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Intra-population genetic diversity modeling of date palm (*Phoenix dactylifera* L.) population in Niger

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ABSTRACT

Genetic variability can provide important information on how populations behave internally and can also serve as a valuable guide for conservation. In the case of cultivated plants, the conservation of genetic variability contributes significantly to the stabilization of agricultural production. Then, this study aims to assess the intra-population genetic variability of the date palm in Niger. To achieve this objective, various indices of intra-population variability were estimated, a clonal reproduction test was conducted across different populations, from multilocus genotypes using 18 nuclear SSR (Simple Sequence Repeats) molecular markers. These analyses showed that, in general, the date palm population in Niger is genetically highly diverse, with the observed number of multilocus genotypes per subpopulation (MLG= 130), the expected number of multilocus genotypes (eMLG= 66.70), the Shannon-Wiener diversity index ($H = 4.84$), the probability that two randomly selected genotypes will differ ($\lambda = 0.992$), the equilibrium of genotype abundance distribution ($E_5 = 0.96$), the Nei index of genetic diversity or expected heterozygosity ($H_{exp} = 0.635$) and the random association index for each population ($\bar{r}_d = 0.039$, P-value= 0.000). Genetic variability is high and the population dynamics are stable in these populations. But, the sahelian subpopulation is less diverse and is converging toward homogeneity.

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INTRODUCTION

Understanding the patterns of genetic variability can provide important insights into how populations behave internally, as well as serve as guide for future collections. In the case of crop plants, the conservation of genetic variability can make a significant contribution to the stability of agricultural production. Indeed, it is generally considered that variation among ecotypes, varieties, or cultivars of a species allows for the selection of the form best suited to the specific production conditions of a given environment (Arnholdt-Schmitt, 2005). This variation also forms the basis of several genetic improvement programs aimed at developing cultivars tolerant to specific stressors such as drought, salinity, and climatic conditions (Arnholdt-Schmitt, 2005) or at developing more productive cultivars. Within a population, the variation in yield or profitability observed among individuals of the studied species is generally considered a factor that negatively impacts final yield. Nevertheless, this intra-population variation could also be adaptive in response to unpredictable environmental variations related to climate (Lambdon *et al.*, 2003) and human activities. There is therefore a divergence of views regarding the agronomic value of genetic variability. The high intra-population genetic variability observed in several species indicates a considerable increase in gene flow between populations (Hassel *et al.*, 2005). High genetic diversity within populations ensures the continuity and maintenance of genetic diversity at the metapopulation level (Nahla, 2017). In this context of environmental change, biodiversity and more specifically genetic diversity is more threatened because it is essential for ensuring the viability and evolutionary potential of natural populations. Indeed, sufficient genetic diversity in a natural population allows for greater adaptability to environmental changes, reduces the risk of inbreeding depression affecting fertility and survival, and thus lowers the risk of extinction for the species (Frankham, 2005). Genetic variability can be considered the driving force of natural selection. More broadly, it ensures that populations

maintain the ability to adapt to a changing environment and is a prerequisite for their survival over time and across space. It is therefore necessary to manage the genetic variability of populations, which requires conducting an assessment using a variety of indicators. The intra-population variability within a species regarding proactivity and quality allows for significant opportunities to create more adapted and profitable genotypes (Diagby *et al.*, 1999).

Nevertheless, research on the association between genetic variability and the phenotypic performance of date palm individuals remains very scarce. Yet any attempt to implement species improvement programs necessarily relies on a targeted inventory of the variability offered by the considered species. Then, this study aims to assess the level of variability within subpopulations and specifically : (i) Determine clonal reproduction within date palm populations and (ii) Evaluate indices characterizing intra-population genetic diversity.

MATERIALS AND METHODS

Study area

The plant material used consists of a collection of leaf samples from the date palm population in Niger. The samples were collected across the species' geographic range to consider the greatest possible genetic diversity, in the two main date palm production areas of Niger : the saharan zone and the sahelian zone (Fig. 1).

