Genet Resour Crop Evol (2012) 59:1883–1898
DOI 10.1007/s10722-012-9905-8

NOTES ON NEGLECTED AND UNDERUTILIZED CROPS

Morphological variation among shea tree (*Vitellaria paradoxa* subsp. *nilotica*) 'ethnovarieties' in Uganda

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Received: 9 May 2012 / Accepted: 30 August 2012 / Published online: 14 September 2012

Abstract *Vitellaria paradoxa* C. Gaertn. (shea butter tree) is an indigenous African tree species that is widely distributed in the dry areas of northern and eastern Uganda. The species is widely known for its oil which is used in cooking, cosmetics and traditional medicine. Local folk classification recognises the presence of different ethno-varieties on the basis of fruit and nut characters. In the present study, 176 trees representing 44 ethno-varieties from three farming systems of Uganda were assessed to determine the patterns of morphological variation and establish the congruence between morphological variation and folk classification. The results show high variation in pulp weight (CV = 35.9 %), stem diameter (CV = 28.48 %), fruit weight (CV = 27.81 %) and canopy diameter (CV = 26.69 %). There was a strong positive correlation between pulp and fruit weight (r = 0.963, $p < 0.001$), leaf length and leaf width (r = 0.652, $p < 0.001$) and between petiole length and leaf length (r = 0.788, $p < 0.001$). There was no underlying quantitative morphological structuring among the 44 ethno-varieties. Hierarchical cluster analysis using quantitative morphometric data produced three groups without clear aggregation based on ethnographic or geographic separation. However, a combination with qualitative traits as perceived by farmers provided good congruence with folk classification. Quantitative morphological data alone does not resolve any discrete forms of *V. paradoxa* that are related to folk classification. There is need to utilise biochemical and molecular markers to unravel the underlying variation for use in selection and improvement of shea butter tree ethno-varieties.

Keywords Ethno-varieties · Folk classification · Morphological variation · Qualitative traits · Quantitative traits · *Vitellaria paradoxa*

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Introduction

The shea butter tree (*Vitellaria paradoxa* C. F. Gaertn.—Family Sapotaceae) is a multipurpose tree species of the Sudano-Sahelian belt of Africa (Hall et al. 1996; Hemsley 1968). It is a semi-domesticated species distributed in a wide belt over 1 million km^2 i.e. between western Senegal and eastern Uganda (Hall et al. 1996; Salle et al. 1991). It is currently divided into two subspecies (*V. paradoxa* subspecies *paradoxa*—found in Western Africa and *V. paradoxa* subsp.

nilotica (Kotschy) A.N. Henry, Chithra et N.C. Nair—found in eastern Africa). The shea butter tree takes on various forms, which may be influenced by environmental factors, but nonetheless are recognised by farmers in variety classification. The fruits contain a large solitary seed (sometimes the seeds can be 2 or 3) and the cotyledons contain abundant fat and oil. Within Uganda, the subspecies *nilotica* covers the whole range of the savanna drylands above 1° North. The southernmost distribution is in Pallisa district in eastern Uganda while to the west, it occurs in Masindi and spreads into the Democratic Republic of Congo (DRC). To the north, its occurrence is contiguous with its southern Sudan distribution. The species therefore occurs in eastern, mid-western and northern Uganda. The highest density of *V. paradoxa* subsp. *nilotica* is reported to be in Otuke county in Lira district (Masters and Puga 1994).

Interest in this species arises out of the multiple uses of the tree and its products. The most important product is fat/oil that is extracted from the kernels of the shea fruit. This oil is used for a variety of purposes including cooking (Abbiw 1990), medicinal, hair and skin ointments and as a base for industrial manufacture of confectioneries (Cidell and Alberts 2006). It is also used for various traditional and social rituals and ceremonies such as marriages, funerals, coronations and rainmaking (Ferris et al. 2004; Gwali et al. 2012; Hall et al. 1996; Moore 2008).

Morphological characters have been widely used in descriptive accounts of this species (Hall et al. 1996; Hall and Hindle 1995; Hemsley 1968; von Gaertner 1807; Kotschy 1865; Andrews 1952; Pennington 1991) and in identifying useful phenotypes of *V. paradoxa* for domestication (Chevalier 1943, 1948; Diarrassouba et al. 2007; Ruyssen 1957; Sanou et al. 2005, 2006; Ugese et al. 2010). Based on fruit and leaf variation, Chevalier (1943) distinguished eight varieties (i.e. *cuneata, ferruginea, floccosa, mangifolia, nilotica, parvifolia, poissoni* and *serotina*). Ruyssen (1957) utilised tree shapes and sizes, fruits, nuts and leaves to report *V. mangifolium* as a subspecies consisting of two varieties (*viridis* and *rubifolia*). Correlation between different morphological characteristics has been demonstrated in many West African countries such as Burkina Faso (Lamien et al. 2007), Cameroon (Diarrassouba et al. 2007), Ghana (Lovett and Haq 2000b), Mali (Sanou et al. 2005, 2006) and Nigeria (Ugese et al. 2010). High variation has been reported for shea butter tree trunk, leaves, fruits and nut characters (Kelly et al. 2004; Lovett and Haq 2000a). Five phenotypes based on fruit morphology (round, ovoid, reversed pear, fusiform, and oblong) have been recorded for shea butter trees in Cameroon (Diarrasouba et al. 2007). Nut colour, crown shape and habitat types have been used in addition to dendrometric and fruiting variables to assess shea butter tree variation (Diarrasouba et al. 2007; Lamien et al. 2007).

