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Morphological variation in *Balanites aegyptiaca* fruits and seeds within and among parkland agroforests in eastern Niger

Tougiani Abasse · John C. Weber · Boubacar Katkore · Moussa Boureima · Mahamane Larwanou · Antoine Kalinganire

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Abstract *Balanites aegyptiaca* (L.) Delile. is one of the priority indigenous fruit trees for rural communities in the West African Sahel. As part of a participatory tree domestication program in Niger, phenotypic variation in fruit and seed morphology was assessed in four natural populations in eastern Niger. Measured variables were weight of the fruit, seed coat and kernel; length and width of the fruit and seed (25 trees per population, 30 fruits per tree). Derived variables were the tree's coefficient of variation (CVs) for each measured variable, and two sets of factor scores from principal components analysis of tree means and CVs. ANOVA indicated significant variation in all measured variables due to trees nested in populations. ANOVA and simple linear regression indicated significant geographic variation in some variables: the drier parts of the sample region tended to have heavier fruits and kernels, longer/narrower seeds, and lower within-tree variability in fruit and seed width. Length and width were strongly correlated between fruits and seeds, fruit weight was moderately correlated with seed dimensions, and CVs of fruit weight and width were moderately correlated with the CV of seed width. Some hypotheses for the geographic variation are presented, and some practical implications of the correlations for tree domestication programs are discussed.

Keywords *Balanites aegyptiaca* · Domestication · Fruit and seed morphology · Selection

Introduction

Balanites aegyptiaca (L.) Delile. (Zygophllaceae family [formerly Balanitaceae]) is native to semi-arid regions in sub-Saharan Africa and provides essential wood and non-wood products for rural communities (Hall and Walker 1991). It is one of the priority species for rural communities in the West African Sahel, where it is cultivated with annual food crops in the traditional parkland agroforests (World Agroforestry Centre 2009). It sprouts vigorously after coppicing, spreads asexually from sucker shoots, and can live for more than 100 years. Fruit production starts after 5–7 years, and the seeds can be dispersed

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T. Abasse · B. Katkore
Institut National de Recherche Agronomique du Niger,
BP 240, Maradi, Niger

J. C. Weber (✉) · A. Kalinganire
World Agroforestry Centre (ICRAF), BP E 5118,
Bamako, Mali
e-mail: johncrweber@aol.com

M. Boureima
Institut National de Recherche Agronomique du Niger,
BP 421, Tahoua, Niger

M. Larwanou
African Forest Forum, c/o World Agroforestry Centre
(ICRAF), PO Box 30677-00100 GPO, Nairobi, Kenya

over potentially long distances, mainly by humans and animals such as cattle and goats (Hall and Walker 1991). The long distance seed dispersal would tend to increase genetic variation within populations and reduce differences among populations (Hamrick et al. 1992). Unfortunately, desertification has reduced its abundance in the West African Sahel (Gonzalez 2001).

There is considerable potential for commercialization of *B. aegyptiaca* fruit and seed (Faye et al. 2010). The nutritious pulp is consumed fresh or dry, and the seed is a source of oil for cooking, pharmaceuticals and the preparation of soap. All of these uses are important to rural communities, and many communities also sell dried fruit and seed for industrial processing.

A participatory domestication program for *B. aegyptiaca* was initiated with rural communities in eastern Niger (World Agroforestry Centre 2009). Rural communities prefer to develop the domestication program based on sexual rather than asexual propagation methods because, in their experience, propagation from seed is easier and often results in higher survival than vegetative propagation. As part of this program, studies of phenotypic variation in fruit and seed morphology (and other traits) were initiated within and among natural populations. The existence of phenotypic variation within and among natural populations is important for tree domestication programs since it is the base for selection and improvement (Simons and Leakey 2004).

