

## Full Length Research Paper

# Exploring genetic diversity and structure of *Acacia senegal* (L.) Willd. to improve its conservation in Niger

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The genetic diversity of African forest resources is poorly documented while it can be the basis for adapting these resources to climatic variations. This study aimed to characterize the genetic diversity of the *Acacia senegal* (L.) Willd in its natural range in Niger. 252 individuals from 10 populations of the species, across three gum basins were analyzed with 9 nuclear microsatellite markers. Genetic diversity indexes are high in all the populations studied: number of allele ( $N_a$ ) varies from 4.00 to 5.44; allele richness ( $R$ ) varies from 3.42 to 4.49; observed heterozygosity ( $H_o$ ) and expected heterozygosity ( $H_e$ ) range from 0.44 to 0.56 and from 0.46 to 0.63, respectively. The values of differentiation index ( $F_{st}$ ) per pair of population range from 0.0057 to 0.110 and 20% of these values are not significant indicating a low differentiation between populations. In addition, molecular variance analysis shows that 93% of total variation is within populations. Through Bayesian model, a structure of population into three groups is observed. These results could form the basis for building sustainable management and conservation strategies of genetic resources of *A. senegal* in Niger.

**Key words:** Genetic diversity, microsatellites, *Acacia senegal*, climate change, Niger.

## INTRODUCTION

The major challenge of biological conservation is the preservation of genetic diversity in the maintenance of the evolutionary process of species (Assogbadjo et al., 2006). Using genetic data to determine evolutionary relationships between species and populations significantly contributes to their conservation (Chiveu et al.,

2008). Genetic variation in several trees species on earth is a trans-generational resource of great social, economic and environmental importance. Commonly referred to as "forest genetic resources", these variations are expressed by differences between species, populations, and individuals or chromosomes and have an actual or

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potential value (Young et al., 2001).

The management of forest genetic resources has caused serious national and international concern over the past few years due to overexploitation and unfavorable climatic conditions which have led to severe degradation of ecosystems. This phenomenon affects particularly the Sahelian region including Niger.

Among African forest species, *Acacia senegal* (L.) Willd. has a wide distribution in the arid and semi-arid regions of Africa, from South Africa northwards to Sudan (Maydell, 1983), because it tolerates aridity and eroded soils (Raddad et al., 2005; Chiveu et al., 2008). *A. senegal* (L.) Willd is a leguminous multipurpose species belonging to the subgenus *Aculeiferum* (Arce and Blanks, 2001). The international botanical community accepts the retyfying *Acacia* with a new type which would place most species ascribed to the present subgenus *Aculeiferum* into the genus *Senegalia* (Boatwright et al., 2014; Kyalangalilwa et al., 2013; Haddad, 2011).

In Niger, *A. senegal* is distributed along a climatic gradient between the isohyets 620 and 250 mm (Elhadji et al., 2012, 2016), forming a band from west to east and of which three gum basins are distinct (western basin, central basin and eastern basin) (FAO, 2003). However, since the droughts of 1974 and 1982, natural stands of *A. senegal* are constantly degrading under combined effects of anthropogenic actions and climatic variability (Amani, 2010). The deforestation of the natural stand of the gum groves for installation of crop fields, the exploitation of wood for domestic energy and mutilation of trees to feed animals constitute some factors of deterioration (Ichaou, 2008). In addition to the aforementioned factors, aging of trees, their high mortality and low capacity of regeneration are added (Maisharou and Nourou, 2004). Indeed, the natural stand regeneration, which is mainly done by seeds coming from the trees *in situ*, would depend on the maintenance of genetic diversity of the populations. The genetic diversity would also help to cope with unpredictable climatic changes or to establish breeding programs (Blanc et al., 1999). It is important to know the structure of genetic diversity which constitutes the partition of variation between different populations and which could be their capacity to adapt to environmental changes.

While the importance of *A. senegal* in rural economy (Guinko et al., 1996) and soil stabilization and fertility (Abdou et al., 2013; Wickens et al., 1995) is undeniable, the importance of genetic diversity of natural populations in Niger is still very poorly studied. The knowledge of the partitioning of genetic variation within species is a prerequisite for defining strategies for conservation, management and sustainable use of the species' resources. The main objective of the study is to analyze the genetic diversity and structure of the natural stands of *A. senegal* in Niger through (i) the quantification of genetic diversity within each population, (ii) the determination of genetic structure of populations and (iii)

the estimation of gene flow between these populations.

## MATERIALS AND METHODS

### Presentation of study sites

The study is conducted in the three basins of gum arabic production in Niger, namely western basin, central basin and eastern basin (Figure 1). The sites of western basin (Kiki, Kokoyé, Tempena and Bégorou) are characterized by a Sahelian climate with two seasons (a rainy season from June to October and a dry season from November to May) with rainfall varying between 620 and 400 mm. For the sites of the central basin (Aseye, Dakoro and Bader), the annual rainfall varies between 400 and 350 mm and the climate is Sahelo-Saharan with a long dry season (9 months) and a short rainy season. In the sites of the eastern basin (Malam Mainari, Gouré and Nguel kolo), annual rainfall varies between 300 and 250 mm and this site is characterized by a dry climate (a long dry season and rainy season hardly reaching 3 months in the year). In all the sites, the vegetation consists of woody species: *Acacia tortilis*, *Acacia seyal*, *Acacia laeta*, *Acacia dudgeoni*, *Balanites aegyptiaca*, *Boscia senegalensis*, *Combretum glutinosum*, *Combretum micratum*, *Calotropis procera*, *Leptadenia pyrotechnica*, *Maerua crassifolia*, *Ziziphus mauritiana*, *Tamarandis indica* and Herbaceous: *Alysicarpus avalifolius*, *Cyperus indica*, *Eragrostris tremula*, *Acanthospermum hispidum*, *Cenchrus biflorus*. But *A. senegal* is dominant. The highest average daily temperature (38.50°C) is observed to the east and north center of Niger, corresponding to the sites of the eastern and central basins in April and May of the year. While in the west, it varies between 35 and 36.50°C (western basin).

