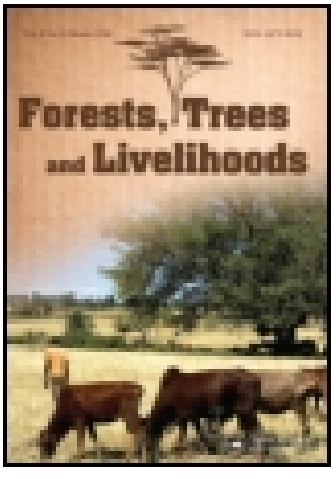

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Genetic diversity of Faidherbia albida (Del.) A. Chev accessions held at the World Agroforestry Centre

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Genetic diversity of *Faidherbia albida* (Del.) A. Chev accessions held at the World Agroforestry Centre

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This study assessed the extent and distribution of genetic diversity of 29 *Faidherbia albida* provenances from 10 African countries by employing amplified fragment length polymorphism with an aim of providing crucial genetic diversity information for *in situ* and *ex situ* management and utilization of the collections. Plant materials consisted of *F. albida* accessions held at World Agroforestry Centre [International Center for Research in Agroforestry (ICRAF)] seed bank. A total of 676 bands ranging from 50 to 499 base pairs were scored using five primer sets. The average percentage of polymorphic loci over all populations was 31.7. The collection from the Taveta (Kenya) provenance had the highest percentage of polymorphic loci (69.5%), while those from Manapools (Zimbabwe) had the lowest (13.5). The average heterozygosity ranged from 0.05 to 0.28 with a mean of 0.16 across all the provenances. There was high and quite significant population differentiation among the populations (PhipT = 0.64, $p = 0.001$). Analysis of molecular variance revealed that 64% of the total variation was partitioned among the populations and 36% within the populations. Unweighed pair-group method with arithmetic averaging clustering generally reflected the geographical origins and similarity of the germplasm except West African provenances indicating complex evolutionary trends that have shaped the population structure and distribution of the species. The results show that the germplasm held at ICRAF seed bank is of low genetic variability with the western and some of the eastern Africa provenances having the highest diversity. More collections need to be done to cover the entire distribution range of this species to capture more diversity and enrich this gene pool.

Keywords: amplified fragment length polymorphism; genetic diversity; *Faidherbia albida*; germplasm conservation; heterozygosity; provenances; population differentiation

Introduction

Faidherbia albida, formerly referred to as *Acacia albida*, is a tree species native to Africa and the Middle East. It is a leguminous woody species belonging to the Mimosoidae subfamily and commonly known as Apple-ring Acacia, Ana tree or Winter Thorn. *F. albida* is an important agroforestry tree promoted in the evergreen agriculture within the arid and semi-arid zones of Africa for soil conservation and fertility improvement (Garrity 2011). Its importance is underscored by a peculiar reverse phenology that makes it highly compatible with crops since it does not compete with them for nutrients and light (International Center for Research in Agroforestry [ICRAF] 1989). Shedding leaves during the rainy season at the time of higher microbial activity improve the soil structure, permeability and retaining leaves in the dry season provide shade and mulch thus

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conserving soil moisture (Dangasuk 2006). Besides the reverse phenology benefits, the tree is a nitrogen fixer which improves the soil fertility (Payne et al. 1998). Its leaves and pods provide crucial source of fodder in the dry season for livestock and it is also a chief source of wood and medicine. The species is also crucial in agroforestry systems and in desertification control through curbing soil erosion (Dancette & Poulain 1969; Cossalter 1991; Heshmati & Squires 2013). The importance of this species and the need for its conservation were recognized by the FAO (1974) Panel of Experts on Forestry Gene Resources. Between 1990 and 1994, a *F. albida* seed collection mission was initiated by the Oxford Forestry Institute (OFI) collaborating with several national tree seed centers and genebanks, and the collection was made from more than 40 stands in 10 African countries. Seed collection was carried out from 25 individual trees randomly selected from each provenance. Provenance collection criteria were based on geographical discontinuity from other populations, sites with differences in climate (altitude, soils, and ecology), selection from both undisturbed natural populations and populations in agricultural systems where there was a choice and distinctive morphological and phenological attributes (Fagg 1992). In 2001, ICRAF genebank received about 800 accessions of *F. albida* collection from the OFI. These accessions have been distributed to various evergreen agriculture projects over the years. Due to the increased demand for *F. albida* seeds the ICRAF genebank stock has become depleted warranting the need for restock through regeneration for multiplication or undertake a fresh collection where the original wild stands are still intact. However, either approach requires capital investments; undertaking a fresh collection requires surveys to ensure the existence of the wild stands. Regeneration is expensive and time consuming, especially for perennial tree species such as *F. albida* which may not flower until about 7 years after planting, and comes with risks to genetic integrity (Jorge & Hanson 2010). Regeneration of a tree species has to take into account the outcrossing nature of the species, space and the breeding cycle of the species and overall cost of maintaining a seed orchard (FAO 2014). To optimize on these costs in conservation for use approach, it is therefore important to evaluate genetic diversity of the genebank collection mapping it on the natural distribution to identify key areas to target for collection and accession that can be placed in the seed stand.