Folk classification recognises the presence of a diversity of shea butter tree forms (ethno-varieties) across different ethnic groups in Uganda (Gwali et al. 2011). According to the authors, ethno-variety classification across the shea butter tree range in Uganda is similar and consistent among different ethnic groups. However, the recognition of many different forms (ethno-varieties) purely on the basis of local selection criteria cannot produce an adequate understanding of the range of variation within the species. Folk taxonomy and phenotypic observations can only describe a small portion of the underlying genetic diversity present in a species. Nevertheless, it is important to document the folk taxonomy or classification systems of useful and yet undomesticated species as a first step in the selection process. In West Africa, farmers are reported to utilise this folk classification to actively select and preserve superior shea (Lovett and Haq 2000b) and other priority trees on farm (Assogbadjo et al. 2008). However, there is only scanty documentation of shea butter tree folk classification in Uganda. There are no studies in Uganda to-date that have quantified phenotypic variation of shea butter trees across their range. Although genetic diversity studies have been undertaken for shea butter trees across the whole range and have included Ugandan populations, the criteria for sampling did not include folk classification and phenotypic variation. Although the reproductive biology and flowering and fruiting of subspecies *nilotica* in Uganda were studied by Okullo (2004), additional studies are needed to consider folk classification, phenotypic and genetic variability of subspecies *nilotica*. According to many authors (Kovach et al. 2007; Sweeney and McCouch 2007; Vodouhè et al. 2011), folk classifications can be the basis for domestication or breeding programmes. Therefore, understanding the morphological variation of the ethno-varieties is important for the management, conservation and domestication of shea trees in Uganda. A sound knowledge of the relationships between folk taxonomy, phenotypic variation and the underlying genetic variability is useful in developing efficient selection strategies for shea butter trees in Uganda.

In the present study, we investigated the morphological variation among shea butter tree (*Vitellaria paradoxa* subsp. *nilotica*) ethno-varieties in Uganda on the basis of the recently documented folk classification of shea butter trees in Uganda (Gwali et al. 2011) and established the extent of congruence between morphological and folk classification.

Materials and methods

Study area

The study was conducted in the shea belt of Uganda. Sampling was carried out in the Teso, Northern and West Nile farming systems (Fig. 1). The vegetation in the study area is classified as *Combetrum*/*Vitellaria* and grass savannas (Langdale-Brown et al. 1964). The rural people are agro-pastoralists and depend on subsistence mixed annual cropping as well as livestock production for their livelihoods (Okorio et al. 2004; Oluka et al. 2002). The rainfall pattern is bimodal in the Teso farming system with a mean annual precipitation of 1,300 mm (Ebanyat et al. 2010; Gavigan et al. 2009); while the Northern and West Nile farming systems receive less markedly bimodal rainfall, consisting mainly of one major rainfall season per year, with mean annual precipitation of 800 mm (Mwebaze 2010).

Plant material used and their characteristics

Shea butter trees come in all sorts of shapes. Many trees have a porous crown with spreading branches, sometimes branching very low (Fig. 2). Sometimes, the crown takes on a rounded shape with drooping or sagging branches. Some trees have conical shapes, with the branches growing skyward thereby forming an "inverted cone-shaped" crown. At seedling level however, it is not possible to know which tree shape it will grow into. Nursery trials conducted in the present study show some ethno-varieties grow more vigorously than others. However, farmers use mainly fruit/nut morphological and organoleptic properties for classification of shea butter tree phenotypes (Gwali et al. 2011). In this study, we investigated 176 shea butter trees representing 44 ethno-varieties from the three farming systems. Shea butter tree folk classification is consistent across all ethnic groups in the shea butter tree zone of Uganda (Gwali et al. 2011). The prefix 'ethno-variety' is used to refer to a grouping of shea butter trees that are identified by a single name by farmers of a particular ethnic group (sensu Sturtevant 1964; Rivera et al. 2006). The different ethno-varieties and characteristics used by farmers to classify them as documented by Gwali et al. (2011) are presented in Table 1.

Data collection

Morphological variation was investigated based on a maximum of five trees sampled from each ethno-variety in each farming system. A total of 40–50 mature leaves and 20–30 fallen ripe fruits were collected from each tree between April and June 2009. Only 3–5 leaves were taken from the distal end of each leafing twig on a tree to ensure comparability between sampled trees. The location of each tree was geo-referenced using a global positioning system (GPS). Data were collected from six qualitative and 14 quantitative phenotypic and morphological variables (Table 2). Diameter at breast height (DBH) was measured at 1.3 m high using a diameter tape while a measuring tape was used to determine the canopy diameter (Table 2). Canopy diameter was measured in the N–S and E–W directions after which a mean value was derived for each tree. Leaf morphometric parameters were determined using a graduated rule or calliper. Fruit and nut weight was measured using a Mettler PJ3600 Delta Range 0.001 g sensitive balance.

Data analysis

Means and standard deviations were calculated for each quantitative variable of all the leaf and fruit samples of each ethno-variety. Quantitative variables were tested for normality at the 95 % confidence level using the one-sample Anderson–Darling (A–D) test in Minitab version 14. Only eight out of the 14 quantitative variables were normally distributed at the 95 % confidence level. To achieve normality, the data set was transformed using the Box-Cox transformations within the control charts command of Minitab at a Lambda value of −0.13 (Fig. 3).

