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Genetic variability and divergence of seed traits and seed germination of five provenances of *Faidherbia albida (Delile)* A. Chev

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Establishment of *Faidherbia albida* trees on farm is often difficult despite the plant survival adaptive mechanisms such as drought and disease resistance. Adoption of the tree to agroforestry systems is also limited due to lack of knowledge on genetic variation of its provenances. Morphological characterization of *F. albida* provenances is therefore necessary to screen for natural genetic variation in seeds traits for selection of germplasm for long term agroforestry, timber production, fodder, soil fertility increment and environmental sustainability. In this study, seed traits of five provenances of *F. albida*: Taveta Wangingombe, Lupaso, Kuiseb and Manapools were examined. Divergent studies were analyzed based on seed morphology and geo-climatic conditions of the provenances. Seed length, width, thickness and weight were analyzed to determine the extent of phenotypic and genotypic variance and heritability. This study revealed significant differences among provenances (P≤0.05) for all the studied characters indicating substantial genetic variability. Genetic variance for all seed traits was higher than environmental variance suggesting that the expressions of these traits are under genetic control. This result was supported by high heritability values for seed length (0.92), width (0.99), thickness (0.99) and weight (0.99). Seed germination test involved 4 replicates of 25 randomly selected seeds per provenance. Mean germination percentage among provenances was 83.3% with the highest being 97% and the lowest 71%, P≤0.05. Relationships among these variables were analyzed using principal component analysis and cluster analysis resulting in separation of provenances into three distinct clusters. Manapools (760 mm), Lupaso (1165 mm) and Wangingombe (628 mm) with high rainfall were placed in cluster one. Taveta (545 mm) cluster two and Kuiseb (<50 mm) cluster three. Wangingombe (1700 m a.s.l.) clustered closely to Lupaso (500 m a.s.l.) than Taveta (760 m a.s.l.). High heritability (h^2>0.5) for all traits suggests that selection based on morphological traits can be made with a high degree of confidence.

Key words: Provenances, selection, clinal distribution, geographical differentiation, genetic variation, heritability.

INTRODUCTION

Faidherbia albida (Del.) A. Chev. is a leguminous trees species belonging to *Mimosoideacea* subfamily, tribe *Acaciacea*. It is locally referred to as Apple-Ring Acacia, Ana tree, Balanzan tree and Winter Thorn (Fagg and Barnes, 2003). Due to its phytochemical properties, pollen structure and phenology, it is placed in a monotypic genus

Faidherbia (Bernard, 2002; Hyde and Wursten, 2010*). F. albida* is an important agroforestry appreciated due to it compatibility with cropping systems (Roupsard et al., 1999; Payne, 2000; Ibrahim and Tibin, 2003). The tree is used in dry lands for soil conservation (Dangasuk et al., 2001). It can grow among field crops without overshadowing them during the rainy season and provides shade during dry season (Orwa et al., 2009). Falling leaf mulch and the canopy shade creates a microclimate with better infiltration and reduced evapotranspiration which is crucial for plants (Gassama-Dia et al., 2003).

Despite the immense benefits of *F. albida*, broadening the utilization, breeding and conservation of the species still remain a challenge. *F. albida* is faced with threats to its gene pool due to drought and land use pressure; the situation is worsened by lack of natural regeneration and artificial propagation by seed or suckers among the people living in the Sahel (Weber and Hoskins, 1983; Bonkoungou, 1992; McGahuey, 1992). However, the *F. albida* trees currently growing in the Sahel regenerate naturally (Weber and Hoskins, 1983) and attempts of artificial regeneration have met failures due to poor survival and highly variable growth in early stages (McGahuey, 1985). It is therefore important to test seeds in order to screen for naturally available genetic variation for selection of germplasm for long term agroforestry, sustainability of timber production, fodder and soil fertility increment and environmental sustainability.