Phenotypic variation in fruits and seeds may reflect the interaction of several effects. For example, natural selection related to rainfall gradients in the West African Sahel may produce clinal variation in adaptively important traits among populations (Weber et al. 2008; Sotelo Montes and Weber 2009; Weber and Sotelo Montes 2010; Sotelo Montes et al. 2010), and seed size and shape may be adaptively important (Maranz and Wiesman 2003). In addition, selection by humans can produce significant differences in fruit size within and among regions (e.g., Maranz and Wiesman 2003; Leakey et al. 2004, 2005b; Assogbadjo et al. 2005). In the case of *B. aegyptiaca*, rural people value the fruit pulp for consumption and the seed kernel for oil, pharmaceuticals and soap. This could affect the variation in fruit/seed morphology as well as the strength of correlations between fruit and seed variables within tree populations. For example, if people select some fruits primarily for consumption (i.e., much pulp with small kernels) and other fruits primarily for oil (large kernel with little pulp) and sow the seeds from both selected types, there could be considerable variation in fruit, pulp and kernel weights, and relatively weak correlations between kernel and fruit weights within populations.

In this study, we investigated phenotypic variation in fruit/seed size and shape within and among parkland agroforests of *B. aegyptiaca* in eastern Niger. The major objectives were to determine (a) if there was significant phenotypic variation within and among populations; (b) if within-tree variation differed among populations; (c) if the variation was related to latitude and longitude and, by hypothesis, rainfall gradients in the region; and (d) if correlations among fruit and seed variables were similar within populations. Results are compared with other studies of phenotypic variation in indigenous fruit trees in Africa, and some practical implications for tree domestication programs are discussed.

Materials and methods

Sample region and measured variables

Fruits of *B. aegyptiaca* were collected in four extensive parkland agroforests, hereafter referred to as populations, in the Maradi region of eastern Niger in 2007 (Table 1). The sample region is approximately 170 km from south to north and 100 km from west to east. Mean annual rainfall in the sample region decreases slightly from south to north and from west to east (~450–400 mm: data obtained from WorldClim database described by Hijmans et al. 2005). Mean annual temperature is ~29°C (Sivakumar et al. 1993), and soils are sandy and infertile (arenosols: FAO 2007). The first three populations are located in the sites of the participatory tree domestication program, and the fourth is the northernmost population in the region. These populations were chosen because participating communities wanted to establish provenance/progeny tests in their parklands to compare their local provenance with a provenance from a drier zone, which they hypothesized would be better adapted to drought (World Agroforestry Centre 2009).

Table 1 Mean latitude, longitude and elevation of four populations of *Balanites aegyptiaca* in the Maradi region of Niger

Code	Population	Latitude (°N)[a]	Longitude (°E)[a]	Elevation (m)[a]
P1	Sajamanja	13°12″58″	7°28′48″	423
P2	Elgueza	13°16′6″	7°32′22″	403
P3	Dansaga	13°24′49″	7°26′57″	413
P4	Kanambakache	13°27′53″	7°25′22″	400

[a] Mean of 25 trees per population

In each population, mature fruits were collected from 25 trees that had sufficient fruits for this study and the provenance/progeny tests, and no visible insect damage or disease symptoms. Fruits were sampled from the lower, middle and upper parts of the four quadrants in the canopy: the average number of fruits collected per tree was approximately 600. A minimum distance of 100 m was maintained between each selected tree in order to reduce the chance of sampling siblings. Stem diameter at breast height (DBH, 1.3 m above ground) of sampled trees was measured to the nearest cm using a diameter tape. Latitude, longitude and elevation (±7–10 m) of sampled trees were recorded using a GPS. Mean latitude, longitude (decimal format) and elevation of the populations were calculated from the values for the 25 trees in each population: decimal values for population latitude and longitude were then transformed into degrees-minutes format for descriptive purposes.