### Sampling

Ten natural *A. senegal* populations scattered in the three gum basins were sampled (Figure 1 and Table 1). The number of sample per population and basin is consigned in Table 1. A total of 252 trees (young and adult) distant at least 50 m fresh leaves were collected to avoid sampling related to trees. Such a sampling plan makes it possible to capture the maximum of variability within a population. Leaf samples were dried using silica gel before shipment to the genetics laboratory of the IRD (Niamey) representation in Niger.

### DNA extraction and SSR marker analysis

DNA was extracted from 0.5 g of dried leaves using the protocol described by Ky et al. (2000). The quality of DNA was assessed by electrophoresis on a 1% agarose gel and quantified using a nano-drop spectrophotometer (ND1000, Thermo Scientific, USA) at Center for Medical Research and Sanitary (CERMES) in Niamey, Niger. Nine nuclear SSR markers (mAsCIRB10, mAsCIRC07, mAsCIRE06, mAsCIRE07, mAsCIRE10, mAsCIRF02, mAsCIRF03, mAsCIRH01 and mAsCIRH09) developed in *A. senegal* var. *senegal* by Assoumane et al. (2009) were used for diversity analysis. The 252 samples were genotyped at the ICRISAT Plant Genetics Laboratory in India.

### Data analysis and statistical test

#### Genetic diversity

The following five parameters were used to quantify genetic

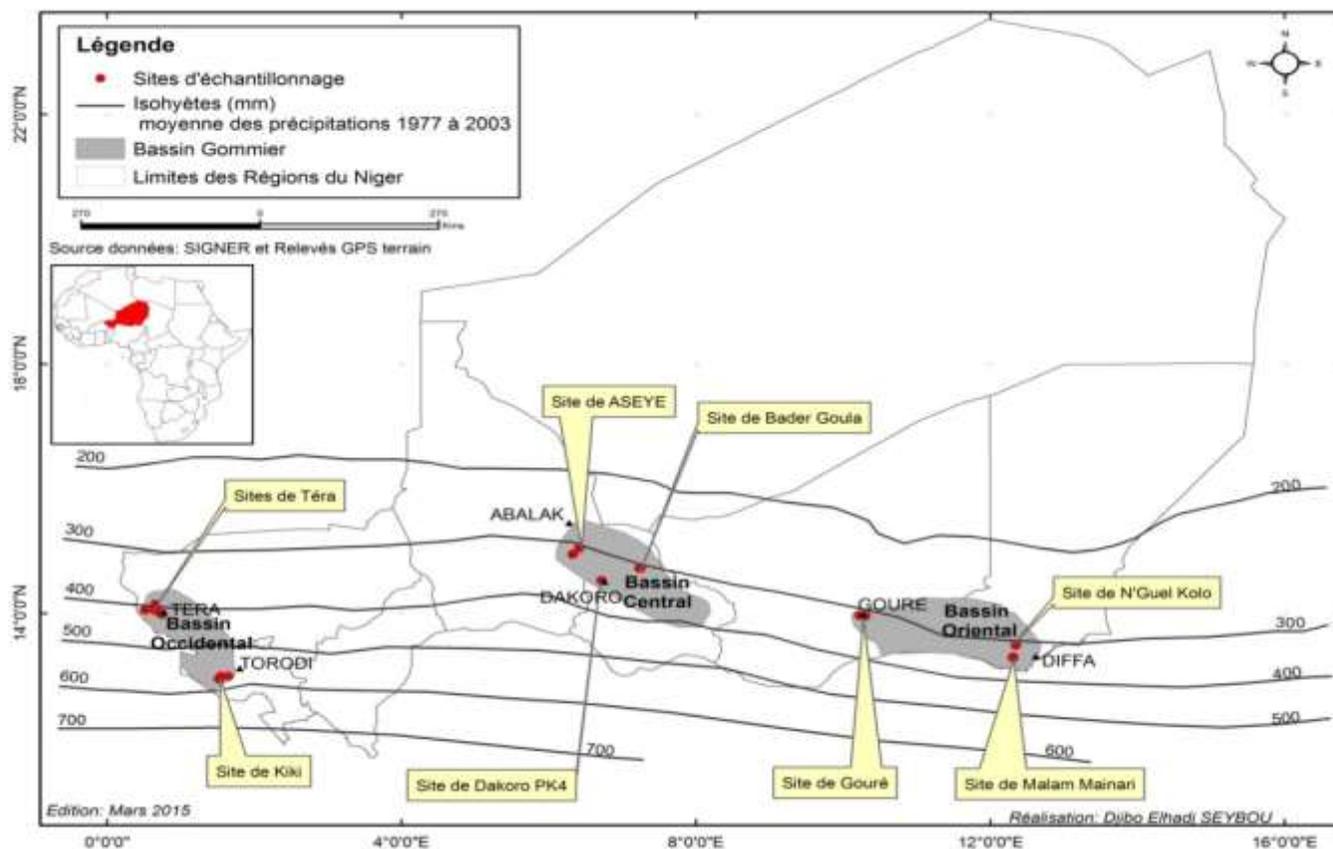


Figure 1. Location map of the study sites.