Seed morphology is an evolutionary trait contributing to genetic diversity (Aniszewski et al., 2001). Seed morphology influence water relation and seed dispersal, emergence, survival and seedling establishment (Milberg and Lamont, 1997); large and heavy seeds germinate rapidly with high survival and fast growth as compared to small seeds. Seed morphology is linked to fitness hence successful establishment (Zhang, 1998). Seeds traits that show high morphological variation are useful for selection of germplasm for conservation and propagation (Khurana and Singh, 2001). It has generally been reported that large seeds produce seedlings that have high survival rates (Moles and Westoby, 2004; Turnbull et al., 2008; Westoby, 1998) and trees with small seeds may produce more seeds per individual but with low seedling survival rates (Rees, 1995; Turnbull et al., 1999; Eriksson et al., 2000; Leishman and Murray, 2001). Knowledge of genetic variation among seed traits provides useful information for adaptation to heterogeneous environment. Seed traits that have high heritability values ($h^2 \geq 0.05$) are useful markers for selection (Akbar et al., 2003).

Variability studies are important in improvement of tree as it provides information relevant for selection of quality germplasm (Bhat and Chauhan, 2002). Germplasm quality affects the quality of trees propagated (IFSP, 2000) and should be considered during selection. Ibrahim (1996) and Dangasuk et al*.* (1997) examined the variation in seed and seedling traits of *F. albida* but did not provide any information on genetic and phenotypic variance, phenotypic and genotypic coefficient of variation and heritability of *F. albida* provenances. The current study is novel and aims at testing the reliability of selection of *F. albida* provenances based on seed morphological traits and to determine the genetic relationships among the provenances under study based on seed morphology and geo-climatic conditions.

MATERIALS AND METHODS

Study site

Morphological characterization of the seeds was conducted in April 2014 at the seed laboratory of the World Agroforestry Centre (ICRAF) in Nairobi, while the seeds were germinated in the ICRAF nursery greenhouse. ICRAF is located about 20 km south east of Nairobi, Kenya at latitude of 1° 33' S longitude 37° 14' E and an altitude of 1580 m above sea level. The mean annual rainfall ranges between 500 and 1370 mm and the mean temperature of 21°C.

Seed sources

The seeds of five provenances, obtained from ICRAF seed bank were used for the study. The seeds were collected by Oxford Forest Institute (OFI) in 1990 for international provenance trials. The seeds were then processed and sent to ICRAF seed bank. For each provenance, OFI selected trees that had geographical discontinuity from other populations. The selected trees were obtained from sites with varying climate, soil, altitude and ecology. Undisturbed natural populations with distinct morphological and phenological traits were selected.

OFI collected 25 mother trees to represent a provenance. The mother trees were spaced 100 m apart to avoid collections from related individuals and to capture a large proportion of the natural genetic variation within the provenance (Ofori, 2001). The geographical range of the seeds varied from 3°24'S, 37°42'E to 23°34'S, 15°02'E longitude and altitude of 360 to 1700 m above the sea level. Taveta and Wangingombe represented eastern Africa provenances while Lupaso, Kuiseb and Manapools represented southern Africa provenances (Figure 1 and Table1).

Characterization of seed morphology

To investigate variation in seed length, width, weight and thickness, 100 seeds per provenance were randomly selected from the seed bulk. The seed were organized in a completely randomized experimental design with 25 seeds replicated four times per provenance (25 x 4 x 5) = 500 experimental units (Table 2). A Vernier caliper calibrated to two decimal places was used to measure seed length, width and thickness. Seed length was measured over the seed coat along the longest axis of the seed;

