Research Article

Structure of Needle Highlights Ecological Adaptability and Microevolution of Natural Populations of *Cedrus atlantica* in Morocco

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Received 13 April 2022; Accepted 7 June 2022; Published 29 June 2022

Academic Editor: Anna Žrobek-Sokolnik

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The study of morphological and anatomical characteristics of leaves is important for assessing the geographical variation of species. The ecological adaptability of forty individuals from four populations of *Cedrus atlantica* were studied, based on analysis of morphological and anatomical traits. The results of the Spearman nonparametric coefficient of correlation showed that the number of stomatal lines (NLS) and the length of the needle (NL) are negatively correlated to altitude and positively to latitude and precipitation sums, while the width of the needle (NW), the thickness of the cuticle (CT), and the number of needles per rosette (NN/R) were negatively related to temperature. In addition, the sum of precipitation is negatively correlated with NW. The first two principal components account for 58.18% of the variation. According to Tukey’s test and Kruskal–Wallis test, all populations had at least three characters separating them at a statistically significant variation. Moreover, the hierarchical classification led us to the individualization of three main groups. All these results show an adaptation of the structure of the needles of *C. atlantica* from Morocco to the geographical position and the climatic conditions of the populations.

1. Introduction

Atlas cedar (*Cedrus atlantica* Manetti) is a relict and endemic endangered species in the mountains of North Africa, whose distribution range has undergone a dramatic reduction over recent decades, that is attracting increasing international interest in its use in reforestation of degraded lands due to its large ecological range [1–4]. It occupies surfaces of unequal importance and spontaneously forms seven geographical blocks in North Africa, three of which are located in the Moroccan mountains: Rif, Middle Atlas, and High Atlas [5, 6]. *C. atlantica* is the most important timber resource in Morocco, occupying a surface area of 132,000 ha and representing 2.3% of the national forest [7]. In the central Middle Atlas, two groups of the geological formations are distinguished by their morphological and phytocological structure: the group of the causee of the tabular Middle Atlas in the north mainly made up of dolomitic limestones from the Lower Jurassic, which surmount the Triassic series formed by red argillites and basalts [8–10]; and the group of the Middle Atlas pleated to the south and differs from the subtabular causee by the presence of wrinkles which form reliefs oriented in the general direction of the chain. These anticlinal wrinkles frame synclinal depressions, which continued to function during the Middle Jurassic as fairly thick marly and marnocalcary depocenters [11–13].

Needles are the most vigorous assimilation organs, especially in pine, because they have important effects on physiological and ecological adaptabilities [14, 15]. Although most of the morphological and anatomical traits of needles are more or less specific for the species, the genetic investigations have demonstrated intraspecies genetic variations [16, 17]. Adaptation of needle characteristics to the environment was also described [19–23], as well as
microevolution within species and needle evolution by comparing morphology and anatomy [24–27]. Nagy et al. [28] proposed the theory of the altitude-related biological phenomenon, which has had negative effects on plant communities reducing the number of plant species [29], the plant productivity [30], the organ size trends [31], the physiology and morphology of plants [32], the gene ecology [33] and the characteristics of the history of life [34]. In addition, Friend and Woodward [35] and Nagy [28] showed that the physical factors such as tree growth, altitude, decrease of air temperature with altitude, influence of exposition, solar radiation, access to the light, atmospheric pressure, increased precipitation, and wind speed affect plant development. The only studies published over the past decade on the taxonomic and geographical differentiation of conifers show that morphological and anatomical characteristics of needles are important in the recognition of phylogenetic relationships and geographic pattern of variation in Pinaceae [14, 35–39]. In Morocco and in Algeria, some morphological traits have been used as criteria for differentiating species and trees in nurseries and natural populations [40, 41]. These findings revealed that the populations of the High Atlas and the Rif are easier to characterize, while those of the Middle Atlas are morphologically more complex and require more detailed investigations on the morphology of needles. Despite the importance of the Moroccan forest genetic resources, few studies have focused on the variation of needle traits of Cedrus in nature [14], and the little information exists on the morphological traits and coniferous species [40–43].

The main objectives of the present study were to reveal the variations in needle morphological and anatomical traits among populations, illustrate the variations in needle traits among individuals within populations, and be interested in finding the link between the variation of traits with geography and environmental conditions that will be useful to understand the ecological adaptability and microevolution of C. atlantica.