A number of studies have been done toward understanding the ecology, growth and genetic dynamics of the species. Dangasuk et al. (2001) observed that early growth performance variance in *F. albida* populations was a factor of climatic selection pressure and soil properties. Dangasuk and Gudu (2000), using isozyme analysis showed a significant deviation from the Hardy–Weinberg equilibrium and deficiency in heterozygotes which was associated with inbreeding. Studies conducted by Joly (1992), using isozyme as genetic markers revealed that *F. albida* populations were highly variable for the loci examined. In most cases the percentage of polymorphic loci was 90%, only the population of Mana Pools, Zimbabwe exhibited a low level of heterozygosity. The level of heterozygosity, which can be considered a measure of allelic diversity (Nei 1977) was very high for the West African populations ($H = 0.400$) as compared with the East African populations ($H = 0.265$). Random amplified polymorphic DNA (RAPD) analysis carried out by Dangasuk (2006) reported a high degree of polymorphism among 16 African provenances with Tot and Kainuk provenances from Kenya having the least polymorphism in the East African region. Information generated by these studies can be complemented by data obtained by engaging a more reproducible and reliable technique with a bearing on conservation and utilization of the germplasm.

This study used one of the most widely applied polymerase chain reaction-based marker technologies, amplified fragment length polymorphism (AFLP), to assess the

genetic diversity of *F. albida* provenances in ICRAF seed bank. The marker has been employed to assess genetic structuring in the tree species such as *Calycophyllum spruceanum* (Russell et al. 1999), *Pinus pinaster* (Mariette et al. 2001), and *Warbugia ugandensis* (Muchugi et al. 2008). Information generated will be essential in collection and development of better procedures for regeneration of germplasm for example by targeting unrepresented provenances. Through improved characterization and development of core collections based on this diversity information, it will be possible to exploit *Faidherbia* genetic resources valuably and reduce the number of redundant accessions (Malice & Baudoin 2009).

Materials and methods

At total of 29 *F. albida* provenances held at World Agroforestry Centre genebank were used (Table 1). Selection was based on the regional distribution of the material. Seeds were selected to cover varying elevations of the major phytochoria of Africa where *F. albida* is endemic. Equal number of seeds was randomly sampled from each of the 25 trees per provenance to constitute a bulk sample for germination. A sample of 50 pure seeds from each provenance was pretreated by mechanical scarification, nicking the distal end of each of the seeds with a nail clipper as proposed by Bechman (1992). The seeds were sown in forest soil mixed with compost medium filled in polythene tubes at 15 mm depth. The leaves from 20-day-old seedlings were harvested for DNA extraction.

Genomic DNA was extracted according to Doyle and Doyle's (1987) cetyltrimethylammonium bromide procedure. AFLP procedure was employed as described by Vos et al. (1995). The same procedure has been adapted in the AFLP™ *Plant mapping protocol* of the Applied Biosystems (ABI) and by Hemeida et al. (2004). Five primer sets (EcoRI–ACA/MseI–CAT, EcoRI–ACT/MseI–CTC, EcoRI–AAG/MseI–CTT, EcoRI–ACC/MseI–CAT and EcoRI–AGC/MseI–CTC) that produced clear and scorable bands were utilized for the analysis.