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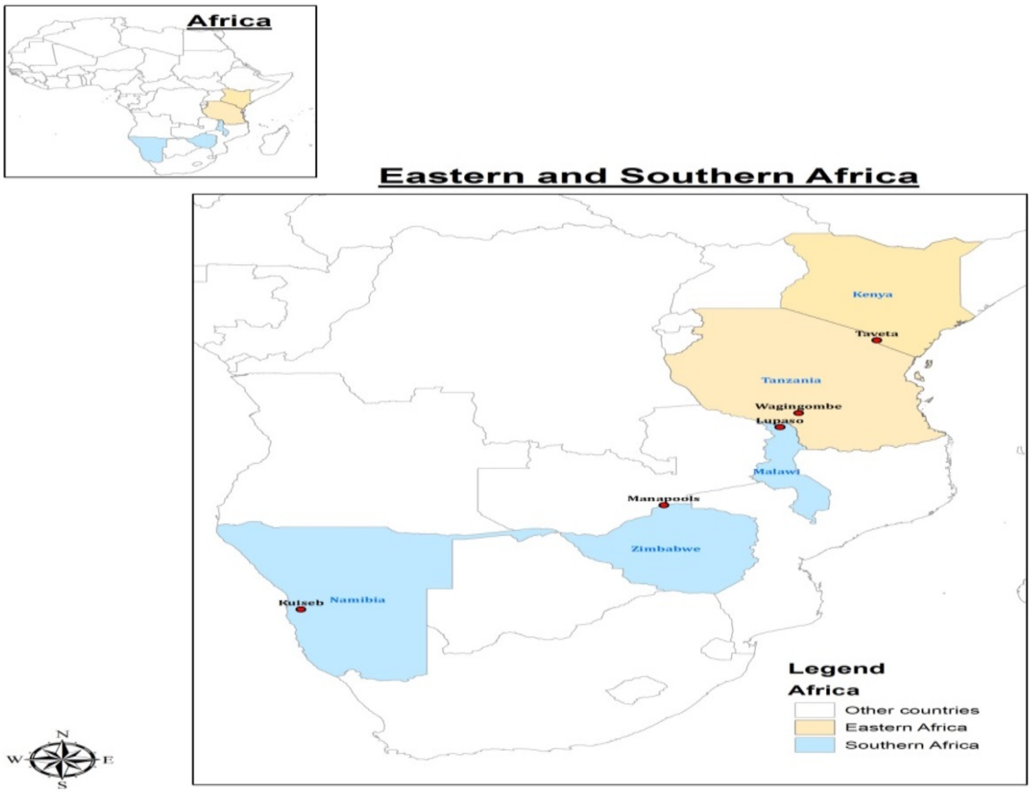

Figure 1. Map of the collection site for *Faidherbia albida* provenances under study.

Table 1. Geo-climatic (latitude, longitude, altitude, rainfall and temperature) of the different provenances of *F. albida* under study.

Country	Region	Provenance	Location	Altitude (m asl)	Rainfall (mm)	Temperatures (°C)
Kenya	Eastern Africa	Taveta	3°24'S, 37°42"E	760	545	28.1
Malawi	Southern Africa	Lupaso	9°55'S, 33°53'E	500	1165	24.8
Namibia	Southern Africa	Kuiseb	23°34'S, 15°02'E	400	<50	15.2
Tanzania	Eastern Africa	Wangingombe	8°51'S, 34°38'E	1700	760	27.1
Zimbabwe	Southern Africa	Manapools	15°45'S, 29°20'E	360	628	25.1

Table 2. Completely randomized experimental design for characterization of seed morphology and seed germination test

Provenance	Number of seeds per replicate				Total
	Replicate 1	Replicate 2	Replicate 3	Replicate 4	
Taveta	25	25	25	25	100
Wangingombe	25	25	25	25	100
Lupaso	25	25	25	25	100
Kuiseb	25	25	25	25	100
Manapools	25	25	25	25	100
Total	100	100	100	100	500

seed width measurements were taken on one of the widest faces at the middle of the seed; seed coat thickness was measured without the removal of seed coat from the seed. An electronic top pan model was used to weigh each seed for all replicates.

Table 3. Morphological variation in seed length, width, thickness and seed weight among the five provenances of *F. albida*

Provenance	Seed length(mm)	Seed width(mm)	Seed thickness (mm)	Seed weight (mg)
Taveta	6.73c	4.98d	2.96c	83.83d
Lupaso	8.86b	5.18c	3.05a	126.43c
Kuiseb	10.21a	5.89ab	3.01ab	160.62a
Manapools	10.44a	6.00a	3.03ab	167.15a
Wagingombe	9.30b	5.75b	3.04ab	143.20b
CV	12.26%	6.80%	0.16%	30.41%
SD	1.74	0.55	0.014	50.9

CV = coefficient of variation, SD = standard deviation. Means followed by a different letter within a column are significant different according to LSD post-hoc test for all the traits.