Thirty fruits per tree were randomly selected and air-dried to a constant weight prior to measurement. Each fruit was measured individually. Measurements were not made on fresh fruits because it was not possible to maintain them in a fresh condition without fungal infection during the collection. The measured variables used in the analyses were weights of the fruit, hard seed coat and kernel to the nearest 0.1 g; and lengths and widths of the fruit and seed (kernel plus seed coat) to the nearest mm. Fruit weight included weight of the fruit coat, pulp, seed coat and kernel. Individual weights of the fruit coat and pulp were not analyzed because they could not be accurately estimated: the pulp adhered to the fruit coat and in particular to the seed coat, so it had to be dissolved and scraped off the seed coat.

Statistical analysis of measured and derived variables

The SAS® statistical package (SAS Institute Inc. 2004) was used for all analyses. Departure from the normal distribution and homogeneity of variance were tested for the residuals from the analysis of variance (ANOVA) models presented below, using statistics provided by the UNIVARIATE procedure. The significance level was $\alpha \leq 0.05$ for all tests.

Three sets of variables were derived from the measured variables for each tree. These included the coefficient of variation (CV) of each measured variable, and standardized factor scores from principal component analysis (PCA) of the means and CVs of the measured variables (PC-Means and PC–CVs, respectively). Principal components were factored from the matrix of Pearson *r* correlation coefficients among tree means and among CVs (PRINCOMP procedure).

ANOVA was used to determine if there were significant differences in the measured variables due to populations and trees nested in populations, and in the derived variables due to populations (GLM procedure, type III sums of squares). Sources of variation were populations, trees nested in populations and residual (i.e., pooled within-tree variation) for the measured variables; and populations and residual (i.e., trees nested in populations) for the derived variables. Populations and trees nested in populations were treated as random factors. Numerator/denominator degrees of freedom of F ratios were 3/96 for populations and 96/2900 for trees nested in populations. For variables with significant differences due to populations, least-squares means of populations were compared using Tukey's "honestly significant difference test": this test was chosen to control the "maximum experimentwise error rate" for equal sample sizes (Steel et al. 1997).

Multiple linear regression analysis was used to investigate variation among trees in relation to latitude, longitude and elevation (REG procedure). The dependent variables were the tree means and CVs of each measured variable and standardized factor scores from PCA of the means and CVs. The independent variables included the linear and quadratic terms for tree latitude, longitude and elevation; and the two-way interactions between linear latitude, longitude and elevation. Models were selected using the stepwise technique.

Pearson *r* correlation coefficients were used to investigate linear relationships among the measured variables (CORR procedure). Correlations were based on all fruits, and separately among fruits in each population in order to assess whether correlations varied among populations.

Results

Stem diameter of sampled trees

Mean stem diameter and the range in stem diameter of sampled trees were greater in the two southernmost populations and lower in the two northernmost populations. The mean, range and CV of DBH, respectively were 117 cm, 136 cm and 30% in Sajamanja; 117 cm, 176 cm and 34% in Elgueza; 34 cm, 35 cm and 26% in Dansaga; 37 cm, 38 cm and 28% in Kanambakache.

Variation in measured and derived fruit/seed variables

Mean weights of the seed coat and kernel were ~41% of the entire fruit weight (Table 2). Therefore, mean weights of the fruit coat and pulp were ~59% of the entire fruit weight. There was considerable variation in weights and dimensions of *B. aegyptiaca* fruits and seeds. Judging from the CVs, there was relatively greater variation in weights than in lengths and widths. All variables exhibited continuous variation (plots not shown). It should be emphasized that this is phenotypic variation, which reflects the genotype, environment and genotype by environment interaction.