2. Materials and Methods

2.1. Sampling and Measurements. The material used in this study was collected in 2015 in four geographical populations of C. atlantica: Moudemame (M), Aït Ouèlfa (O), Aït Ayach (A) [23], and Tazekka (T), respectively, located in the central Middle Atlas and in the High Atlas and in eastern parts of the Middle Atlas (Table 1). The pure and dense population of M is formed on a basalt–calcareous substratum and characterizes with a fresh and stable wet bioclimate. The population of T represents one of the largest reserves of Atlas cedar and is a protected area for more than fifty years. This cedar forest covers area more than 850 hectares on a noncalcareous, primary shales substratum in a cold, perhumid bioclimate. The Aït Ouèlfa (O) forest covers an area of 5 650 ha located on the southern edge of the Middle Atlas about 40 km northwest of Midelt on a calcareous substratum [44]. The general climate of O is characterized by a low rainfall and a marked drought for a long part of the year [45]. The population of A is less than 7 km from Cirque de Jaaffar and is characterized by the presence of C. atlantica and Quercus ilex L. on a calcareous substratum with a semiarid continental climate. Ten adult and carrying cones trees were randomly sampled from each population, at distance of at least 30 m each other. Ten mature brachyblasts undamaged, fully developed with needles with no visible insect and/or fungi damage, from well-illuminated, north-facing parts of the tree crown about 2-3 m above ground level were collected from each tree. After collection, the lengths of the two-year-old needles were measured, and the plant material was then preserved in 70% ethanol and stored at 20°C until analysis [46, 47]. Semidurable preparations from the central part of ten needles representing the ten brachyblasts from each individual in each population were made by a cross-section. The anatomical preparations were performed freehand on the central part of each needle, and the crosssections were treated with 5% NaOH for 4 h at 70°C, according to Arnott [48] and Brady et al. [49] cited by Ruzin [50]. In this study, six morphological and anatomical characters of needles were studied. The length of the needle (NL) was manually determined on fresh material with an accuracy of 0.25 mm. The number of the needle/brachyblast (NN/R) was counted for each sample (Figure 1). The number of facets (NF) was determined from the cross-sections in the central part of the needle. The number of stomatal lines (NLS) was determined for ten cross-sections of the same needle and keeping the highest number among the ten values obtained (Figure 1). Measurements of NF and NLS were taken under the optical microscope (Optika DM-15), and the preparations were then photographed with the integrated camera. Measurement of needle width (NW) and cuticle thickness (CT) (Figure 1) was determined with an accuracy of 1 μm using the best image of a section for each needle, using the software Opnias ver.1.0. The climatic data in each geographic location of the population (Table 1) were obtained from https://www.climate-data.org.

2.2. Data Analysis. The average values and coefficients of variation (CV) for each trait within populations were determined. Before starting the multivariate analysis, we used the Kolmogorov–Smirnov test to check the normality of the data and the Levene test to assess the homogeneity of the variances of the data. In addition, mean values were compared using the Tukey test at a level of significance of $P \leq 0.01$ and $P \leq 0.05$ for characters with a normal and Kruskal–Wallis test at $P \leq 0.05$ for those of biased distribution (NW and NF). The Pearson correlation at the 0.01 and 0.05 thresholds between the pairs of characters studied was performed on the raw values of all the samples. The correlation between populations for each morphological trait and environmental factors such as altitude, latitude, longitude, temperature, and precipitation was studied using Spearman’s nonparametric correlation coefficient. This correlation coefficient is adequate for samples of small size and nonnormal distributions. Principal component analysis (PCA) was performed on the average of each tree. Finally, the agglomeration of the populations on the closest Euclidean distances according to Ward’s method was carried...
out using all the characters to check out the affinities between *C. atlantica* populations. All statistical analyzes were performed using IBM SPSS software version 20.0.

### 3. Results

#### 3.1. Variation within Population

The average values and variation coefficients (CV) of six needle traits in each population are given in Table 2. To estimate the proportion of within-population variation, we calculated the CV in the population according to means and standard deviations (SD) for each character (Table 2). Our results showed that the highest values of the coefficient of variation (CV >20%) in all populations were detected for cuticle thickness (CT) and the number of stomatal lines (NLS). The values of the coefficient of variation below 20% were recorded for needle length (NL) and needle width (NW) in most populations (Table 2). The remaining characters were as follows: the number of facets (NF) and the number of needles per brachyblast (NN/R) show a considerable variation from 15.26 to 32.16% (Table 2). The description parameter of character distribution (curtosis) shows a similarity between population *T* and population *A* (Table 2). These two populations showed negative flattening values, so their characters are less clustered around the mean, with the exception of NL (needle length) of the population of *T* and NL and NN/R (length and number the needles per rosette) of the population of *A* (Table 2). While for the other two populations (*M* and *O*), the distribution character (curtosis) showed negative values for three characters at *M* and four characters at *O* and positive values for the rest of characters. The values of these characters are therefore less grouped around the mean.