Seed germination test

After recording the variation in seed morphology, the seeds were germinated. The seeds were nicked (Bewley and Black, 1994) at the distal end near the microphyle (Manz et al., 2005; Wojtyla et al., 2006) using a nicking caliper. The seeds were then soaked in water for 24 h before sowing. Rapid influx of water was observed during the first twelve hours due to low water potential of dry seeds (Obroucheva and Antipora, 1997). Polythene tubes measuring 10 x 20 cm, filled with sterilized sand were used to germinate the seeds. The sand was sterilized using the oven method. Prior to sterilization, the sand was cleaned in tap water then placed in metal baking pans up to four inches in depth. The metal pans were then tightly covered with aluminum foil and placed in the oven at temperatures between 180 to 200°F; the temperatures were maintained for 30 min. After heating, the oven was cooled and metal pans removed. The aluminum foil covering the metal pans was left intact to prevent the sand from contamination. The sand was watered to field capacity before sowing the seeds. The polythene tubes containing the seeds were kept under a temperature range of 25-30°C and photoperiod of 12 h light and 12 h dark. Seed germination was monitored for thirty days and mean germination percentage was calculated following ISTA (1993).

Statistical analysis

Seed morphological data and germination percentage were subjected to one-way analysis of variance after testing for homogeneity of variance and normality (Zar, 1996). The genotype means were further separated and compared using least significant difference test at a 0.05 significance level. The genetic, phenotypic and environmental variance, genotypic, environmental and phenotypic coefficient of variation and heritability for each trait were calculated from one way analysis of variance using formulas formulated by Zobel and Talbert (1991) as shown below:

$$\sigma^2_g = \frac{(MSG - MSE)}{r}$$

$$\sigma^2_p = \frac{(MSG)}{r}$$

$$\sigma^2_e = \left(\frac{MSE}{r}\right)$$

$$h^2 = \frac{\sigma^2_g}{\sigma^2_p}$$

$$PCV = \frac{\sqrt{\sigma^2_p}}{\bar{x}} \times 100$$

$$GCV = \frac{\sqrt{\sigma^2_g}}{\bar{x}} \times 100$$

Where

σ^2_g = Genotypic variance, σ^2_p = phenotypic variance, σ^2_e = environmental variance MSG = mean sum square for genotype, MSE = mean sum square for error and r, is the number of replications, h² = narrow sense heritability, PCV = phenotypic coefficient of variation, GCV = genotypic coefficient of variation and $\bar{x}$ = grand mean.

Pearson correlation coefficient for seed traits and among seed traits with geo-climatic conditions of seed source was determined. In order to examine differences and relationship among seed traits and geo-climatic conditions, principal component analysis and cluster analysis were used in Multivariate Statistical Package (MVSP). PCA solutions were accepted when Eigen values were greater than one (Kaisers criterion) and compatible with Cat tells scree rule. Component scores and factor loading were calculated after varimax rotation. Factors equal or greater than 0.7 were considered as defining part of PCA. Hierarchical cluster analysis was used to group provenances. The nearest neighbour method was utilized for classification and Square Euclidean method used as dissimilarity. Discriminant analysis was used to determine the variables responsible for the cluster formation. Dendograms were plotted to determine phylogenetic relationships among the five provenance of *F. albida*.

RESULTS

Morphological variation in seed traits

There were significant differences ($p \leq 0.05$) among provenances in all seed traits measured except seed coat thickness (Table 3). The coefficient of variation (CV) was 30.41 % for seed weight and 12.26% for seed length. Seed thickness and seed width (CV 1.2 and 6.8% respectively) recorded a lower coefficient of variation suggesting minimal environmental effect on expression of these traits. On average, seed length among provenances ranged from 6.73 ± 0.01 (Taveta) to 1.04 ±

Table 4. Genetic variance components ($σ^2_g$, $σ^2_p$ and $σ^2_e$), genotypic (GCV) and phenotypic (PCV) coefficient of variation along with heritability (h^2) for seed traits of the five provenances of *F. albida*