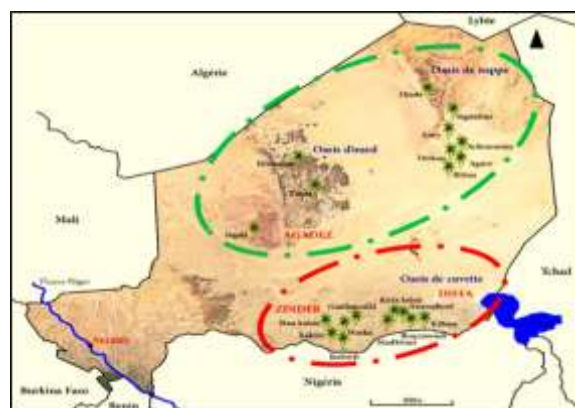


Fig. 1. Location of the study area: Sahara (band in green) and Sahel (band in red) (Ibrahim *et al.*, 2020)

Data collection

This study was conducted by shuffling the actual data. The collected data consists of 18 nuclear microsatellite markers (SSRs) (Simple Sequence Repeats) from diploids with independent alleles. These markers were used to genotype 140 date palm samples from two (02) main regions (Sahara and Sahel), five (04) subregions, and twenty (20) palm groves. To cover all of Niger's main date-palm areas, 60 producers were surveyed in the 20 palm groves representative of the two date-palm areas, with three producers per palm grove. These interviews made it possible to compile an inventory of date palm cultivars in the areas under consideration, as well as a list of the most favored and most profitable cultivars from the growers' perspective.

Data analysis

Index of intra-population genetic variability

Genetic diversity within the date palm population was analyzed in terms of intra-population variability. The aim of this approach was to characterize the date palm population and the genetic relatedness of individuals using a set of variability parameters. To describe intra-population genetic variability, six (06) genetic diversity indices were considered. These genetic diversity indices do not require the Hardy-Weinberg equilibrium assumption. They are estimated for each locus, and the average is taken across all loci. In terms of intra-population genetic variability, a direct comparison of allele frequencies per individual is not always easy to perform. However, there are parameters capable of synthesizing, through an overall value, the most important information such as : the number of observed (MLG) and expected (eMLG) multilocus genotypes, the Shannon-Wiener diversity index (H), the Simpson index lambda (λ), the index of genotypic dominance in the population (E.5), Nei's genetic diversity index (H_{exp}) or expected heterozygosity index, the standardized association index in a population ($\bar{r}_d$).

The indices presented above were estimated using permutations to test the statistical significance of the

results obtained. All calculations were repeated 100,000 times, and the results are presented as simulation histograms compared to the observed values, to assess in how many scenarios the same results are obtained and/or in the form of a P-value, which indicates the probability that the observed variations are due to random processes (P-value of 0.05 indicates a 95% chance that the observed variations are not due to chance).

The Shannon-Wiener diversity index (Shannon, 1948) was estimated to assess the abundance and distribution of genotypes, taking entropy into account.

$$H = - \sum_{i=1}^l P_i \log_b P_i$$

The Simpson's index (lambda) was estimated to determine the probability that two genotypes randomly selected from a population will be different. This index ranges from 0 (if all genotypes are identical) to 1 (if all genotypes are very different).

$$\lambda = 1 - \sum_{i=1}^l P_i^2$$

Where P_i is the frequency of the $i^{ème}$ allele at $l^{ème}$ locus.

The genotypic dominance index in a population (E.5) was estimated to determine whether the population is dominated by a single genotype or a group of genotypes. It ranges from 0 (if the population is dominated by a single genotype) to 1 (if all genotypes are different).

$$E.5 = \frac{\left(\frac{1}{\lambda}\right) - 1}{e^H - 1}$$

Where $1/\lambda$ the Stoddart and Taylor index (Stoddart and Taylor, 1988) and H the Shannon-Wiener diversity index (Shannon, 1948).