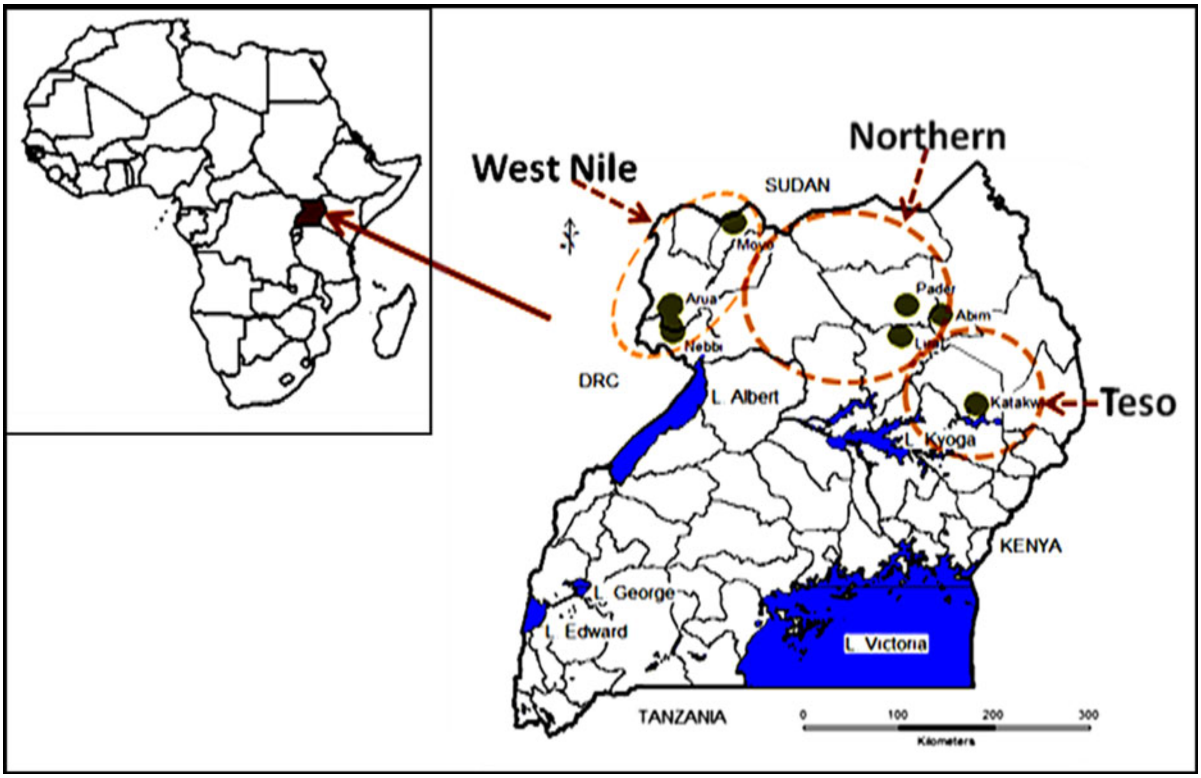

Fig. 1 Location of the seven study sites (*shaded circles* in map) in the three farming systems (bounded by *dark dashed lines* in map) of the shea belt of Uganda. Inset: Map of Africa showing location of Uganda

Pair wise comparisons of all variables were calculated using Minitab 14.0. First order (Pearson's) and second order (partial) correlation coefficients were computed. Partial correlation analysis is aimed at finding correlation between two variables after removing the effects of other variables. Partial correlation helps to spot correlations explained by the effect of other variables as well as to reveal those correlations masked by the effect of other variables (Pillai and Mohankumar 2010). Partial (second order) correlations were calculated from the bivariate correlations using the following formula:

$$r_{ijk} = \frac{r_{ij} - (r_{ik} \times r_{jk})}{\sqrt{(1 - r_{ik}^2) \times (1 - r_{jk}^2)}}$$

where r_{ijk} refers to the partial correlation coefficient between variable i and j controlling for k (ethno-variety). r_{ij}, r_{ik} and r_{jk} are Pearson's correlation coefficients between variables i, j and K (ethno-variety).

Principal component analysis (PCA) was performed on the quantitative variables to produce a few representative components of the variables and hence assess quantitative morphological similarity of different shea butter tree ethno-varieties. Only components with eigenvalues of more than 1.0 were extracted. Morphological variables that loaded PCA coefficient values greater than 0.3 were considered relevant for a particular principal component (Jeffers 1967). An agglomerative hierarchical cluster analysis (HCA) was then performed based on a pair-wise similarity matrix of 14 standardised variables using Ward's method and squared Euclidean distance. A second hierarchical cluster analysis was performed in combination with the qualitative variables as perceived by farmers.

Results

Morphological variation of shea butter tree ethno-varieties

The highest variation was found in pulp weight (Table 3) followed by DBH, fruit weight and canopy

Fig. 2 Diversity of shea butter tree (**A–C**) and fruit (**D–E**) shapes and nut sizes/colours/shapes (**F–H**)

Table 1 List of ethno-varieties (including their corresponding descriptors) documented by Gwali et al. (2011) and utilised in assessment of morphological variation

Descriptor	Ethno-variety	Provenance	Farming system
Pulp taste			
Astringent pulp	Egeget	Katakwi	Teso
	Etria	Moyo	West Nile
	Menacwot	Abim	Northern
	Nyangili-macwot	Nebbi	West Nile
	Udanyo-macwot	Nebbi	West Nile
Sweet pulp	Abono	Lira	Northern
	Ewiny	Katakwi	Teso
	Limi	Moyo	West Nile
	Mbilimbili	Arua	West Nile
Tasteless pulp	Asa	Arua/Moyo	West Nile
	Epiana	Katakwi	Teso
Pulp quantity			
Little pulp	Ajiki	Abim	Northern
	Upende-aboro	Nebbi	West Nile
Much pulp	Amoo	Abim	Northern
	Mudaa	Moyo	West Nile
Fruit/nut size			
Big fruits/nuts	Enyii	Moyo	West Nile
	Mbele	Arua	West Nile
Small fruits/nuts	Abor	Abim	Northern
	Alindiri	Lira	Northern
	Ciria	Moyo	West Nile
	Nyiri	Arua	West Nile
	Yao-matino	Pader	Northern
Fruit/nut shape			
Oval/elliptical fruits/nuts	Acula	Abim/Lira	Northern
	Aloto	Pader	Northern
	Coloa	Moyo	West Nile
	Julu	Arua	West Nile
	Nasomel	Katakwi	Teso
Round fruits/nuts	Alulung	Lira	Northern
	Gburua	Moyo	West Nile
	Mangulungulu	Nebbi	West Nile
	Mulunge	Pader	Northern
	Nalungur	Katakwi	Teso
	Ngulu	Arua	West Nile
Pulp hardness			
Hard pulp	Acogo	Lira	Northern
	Ngorokwa	Moyo	West Nile
	Nyangili-acogo	Nebbi	West Nile
	Yao-atega	Pader	Northern
Soft pulp	Apocopoco	Lira	Northern
	Mayom	Nebbi	West Nile
	Upende-appi	Nebbi	West Nile

Table 1 continued

Descriptor	Ethno-variety	Provenance	Farming system
Fruit hairiness			
Hairy fruit	Ajayer	Lira	Northern
	Layer	Pader	Northern
	Nacekum	Katakwi	Teso
	Nyangili-ayir	Nebbi	West Nile