Data analysis

The AFLP products were separated by capillary electrophoresis using the ABI PRISM 3730® system. GeneMapper® software was employed to score molecular data as allele frequencies in binary and to generate AFLP electrophoregrams of DNA fragments produced by the most optimal primer combinations. The analysis of molecular variance (AMOVA; Excofferier et al. 1992) was conducted by employing GenALEx 6.41 (Peakall & Smouse 2006) software to reveal the partitioning of the variation across the populations. The variance components were used to calculate PhipT statistics which are analogous to *F*-statistics and useful for analysis of dominant markers. This analysis was based on AFLP genotypes consisting of 676 band states. Levels of significance were based on 99 iterative permutations. Fisher's exact test for population differentiation was used to further test the null hypothesis that there is no differentiation among the populations. The GenALEx was also used to compute principle component analysis (PCA) to display provenance relationships by interpreting patterns in the composition of the samples. Similarity matrix based on Nei's (1978) genetic distances was generated with tools for population genetic analysis tools for population genetic analysis (TFPGA) 1.3 (Miller 1997) software. A dendrogram was then generated by employing the unweighed pair-group method with arithmetic averaging (UPGMA; Sneath & Sokal 1973). Validation of the cluster analysis was done by computing 5000 bootstrap samples using TFPGA. To establish genetic

Table 1. Details of provenances sampled.

Country	Provenance	Location	Sample size[a]	Seed source no.	Population designation
Mozambique	Guijalimpopo	24.30S, 33.02E	16	140/94	1
Zimbabwe	Manapools 1	15.45S, 29.20E	15	24/90	2
Malawi	Bolero	10.58S, 33.43E	15	78/90	3
Malawi	Chawanje	14.39S, 34.48E	20	7/92	4
Ethiopia	South harar	9.17N, 42.06E	14	120/94	5
Ethiopia	Lake koka	8.20N, 38.59E	16	119/94	6
Tanzania	Wagingombe	8.51S, 34.38E	15	5/92	7
Zimbabwe	Manapools 2	15.45S, 29.20E	15	19/92	8
Senegal	Bignona	12.45N, 16.25W	15	8/92	9
Malawi	Lupaso	9.55S, 33.53E	14	77/90	10
Namibia	Okangwati	17.25S, 13.17E	11	16/94	11
Zambia	Chizombo	13.08S, 32.45E	9	75/90	12
Kenya	Maseno	0.01S, 34.6E	15	–	13
Kenya	Taveta	3.24S, 37.42E	15	179/92	14
Ghana	Bolgatonga	10.46N, 1.00W	15	74/90	15
Ethiopia	Gelemso	8.45N, 40.27E	14	117/94	16
Zimbabwe	Bubye river	21.42S, 30.29E	14	27/93	17
Zimbabwe	Duvure	20.10S, 32.10E	16	47/90	18
Zimbabwe	Tegwani/Masiti dam	19.55S, 27.07E	16	25/93	19
Zimbabwe	Ghona re-Zhou	21.18S, 32.22E	16	30/92	20
Zimbabwe	Kapula	18.42S, 26.17E	8	23/93	21
Zimbabwe	Nyanyadzi	19.45S, 32.26E	8	25/92	22
Zimbabwe	Kuiseb	23.34S, 15.02E	13	60/90	23
Zambia	Kafue flats	15.31S, 26.40E	16	76/90	24
Ethiopia	Lake Awassa	7.03N, 38.28E	16	24/94	25
Tanzania	Mwembe	4.08S, 37.51E	16	10/92	26
Tanzania	Mfumbi	8.50S, 34.00E	15	9/92	27
Zimbabwe	Dumisa	22.13S, 31.24E	10	76/92	28
Ethiopia	DebreZeit	8.48N, 38.59E	13	118/94	29

[a] Fifty seeds for each provenance were sown. Not all seeds germinated. The number of actual samples we could collect per provenance is shown in this column.

diversity of the provenances, the percentage of polymorphic loci at 99% confidence interval and unbiased average heterozygosity were computed using TFPGA. Here the allele frequencies were estimated based on the square root of the null genotype and Hardy–Weinberg equilibrium was assumed.

Results

Analysis of molecular variance

The AMOVA showed significant provenance differentiation with 64% of the variation attributed to among populations and 36% to within populations (Table 2). Fisher's exact

Table 2. Summary of the AMOVA within and among *Faidherbia albida* provenances.