The Nei genetic diversity index (H_{exp}), also known as the expected heterozygosity index (Nei, 1978), was estimated to assess genetic diversity without bias ; it ranges from 0 (population homogeneity) to 1 (very high diversity).

$$H_{exp} = \sum_{i=1}^m h_i / m \text{ and } h_i = \left(\frac{n}{n-1}\right) 1 - \sum_{i=1}^k P_i^2$$

Where P_i the frequency of $i^{ème}$ allele at a given locus in the population, k the number of alleles at a given locus, n the number of alleles observed in a given population, h_i the value of h at $i^{ème}$ locus and m the total number of loci.

The standardized association index in a population ($\bar{r}_d$) to assess the level of clonal reproduction in a population ; if significant, the population is far from being clonal (few identical individuals in the population).

$$\bar{r}_d = \frac{V_o - V_E}{2 \times \sum_{l=1}^m \sum_{k=1}^m \sqrt{Var(d_j) \times Var(d_k)}}$$

Where $V_o = Var(D)$ the total observed variance, $V_E = \sum_{l=1}^m Var(d_j)$ the expected variance, m the total number of loci, k the ploidy, D the matrix of distances between individuals across all loci, d_j the distance

between individuals at a locus and d_k The distance between two individuals at a locus based on allelic forms and ploidy levels k and Var is synonymous with variance.

All estimates and analyses were performed using R software version 4.5.2 (R Development Core Team, 2025) via the *poppr* and *adegenet* packages.

RESULTS

Fig. 2 shows the characteristics of the 17 microsatellite markers used and the number of samples per area included in this study (Fig. 2a and 2d). The markers exhibit variable allele frequencies by locus (Fig. 2b), and the difference between expected and observed heterozygosity is positive for most markers (Fig. 2c).

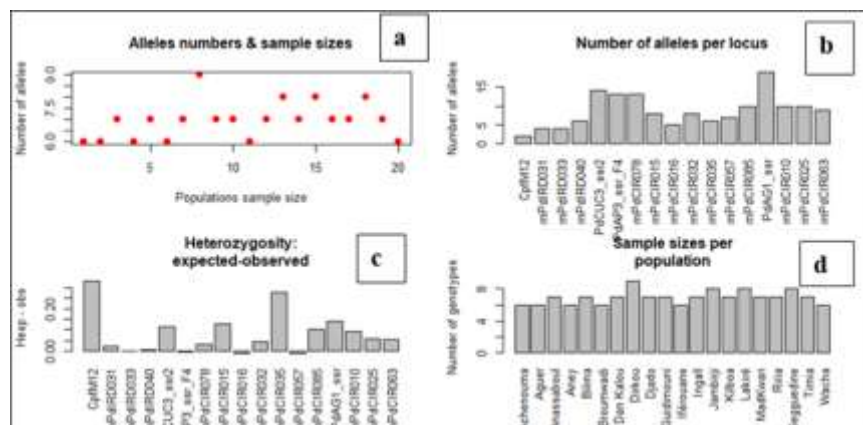


Fig. 2. Distribution of the number of alleles per locus (b), sample size by region (a and d), and the difference between expected and observed heterozygosity (c)