Table 2 Quantitative and qualitative variables and their measurement methods

Variables and units	Code	Equipment/method used
Pulp taste	PlpTst	Farmers' perception
Fruit size	FrtSze	Farmers' perception
Pulp quantity	PlpQty	Farmers' perception
Fruit pubescence	FrtPbs	Farmers' perception
Fruit shape	FrtShp	Farmers' perception
Pulp eubstance	PlpEbst	Farmers' perception
Canopy diameter (m)	CanDia	Measuring tape
Diameter at breast height (cm)	DBH	Measuring tape
Fruit length (cm)	FrtLgth	Vernier callipers
Fruit width (cm)	FrWdth	Vernier callipers
Fruit weight (g)	FrWght	0.001 g sensitive balance
Nut weight (g)	NtWght	0.001 g sensitive balance
Pulp weight (g)	PlpWght	0.001 g sensitive balance
Nut length (cm)	NtLgth	Centimetre rule
Nut width (cm)	NtWdth	Centimetre rule
Leaf length (cm)	LfLgth	Centimetre rule
Leaf width (cm)	LfWdth	Centimetre rule
Petiole length (cm)	PtlLgth	Centimetre rule
Lamina base angle (degrees)	LmBseAng	Protractor
Lamina apex angle (degrees)	LmApxAng	Protractor

diameter. The lowest variation was recorded in nut width, nut length and lamina apex angle. With the exception of petiole length, nut length and width, variation in fruit morphology was generally higher than that in leaf variables.

'Apocopoco' had the heaviest fruits, nuts and pulp at mean values of 43.94, 14.08 and 29.86 g respectively. 'Acula' had the longest fruits with a mean value of 4.28 cm while the highest variation in fruit length was recorded in 'Apocopoco' (CV = 26.94 %). The longest nuts were recorded in 'Ewiny' with a mean length of 2.95 cm. In terms of nut width, 'Ewiny' and 'Nalungur' had the widest nuts at mean values of 2.06 and 2.06 cm respectively. 'Nyiri', 'Yao-matino' and 'Alindiri' had the smallest fruits and nuts. Leaf lengths were higher in ethno-varieties from the West Nile farming system with 'Gburua' having the longest leaves at mean values of 28.69 cm. Other ethno-varieties with long leaves were 'Coloa' (mean = 7. 74 cm) and 'Ngorokwa' (mean = 27.17 cm). The shortest leaves were recorded among 'Nasomel' and 'Epiana' of the Teso farming system. Ethno-varieties from the northern and West Nile farming system also had wider leaves. 'Apocopoco' leaves had a mean width of 9.22 cm while 'Nyangili-Acogo' and 'Gburua' had leaves measuring 8.59 and 8.59 cm wide respectively.

There was strong correlation between most of the fruit and nut (length, width, weight) variables (Table 4; Fig. 5). The strongest correlation was between pulp weight and fruit weight (r = 0.963, $p < 0.001$). While there was strong significant correlation between leaf length and leaf width (r = 0.652, $p < 0.001$) and between petiole length and leaf length (r = 0.788, $p < 0.001$), the rest of the relationships among the leaf variables were weak (r < 0.5). A partial (second order) correlation analysis controlling for ethno-varieties revealed only very little difference when compared to the first order correlation analysis. For example, compared to first order correlations, the second order (partial) correlation between pulp weight and fruit weight was 0.960 while that between petiole length and leaf length was 0.787, a difference of only 0.3 and 0.1 % respectively. This means that quantitative morphological variation in shea butter tree ethno-varieties is not structured according to folk classification (Fig. 4).

There were weak but significant correlations between most morphological and geographical variables (latitude, longitude and altitude; Table 5). Only

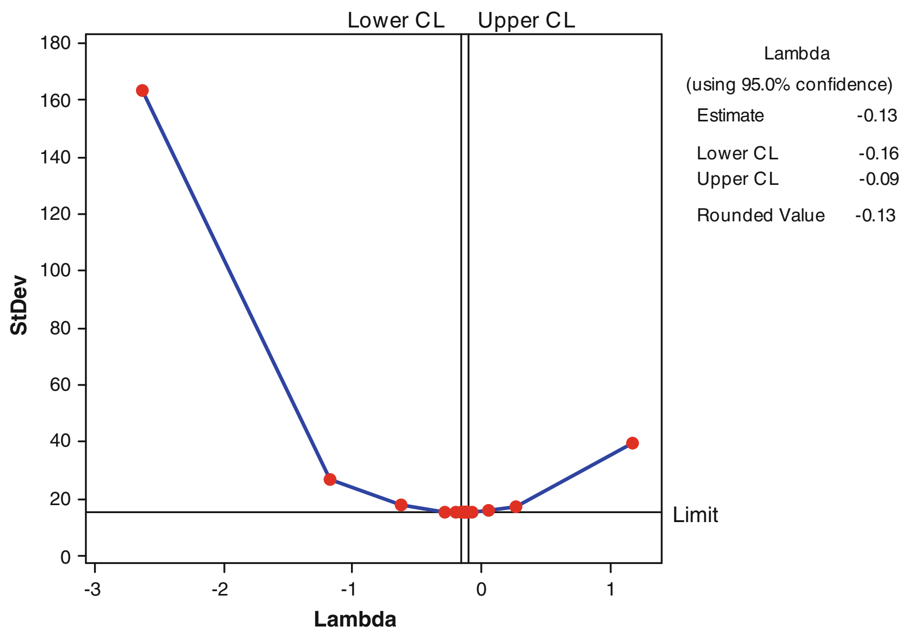

Fig. 3 Box-Cox plot of estimated lambda value based on standard deviations at 95 % confidence for 14 morphometric variables

Table 3 Variation of morphological traits of *Vitellaria paradoxa* in Uganda

Variable	Minimum	Maximum	Mean	SE mean	CV
Canopy diameter (m)	4.40	21.75	13.44	0.27	26.69
Diameter at breast height (cm)	35.00	111.05	62.77	1.34	28.48
Fruit length (cm)	2.43	5.18	3.52	0.04	13.66
Fruit width (cm)	1.92	4.14	2.86	0.02	11.59
Fruit weight (g)	11.70	53.75	24.22	0.51	27.81
Nut weight (g)	5.06	19.48	9.50	0.16	22.73
Pulp weight (g)	5.79	37.65	14.72	0.40	35.90
Nut length (cm)	1.98	3.29	2.65	0.02	9.48
Nut width (cm)	1.38	2.26	1.88	0.01	7.88
Leaf length (cm)	15.08	33.31	24.05	0.27	15.16
Leaf width (cm)	4.61	9.80	7.32	0.08	15.41
Petiole length (cm)	2.82	10.78	6.10	0.10	21.03
Lamina base angle (degrees)	56.40	128.28	84.01	0.99	15.65
Lamina apex angle (degrees)	69.56	118.75	89.65	0.66	9.72

canopy diameter and lamina apex angle were not significantly related to any of the geographical variables. All fruit variables were negatively correlated with latitude but positively correlated with longitude and altitude. On the other hand, leaf variables were positively correlated with latitude but negatively correlated with longitude and altitude.