Seed traits	$σ^2_g$	$σ^2_p$	$σ^2_e$	GCV	PCV	h^2
Length	0.53	0.57	0.04	75.7	79.1	0.92
Width	0.03	0.03	0	75.72	35.71	0.99
Thickness	0.0003	0.0002	0.0001	4.69	4.54	0.99
Weight	0.02	0.02	0	121.2	122.31	0.99

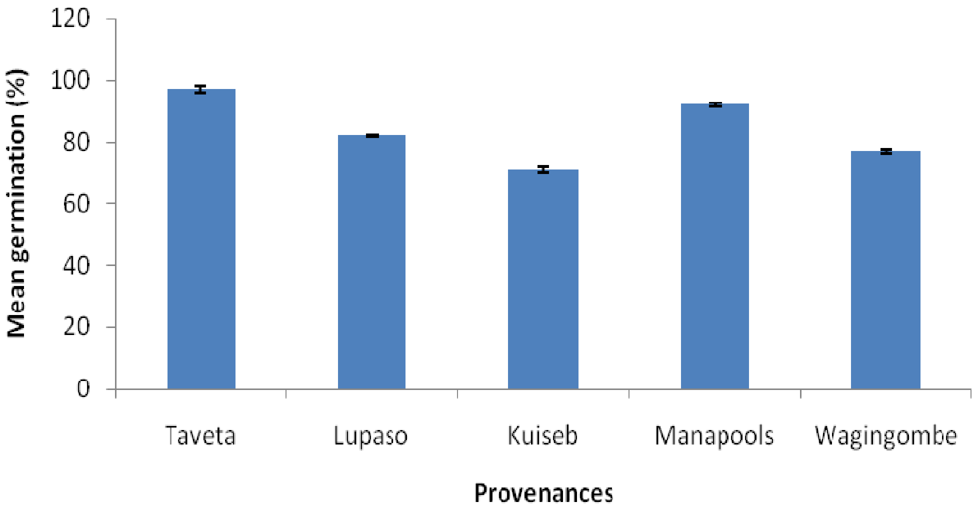

Figure 2. Mean germination percentage of five provenances of *F. albida* at four weeks after sowing.

0.008 mm (Manapools) with a grand mean of 9.11 ± 0.003 mm. The mean seed length for Wangingombe, and Eastern African provenance was higher than Lupaso (southern Africa provenance) though the difference was not statistically significant (P ≤0.05). Southern African provenances recorded higher mean seed length as compared to East Africa provenances. Manapools recorded the maximum seed width 0.60 ± 0.003 mm followed by Kuiseb with 0.58 ± 0.004 mm. Taveta recorded lowest mean seed width as compared to the other provenances; seed width ranged from 0.49 ± 0.003 to 0.60 ± 0.003 mm. Seed weight was smaller in eastern Africa provenances than in southern African provenances. One way analysis of variance of seed thickness separated *F. albida* seeds into two thickness groups ranging from 0.29 to 0.305 mm. Seed thickness did not follow the same pattern as for seed length and seed width.

Genetic variance components

Genetic variance components are represented in Table 4. Seed length recorded the highest variation but the lowest heritability index. Nonetheless, heritability indices ranging from 0.92 to 0.99 suggest that environmental influence on seed characteristics is minimal and hence genetic factors have a lot of influence on the seed traits analyzed. This suggests that selection based on morphological traits can be made with a high degree of confidence.

Seed germination

There were significant differences (p ≤ 0.05) among provenances in seed germination percentage (Figure 2). Seed germination percentage was highest for Taveta (97%) followed by Manapools (95%) and was lowest in Kuiseb (71%). Mean germination in nursery averaged 83.3% varying from 97 to 71% and was significantly different among provenances (p ≤ 0.05). Taveta with the smallest seeds recorded the highest seed germination. No significant correlation (r=0.15 p>0.05) was observed between seed size or seed weight with mean germination.