Table 1. Samples per site and localisation of the sites.

| Basin      | Site          | Sample | Localization              |
|------------|---------------|--------|---------------------------|
| Occidental | Tempena       | 17     | N12°57'04,1" E01°31'14,6" |
|            | Kiki          | 22     | N12°59'35,8" E 01°32'59"  |
|            | Begorou       | 23     | N14°03'3,9" E00°38'58,1"  |
|            | Kokoyé        | 32     | N13°59'10,30" E 00°44'35" |
| Central    | Aseye         | 36     | N15°02'46,2" E06°24'53,7" |
|            | Bader         | 25     | N14°43'19,7" E07°14'2,6"  |
|            | Dakoro        | 12     | N14°31'42,9" E06°42'53,1" |
| Oriental   | Gouré         | 22     | N13°58'06,8" E10°13'33,3" |
|            | Malan Mainari | 32     | N13°17'26,2" E12°18'29,2" |
|            | N'guel kolo   | 31     | N13°29'24,2" E12°20'51,9" |
| Total      | 10            | 252    | -                         |

diversity in the studied populations: Number of alleles per locus ( $N_a$ ), Allelic richness ( $R$ ); this parameter determines the mean number of alleles taking into account sample size, which conditions the number of alleles observed in the population, observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), and Wright (1965) fixation index ( $F_{is}$ ). Fstat software 2.9.3 (Goudet, 2001) was used to calculate these diversity parameters.

#### Population's genetic structure

Four methods of analysis were used: (1)  $F_{st}$  calculation using Fstat 2.9.3 software (Goudet, 2001); (2) genetic distance tree using Darwin 5.0.85 software (Perrier and Jacquemond-Collet, 2006); (3) Bayesian model using STRUCTURE 2.3.1 software (Pritchard et al., 2000) and (4) Analysis of Molecular Variance Analysis

**Table 2.** Parameters of genetic diversity in 10 natural populations of *Acacia senegal* distributed in the three gum basin in Niger.

| Gum basins    | Population    | Average rainfall (mm) | Na   | R    | Ho   | He   | Fis (W&C)            | N  |
|---------------|---------------|-----------------------|------|------|------|------|----------------------|----|
| Western basin | Kokoye        | 414.2                 | 5.22 | 4.17 | 0.50 | 0.58 | 0.143**              | 32 |
|               | Begorou       | 414.2                 | 4.67 | 3.93 | 0.49 | 0.54 | 0.093 <sup>ns</sup>  | 23 |
|               | Tempena       | 621.6                 | 5.00 | 4.49 | 0.56 | 0.63 | 0.123*               | 17 |
|               | Kiki          | 621.6                 | 4.33 | 3.80 | 0.49 | 0.56 | 0.118*               | 22 |
| Eastern basin | Malan Mainari | 309.2                 | 4.56 | 3.53 | 0.44 | 0.49 | 0.102*               | 32 |
|               | N'guel kolo   | 309.2                 | 4.33 | 3.48 | 0.46 | 0.48 | 0.033 <sup>ns</sup>  | 31 |
|               | Goure         | -                     | 4.00 | 3.42 | 0.46 | 0.46 | -0.008 <sup>ns</sup> | 22 |
| Central basin | Dakoro        | 436.5                 | 4.22 | 4.15 | 0.52 | 0.57 | 0.076 <sup>ns</sup>  | 12 |
|               | Bader         | 375.7                 | 5.22 | 4.41 | 0.48 | 0.55 | 0.126**              | 25 |
|               | Aseye         | 350                   | 5.44 | 4.07 | 0.48 | 0.55 | 0.131**              | 36 |

Na: Average number of alleles; R: allelic richness; Ho: observed heterozygosity; He: expected heterozygosity; Fis: fixing index estimated by Weir and Cockerham (1984); N: number of samples. Level of significance: \*P <0.05; \*\*P <0.01 and ns not significant.

(AMOVA) using the GenAEx 6.5 program (Peakall and Smouse, 2012).

**Fst calculation:** The significance of Fst values were tested at the 5% threshold after 1000 permutations of alleles within populations.

Gene flow between populations was estimated by the indirect method based on the assumption of mutation-drift equilibrium. The number of migrants per generation (Nm) is calculated from the average of Shannon diversity index. The calculation was done with the GenAEx version 6.5 software (Peakall and Smouse, 2012) according to the following classical formula:

$$Nm = \frac{1 - Fst}{4Fst}$$

Fst: index of population differentiation.

**Genetic distance tree:** Jaccard's distance was used to calculate the matrix of genetic distances because some individuals had more than two alleles for a locus. Jaccard's distance makes it possible to obtain an unbiased estimate of the genetic distance between individuals, as it does not consider the absence of the allele (0) as a similarity. It is calculated by the following formula:

$$d_{ij} = \frac{b + c}{a + (b + c)}$$

where dij = dissimilarity between two units i and j; a = number of variables for which xi = presence and xj = presence; b = number of variables for which xi = presence and xj = absence; c = number of variables for which xi = absence and xj = presence; xi and xj being the values of the variables for units i and j.

A Neighbour-Joining genetic distance tree (Saitou and Nei, 1987) was constructed from the genetic distance matrix for all samples.