Congruence between morphological variation and folk classification

Principal component analysis of 14 quantitative variables extracted four components (with eigenvalues $\geq$1) which explained 77 % of the total variation in shea butter tree ethno-varieties. The first component

Table 4 Pearson correlation test of morphological variables of shea butter tree ethno-varieties in Uganda

	CanDia	DBH	FrtLgth	FrtWdth	FrtWght	NutWght	PlpWght	NutLgth	NutWdth	LfLgth	LfWdth	PtlLgth	LmBseAng	LmApxAng
CanDia		0.000	0.317	0.575	0.944	0.462	0.886	0.947	0.549	0.132	0.385	0.845	0.781	0.225
DBH	0.575		0.026	0.020	0.005	0.018	0.007	0.001	0.069	0.236	0.024	0.033	0.007	0.079
FrtLgth	0.076	−0.168		0.000	0.000	0.000	0.000	0.000	0.000	0.409	0.934	0.747	0.001	0.271
FrtWdth	0.043	−0.176	0.776		0.000	0.000	0.000	0.000	0.000	0.383	0.545	0.999	0.016	0.187
FrtWght	−0.005	−0.213	0.812	0.864		0.000	0.000	0.000	0.000	0.721	0.654	0.689	0.020	0.377
NutWght	−0.056	−0.178	0.586	0.695	0.800		0.000	0.000	0.000	0.723	0.774	0.960	0.122	0.328
PlpWght	0.011	−0.201	0.812	0.832	0.963	0.615		0.000	0.000	0.654	0.554	0.634	0.016	0.483
NutLgth	−0.005	−0.245	0.803	0.682	0.843	0.814	0.753		0.000	0.878	0.758	0.742	0.002	0.973
NutWdth	0.045	−0.138	0.447	0.624	0.640	0.755	0.514	0.713		0.834	0.756	0.794	0.949	0.916
LfLgth	−0.114	0.090	0.063	0.066	0.027	0.027	0.034	−0.012	0.016		0.000	0.000	0.811	0.041
LfWdth	−0.066	0.170	−0.006	0.046	0.034	0.022	0.045	−0.023	0.024	0.652		0.000	0.000	0.008
PtlLgth	−0.015	0.160	0.025	0.000	−0.030	0.004	−0.036	−0.025	0.020	0.788	0.425		0.171	0.329
LmBseAng	0.021	0.204	−0.252	−0.181	−0.175	−0.117	−0.182	−0.236	−0.005	0.018	0.270	0.104		0.000
LmApxAng	0.092	0.133	−0.083	−0.100	−0.067	−0.074	−0.053	0.003	−0.008	−0.154	0.200	−0.074	0.265	

Numbers below the diagonal blank line indicate Pearson's rank correlation coefficient. The numbers above the diagonal are related p values

explained 39.4 % of the total variation and received relatively high negative loadings from fruit variables (Table 6). The second component explained a further 16.8 % of the total variation and received high positive loading from leaf variables. The third component received relatively high loadings from tree (canopy diameter and DBH) variables and explained another 11.8 % of the total variation while the fourth component received loadings from lamina characters (base and apex angles) and explained 9.1 % of the total variation available.

For further analysis of quantitative variation among the ethno-varieties, we considered the first two principal components which carry most of the variation and are utilized in folk classification. Hierarchical cluster analysis (HCA) using all variables that contributed to PC1 and PC2 showed no clear aggregation on the basis of ethnographic (folk classification) or geographic separation across the three farming systems (Fig. 5). Ethno-variety membership widely overlapped in separate clusters. Examination of the dendrogram (Fig. 5) revealed three groups (at a similarity level of 51.5 %):

1. Group one consisted of seven ethno-varieties that are characterized by possession of heavy fruits. The mean fruit, pulp and nut weights in this group were over 29, 16.6 and 10.8 g respectively. With the exception of 'Ewiny' and 'Upende-Appi' from the Teso and West Nile farming systems, the rest of the ethno-varieties in this group are from the northern farming system.
2. Group two comprised of ethno-varieties that are characterized by possession of short leaf petioles. Membership of this group was dominated by ethno-varieties from the Teso and northern farming systems. Mean petiole length as well as leaf length and width ranged from 4.5 to 6.9 cm. The shortest petioles were recorded in ethno-varieties from the eastern fringes of the northern farming system and the Teso farming system namely, 'Ajiki', 'Nasomel', 'Egeget', 'Epiana', 'Menacwot' and 'Nalungur' (Fig. 5). Petiole lengths among these ethno-varieties ranged from 4.5 to 5.5 cm.
3. Group three consisted of 13 ethno-varieties that are characterized by possession of small fruits/nuts and long leaf petioles. This group was separated into two sub-groups. One sub-group consists of small-sized and light-weight fruits and

