	0.1
	Argana	2.6	2.9	2.3	7.3
	Ait Baha	2.8	3.1	2.5	5.0

types ($\sigma^2_{\text{genotype}}$) and a variance due to genotype \times population interaction ($\sigma^2_{\text{genotype} \times \text{population}}$). Then, it was not possible to extract genotype nor environment variance for an unbiased estimate of heritability. Under these limitations, repeatability (a broad sense heritability estimates) were higher for FL, SL, SR, FE, SE, SW than for FR and ES which were intermediate or for FW and FC which were lower (Table 2). As it is, for

Table 4. Correlation coefficient between canonical components axes and argan fruit and stone weight, length, width and width / length ratio (FE, FL, FW, FR, SE, SL, SW, SR), flesh weight (FS), fruit color (FC) and stone chamber number(CN) and partition of variation.

Variables	Axis 1	Axis 2
FC	1.00	0.00
FE	-0.36	0.93
FL	0.71	0.71
FW	-0.82	0.57
FR	-0.96	-0.29
SE	0.15	0.99
SL	0.70	0.71
SW	0.04	1.00
SR	-0.85	-0.53
FS	-0.86	0.52
CN	-0.92	0.39
Eigenvalues	0.97	0.2
Percentage of variation	82.8	17.2

Table 5. Mahalanobis distance D^2 (above diagonal) and similarity coefficient between populations ($100 - D^2$) (below diagonal).

Population	Ait Melloul	Argana	Ait Baha
Ait Melloul	-	5.2	4.0
Argana	94.8	-	1.3
Ait Baha	96.0	98.7	-

Table 6. Clustering pattern of argan trees based on average linkage cluster analysis (Euclidean distance)

Cluster	Euclidean distance	Ait Meloul	Argana	Ait Baha
1	3.2	9	5	2
2-1	2.3	14	14	14
2-2	2.3	7	11	14

these characters, comparing population and tree/population it clearly appears that inter-population variance was lower than intra-population variance.

Diversity analysis

The first canonical variates of the discriminant function analysis (DFA) explained 82.8 % of total variance between populations (Table 4). It is first determined by

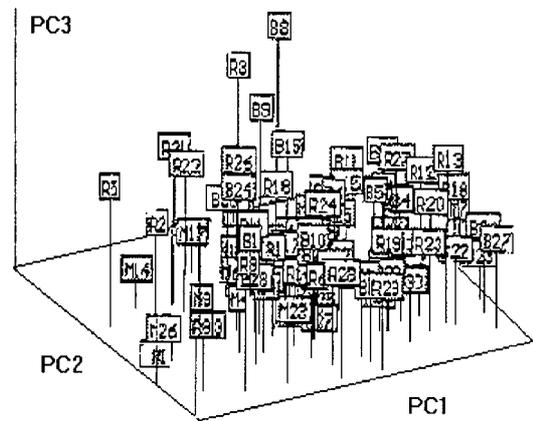


Figure 3. Factor scores for the first three principal components (PC 1: 43.8 %, PC 2: 30.3 % and PC 3: 12.5 % of total variance) of tree means of argan fruit and stone morphological characters. A letter (A for Ait Baha, M for Ait Melloul and R for Argana) followed by a number identify individual trees of a population.

FC, FR and CN. The second canonical vector is determined by SW, SE, and FE and explained 17.2 % of total variance between populations. Hence, discrimination between population is mainly dependant upon criterions with the lowest variability. This translates into high phenotypic similarity between the three population, estimated by Mahalanobis distance D^2 (Table 5). Though within D^2 restricted interval, Ait Melloul and Ait Baha populations were extremes and Argana at an intermediate position. A dendrogram three clusters visualizing Euclidean distances among trees as generated from matrices of multivariate information supported by fruit and stone morphological characters, was summarized for convenience in table 6. Any one of these clusters is formed of a combination of trees from each of the three populations. Again none of the populations is dominating a cluster. Variables FL and SL had the highest repeatabilities. So little diversity between the three populations was showing out of the 3-D projection of principal components, generated from matrices of characters, as a close to random agglutination of different phenotypes from the three populations (Figure 3). The three first principal components (PCA) account for 86.6% of the total observed variance (Table 7). The first component which accounts for the highest proportion of variability, is linked to FE, SE, SL, FL and FS; the second component is linked to FR, SR and SW; whereas the third component is linked to FC and CN. Long narrow and heavy fruits are projected to the negative side of the first PC axis, equally as long as wide fruits to the negative side of the second axis and dark fruits with a large chamber number to the positive side of the third axis. Hence within anyone of the three popula-

Table 7. Correlation coefficient between principal Components axes and argan fruit and stone weight, length, width and width / length ratio (FE, FL, FW, FR, SE, SL, SW, SR), flesh weight (FS), fruit color (FC) and stone chamber number(CN) and partition of variation.