**Bayesian model:** The genetic structure was also described by a Bayesian model using the software STRUCTURE 2.3.1 (Pritchard et al., 2000). In the STRUCTURE program, the admixture correlated allele model was used. This model assumes that all individuals share common ancestors and that alleles are correlated within populations. Thirteen "runs" were made to test independent K-values using 400,000 MCMC (Markov Chain Monte Carlo) and

40,000 burn-in periods.

**Analysis of Molecular Variance (AMOVA):** The distribution of genetic variation was evaluated specifying that the population groups constituting the three basins. AMOVA applied formula is:

$$F_{rt} = AR / (WI + AI + AP + AR) = AR / TOT$$

where AR = Estimated variance among basins; AP = Estimated variance among populations; AI = Estimated variance among individuals; and WI = Estimated variance within individuals.

## RESULTS

### Genetic diversity

The diversity parameters data are shown in Table 2. The number of alleles per locus (Na) varies from 4 (Gouré) to 5.44 (Aseye). The allelic richness (R) varies from 3.42 (Gouré) to 4.49 (Tempena). The heterozygosity is also higher in Tempena (He = 0.63, Ho = 0.56) and lower in Goure (He = 0.46; Ho = 0.46). These parameters (Na, R, Ho and He) reveal a fairly high genetic diversity in the natural populations studied. The fixation index (Fis) is different from zero and positive in all populations except in Bégorou, N'guelKolo, Dakoro and Gouré populations, where Fis is not significantly different from zero. The overall value of Fis is 0.104 and is significantly different from zero.

### Genetic structure

#### Differentiation detected by Fst

Table 3 presents the matrix of differentiation index (Fst) calculated by population pair. The populations of same gum basin have low Fst values that are not often

**Table 3.** Fst matrix per population pair.

| Population air | Western basin        |                      |                      | Eastern basin |                      |         | Central basin        |                      |                       |
|----------------|----------------------|----------------------|----------------------|---------------|----------------------|---------|----------------------|----------------------|-----------------------|
|                | Pop2                 | Pop3                 | Pop4                 | Pop5          | Pop6                 | Pop7    | Pop8                 | Pop9                 | Pop10                 |
| Pop1           | 0.0057 <sup>ns</sup> | 0.0206 <sup>ns</sup> | 0.0145 <sup>ns</sup> | 0.1063*       | 0.0926*              | 0.0808* | 0.0081 <sup>ns</sup> | 0.0409*              | 0.0282*               |
| Pop2           |                      | 0.0349 <sup>ns</sup> | 0.0067 <sup>ns</sup> | 0.0962*       | 0.0817*              | 0.0538* | 0.0269 <sup>ns</sup> | 0.0618*              | 0.0376*               |
| Pop3           |                      |                      | 0.0036 <sup>ns</sup> | 0.0803*       | 0.0944*              | 0.0786* | 0.0529*              | 0.0513*              | 0.0565*               |
| Pop4           |                      |                      |                      | 0.1103*       | 0.1107*              | 0.0892* | 0.0536*              | 0.0784*              | 0.0644*               |
| Pop5           |                      |                      |                      |               | 0.0075 <sup>ns</sup> | 0.0451* | 0.0944*              | 0.0531*              | 0.0885*               |
| Pop6           |                      |                      |                      |               |                      | 0.0641* | 0.0971*              | 0.0640*              | 0.0917*               |
| Pop7           |                      |                      |                      |               |                      |         | 0.0716 <sup>ns</sup> | 0.0371*              | 0.0553*               |
| Pop8           |                      |                      |                      |               |                      |         |                      | 0.0220 <sup>ns</sup> | -0.0064 <sup>ns</sup> |
| Pop9           |                      |                      |                      |               |                      |         |                      |                      | 0.0212 <sup>ns</sup>  |

ns: Non significant; \*Significant at 5% threshold ; Pop1: Kokoye; Pop2: Begorou; Pop3: Tempena; Pop4: Kiki; Pop5: Malan Mainari; Pop6: N'guel kolo; Pop7: Goure; Pop8: Dakoro; Pop9: Bader ; Pop10: Aseye.

**Table 4.** Matrix of mean gene flux values (Nm) between populations calculated from Shannon Diversity Index means over 9 loci.

| Pop1   | Western basin |       |       | Eastern basin |       |       | Central basin |       |       | Population |
|--------|---------------|-------|-------|---------------|-------|-------|---------------|-------|-------|------------|
|        | Pop2          | Pop3  | Pop4  | Pop5          | Pop6  | Pop7  | Pop8          | Pop9  | Pop10 |            |
| 0.000  |               |       |       |               |       |       |               |       |       | Pop1       |
| 15.635 | 0.000         |       |       |               |       |       |               |       |       | Pop2       |
| 5.271  | 3.169         | 0.000 |       |               |       |       |               |       |       | Pop3       |
| 8.179  | 7.788         | 8.267 | 0.000 |               |       |       |               |       |       | Pop4       |
| 0.993  | 1.618         | 1.076 | 1.016 | 0.000         |       |       |               |       |       | Pop5       |
| 1.126  | 1.863         | 0.857 | 1.006 | 18.543        | 0.000 |       |               |       |       | Pop6       |
| 1.517  | 2.900         | 1.045 | 1.320 | 5.506         | 4.724 | 0.000 |               |       |       | Pop7       |
| 5.546  | 3.177         | 1.032 | 1.344 | 1.768         | 1.603 | 2.119 | 0.000         |       |       | Pop8       |
| 2.420  | 2.069         | 1.393 | 1.130 | 1.871         | 1.494 | 2.673 | 3.448         | 0.000 |       | Pop9       |
| 2.960  | 2.479         | 1.393 | 1.357 | 1.408         | 1.179 | 2.771 | 5.743         | 8.557 | 0.000 | Pop10      |