Fig. 4 Morphometric relationships between fruit variables

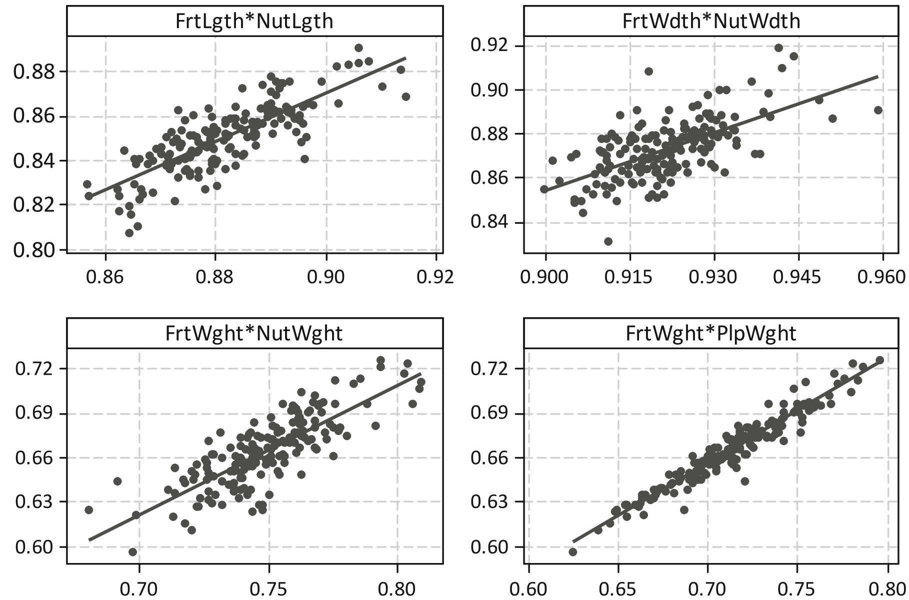

Table 5 Pearson's rank correlation coefficients between morphological variables and geographical variables (latitude, longitude and altitude)

	Latitude	Longitude	Altitude
Canopy diameter (m)	0.035	−0.003	−0.066
Diameter at breast height (cm)	−0.160*	0.436***	0.325***
Fruit length (cm)	0.075	−0.313***	−0.282***
Fruit width (cm)	0.108	−0.258**	−0.210**
Fruit weight (g)	0.214**	−0.355***	−0.365***
Nut weight (g)	0.207**	−0.174*	−0.257**
Pulp weight (g)	0.179*	−0.386***	−0.359***
Nut length (cm)	0.235**	−0.351***	−0.371***
Nut width (cm)	0.198**	−0.234**	−0.268***
Leaf length (cm)	−0.325***	0.299***	0.331***
Leaf width (cm)	−0.248**	0.293***	0.311***
Petiole length (cm)	−0.244**	0.284***	0.302***
Lamina base angle (degrees)	−0.178*	0.256**	0.244**
Lamina apex angle (degrees)	−0.074	0.037	0.063

Asterisks represent significant p values: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

nuts, namely, 'Alindiri', 'Nyiri', 'Layer', 'Mangu-lungulu', 'Yao-matino', 'Nyiri' and 'Nacekum'. The second sub-group comprised long-leaved ethno-varieties with petioles that measured over 7 cm long. With the exception of 'Nacekum', the rest of ethno-varieties in this group are from the northern and west Nile farming systems.

Inclusion of qualitative traits as perceived by farmers produced a dendrogram with eight clear groups with considerable congruence to folk classification (Fig. 6):

(a) Cluster one comprised six ethno-varieties grouped together on the basis of fruit weight. Fruit, nut and pulp weights of these ethno-varieties were the heaviest, having mean values ranging between 28 and 44 g, 10.6–14 g and 16.7–29.9 g respectively.
(b) Cluster two comprised three ethno-varieties grouped together on the basis of fruit size. However, while 'Enyii' and 'Mbele' were described by farmers as ethno-varieties that produced big fruits, they classified 'Abor' among those that produce small fruits. However, in the morphometric analysis, 'Abor' fruits were considerably longer and broader (4 × 3 cm).
(c) Cluster three comprised of four ethno-varieties grouped together on the basis of pulp quantity. Farmers described 'Amoo' and 'Mudaa' fruits as containing a lot of pulp while those of 'Ajiki' and 'Upende-aboro' were described as containing little pulp.
(d) Cluster four comprised of five ethno-varieties grouped together on the basis of pulp taste.

Table 6 Principal component analysis (PCA) of 14 quantitative variables of shea butter tree ethno-varieties in Uganda

PCA	Axis			
	PC1	PC2	PC3	PC4
Eigenvalue	5.5229	2.3472	1.6462	1.2712
Explained proportion of variance (%)	39.4	16.8	11.8	9.1
Cumulative proportion of variance (%)	39.4	56.2	68	77.1
Variable	**PCA coefficients**			
Canopy diameter (m)	0.008	0.008	**−0.620**	−0.410
Diameter at breast height (cm)	0.116	0.193	**−0.570**	−0.289
Fruit length (cm)	**−0.365**	0.016	−0.037	−0.135
Fruit width (cm)	**−0.379**	0.034	−0.046	−0.046
Fruit weight (g)	**−0.411**	0.011	−0.039	0.020
Nut weight (g)	**−0.361**	0.020	−0.026	0.103
Pulp weight (g)	**−0.383**	0.011	−0.037	−0.017
Nut length (cm)	**−0.389**	−0.022	−0.032	0.050
Nut width (cm)	**−0.315**	0.034	−0.111	0.159
Leaf length (cm)	−0.016	**0.590**	0.218	−0.149
Leaf width (cm)	−0.001	**0.526**	−0.025	0.237
Petiole length (cm)	0.007	**0.547**	0.121	−0.168
Lamina base angle (degrees)	0.105	0.182	−0.270	**0.521**
Lamina apex angle (degrees)	0.042	0.030	−0.367	**0.558**