Source of variation	df	SS	MS	Est. var.	%	Stat	Value	*p*-Value
Among populations	28	25,595.442	914.12	62.108	64			
Within populations	382	13,365.774	34.99	34.989	36			
Total	410	38,961.217		97.097	100	PhipT	0.64	0.001

test for population differentiation also revealed that the populations were significantly differentiated ($p = 0.00$).

Cluster analysis

Nei's genetic distances were used to generate genetic similarity estimates based on all the 676 AFLP loci using the UPGMA cluster analysis in order to present genetic relationships as dendrogram (Figure 1). Validation of the cluster analysis was done by computing 5000 bootstrap samples. The dendrogram generated showed five major population clusters. The highest genetic distance (0.488) was observed between Manapools 1 and Bubye river provenances which interestingly are accessions from the same country while the lowest genetic distance (0.012) was observed between Bolero and Chawanje provenances from Malawi. Bolgatonga (Ghana) and Bignona (Senegal), though both from West Africa, are in different clusters with a genetic distance of 0.392. Two provenances from Ethiopia (South Harar and Lake Koka) are clustering together with a genetic distance of 0.031 but distantly with Gelemso accessions from the same country with genetic distances of 0.304 and 0.309, respectively. The two Kenyan provenances, Taveta and Maseno, are in different clusters, and quite distantly related (0.308). Taveta is clustering with Gelemso (0.06) and Maseno with Wagingombe, Tanzania, (0.11). Most of the South African provenances are showing a regional similarity.

Principle coordinate analysis

Principle coordinate analysis delineated three general groups by combining together the three middle groups in the dendrogram which comprised of 73.3% of East African provenances. Bignona (Senegal) appeared to be a bit distantly related from the rest of the

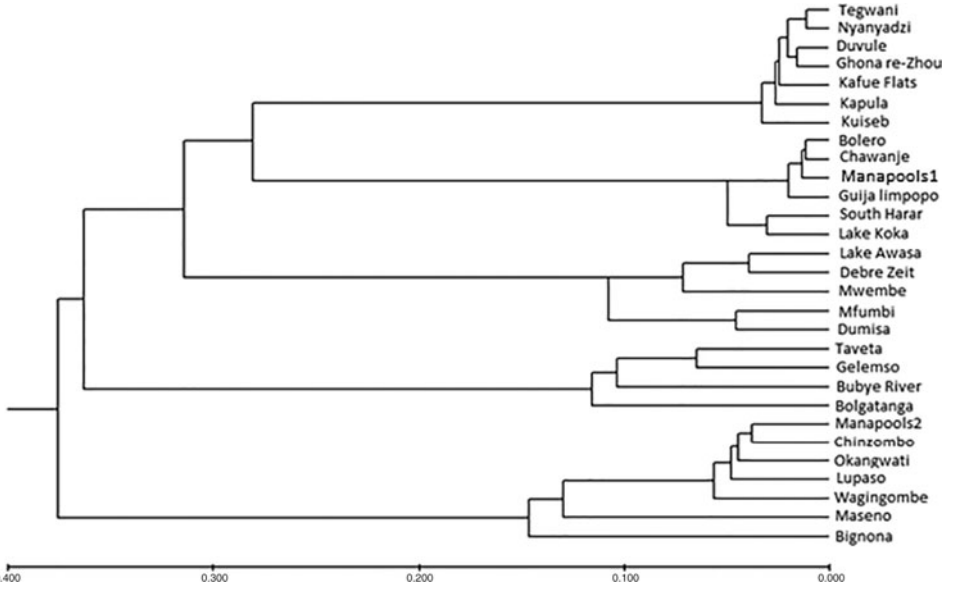

Figure 1. An UPGMA dendrogram showing relationship among 29 provenances of *Faidherbia albida* based on 676 AFLP loci amplified by five primer sets.

provenances in the respective groups. The first three coordinates explained 97.6% of the total variation.

Measures of genetic diversity

The mean heterozygosity (Nei's genetic diversity) based on the 676 loci across the 29 populations ranged between 0.05 and 0.28. The percentage of polymorphic loci ranged between 13.46 and 69.5 with Manapools 1 accessions having the lowest diversity and percentage of polymorphism and Taveta having the highest (Table 3). It was observed that the percentage of polymorphism values and average genetic diversity values are in agreement to the extent that the population showing a low percentage population is also showing low *H*.