Pop1: Kokoye; Pop2: Begorou; Pop3: Tempena; Pop4: Kiki; Pop5: Malan Mainari; Pop6: N'guel kolo; Pop7: Goure; Pop8: Dakoro; Pop9: Bader ; Pop10: Aseye.

significant at the 5% threshold. The overall Fst is 0.059; this reflects moderate differentiation according to Wright's ranking. In addition, overall average number of migrants (Nm) per generation is 3.288. It is high between populations in same basin and moderately low between populations of different basins (Table 4).

### Structure detected by genetic distance tree

The individual genetic distance tree of the Neighbour-Joining type (Saitou and Nei, 1987) presents a low individualization of branches. However, almost 3 distinct groups can be observed corresponding to 3 gum basins and two pools gathering individuals from all the basins (Figure 2).

### Structure detected by Bayesian model

For K = 3, the model highlights three groups corresponding

exactly to 3 gum basins (Figure 3). Nevertheless, in each group, individuals with a genetic proportion coming from the neighbouring groups were observed.

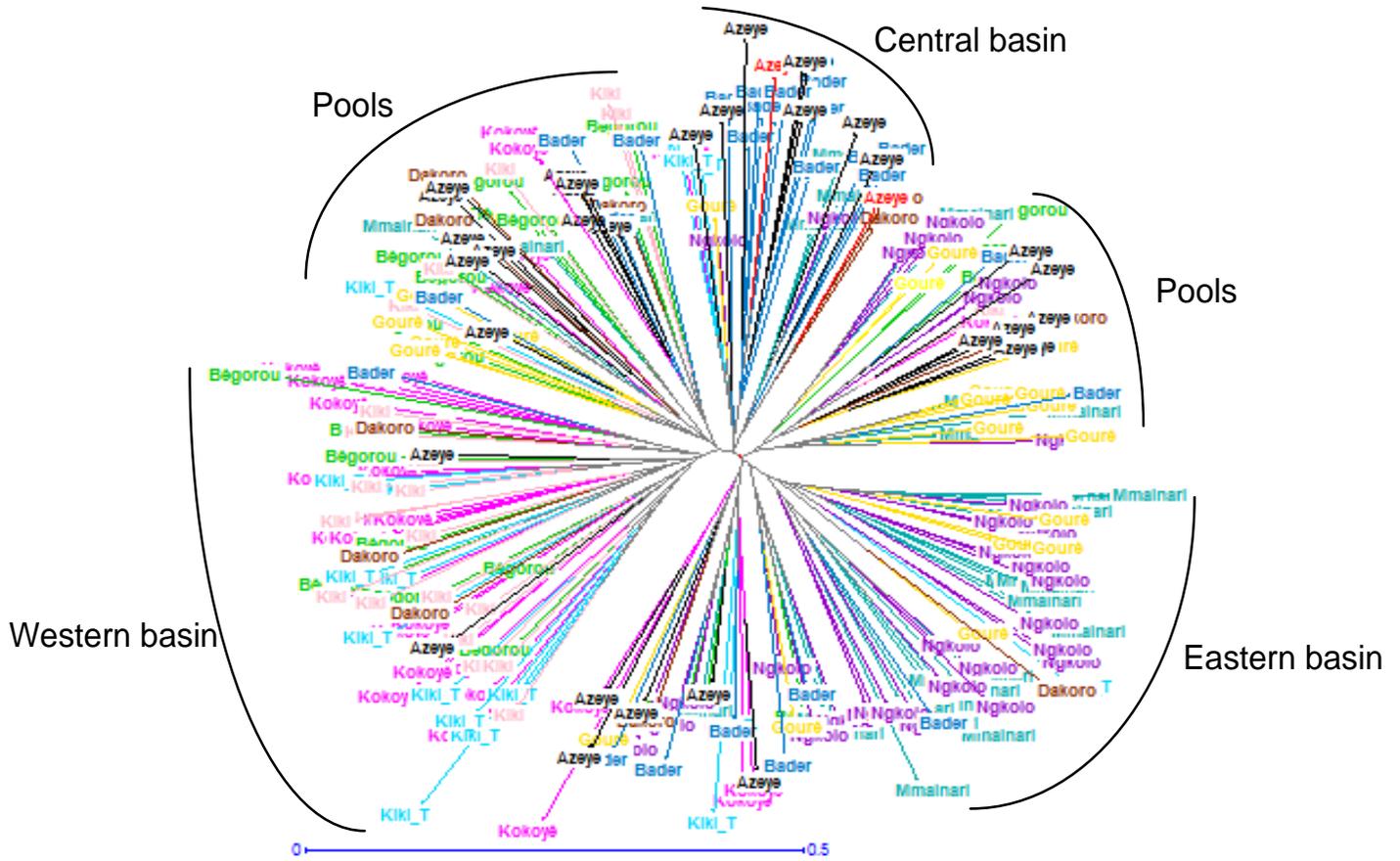
When using a K = 2 value to evaluate population structure, populations of western basin and central basin formed a single group and eastern basin populations form a second group (Figure 4).