Correlation among seed traits

Correlation of seed traits showed that seed weight correlated with seed length (r = 0.494, p ≤ 0.05) and seed width (r = 0.433, p ≤ 0.05) (Table 5). Seed length and

Table 5. Mean correlation coefficient (r) between seed traits and germination percentage of *F. albida* provenances

Seed traits	Length	Width	Thickness	Weight
Width	0.597**			
Thickness	0.133**	0.104*		
Weight	0.494**	0.433**	0.094*	
Germination percentage	0.12	0.09	0.04	0.15

*, **Significance at 5 and 1% probability level, respectively.

Table 6. Pearson correlation coefficient (r) for seed trait and geo-climatic condition of the seed origin of the five provenances of *F. albida.*

Variables	Length	Width	Thickness	Weight	Altitude	Rainfall
Width	0.562**					
thickness	-0.054	-0.095				
weight	0.545**	0.527**	-0.053			
altitude	-0.306**	-0.165	0.064	-0.117		
Rainfall	-0.262**	-0.353**	0.139	-0.121	0.219*	
Temperature	-0.435**	-0.371**	0.023	-0.264**	0.248*	0.659**

*, **Significance at 5 and 1% probability level, respectively.

Table 7. Factor loading for each variable on the component of PCA analysis.

Variables	PC1	PC2
Length	**0.964**	-0.21
Width	**0.93**	-0.247
Thickness	**0.921**	0.372
Weight	**0.966**	-0.222
Altitude	0.077	0.618
Rainfall	-0.127	**0.864**
Temperatures	-0.37	**0.756**
Eigen values	3.74	1.99
Percentage of variance	53.35	28.48
Cumulative variance (%)	53.35	81.83

Values in bold (>0.7) are the principal components that explain most of the observed variation.

seed width also showed a significant positive correlation (r=0.597 p≤0.05). Seed thickness showed a weak correlation with seed weight, width and length (r = 0.094, 0.104, and 0.133 p≤ 0.05). No significant correlation was recorded between seed size and seed weight with mean germination percentage.

Correlation between seed traits and geo-climatic conditions of the seed origin

Correlation among seed data and geo-climatic data showed that seed length, width and weight were significantly negatively correlated to altitude, rainfall and temperature of the seed collection zone. Correlations among seed traits with geo-climatic condition of the provenances suggest the possibility of ecoclinal distribution of *F. albida* provenances (Table 6).

Genetic divergence

Genetic divergence of seed traits were analyzed using principal component analysis and cluster analysis. An acceptable solution of component analysis was reached when two dimension models were found to be significant and explained 81.83% of the total variance observed. The total variance was partitioned into the two principal components as: 53.35% of the total variance/variation for the first component (PC1) which was dominated by seed weight, seed width and seed length and seed thickness, 28.48% for the second component (PC 2) defined by rainfall and temperature (Table 7). PCA dendrogram analysis based on squared Euclidean distance for dissimilarity from these three principal components revealed three clusters (Figure 3). Cluster 1 composes of Lupaso, Manapools and Wangingombe which receive high rainfall and temperatures; their seeds have large to moderate sizes and are heavy. Kuiseb and Taveta were placed in separate clusters. Taveta (cluster 2) on the other hand has the smallest and lightest seeds and receive higher rainfall and temperature as compared to Kuiseb (545 mm, 28.1°C annually). Kuiseb in cluster