Table 2 Descriptive statistics of fruit/seed variables of *Balanites aegyptiaca* from the Maradi region of Niger

Variable	Mean	Range	SD	CV
Fruit weight (g)	6.28	11.2	1.65	26.23
Seed coat weight (g)	2.02	1.7	0.59	29.15
Kernel weight (g)	0.58	1.8	0.23	38.89
Fruit length (cm)	2.78	7.5	0.38	13.81
Fruit width (cm)	2.22	3.7	0.25	11.45
Seed length (cm)	2.51	3.1	0.35	13.95
Seed width (cm)	1.82	1.9	0.22	12.09

Sample size = 3000 for all variables (100 trees, 30 fruits per tree), *SD* standard deviation, *CV* coefficient of variation

Interpretation of the derived variables from PCA was based on the sign and magnitude of the eigenvectors (Table 3). Trees with larger factor scores were interpreted to have the following characteristics: PC1-Means = longer, wider fruits and seeds, and heavier fruits; PC2-Means = longer, narrower fruits and seeds, and heavier seeds; PC1–CVs = greater within-tree variation in fruit and seed size and fruit weight; PC2–CVs = greater within-tree variation in kernel weight, fruit and seed length, but lower within-tree variation in seed width.

Fruit weight, kernel weight, CV-fruit width, CV-seed width and PC1–CVs differed significantly among populations (ANOVA not tabled: $P < 0.01$ for fruit weight and CV-fruit width, $P < 0.05$ for others). All seven measured variables differed significantly among trees within populations ($P < 0.001$). Fruit and kernel weights were greater in the northernmost and easternmost populations (P4 and P2, respectively: Table 4). CVs of fruit and seed width and PCI–CVs decreased from the southernmost to the northernmost population (P1 to P4: Table 4).

Table 3 Eigenvectors for first two principal components of tree means and CVs of fruit/seed variables of *Balanites aegyptiaca* from the Maradi region of Niger

Variable	PC1-Means	PC2-Means	PC1–CVs	PC2–CVs
Fruit weight	0.509	−0.131	0.500	−0.139
Seed coat weight	0.081	0.378	−0.141	0.332
Kernel weight	0.044	0.447	−0.040	0.727
Fruit length	0.445	0.376	0.351	0.346
Fruit width	0.427	−0.388	0.477	0.129
Seed length	0.425	0.429	0.296	0.365
Seed width	0.415	−0.405	0.538	−0.270

Percent of total variance: PC1-Means = 45%, PC2-Means = 21% (total = 66%)

Percent of total variance: PC1–CVs = 31%, PC2–CVs = 18% (total = 50%)

Table 4 Multiple comparison test of population means of *Balanites aegyptiaca* from the Maradi region of Niger

Variable	Populations (P1–P4)			
	P1	P2	P3	P4
Fruit weight (g)	5.97	6.78a	5.60	6.80a
Kernel weight (g)	0.53	0.63	0.59a	0.60a
CV-fruit width	9.00a	7.97ab	7.13b	6.85b
CV-seed width	8.84a	7.81ab	7.44ab	7.12b
PC1–CVs	0.48a	0.08ab	−0.21ab	−0.35b

Means with different letters are significantly different ($P < 0.001$ for fruit and kernel weights, $P < 0.05$ for others), and means with the same letter are not significantly different ($P > 0.05$)

Values for five variables varied with latitude or with the latitude by longitude interaction in the sample region (Table 5). Mean kernel weight and PC2-Means of trees increased from the southwest to the northeast (i.e., with the latitude by longitude interaction). The trend in PC2-Means indicates that trees in the northeast tended to have longer, narrower fruits and seeds, and heavier seeds. CVs of fruit and seed width and PC1–CVs of trees decreased from south to north, indicating that trees in the north tended to have relatively lower within-tree variability in fruit weight and fruit and seed dimensions. Although statistically significant, the regression models generally explained less than 10% of the variation among trees.

Correlations among fruit/seed variables

All significant correlation coefficients among the measured variables were positive in the analysis across populations (Table 6). The strongest correlations were between the length of fruits and seeds, and between the width of fruits and seeds. Fruit weight had a stronger correlation with width than with length of both fruits and seeds. The correlation between seed coat and kernel weights was moderately strong, while correlations among dimensions of fruits and seeds were relatively weak. Seed coat and kernel weights had very low or insignificant correlations with fruit weight, and with fruit and seed dimensions.