### Genetic variability partitioning by AMOVA

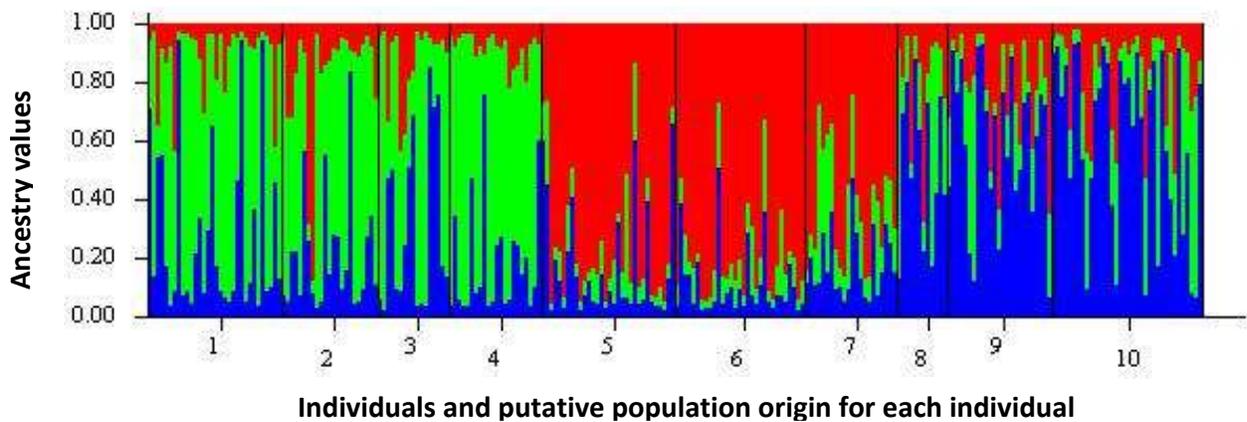
The AMOVA showed that 83% of variation is within individuals, 10% between individuals, 2% between populations and 5% between basins (Table 5).

### DISCUSSION

The distribution of forest tree species has a major impact on the extent of their genetic variability and structure. *A. senegal* is widely distributed in Niger, from west to east



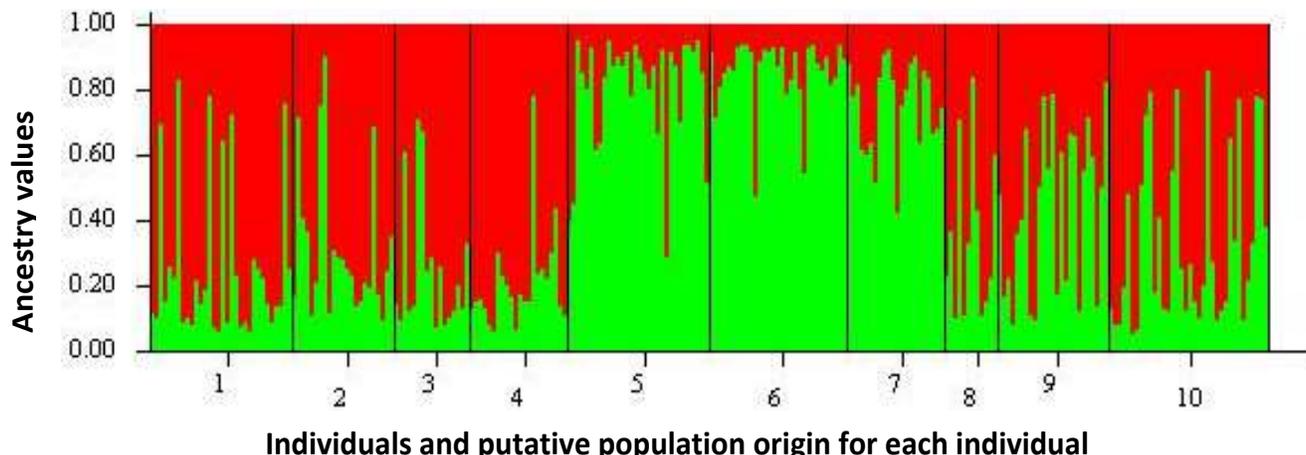
**Figure 2.** Neighbour-joining tree realized according to Jaccard distance. Individuals in the same color belong to the same population.



**Figure 3.** The grouping of individuals and populations realized using the model "admixture alleles correlated" and  $K = 3$ . The groups are represented by different colors (green, red and blue) and individuals are represented by vertical lines. The same color in different individuals indicates that these individuals belong to the same group. Different colors in the same individual group indicate the posterior probability of belonging to different groups. Populations 1, 2, 3 and 4 belong to the western basin; populations 5, 6, and 7 belong to the eastern basin and populations 8, 9 and 10 belong to the central basin.

forming a broad band in which three large gum basins were singled. In this study, the populations of these gum basins have a fairly high mean genetic diversity ( $H_o =$

0.48,  $H_e = 0.54$ ) compared to values found for other forest species analyzed with the same types of markers (Table 6). Genetic diversity in *A. senegal* species is



**Figure 4.** The grouping of individuals and populations realized the model "admixture alleles correlated" and  $K = 2$ . The groups are represented by different colors (green, red) and individuals are represented by vertical lines. The same color in different individuals indicates that these individuals belong to same group. Different colors in the same individuals indicate the posterior probability of belonging to different groups. Populations 1, 2, 3 and 4 belong to the western basin; populations 5, 6, and 7 belong to the eastern basin and populations 8, 9 and 10 belong to the central basin.