Generally, the accessions from West and East Africa (Bignona – 52.1, Bolgatonga – 55.3, Kenya – 69.5, Gelemso – 53.3) and Lake Awassa (50.9) had higher percentage of polymorphic loci and average heterozygosity compared with the accessions from South Africa (Manapools 1–13.46, Bolero – 15.5 and Chawanje – 16.6). Only Bubye river provenance from Mozambique had comparatively high genetic diversity (0.17) and

Table 3. Mean genetic diversity estimates for 29 *Faidherbia albida* provenances based on five primer sets and 676 loci.

Provenance	Country	Number of individuals	Average heterozygosity	% Polymorphic loci
Guija Limpopo	Mozambique	16	0.08	21.30
Manapools 1	Zimbabwe	15	0.05	13.46
Bolero	Malawi	15	0.06	15.53
Chawanje	Malawi	20	0.06	17.60
South Harrar	Ethiopia	14	0.06	15.09
Lake koka	Ethiopia	16	0.06	17.01
Wagingombe	Tanzania	15	0.14	41.27
Manapools 2	Zimbabwe	15	0.13	34.61
Bignona	Senegal	15	0.19	52.07
Lupaso	Malawi	14	0.13	39.05
Okangwati	Namibia	11	0.11	27.66
Chinzombo	Zambia	9	0.13	31.51
Maseno	Kenya	15	0.10	28.69
Taveta	Kenya	15	0.28	69.53
Bolgatonga	Ghana	15	0.21	55.33
Gelemso	Ethiopia	14	0.22	53.25
Bubye River	Zimbabwe	14	0.17	45.71
Duvure	Zimbabwe	16	0.10	35.79
Tegwani/Masiti Dam	Zimbabwe	16	0.09	26.33
Ghona re-Zhou	Zimbabwe	16	0.09	28.11
Kapula	Zimbabwe	8	0.08	22.78
Nyanyadzi	Zimbabwe	8	0.09	23.96
Kuiseb	Namibia	13	0.07	20.85
Kafue flats	Zambia	16	0.10	25.89
Lake Awasa	Ethiopia	16	0.19	50.89
Mwembe	Tanzania	16	0.09	29.14
Mfumbi	Tanzania	15	0.09	25.44
Dumisa	Zimbabwe	10	0.07	24.85
DebreZeit	Ethiopia	13	0.09	25.00

percentage of polymorphic loci (45.7). South harar (15.1) and Lake Koka (17) accessions from Ethiopia had the lowest estimates among the east African provenances.

Discussion

Measures of genetic diversity results based on five primer combinations showed that *F. albida* accessions held at ICRAF seed bank are generally of low variability. Taveta provenance from Kenya had the highest diversity estimate values ($H = 0.28$), while Manapools 1 from Zimbabwe had the least ($H = 0.05$). The same trend was manifested by the percentage of polymorphic loci estimates. The mean percentage of polymorphic loci (33.98) and the mean heterozygosity (0.13) for all the populations were in the range of those observed by Harris et al. (1997) using isozymes (33.98 and 0.17). On average, the West African provenances manifested higher genetic variation followed by eastern populations, while the South African provenances had the lowest levels. This is in agreement with the findings of Dangasuk (2006) using RAPD analysis and Harris et al. (1997) using isozymes. This trend suggests West Africa as the possible center of origin and center of diversity of *F. albida* and a subsequent east to south spread. This school of thought was first postulated by Chevalier (1934) and Wickens (1969).

The diversity estimates were, however, lower than those reported by Dangasuk (2006) based on RAPD (West Africa $H = 0.7$, East Africa $= 0.67$ and South Africa $= 0.47$). This could be possible owing to the differences in the methodology; however, the overall trend was virtually similar. The high genetic diversity recorded in West (Bignona and Bolgatonga) and East (Taveta) African accessions makes them potential seed sources for introduction and domestication of *F. albida*. The accessions from South Harar and Lake Koka (Ethiopia), Bolero and Chawanje (Malawi) and Manapools 1 had the lowest diversity estimates. This is in agreement with the results observed by Harris et al. (1997). Indeed, he observed that there was absence of heterozygotes in Bolero ($H = 0.00$). These patterns of variation point to a possibility of severe founder effects or genetic erosion due to anthropogenic factors acting on these populations long before the time of collection.