There were some notable differences among populations in the sign of some statistically significant correlations involving seed coat and kernel weights (Table 6). For example, the correlations between the weight of fruits and kernels, and between kernel weight and the width of fruits and seeds were positive in population 4 but negative in population 2; the correlation between weight of fruits and seed coats was positive in populations 1 and 4 but negative in population 3; and the correlations between seed coat weight and the length of fruits and seeds were positive in populations 1 and 2 but negative in population 4. Although most correlations involving seed coat and kernel weights were relatively low, the differences

Table 5 Linear regression of fruit/seed variables of *Balanites aegyptiaca* trees with geographic location in the Maradi region of Niger

Dependent variable[a]	Regression equation[b]	SE[c]	P[d]	R^{2}[e]
Kernel weight	−7.183 + 0.078(Lat*Long)	0.024	**	0.094
CV-fruit width	113.640 − 7.938(Lat)	2.322	***	0.107
CV-seed width	85.164 − 5.799(Lat)	2.204	**	0.067
PC2-Means	−54.269 + 0.544(Lat*Long)	0.193	**	0.075
PC1–CVs	40.297 − 3.021(Lat)	0.935	*	0.096

[a] Dependent variables: kernel weight = seed kernel (g); CV-fruit width and CV-seed width, respectively = coefficients of variation of fruit and seed width within trees; PC2-Means and PC1–CVs, respectively = standardized factor scores of trees for principal component 2 based on tree means and for principal component 1 based on tree coefficients of variation

[b] Independent variables: Lat and Long = latitude and longitude (decimal °N and °E, respectively), Lat*Long = Lat × Long interaction

[c] SE = standard error of regression coefficient

[d] P = significance of regression coefficients: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$

[e] R^2 = coefficient of determination of model, $N = 100$

Table 6 Pearson *r* correlation coefficients among fruit/seed variables across and within populations of *Balanites aegyptiaca* from the Maradi region of Niger

Variable	Fruit weight	Seed coat weight	Kernel weight	Fruit length	Fruit width	Seed length	Seed width
Across populations							
Fruit weight	–						
Seed coat weight	0.076***	–					
Kernel weight	NS	0.332 ***	–				
Fruit length	0.462***	0.077 ***	0.038 *	–			
Fruit width	0.613***	0.044 *	NS	0.219 ***	–		
Seed length	0.449***	0.081 ***	0.048 **	0.836 ***	0.172 ***	–	
Seed width	0.628***	0.044 *	NS	0.159 ***	0.682 ***	0.140 ***	–
Populations 1 below and 2 above diagonal							
Fruit weight	–	NS	−0.160 ***	0.338 ***	0.656 ***	0.319 ***	0.763 ***
Seed coat weight	0.145***	–	0.360 ***	0.131 ***	NS	0.114 **	−0.104 **
Kernel weight	NS	0.228 ***	–	NS	−0.138 ***	NS	−0.183 ***
Fruit length	0.484***	0.267 ***	NS	–	NS	0.904 ***	NS
Fruit width	0.584***	0.104 **	NS	0.446 ***	–	NS	0.774 ***
Seed length	0.484***	0.282 ***	NS	0.805 ***	0.428 ***	–	NS
Seed width	0.463***	0.081 *	NS	0.269 ***	0.561 ***	0.275 ***	–
Populations 3 below and 4 above diagonal							
Fruit weight	–	0.100 ***	0.203 ***	0.450 ***	0.538 ***	0.502 ***	0.680 ***
Seed coat weight	−0.086*	–	0.277 ***	−0.131 ***	0.074 *	−0.163 ***	0.112 **
Kernel weight	NS	0.497 ***	–	0.122 ***	0.125 ***	0.123 ***	0.171 ***
Fruit length	0.513***	NS	NS	–	0.184 ***	0.745 ***	0.111 **
Fruit width	0.689***	NS	0.074 *	0.186 ***	–	0.151 ***	0.644 ***
Seed length	0.470***	NS	NS	0.895 ***	0.162 ***	–	0.130 ***
Seed width	0.654 ***	NS	NS	0.213 ***	0.757 ***	0.182 ***	–

Probability of Pearson *r*: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, NS $P > 0.05$; N = 3000 across and 750 within populations

in sign among populations explain why the correlations were very low or insignificant across populations.