Relative loading on the first four PCA axes are indicated in bold face

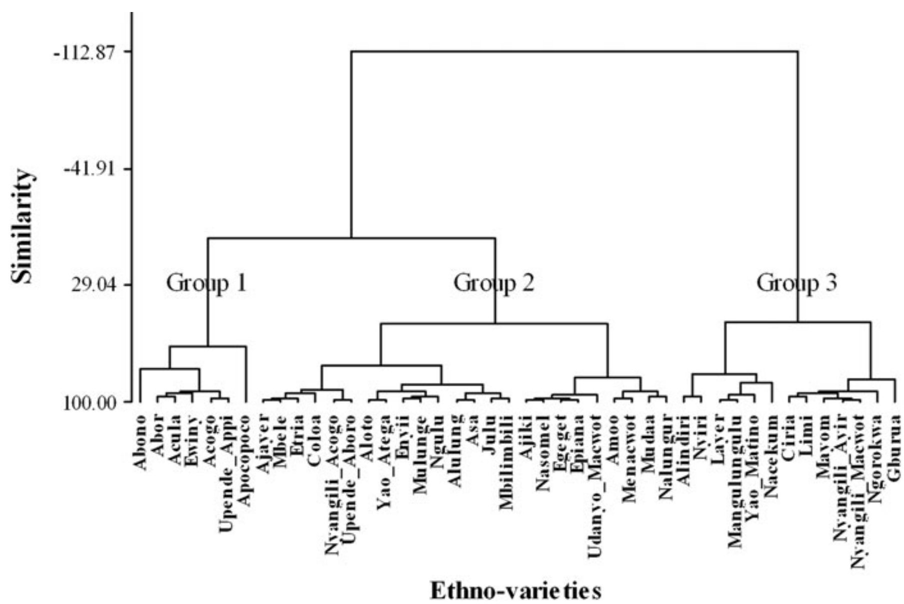

Fig. 5 Cluster analysis of seven fruit (PC1) and three leaf (PC2) quantitative variables based on Ward's linkage and squared Euclidean distances

The fruit pulp of 'Egeget', 'Etria', 'Menacwot' and 'Udanyo-macwot' were described by farmers as astringent while that of 'Epiana' was described as tasteless. Due to morphometric variation, some ethno-varieties that were classified by farmers according to pulp taste were grouped in different clusters.

(e) Cluster five comprised of 11 ethno-varieties grouped together on the basis of fruit and nut shape. Due to ethnographic limitations, farmers

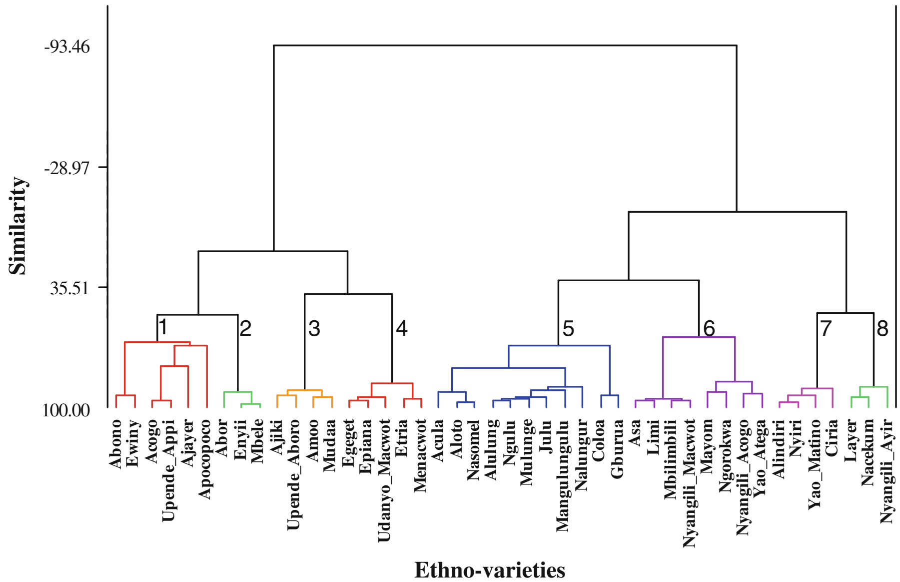

Fig. 6 Cluster analysis of seven fruit (PC1) and three leaf (PC2) quantitative variables in combination with six qualitative variables based on Ward's linkage and squared Euclidean distances

broadly grouped fruit and nuts shapes into two, that is, round and oval or elliptic.

(f) Cluster six comprised of eight ethno-varieties grouped together on the basis of pulp taste and eubstance, that is, the hardness or softness of ripe fruit pulp. This cluster was made up of two sub-clusters. One sub-cluster comprising 'Asa', 'Limi', 'Mbilimbili' and 'Nyangili-macwot' can be defined by pulp taste while another sub-cluster comprising 'Nyangili-acogo', 'Ngorokwa' and 'Yao-atega' can be defined by pulp hardness.

(g) Cluster seven comprises four ethno-varieties grouped together on the basis of fruit size. From morphometric assessment, 'Alindiri', 'Nyiri', 'Yao-matino' and 'Ciria' ethno-varieties had the lowest mean length and breadth values for fruits and nuts, ranging from 2.6 to 2.0 × 2.2–2.5 cm and 2.3–2.4 × 1.6–1.8 cm respectively.

(h) Cluster eight comprised of three ethno-varieties grouped together on the basis of fruit pubescence. Fruits of 'Layer', 'Nacekum' and 'Nyangili-ayir' were described by farmers as pubescent.

Discussion

General trends in morphological variation

The primary aim of this study was to establish the patterns of morphological variation in shea butter tree ethno-varieties in Uganda. Although, at first, this seemed at odds with folk descriptors of ethno-varieties which span beyond morphology, a pattern of morphological variation was eventually discerned. Up to 23 % of the total variation was not explained by tree, fruit and nut characteristics. Variation was higher in fruit and nut variables compared to leaf variables. Principal Component and Hierarchical Cluster analyses in the present study showed that fruit and nut traits were the most important in quantification of morphological variation. Fruit and nut traits have been found to be important in structuring morphological variation in many tropical trees, such as *Tamarindus indica* L. (Fandohan et al. 2011) and *Balanites aegyptiaca* (L.) Delile (Abasse et al. 2011). It is clear therefore that fruit and nut traits provide a very considerable opportunity for identification and selection of plus trees for domestication.