**Table 5.** AMOVA of 252 individuals belonging to 10 populations of *Acacia senegal* distributed in the three gum basins in Niger.

| Source of variation | df  | SS      | MS    | Est. Var. | %/total | P-value |
|---------------------|-----|---------|-------|-----------|---------|---------|
| Among-basins        | 2   | 55.51   | 27.75 | 0.13      | 5       | <0.001  |
| Among-populations   | 7   | 35.92   | 5.13  | 0.05      | 2       | <0.001  |
| Among-individuals   | 242 | 647.14  | 2.67  | 0.25      | 10      | <0.001  |
| Within-individuals  | 252 | 546.50  | 2.17  | 2.17      | 83      | -       |
| Total               | 503 | 1285.07 | -     | 2.60      | 100     | -       |

higher than average genetic diversity of tropical trees ( $H_e = 0.211$ ) and conifers ( $H_e = 0.207$ ) (Borgel et al., 2003). However, the genetic diversity observed in *A. senegal* is lower than that found in *Acacia mangium* ( $H_e = 0.70$ ) by Butcher et al. (2000) or in *A. senegal var. kerensi* ( $H_e = 0.63-0.70$ ) by Omondi et al. (2009).

The fixation index ( $F_{is}$ ) indicated a deficiency in heterozygosity from expected results under the assumptions of Hardy Weinberg. A positive value of  $F_{is}$  indicates a heterozygosity deficiency relative to the panmictic balance. A deficiency in heterozygosity can be explained mainly by 3 factors (Assoumane, 2011; Mohamed et al., 2010; Jordana, 2003): breeding regime that does not favor cross-breeding, existence of null alleles and effect of Wahlund. Indeed, for crossbreeding between relatives, it is well known that inbreeding (mating between an individual and his ascendants, his collaterals and/or his descendants) modifies the genotypic frequencies resulting in loss of genetic variability over generations. The second factor may be inherent to the existence of null alleles for some loci. Null alleles are alleles which do not amplify during polymerase chain reaction (PCR) due to mutation in the binding of the primer region. Then,

individuals are considered homozygous for these loci, while they are heterozygous and this phenomenon would reduce the number of heterozygous. The last factor refers to the presence of subpopulations within populations considered (substructure) can induce Wahlund effect. The presence of null alleles was not tested in our data. Nevertheless, a Wahlund effect can be assumed because at Aseye population where two groups distant about 10 km were sampled, a  $F_{is}$  value ( $F_{is} = 0.131$ ) was found which is significant at the 1% threshold. Then the two groups can be considered as different populations. The  $F_{is}$  (0.104) is comparable to that  $F_{is}$  (0.08) measured by Assoumane et al. (2012) and significantly different from zero in a population of *A. dudgeoni* (Dogona) in the western areas of Niger.

The  $F_{st}$  calculated among all populations ( $F_{st} = 0.059$ ) indicates moderate differentiation among populations. In addition,  $F_{st}$  observed in the study is comparable to those found in Table 6 in forest species with same markers. The genetic differentiation level is due to the existence of gene flow among populations.

The importance of gene flow between populations could be explained by the mode of seed dispersal and

**Table 6.** Parameters of diversity and genetic differentiation among populations of some forest species, estimated with nuclear microsatellites.

| Specie                                | Distribution | Dispersion mode         | N   | He        | Fis         | Fst   | Reference                |
|---------------------------------------|--------------|-------------------------|-----|-----------|-------------|-------|--------------------------|
| <i>A. senegal</i> (L) Willd.          | Continental  | Anemochore/Zoochore     | 252 | 0.46-0.63 | -0.01-0.143 | 0.059 | This study               |
| <i>Dacryodes buettneri</i>            | Continental  | Barochore/Anthropochore | 170 | 0.35      | 0.25        | 0.08  | Todou et al. (2013)      |
| <i>Dacryodes edulis</i>               | Continental  | Barochore/Anthropochore | 524 | 0.47      | 0.12        | 0.03  | Todou et al. (2013)      |
| <i>A. senegal</i> (L) Willd.          | Continental  | Anemochore/Zoochore     | 469 | 0.41-0.60 | -0.21-0.08  | 0.09  | Assoumane (2011)         |
| <i>A. senegal</i> var. <i>kerensi</i> | Continental  | Anemochore/Zoochore     | 300 | 0.63-0.70 | -0.20-0.04  | 0.04  | Omondi et al. (2009)     |
| <i>Pterocapus officinalis</i> Jacq.   | Insular      | Barochore/Hydrochor     | 202 | 0.25-0.59 | -0.04-0.37  | 0.29  | Muller et al. (2008)     |
| <i>Santalum insulare</i>              | Insular      | Zoochore                | 162 | 0.27-0.56 | -0.10-0.14  | 0.23  | Lhuillier et al. (2006)  |
| <i>Vitellaria paradoxa</i>            | Continental  | Barochore/Zoochore      | 169 | 0.25-0.42 | -0.22-0.18  | 0.05  | Sanou et al. (2005)      |
| <i>Vouacapoua americana</i>           | Continental  | Zoochore                | 408 | 0.34-0.52 | 0.09-0.22   | 0.08  | Dutech et al. (2004)     |
| <i>Swietenia macrophylla</i>          | Continental  | Barochore/Zoochore      | 194 | 0.78-0.81 | 0.06-0.10   | 0.1   | Lemes et al. (2003)      |
| <i>Swietenia macrophylla</i>          | Continental  | Barochore/Zoochore      | 284 | 0.59-0.80 | 0.07-0.24   | 0.11  | Novick et al. (2003)     |
| <i>Grevillea macleayana</i>           | Continental  | Barochore               | 130 | 0.42-0.53 | 0.07-0.31   | 0.22  | England et al. (2002)    |
| <i>Caryocar brasiliense</i>           | Continental  | Barochore/Zoochore      | 314 | 0.58-0.85 | 0.07-0.05   | 0.11  | Collevatti et al. (2001) |
| <i>Melaleuca alternifolia</i>         | Continental  | Barochore/Zoochore      | 500 | 0.13-0.92 | 0.07-0.29   | 0.07  | Rossetto et al. 1999     |
| <i>Symphonia globulifera</i>          | Continental  | Barochore/Zoochore      | 914 | 0.72-0.85 | 0.2         | -     | Aldrich et al. (1998)    |