There were some positive associations between within-tree variability of fruit/seed variables, based on Pearson r correlation coefficients among tree CVs (not tabled). The following significant correlations were observed ($N = 100$): fruit weight with fruit length, fruit width and seed length ($r = 0.250$, 0.343 and 0.570, respectively; $P < 0.05$, 0.01 and 0.001, respectively); seed coat weight with kernel weight ($r = 0.202$, $P < 0.05$); fruit length with fruit width and seed length ($r = 0.223$ and 0.267, respectively; $P < 0.05$ and 0.01, respectively); fruit width with seed length and width ($r = 0.254$ and 0.463, respectively; $P < 0.05$ and 0.001 respectively).

Discussion

Differences in stem diameter of sampled trees between the northern and southern populations

The mean and range of stem diameter of *B. aegyptiaca* trees sampled in this study were lower in the northern than in the southern populations. This may reflect the fact that mean annual rainfall was slightly lower in the north, thereby reducing natural regeneration from seed and seedling/tree growth rates. It may also reflect differences in the age distribution of the sampled trees (i.e., younger in the north). However, tree age was not determined in this study, and stem diameter is not necessarily a reliable indicator of tree age in *B. aegyptiaca*. Stem die-back is common in *B. aegyptiaca* during very dry years, and is often followed by the production of sucker shoots from the roots (Hall and Walker 1991). Some of the stems measured in this study probably developed from sucker shoots, especially in the drier northern populations, and the diameter of these stems underestimates the real age of the tree.

Further research is needed to assess the demographics of tree age and regeneration of *B. aegyptiaca* via sucker shoots and seeds along rainfall gradients. We hypothesize that in the drier zones, regeneration via sucker shoots is relatively high while regeneration via seeds is relatively low compared with the more humid zones and, by implication, genetic diversity is lower in the drier than in the more humid zones.

Variation in fruit and seed variables

All measured fruit and seed variables varied significantly among *B. aegyptiaca* trees in populations (i.e., parkland agroforests) in eastern Niger. This is encouraging because the sample region is relatively small. There is potential, therefore, to select candidate "plus trees" within populations based on fruit/seed morphology. Significant variation in fruits/seeds has also been reported among trees in natural populations of other indigenous fruit tree species in Africa [e.g., *Argania spinosa* (L.) Skeels in Morocco (Bani-Aameur and Ferradous 2001); *Irvingia gabonensis* (Aubrey Lecomte ex O'Rorke) Baillon. (Atangana et al. 2001, Anegbeh et al. 2003) and *Dacryodes edulis* (G.Don) H.J. Lam (Leakey et al. 2002) in west and central Africa; *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokworo (Leakey et al. 2005a, b) and *Uapaca kirkiana* Muell. Arg. (Kadzere et al. 2006, Mwase et al. 2006) in southern Africa].

There was significant geographic variation in some fruit and seed variables based on ANOVA of population means and linear regression of tree means with latitude and longitude. These differences may be due to the historical interaction of several factors such as natural selection, selection by humans and animals, gene flow mediated by humans and animals and random genetic drift (e.g., Hamrick et al. 1992). We cannot of course state which of these factors (and/or others) has had a greater effect in producing the geographic variation. Mean annual rainfall decreases slightly from south to north and from west to east in the sample region. We present a few hypotheses below, related primarily to the rainfall gradients in the sample region, but emphasize that we have no evidence to support the hypotheses.