For a wide range of plant species, the mating system plays a critical role for the patterns of genetic variation both within and among populations (Hamrick et al. 1992). AMOVA results revealed a considerable level of diversity structuring, 64% of which was among populations and 36% within populations. This is contrary to the expected diversity structuring for outcrossing plant species as demonstrated by Rossetto et al. (1995) and Chase et al. (1995). Such structuring means that *F. albida* exhibits some level of selfing. These results are in line with the study done by Joly (1992) where natural populations of *F. albida* revealed a deficit in heterozygotes compared with values expected in open allofertilization confirming a partial selfing. Gassama-Dia et al. (2003) reaffirmed this view while studying reproductive biology of *F. albida*. Due to the mixed mating system suggested by these results, the conservation implication is that many populations should be sampled whereas intra-population sampling need not be very extensive to capture a large proportion of the variation.

The high and significant differentiation observed among the provenances studied, demonstrated the importance of selection pressure in evolution of ecotypes. Different populations were adapted to immediate ecological conditions such as soil type, rainfall patterns, and insolation. This coupled with limited gene flow due to long distances between them led to formation of disjunct distributions of related populations. Details of this population differentiation are therefore clearly important to the conservation of *F. albida* especially where decisions have to be made concerning where and what

populations should be conserved and the need for genetic mixing in introduction programs. The significant differentiation signifies considerable genetic differences among some of the provenances; therefore, the number of provenances to act as future seed source for regeneration and introduction in agroforestry systems is crucial. Some *F. albida* stands are highly endangered due to anthropogenic activities and without detailed knowledge of the spatial population structure of this species, the conservation interest of a particular population may be underestimated (Thompson 1999).

UPGMA cluster analysis on the basis of pair-wise genetic distances showed five main distinct groups. This pattern of clustering was in agreement with the principle coordinate analysis that was chosen to complement the cluster analysis information (Figure 2). Cluster analysis is more sensitive to closely related individuals whereas PCA is more informative regarding distances among major groups (Hauser & Crovello 1982). The dendrogram did not exclusively place provenances according to the geographical origins of the accessions; however, it gave crucial insights into evolutionary processes that result from patterns of colonization and isolation.

The first and second groups were composed of provenances from Southern Africa save for two provenances (South Harar and Lake Koka) with Ethiopian origin. The large genetic distance between the Ethiopian provenances and the four South African provenances in the same cluster (see also position of nodes in Figure 1) points the two as probable seed sources for the colonization of South African countries through migratory herbivores and other human activities. South Harar and Lake Koka share a very small genetic distance that is an indication of a recent divergence. The third and fourth groups were primarily composed of Eastern and Southern Africa provenances. Only Bolgatonga from Ghana (west) featured in this main cluster. A similar pattern was observed by Harris et al. (1997), where Bolgatonga formed part of Ethiopian/Sudanian subcluster rather than the western subcluster. The same case applied to the fifth cluster with only Bignona from Senegal (west) appearing in the group. Based on differences in ecological conditions and geographical isolation it would be expected that natural selection and differentiation will make such closeness impossible. This uniqueness of West African populations being genetically closer to East and South African populations was also observed by Dangasuk (2003), where Bignona clustered together with Rama (Ethiopia). However, Vandenbeldt (1991), and Joly (1992), reported the uniqueness of the Ethiopian provenances of *F. albida* which made them suspect that Ethiopia is the possible species center of origin containing the greatest genetic diversity of the species. This was echoed by Dangasuk et al. (1997). Although this study did not feature Rama in its analysis, the presence of one of the two West African provenances studied in each cluster suggests that they share considerable characteristic with the east and south population. This coupled with their smaller genetic distances to the last common ancestor (see Figure 1) makes West Africa the most likely origin of *F. albida*. A clearer picture about the origin can, however, be obtained if more West African, Sahelian, and North African provenances are included in such a study.