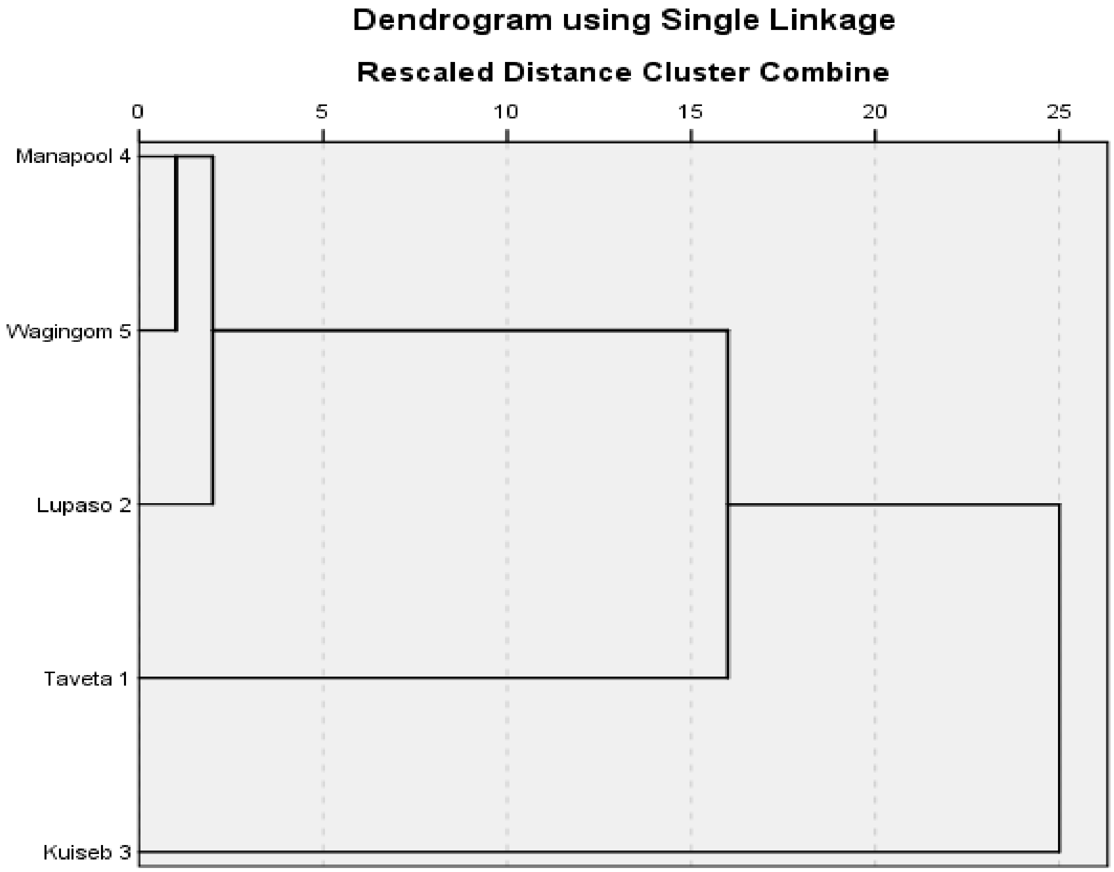

Figure 3. Dendogram for classification of five provenances of *F. albida* based on seed and geo-climatic conditions components from PCA.

three receives extremely low rainfall and temperatures as compared to other provenances under study (<50 mm, 15.2°C annually). Kuiseb has large and heavy seeds.

DISCUSSION

Variation in seed morphology

F. albida exhibited considerable amount of genetic variation in seed morphology, which could be due to its occurrence over a wide range of geo-climatic condition (Joly et al., 1992). Analysis of variance of seed traits showed significant differences, $p<0.05$ indicating high genetic variation among the five provenances of *F. albida* obtained from eastern and southern African provenances. Provenances were not regionally structured, and also showed a higher variability between eastern Africa provenances (Taveta and Wangingombe) than southern African provenances (Manapools, Kuiseb and Lupaso) as revealed by Euclidian distances of the cluster analysis. This could be due to the high variability in environmental conditions within Eastern and Southern Africa regions which is supported by PC2, pointing out that rainfall and temperature have great influence on the phenotypic variation. Ibrahim (1996), Harris et al. (1997) and Dangasuk and Gudu (2000) reported similar results in earlier studies. The variation in seed morphology could be due to interplay of both genetic and varying environmental conditions (interaction among rainfall, temperatures and altitude), exposing the trees to different selective pres-sures, resulting to different degrees of adaptation to climatic conditions (Mathur et al., 1984). The role of genetic and environment in seed morphology is also supported by the correlation between seed trait with geo-climatic conditions of the seed origin. Among all the traits studied, seed weight had the highest coefficient of variation indicating its sensitivity to environmental conditions. In the previous studies of tree species (Gera et al., 2000; Sivakumar et al., 2002; Mkonda et al., 2003), genetic control of seed morphology was observed which is consistent with our finding.