N: Number of samples; He: expected heterozygosity; Fis: fixation index; Fst: differentiation index.

the presence of pollinators. Seed dispersal of *A. senegal* can be ensured by wind (anemophilic mode) after dehiscence of the pods. The socio-economic role of *A. senegal* in rural households (gum arabic) could also contribute to the exchange of plant from region to another and village to another (Ichaou, 2008). In addition to human action (anthropozoic mode), animals through grazing also contribute significantly to gene flows among *A. senegal* populations. Indeed, most of the studied populations constitute grazing areas for transhumant herders moving from one point to another and facilitating seed dissemination.

According to Kremer et al. (2012) and Buckley et al. (2010), improved forest species adaptation to changes in environmental conditions is better when there is more gene flow between populations up. For Slatkin (1987), a low gene flow ( $Nm < 1$ )

results from local differentiation that leads to genetic drift and a higher gene flow ( $Nm > 1$ ) makes population adjustment for survival. Values of 1 to 10 migrants per generation are essential for restoration and resistance to genetic drift and prevention of natural selection (Blanquart and Gandon, 2011; Lopez et al., 2009). In our study, the average number of migrants per generation ( $Nm$ ) is 3.288 and high  $Nm$  are observed between populations in the same gum basin. Low  $Nm$  is recorded between the most geographically distant populations: Kokoyé-Malan Mainari with  $Nm = 0.993$  and Tempena-N'guelkolo with  $Nm = 0.857$ . Indeed, populations of low  $Nm$  are spaced further by 1500 km, which would probably reduce gene flow between them.

The total variability is explained by intra-population variation (93%) and 2 and 5% of variability are attributed, respectively to variations

among populations and among gum basins. This result, which confirms that of  $F_{st}$ , is in agreement with Chavallier and Borgel (unpublished results), who observed that most genetic variability in higher plants and particularly in woody plants is within Populations ( $F_{st} = 8.45\%$ ). However, Rathore et al. (2016) observed in 11 populations of *Gymnema sylvestre* contrary results. These authors found a strong genetic differentiation of populations of the species ( $F_{st} = 70\%$ ) and low gene flow ( $Nm = 0.21$ ) through SSR markers. Their results are explained by the great geographical distance between populations studied, which created a geographic isolation limiting the possibilities of gene flow among populations.

With STRUCTURE program, individuals group by basin mainly due to small difference between populations that constitute the gum basin.

Geographical proximity promotes gene flow

between populations of the same basin. This is confirmed for  $k = 2$ , where we got the grouping of populations of western basin and those of central basin in the same group. The assignment of populations of two gum basins in a group is probably due to gene flow favored by low geographical distance between them.

### Implications for sustainable management and conservation of the species

The assessment of genetic variability among and within forest tree populations is a prerequisite for any restoration or renewal of these species (William and Hamrick, 1996). From results of this study, we can say that conservation of the species in Niger could be done easily through the method of *in situ* conservation. However, the species is threatened by human actions related to abuse of natural resources and degradation of its habitat. Effective and rigorous measures are needed to reverse current trends, because if nothing is done, it will inevitably lead to the disappearance of several populations of the species and these resources. The organization of genetic variability in the species revealed in this study is an important parameter to include in any future sustainable management strategy. Two aspects are of primary importance for the implementation of *in situ* conservation programs: local pedoclimatic conditions of origin and genetic diversity within the species. Indeed, the inclusion of these aspects would avoid the lack of seed germination, seedling mortality and/or long term loss. The effective management of genetic resources requires the identification of priority areas where conservation efforts can be better focused. Structuring by gum basin identified in our study helps to retain basin scale as an *in situ* conservation unit. Any time, if needed, seeds from western basin can be used to repopulate populations of central basin and vice versa, because there is a similarity (low differentiation) between the two gum basins.

### Conclusion

Knowledge of genetic diversity and its partitioning within the species is essential to build any strategy for management and sustainable conservation of natural resources. In this study, a relatively high genetic diversity was found in natural populations of *A. senegal*. The bulk of genetic variability in the species is within populations. The populations belonging to the same gum basin are similar, resulting from gene flows between them. The interpretation of individual's differentiation within populations assumed a Whalund effect. Further studies need to be conducted to confirm this factor or to explore other factors explaining the deficit in heterozygote's observed in more than half of the studied populations. These results could be used as part of the restoration

of degraded lands and rangelands through the plantation of *A. senegal* performed annually by the environmental services, development programs and projects and national, international non-governmental organizations (NGOs). It is recommended to use the seeds from the populations of the catchment area of the intervention zone to set up the nurseries.

### CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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