Balanites aegyptiaca trees in the drier parts of the sample region tended to have heavier kernels, longer and narrower seeds, and less variability in fruit and seed width (based on linear regression). Heavier kernels have potentially greater energy reserves, which could allow more rapid seedling development at the onset of the rainy season (Harper 1977). Seeds with greater kernel weight may, therefore, be favored by natural selection in drier areas. The surface to volume ratio is greater in longer, narrower seeds and this may have a selective advantage in hotter, drier areas. A larger surface to volume ratio could reduce heat load of developing seeds before fruit abscission (Maranz and Wiesman 2003), and also increase the rate of water imbibition (Nobel 1991) thereby favoring more rapid germination and seedling development. Lower within-tree variability in seed width in the drier areas may reflect natural selection for narrower seeds in these areas, as mentioned above. It could also reflect founder effects, i.e. regeneration of the tree population from a very limited genetic base following a period of high tree mortality (such as the protracted droughts in the 1970s: Maranz 2009). Greater within-tree variability in fruit and seed width in more humid areas may also reflect larger human and tree populations, greater market access for tree products, and selection and dispersal by humans of different fruit ideotypes (i.e., for the pulp and kernel: Leakey et al. 2004) for local use and sale in local and regional markets.

The northernmost and easternmost populations of *B. aegyptiaca*, which were from the drier parts of the sample region, had the heaviest fruits and seed kernels (based on ANOVA). Differences in fruit weight do not appear to reflect seed weight because fruit weight was not significantly correlated with weights of the seed coat or kernel across populations. In contrast to these results, some studies of other species have reported heavier fruits and/or kernels in more humid zones in West Africa [e.g. *Vitellaria paradoxa* C.F. Gaertn. (Maranz and Wiesman 2003) and *Adansonia digitata* L. (Assogbadjo et al. 2005)].

Correlations among fruit and seed variables

Length and width of fruits were strongly correlated with those of seeds, indicating that fruit dimensions would be good indicators of seed dimensions.

In addition, fruit weight was moderately correlated with seed dimensions, suggesting that it would be a fairly good indicator of seed dimensions.

In contrast, fruit and kernel weights were not significantly correlated across populations, indicating that fruit weight would be a poor indicator of kernel weight. Similar results were reported for *I. gabonensis* in Cameroon and Nigeria (Atangana et al. 2002) and *S. birrea* subsp. *caffra* in southern Africa (Leakey 2005). However, fruit and kernel weights may be positively correlated in other species [e.g., *Strychnos cocculoides* Baker in Zambia (Mkonda et al. 2003) and *U. kirkiana* in Malawi (Ngulube et al. 1997)] and/or the correlation may vary among populations (discussed below).

These results suggest that it may be challenging for tree domestication programs to simultaneously increase both fruit and kernel weights of *B. aegyptiaca* in the same breeding population. Researchers working on *I. gabonensis* (Atangana et al. 2002) and *S. birrea* subsp. *caffra* (Leakey 2005), which are also valued for the fruit and kernel, observed similar results and recommended that domestication programs develop separate ideotypes for the fruit and kernel. This approach has the advantage of developing improved germplasm for each product and builds on farmers' practices, i.e. selecting some trees for fruit characteristics and others for kernel characteristics. The lack of a strong relationship between these variables indicates that there are opportunities to identify trees with large fruits but small kernels (and by implication a lot of pulp) for consumption, and trees with smaller fruits but larger kernels for oil production (Leakey 2005) but this approach would require extensive sampling. For example, Fig. 1 shows a plot of the factor scores from the principal components analysis of tree means: trees with relatively large fruits and small kernels are in the lower right quadrate (positive PC1-Means, negative PC2-Means), and trees with relatively small fruits and large kernels are in the upper left quadrate (negative PC1-Means, positive PC2-Means). Among the 100 trees, approximately 20% have relatively large fruits with small kernels and approximately 20% have relatively small fruits with large kernels.