The presence of bigger and heavier fruits in the Northern farming system, and larger-leaved trees in the West Nile farming system compared to the smaller-leaved trees of the Teso farming system as revealed by correlation and cluster analyses presents an interesting pattern. This pattern may be explained by environmental and abiotic factors such as rainfall, temperature, soil and altitude. Generally, rainfall in the shea butter tree belt of Uganda decreases from south to north (Kamanyire 2000). The Teso system, the most southerly of the three farming systems, is characterized by two distinct rain seasons separated by a 4 months dry spell. Meanwhile the West Nile and northern systems are characterized by uni-modal rains and a more intense dry season than the Teso system. In the West Nile system, high altitude areas receive much more rainfall (Ebanyat et al. 2010; Mwebaze 2010; Kamanyire 2000; Kabeere and Wulff 2008). In West Africa, shea butter tree agromorphological variables have also been found to be related to climatic gradients, with larger trees being more common in the drier areas (Sanou et al. 2006). The variation in fruit and nut variables recorded here are very close to those estimated by Sanou et al. (2006) in Mali indicating that the magnitude of morphological variability within East and West African shea butter tree populations may be similar. Other tropical fruit trees that exhibit a similar variability pattern include *Balanites aegyptiaca* and *Tamarindus indica* (Soloviev et al. 2004).

There was a small but significant relationship between geographical coordinates (latitude, longitude and altitude) and morphological variables. In Uganda, climatic regimes are strongly associated with geographical location, with areas at low latitudes and high longitudes receiving higher rains and experiencing lower temperatures. Conversely, areas with higher latitudes and lower longitudes receive relatively lower rainfall and experience higher temperatures (Kamanyire 2000). Therefore, in spite of the significant albeit low correlation between morphological and geographical factors, it can be postulated that environmental influences play a role in determining the morphological properties of shea butter tree organs. Other factors that may explain morphological variation include natural selection (Irwin 2000; Tremblay et al. 2010; Darwin 1869), selection by humans (Vaughan et al. 2007) and gene flow mediated random genetic drift (Abasse et al. 2011).

Congruence between morphological variation and shea butter tree folk classification

There was lack of clear separation between ethno-varieties from different farming systems in this study suggesting that shea butter tree ethno-varieties are not aggregated on the basis of ethnographic separation. While ethnographic separation gives rises to variations in folk classification systems, these systems usually arise out of the recognition of and need to maintain diversity. Sometimes folk classification is done for no apparent value but for culinary purposes (Boster 1985). This may partly explain the lack of clear aggregation in morphometric variation on the basis of ethnographic separation. In addition, the use of morphological markers to study folk classification is bedevilled with numerous problems (Quiros et al. 1990). In most cases, farmers may use a single name to describe several phenotypes or several names for a single phenotype (Quiros et al. 1990). In the present study, farmers were observed to utilize a single rather than a combination of morphological traits to describe an ethno-variety. This is usually due to the need to utilize the most important traits that can conveniently communicate and describe particular crop varieties (Bellon 2002). It is, however, possible that these single traits used in folk classifications are genetically inherited hence their stability for use in folk classifications. However, while the use of single trait descriptors may be important in folk classifications, anthropogenic and environmental influences may be under-played in such ethno-variety descriptions. There is high flux and movement of shea fruits/nuts by humans, which facilitates high levels of gene flow and low differentiation in traits of closely related offspring. Hence, shea butter trees have a high level of gene flow due to their out-crossing nature (Hall et al. 1996). This then presents the scenario of unresolved alliances in morphological variation among farmers' ethno-varieties as found in the present study. Similarly low levels of phenotypic differentiation have also been recorded in other African out-crossing and long-living tropical trees (Abasse et al. 2011; Bani-Aameur and Ferradous 2001; Kadzere et al. 2006; Leakey et al. 2005a, b).

Hierarchical cluster analysis on the basis of fruit and leaf quantitative variables revealed three groups. As pointed out from the discussion on general trends in morphological variation above, these groups are neither congruent to folk (ethnographic) classification nor to geographical separation. Therefore, the cause of the inherent differences enunciated by folk classifications may be due to the allogamous nature of shea butter trees. It is known that cross pollination between shea butter trees can give rise to highly phenotypic variants that are largely influenced by environmental factors (McGowen et al. 2010; Williams and Conner 2001). However, phenotypic variation could as well be genetic (Masood et al. 2005). This therefore makes it difficult to identify shea butter tree varieties on morphological evidence alone. However, a combination of quantitative and qualitative variables in the present study resulted into a more powerful resolution of clusters that are highly congruent to folk classification (Fig. 6). Given the lack of clear correspondence in quantitative morphology with an apparently distinct folk classification, there is need to utilize a combination of morphometric and farmers' perspectives of variation. However, given that even a combination of quantitative and qualitative variables may sometimes group similar ethno-varieties into different clusters as seen in Fig. 6, it is important to utilize more powerful biochemical and molecular markers in strategies for wider scale domestication programs.

Conclusion

While folk knowledge in Uganda classifies shea butter trees into 44 ethno-varieties based mainly on fruit and nut morphological traits, evidence presented here shows that there are no discrete groupings from quantitative morphological variation that are congruent with local folk classification. This is possibly due to the plasticity of morphological characters due to environmental variability, the use of a single rather than multiple traits in folk classification and the allogamous nature of shea butter trees. A combination of quantitative and qualitative traits greatly enhances the resolution of inherent variation that is congruent to folk classification. Therefore, quantitative traits alone cannot be used to explain folk classification of shea butter tree ethno-varieties. There is need to utilise even more powerful biochemical and molecular markers to establish the fixed variation and hence validate the present folk classification of shea tree shea butter trees in Uganda.

Acknowledgments We are very grateful to all the shea parkland communities of Amuria, Abim, Nebbi, Moyo, Pader, Otuke and Arua districts of Uganda for their support and cooperation during fieldwork. We are greatly indebted to Richard Amuge, Henry Asindua, Joel Buyinza, Jaspher Okello, Joseph Okello, Slim Abok Openythoo, Paul Okiror and Samuel Oyuko for all their efforts during fieldwork and language translation. Funding for this work was obtained from Makerere University School of Graduate Studies—Carnegie Corporation Competitive Research grant. Additional funding was provided by the European Union INCO—CT Project No. 032037 (Innovative Tools and Techniques for Sustainable Use of the Shea Tree in Sudano—Sahelian zone—INNOVKAR) and the World Agroforestry Centre, Nairobi through the SII/World Agroforestry Project: 'Advancing Agroforestry Research and Development through Training and Education'.

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