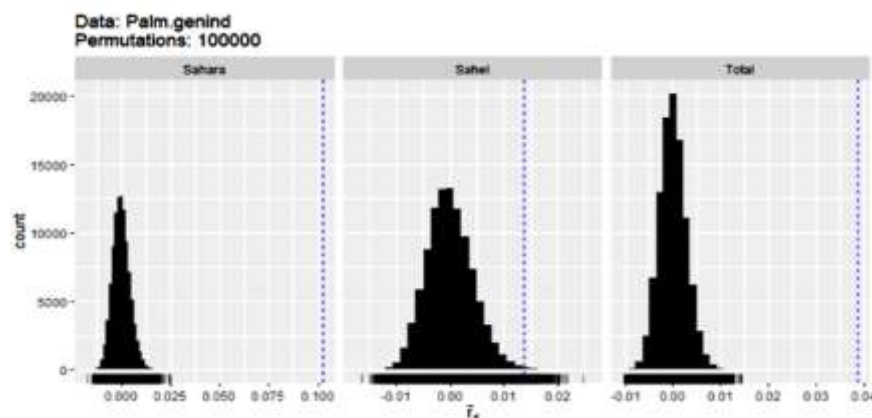
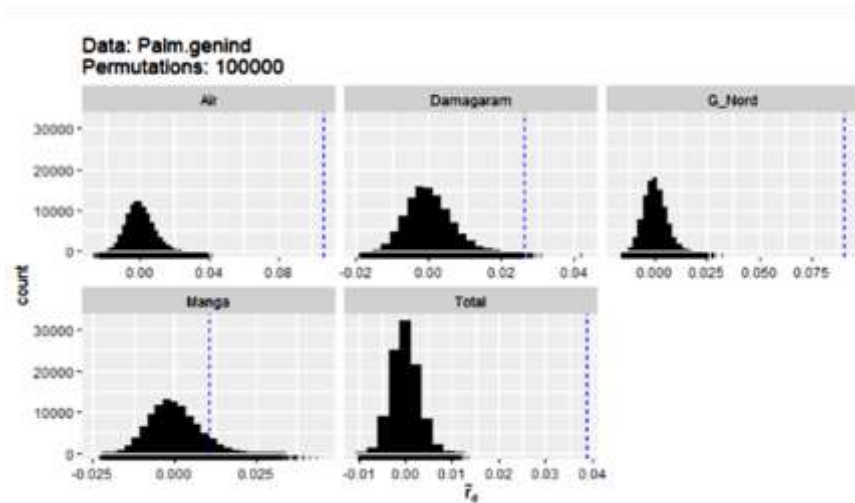


Fig. 3. Simulation histogram $\bar{r}_d$ For each of the two subpopulations (the Saharan and Sahelian populations) and for the overall population

Table 1. Intra-population genetic variability indexes

Population	MLG	eMLG	H	Lambda	E.5	Hexp	$\bar{r}_d$	Pr.($\bar{r}_d$)
Sahara	62.00	62.00	4.09	0.982	0.940	0.611	0.102	0.000
Sahel	68.00	67.10	4.21	0.985	0.984	0.623	0.014	0.002
Total	130.00	66.70	4.84	0.992	0.960	0.635	0.039	0.000

Legend: MLG= Number of multilocus genotypes observed per subpopulation, eMLG= Expected number of multilocus genotypes per subpopulation based on the smallest common sample size; H= Shannon-Wiener diversity index; Lambda= probability that two randomly selected genotypes are different; E.5= Equilibrium (genotype abundance distribution); Hexp = Nei's genetic diversity index (expected heterozygosity); $\bar{r}_d$ = Randomized association index for each population; Pr.($\bar{r}_d$)= P-value de $\bar{r}_d$, P-values in bold are significant.

**Fig. 4.** Simulation histogram $\bar{r}_d$ For each of the four subpopulations (Aïr, Damagaram, Grand Nord, and Manga).

The test for clonal reproduction in the date palm population in Niger generally shows that this population is significantly far from being clonal (Fig. 3, total population). This test in each of the two major subpopulations (Saharan and Sahelian zones) shows that the Saharan subpopulation is significantly far from being clonal (Fig. 3, Sahara), while the Sahelian subpopulation is not clonal but appears to be somewhat close to clonality (Fig. 3, Sahel). Thus, the intra-population genetic structure of the palm groves in the Sahelian zone is less diverse than that of the Saharan zone. The dynamics of genetic diversity are more stable in the Saharan zone. In the Saharan zone, the observed number of multilocus genotypes (MLG = 62) equals the expected number of multilocus genotypes based on the smallest common sample size (eMLG = 62), indicating a dynamic equilibrium of genetic diversity in this zone (Table 1). There is a difference between MLG (68) and eMLG (67.10) in the Sahelian zone ; thus, in this zone, the observed value is slightly higher than the expected