The large genetic distance between Bolgatonga and Bignona could be explained by the two being located in different phytochoria (White 1983). Bignona is part of the Sudanian phytochoria while Bolgatonga is part of Guineo-Congolian regional center of floral endemism. These regions are defined by unique ecological conditions which may have subjected the populations to strong selection forces. The large genetic distances and by implication genetic diversity recorded from West African provenances in this study and by Dangasuk (2003, 2006) and Harris et al. (1997) presented them as crucial diversity centers for germplasm collection. A peculiarity of big genetic distances between Maseno and

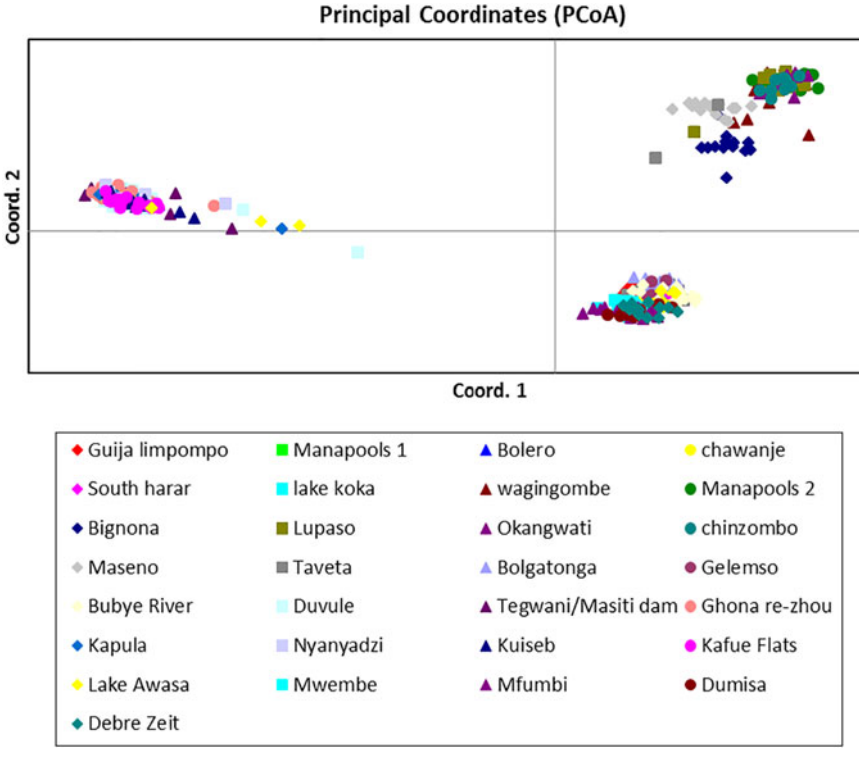

Figure 2. Principle coordinate analysis of the 29 *Faidherbia albida* provenances based on 676 AFLP loci.

Taveta from Kenya, the two Manapools provenances from Zimbabwe and Gelemso from the other Ethiopian provenances was eminent. Such a phenomenon occurs when there is a major barrier to gene flow in terms of pollination and seed dispersal over a number of generations. This could also have been a result of independent colonization events. Going by the global positioning system (GPS) coordinates, the distance between Maseno and Taveta, Bubye River and Manapools 1 are large enough for any substantial gene flow to have occurred and therefore the observed genetic distances could be a result of isolation and divergent evolution over time. Gelemso is found along the eastern highlands of Ethiopia, while Lake Koka is one of the Great Rift Valley lakes. The genetic distance between these accessions could as well be a result of this isolation.

Our results imply that the spatial structuring and diversity of populations does not necessarily reflect their geographical locations. The absence of congruence between phylogenetic branching patterns among related taxa and their geographical distributions could be linked to historical associations among populations, the role of isolation in shaping patterns of disjunct distributions of related taxa, the role of evolutionary forces in shaping traits, the role of human activities on evolution and the interaction between mating systems and the environment.

It is also clear that AFLP is a reliable tool for genotyping a large number of accessions and information obtained is crucial in management of germplasm resources. Generally, accessions from West African provenances have comparatively higher genetic diversity followed by Eastern Africa and Southern Africa populations. The structuring of genetic

diversity revealed that *F. albida* is not entirely outcrossing, a phenomena that has a bearing on the extensiveness of sampling in capturing substantial diversity of accessions. More collections need to be done to cover the entire distribution range of this species and enrich this gene pool. Specifically, South African provenances should be targeted to possibly capture more diversity from this region. This study also confirmed that there are no redundancies among the *F. albida* germplasm analyzed in the seed bank.

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Disclosure statement

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Notes

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