It may be possible to identify populations of *B. aegyptiaca* where the correlation between fruit and kernel weight is positive, which would facilitate selection for large kernels, and other populations where the correlation is negative, thereby facilitating selection for greater pulp mass and small kernels. In this study, for example, the correlation between fruit and kernel weight was weak but positive in the northernmost population and weak but negative in the easternmost population. Slight differences in the strength of the fruit-kernel weight relationship have also been reported among populations of other species, but the relationship was positive in all cases [e.g., *I. gabonensis* in Cameroon and Nigeria (Atangana et al. 2002); *S. birrea* subsp. *caffra* in Namibia and South Africa (Leakey 2005)].

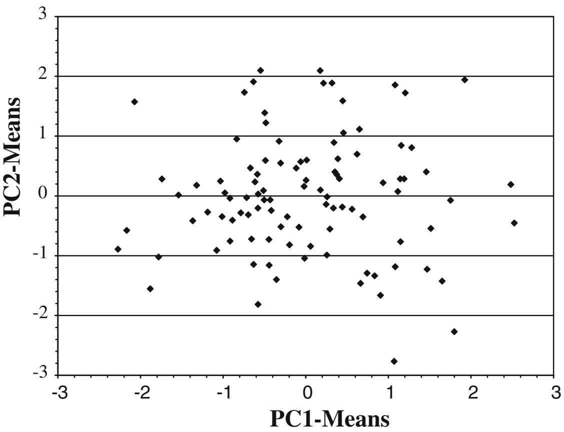

Fig. 1 Plot of factor scores from principal components analysis of fruit/seed variables of *Balanites aegyptiaca* trees from the Maradi region of Niger: Larger values for PC1-Means = longer, wider fruits and seeds, and heavier fruits; larger values for PC2-Means = longer, narrower fruits and seeds, and heavier seeds

The variability within populations suggests that rural people have selected some *B. aegyptiaca* fruits primarily for pulp mass and others for kernel mass, and advertently or inadvertently sown the seeds from both types in their parklands. However, we have no evidence to support this statement. Further research is necessary to assess local selection criteria and domestication histories: such studies could help explain why the fruit-kernel weight relationship varied from negative to positive among the sampled populations.

Conclusions

The existence of significant tree-to-tree variability in *B. aegyptiaca* fruit/seed morphology in a relatively small geographical area is encouraging for the participatory domestication program initiated in eastern

Niger. To the best of our knowledge, however, there are no published reports about genetic variation in fruit/seed traits in *B. aegyptiaca* or other indigenous fruit tree species in Africa, and this information is essential for developing tree domestication and conservation programs. Multi-location provenance/progeny tests of *B. aegyptiaca* and other indigenous fruit tree species are needed to estimate heritability and genotype by environment interaction of fruit/seed traits, genetic correlations among these traits and with tree growth, as well as productivity in different environments. Ideally these should be participatory tests conducted in rural communities, like those established in eastern Niger (World Agroforestry Centre 2009), in order to take advantage of both traditional and scientific knowledge in developing selection criteria to produce high quality fruit products for current and projected markets. In addition to providing essential information, the tests can be managed as in situ and circa situ conservation plots and seed orchards for the production of selected, source identified germplasm (Dawson et al. 2009).

Since the seed of *B. aegyptiaca* is used for several commercial products, there is concern that overharvesting seed in managed and/or natural populations will reduce natural regeneration, especially if national and/or international demand increases for the products. Although the species can regenerate vegetatively from sucker shoots, natural regeneration from genetically diverse seed pools is essential to facilitated adaptation to environmental change, and in particular to projected climate change in the region (Dawson et al. 2010). It is important, therefore, that tree domestication programs work in a participatory manner with rural communities to develop sustainable production and harvesting plans and long-term conservation plans to safeguard the genetic resources of this species.

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