value, indicating that this population is on a slight increase in genetic diversity (Table 1). The Shannon-Wiener diversity index assesses the distribution and abundance of genotypes by considering entropy ; this index is $H = 4.09$ in the Saharan zone and $H = 4.21$ in the Sahelian zone (Table 1). This shows that the Sahelian population converges slightly more toward a higher level of genetic diversity but is more disrupted. The Simpson's index (lambda) indicates the probability that two genotypes chosen at random from a population will be different ; lambda = 0 if all genotypes are identical and equals 1 if all genotypes are different in the studied population (Table 1). Lambda = 0.982 in the Saharan population, lambda = 0.995 in the Sahelian population, and lambda = 0.992 in the total population. These values are very close to 1, implying that in all three cases, most genotypes are different (Table 1). Equilibrium of genotype abundance distribution (E.5) assesses genotype abundance ; if this index equals 1, the population exhibits genotype equilibrium, and if it

equals 0, the population is dominated by a single genotype. $E_5 = 0.94$ in the Saharan population, $E_5 = 0.984$ in the Sahel, and 0.96 in the total population, which generally indicates that the population is highly diverse.

The Nei index or expected heterozygosity (H_{exp}) is 0.611 in the Sahara, 0.623 in the Sahel, and 0.635 for the total population, indicating a good level of diversity within these populations (Table 1). The corrected random-associated index for each population ($\bar{r}_d$) detects clonal reproduction within the population. This index is 0.102, 0.014, and 0.039 in the Saharan, Sahelian, and total populations, respectively, with highly significant (P-values = 0.000) in each case (Table 1). This explains why this population is generally far from being clonally reproducing.

The clonal reproduction test conducted on the four date palm subpopulations under consideration

(Subregion) shows that the subpopulation from the Saharan zone is significantly far from being clonally reproducing (Fig. 4, Aïr and G-Nord), and those from the Sahelian zone (Damagaram and Manga) are not clonally reproducing but appear to be somewhat close to it, especially the one from Manga, where the theoretical distribution is somewhat close to the observed one (Fig. 4, Damagaram and Manga). The dynamics of genetic diversity are more stable in the regions of the Saharan zone. In the Aïr subregion, the observed number of multilocus genotypes (MLG = 19) equals the expected number of multilocus genotypes based on the smallest common sample size (eMLG = 19), indicating a dynamic equilibrium of genetic diversity in this region (Table 2); in the Far North (G-Nord) MLG (43) and eMLG (18.90), in Damagaram MLG (42) and eMLG (19.80), and in the Manga region MLG (26) and eMLG (19.50). In the regions (G-North, Damagaram, and Manga), the observed MLG are higher than expected, indicating an increase in genetic diversity within these populations (Table 2).

Table 2. Intra-population genetic variability index

Sub-Population	MLG	eMLG	H	Lambda	E_5	H_{exp}	$\bar{r}_d$	Pr. ($\bar{r}_d$)
Aïr	19	19.00	2.93	0.945	0.973	0.640	0.107	0.000
G_Nord	43	18.90	3.71	0.974	0.930	0.570	0.091	0.000
Damagaram	42	19.80	3.73	0.976	0.987	0.625	0.026	0.000
Manga	26	19.50	3.24	0.960	0.979	0.614	0.011	0.084

Legend : MLG = Number of multilocus genotypes observed per subpopulation; eMLG = Expected number of multilocus genotypes per subpopulation based on the smallest common sample size; H = Shannon-Wiener diversity index; Lambda = probability that two randomly selected genotypes are different; E_5 = Equilibrium (genotypic abundance distribution); H_{exp} = Nei's genetic diversity index (expected heterozygosity); $\bar{r}_d$ = Randomized association index for each population; Pr. ($\bar{r}_d$) = P-value de $\bar{r}_d$, P-values in bold are significant.