Variables	PCA 1	PCA 2	PCA 3
FC	-0.27	0.33	0.81
FE	-0.93	-0.35	-0.02
FL	-0.83	0.53	-0.01
FW	-0.07	-0.44	-0.03
FR	0.44	-0.88	-0.04
SE	-0.85	-0.40	0.20
SL	-0.85	0.45	0.11
SW	-0.56	-0.70	0.34
SR	0.48	-0.86	0.11
FS	-0.77	-0.17	-0.39
CN	-0.16	0.42	-0.62
Eigenvalues	4.81	3.34	1.37
Percentage of total variance (%)	43.8	30.3	12.5
Cumulated percentage (%)	43.8	74.1	86.6

tions, these type of fruits are expected in similar proportions.

DISCUSSION

Univariate and multivariate analysis, each bringing an answer to a different question, led to similar conclusions about argan (*Argania spinosa* (L.) Skeels) fruit and stone morphological variability. The three populations belong to three geographically different sites (FERRADOUS, BANI-AAMEUR & DUPUIS 1996). In this study, they were not discriminated enough to suggest ecotypes adapted to local environments. These result seem to contradict EL MOUSADIK & PETIT (1996) which looking to progeny data for nine isozyme loci in 10 argan populations concluded to high levels of genetic differentiation of argan populations. Indeed, it appears from their Nei's measure of genetic distances that differentiation between populations from the main area and outsider minor populations was high (0.10–0.30). But they also observed lower levels of differentiation between populations within the main argan area itself ($d = 0.05$), including the three sites used in this study.

Large significant character variances within populations (between trees of a population) were contrasting with low inter-population variances (between populations), qualifying argan as a generalist species. Such a model is expected from a long living woody outcrossing species, dispersed in a large area (GREGORIUS & BARA-

DAT 1992; HAMRICK, GODT & SHERMAN-BROYLES 1992; SIMONS 1992). Indeed, available specific scientific information concerning argan life history under past and/or actual environments is too scarce to allow a better determination of selective forces at work. Even if argan is believed to be a relic from the tertiary era (EMBERGER 1925; EHRIG 1974; BIONDI 1981), it is not actually regenerating under natural conditions (KHAY 1989; ZAHIDI & BANI-AAMEUR 1997; ZAHIDI & BANI-AAMEUR 1998; BANI-AAMEUR & ALOUANI 1999) and its pollination is dominantly entomophilous thus outcrossing (BENLAHBIL & BANI-AAMEUR 1999).

Since environmental induced changes in woody plant morphology and physiology were reported even under very close proximity (DODD, AFZAL-RAFII & POWER 1990; KLEIN *et al.* 1991), since bio-climates of the observed sites in this study were different (EMBERGER 1955; FERRADOUS, BANI-AAMEUR & DUPUIS 1996), environmental effect on stone and fruit phenotypes was expected. The lack of population differences observed in this case may be explained by (1) insignificant biological impact of the differences between the observed sites or (2) by a remarkable degree of plasticity of argan specie. Because argan happens under a highly variable mediterranean arid climate, we tend to favor hypothesis 2). More over, the amplitude of year \times tree/population variances as illustrated by adaptive behavior of trees from Ait Baha (under extreme environmental variation), hints that plasticity within argan populations may play a key role in its adaptation. Though, such interpretation is beyond the scope of this study and more research is needed to fully comprehend argan diversity dispersal and adaptation mechanisms.

Argan fruit is contributing to the local economy. Actually, it is also proposed as a candidate for domestication and a breeding program is emerging. Survey of the genetic material available for the determination of a pool of variable germplasm is the first step in this prospect (DUDLEY & MOLL 1969). The imposed design of this study did not allow repeats of trees between and within sites. As it is, repeatability numerator s^2_{vp} , including an environmental variance, was probably over-estimating genetic variance and repeatability values. However under experimental limitations at this early stage, repeatability (an estimate of broad sense heritability) has to be considered rather as an indicator of variability. Then, some fruit and stone morphological characters exhibited variability that may prove to be useful in an argan breeding program.

Argan is threatened by drought and destructive uses such clearing for urban land, fuel, and animal feed (MELLADO 1989; EL YOUSFI & BENCHKROUN 1992). Preservation of actual gene pool to maintain argan variability and/or reintroduce the specie through refor-

estation or orchard establishment, requires elaboration of a conservation strategy. This study indicated that preserving argan gene pool may necessitate to retain broadly based populations including a maximum of diverse genotypes for conservation and/or as seed sources for regeneration from nursery grown seedlings.

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