Analysis of genetic components of seed traits

Genetic analysis of seed trait revealed the genetic control of seed traits. The phenotypic variance was greater than genotypic variance for seed length and seed width which agrees with earlier findings of Jonah et al. (2013), Tanimu and Aliyu (1997) and Tanimu et al. (1990). Genotypic variance was higher than environmental variance except for seed thickness indicating the role of the environment in determining the extent of the seed thickness. The genotypic coefficient of variation was either equal or greater than phenotypic coefficient of variation which shows the contribution of the environment in expression of seed traits. Jonah et al. (2013) and Agbo and Obi (2005) in their study of Bambara groundnut reported similar finding; indicating that the interaction of genetics and environment plays an important role in selection and tree improvement programs. The 100% heritability for seed width, weight and thickness indicates their high response to selection which is supported by the findings of Vanaja and Luckins (2006).

Seed germination

Seed germination percentage varied significantly among provenances, $p<0.05$ and did not follow a regional pattern as was also shown by the morphological traits. Generally, large seeds are expected to have higher seed germination ability than small seeds (Isik, 1986). Seeds from Manapools provenance, having largest seeds had the second highest seed germination percentage after Taveta provenance which had the smallest sized seeds. This deviates from most findings (Vakshasya et al., 1992; Ginwal et al., 1994), except for Fenner (1991) who observed no significant correlation between seed size or seed weight with the seed germination hence caution should be taken in making such decisions based on seed morphology alone. Seed coat thickness was measured without separating it from the seed which may be another factor; however scarification and soaking of scarified seeds in water for 24 h before sowing might address the physical barriers imposed by seed coat thickness. Hence genotypic factors should not be overlooked and must always be taken into consideration (Ibrahim, 1996; Gera et al., 2000; Jayasankar et al., 1999; Mkonda et al., 2003; Sivakumar et al., 2002). This is supported by the high heritability for the various traits studied (low environmental variance), and thus suggest that most of these traits are under genetic control.

Correlations of seed among seed traits and with geo-climatic conditions of seed sources

Seed characters were highly correlated. Correlated traits are of interest to tree breeding because change of one trait leads to simultaneous improvement of the correlated trait. Correlation among seed traits have been documented in tree species for example, Barracosa et al. (2007) and Dangasuk et al. (1997). The significant correlation among seed traits and geo-climatic conditions of the seed source shows that the environments affect the expression of seed traits and a possibility of clinal distribution of *F. albida* provenance under study.

Seed divergence

High rate of environmental variability within Eastern and Southern Africa regions show that species distribution is discontinuous, with barriers to gene flow among populations, leading to isolation of populations. It is there-fore not expected to observe regional based population structure but rather habitat based structure for instance, Lupaso (Malawi), Manapools (Zimbabwe) and Wangingombe (Tanzania) that clustered together from regions receiving high rainfall and temperatures. Comparing the Eastern Africa provenances, Wangingombe has a higher rainfall (760 mm) and also located in a high altitude (1700 m above sea level) as compared to Taveta that is located in low rainfall area (545 mm) and in a lower altitude (760 m asl). Similarly, Kuiseb from the southern Africa region is located in extremely low rainfall area (<50 mm annually), very low temperature (15.2°C) as well as low altitude (400 m asl) as compared to the other two provenances hence its separation into a different cluster. The results of principal component analysis and cluster analysis indicated the role of interaction among different factors in genetic differen-tiation of *F. albida*.

Conclusions

The high heritability for the traits under study show minimal environmental influence on seed characteristics hence genetic factors have a lot of influence on the seed traits analyzed. This suggests that selection based on morphological traits can be made with a high degree of confidence. The variation in the total germination percentage at the nursery level emphasizes the need for wide-range trials to enhance selection of the best provenances for breeding and conservation of *F. albida* genetic resources. The low germination percentage of Kuiseb could be due to absence of ripen pods during collection or poor handling and processing of the seeds, there is need therefore to recollect the seeds with proper handling for fairer assessments.

The current work is a baseline study aimed at identifying useful traits for selection of the best provenances of *F. albida* for tree improvement, breeding and conservation of its genetic resources. More research is needed to provide more information on the identified traits before a general conclusion is made.

Conflict of Interests

The author(s) have not declared any conflict of interests.

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