The Shannon-Wiener diversity index (H) is 2.93 in the Aïr region, 3.71 in the G-Nord region, 3.73 in the Damagaram region, and 3.24 in the Manga region (Table 2). This indicates that the population of the Aïr region is genetically less diverse than those of the other three regions, which exhibit greater genetic diversity. The Simpson's lambda index is 0.945 in the Aïr region, 0.974 in G-Nord, 0.976 in Damagaram, and 0.96 in Manga (Table 2). These values are very close to 1, implying that genotypes differ across the four regions. The evenness of genotype abundance (E_5) is very close to 1 in the populations of all four

regions, indicating that the genetic structure within these regions is not dominated by a limited number of genotypes. The Nei diversity index (H_{exp}) is 0.64 in the Aïr region, 0.57 in G-Nord, 0.625, and 0.614, indicating that expected heterozygosity is moderately high and the level of diversity within these populations is moderate (Table 2). The corrected random-associated index ($\bar{r}_d$) is 0.107, 0.091, and 0.026 in the Aïr, G-Nord, and Damagaram regions, respectively, with highly significant (P-values = 0.000) in each case (Table 2). This explains why these populations do not reproduce clonally. However, $\bar{r}_d$ is

0.011 in the Manga population, with a non-significant (P-value = 0.084) (Table 2). This explains why the population is converging toward a clonal reproductive regime.

The test of clonal reproduction in various palm groves in Niger shows that the following palm groves Bilma, Kilboa, Lakiré but, those of Timia and Jambirji are not far from being clonal within themselves (Fig. 5). For these palm groves, the theoretical distribution of the

random association index is close to the observed distribution (Fig. 5). Thus, the intra-population genetic structure of these palm groves is less diverse, indicating genetic instability. The observed number of multilocus genotypes (MLG) equals the expected number of multilocus genotypes (eMLG) in all 20 palm groves considered except in the palm groves of Bilma, Lakiré, Kilboa, Jambirji, and Timia (MLG is greater than eMLG); this indicates an imbalance dynamic in genetic diversity within these palm groves (Table 3).

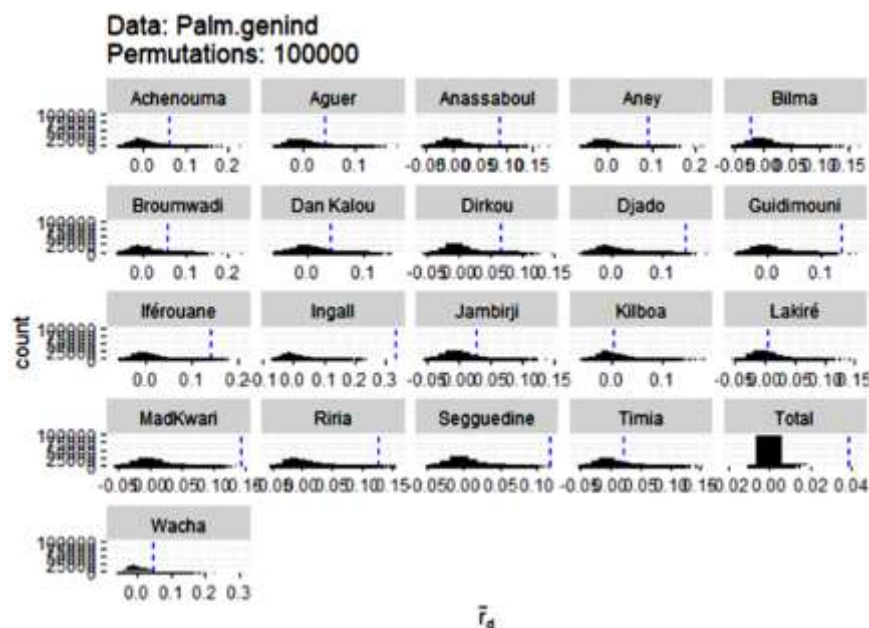


Fig. 5. Simulation histogram r_d For each of the 20 palm groves

Table 3. Intra-population genetic variability index

Population unit	MLG	eMLG	Lambda	E.5	Hexp	$\bar{r}_d$	Pr. ($\bar{r}_d$)
Achenouma	6.00	6.00	0.833	1.000	0.584	0.059	0.031
Aguer	6.00	6.00	0.833	1.000	0.595	0.041	0.075
Dirkou	9.00	6.00	0.889	1.000	0.511	0.067	0.005
Segguédine	8.00	6.00	0.875	1.000	0.604	0.118	0.000
Djado	7.00	6.00	0.857	1.000	0.580	0.145	0.000
Timia	7.00	6.00	0.857	1.000	0.626	0.020	0.182
Iférouane	6.00	6.00	0.833	1.000	0.627	0.141	0.000
Ingall	6.00	5.29	0.816	0.937	0.490	0.330	0.000
Aney	6.00	6.00	0.833	1.000	0.575	0.093	0.004
Bilma	7.00	6.00	0.857	1.000	0.530	-0.021	0.853
Anassaboul	7.00	6.00	0.857	1.000	0.603	0.086	0.003
Broumwadi	6.00	6.00	0.833	1.000	0.628	0.057	0.035
Dan Kalou	7.00	6.00	0.857	1.000	0.557	0.041	0.058
Guidimouni	6.00	5.29	0.816	0.937	0.577	0.138	0.000
Jambirji	8.00	6.00	0.875	1.000	0.648	0.027	0.100
Kilboa	7.00	6.00	0.857	1.000	0.573	0.002	0.420
Lakiré	8.00	6.00	0.875	1.000	0.568	0.004	0.389
MadKwari	6.00	5.29	0.816	0.937	0.569	0.143	0.000
Riria	7.00	6.00	0.857	1.000	0.619	0.126	0.000
Wacha	6.00	6.00	0.833	1.000	0.624	0.046	0.073

The Simpson's index (λ) is approximately 0.8 in each of the palm groves. These values are very close to 1, which implies that in these palm groves, there is at least 0.8 probability that two randomly selected genotypes will be different (Table 3). The equilibrium of genotypic abundance (E_5) is approximately equal to 1 in these subpopulations (Table 3), which generally means that the palm groves are not dominated by a single group of genotypes. The Nei diversity index (H_{exp}) or expected heterozygosity ranges from 0.55 to 0.64 across the different palm groves (Table 3), indicating a moderate level of genetic diversity within these palm groves. The randomized-associated index, corrected for each population ($\bar{r}_d$) yields P-values that are not significant for the following palm groves: Bilma (0.853), Jambirji (0.100), Kilboa (0.420), Lakiré (0.389), and Timia (0.182), with highly significant (P-values = 0.000) in other palm groves (Table 3). This explains why these palm groves are converging toward a clonal reproductive regime.

DISCUSSION

Knowledge of cultivated genetic resources in Sahelian countries where areas are vulnerable and exposed to precarious environmental conditions is of great importance for the development and conservation of agricultural potential. The various indices of intra-population genetic variability used in this study allow to assess the level of intra-population genetic variability from the global population to the palm grove level, including subpopulations. These indices revealed genetic variability ranging from 0.490 to 0.635 from the palm grove level to the total population, implying that the subpopulations are quite diverse within themselves. According to the test for convergence toward clonal reproduction, the subpopulations do not reproduce clonally; therefore, the reproductive system is based on sexual crossing through gamete production via meiosis, and consequently, each individual from population, can pass its alleles to the next generation. However, individuals in certain palm groves such as (Bilma, Timia, Jambirji, Kilboa, Lakiré, and to a lesser extent Wacha and Aguer) appear close to a clonal system;

this explains why the dynamics of intra-population genetic diversity in these palm groves are shifting toward an imbalance characterized by a heterozygote deficit. Clonally reproducing populations multiply by mitosis, whereby any mechanism of genotypic change arises from mutation. Asexual reproduction produces exact copies of the individuals; therefore, it cannot bring about change on its own. However, if populations are of finite size, they may undergo genetic drift (De-Meeûs *et al.*, 2007), hence the importance of slowing clonal reproduction in palm groves where it is high; furthermore, the mode of reproduction in a natural population is a biological property that allows for the prediction of 30 to 40% level of intra-population genetic diversity (Hamrick *et al.*, 1992).

CONCLUSION

The results represent only a contribution to the characterization of date palm populations in Niger. They also provide valuable insights for the implementation of a development program for this species in the country. Furthermore, this work could serve as basis for genetic selection programs for date palm cultivars in Niger. This population is not affected by clonal reproduction. The genetic resource conservation policy for this species should focus on *in situ* conservation, as the intra-population genetic diversity of these resources is not threatened.

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