#### 3.2. Variation among Populations

Tukey’s test for characters with a normal and Kruskal–Wallis test for those of biased distribution (NW and NF) revealed that among all compared populations, at least three characters separate them at

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**Table 1:** Location and geographic characteristics of studied populations of *Cedrus atlantica* in Morocco.

| Populations   | Region            | Latitude    | Longitude   | Altitude (m) | *T* (°C) | *T* max (°C) | *T* min (°C) | *P* (mm) |
|---------------|------------------|-------------|-------------|--------------|----------|--------------|--------------|---------|
| Moudemame     | Middle Atlas central | 33°25’N    | 5°11’W     | 1780         | 14.2     | 24.6         | 6.5          | 779     |
| Tazekka       | Middle Atlas eastern | 34°08’N    | 4°10’W     | 1750         | 12.1     | 22.0         | 3.9          | 456     |
| Aît Oufella   | Middle Atlas central | 32°58’N    | 5°03’W     | 1982         | 14.7     | 25.2         | 6.0          | 263     |
| Aît Ayach     | High Atlas        | 32°31’N    | 4°59’W     | 1972         | 12.0     | 23.1         | 3.1          | 459     |

*T*, annual mean temperature; *T* max and *T* min stand for mean maximum and mean minimum temperature; *P*, annual mean precipitation.

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**Figure 1:** Measured characters of *C. atlantica* needle. (a) The image indicating needles of brachyblast, (b) The image indicating stoma, facet, and needle width. (c) The image indicating cuticle thickness.
Table 2: Descriptive statistics of six quantitative traits of the studied populations of *C. atlantica* in Morocco.

| Populations | Traits                        | Mean ± SD | Min   | Max   | CV  | Skewness | Curtosis |
|-------------|-------------------------------|-----------|-------|-------|-----|----------|----------|
| *M*         | Needle length (mm): NL        | 16.04 ± 1.02 | 14.89 | 17.56 | 10.35 | 0.60  | −1.258   |
|             | Needle width (μm): NW         | 907.21 ± 35.19 | 849.58 | 961.69 | 10.87 | −0.03 | −0.14    |
|             | Cuticle thickness (μm): CT    | 8.93 ± 1.08   | 7.26  | 10.82 | 23.89 | 0.22  | 0.67     |
|             | Number of stomatal lines: NLS | 6.46 ± 1.53   | 3.56  | 8.60  | 20.67 | −0.85 | 1.15     |
|             | Number of facets: NF          | 4.12 ± 0.35   | 3.56  | 4.60  | 30.15 | −0.44 | −0.84    |
|             | Number of needles per brachyblast: NN/R | 62.23 ± 8.75 | 46.56 | 73.20 | 18.79 | −0.64 | 0.04     |
| *A*         | Needle length (mm): NL        | 11.35 ± 1.94  | 8.81  | 15.50 | 19.42 | 1.47  | 4.02     |
|             | Needle width (μm): NW         | 1408.91 ± 101.42 | 1280.65 | 1545.85 | 12.82 | 0.231 | −1.58    |
|             | Cuticle thickness (μm): CT    | 13.62 ± 2.69  | 9.57  | 17.87 | 28.83 | 0.070 | −0.35    |
|             | Number of stomatal lines: NLS | 5.71 ± 1.31  | 4.43  | 8.20  | 18.24 | 0.88  | −0.26    |
|             | Number of facets: NF          | 4.19 ± 0.32   | 3.71  | 4.60  | 33.73 | −0.26 | −1.75    |
|             | Number of needles per brachyblast: NN/R | 71.03 ± 13.13 | 39.25 | 84.71 | 21.52 | −2.01 | 5.04     |
| *T*         | Needle length (mm): NL        | 13.90 ± 1.35  | 11.90 | 16.60 | 13.16 | 0.51  | 0.51     |
|             | Needle width (μm): NW         | 1411.10 ± 146.90 | 1227.47 | 1571.79 | 14.45 | −0.16 | −2.07    |
|             | Cuticle thickness (μm): CT    | 15.44 ± 2.03  | 12.16 | 18.74 | 20.51 | 0.22  | −0.44    |
|             | Number of stomatal lines: NLS | 8.23 ± 1.37   | 6.50  | 10.33 | 19.31 | 0.36  | −1.45    |
|             | Number of facets: NF          | 4.22 ± 0.33   | 3.78  | 4.83  | 23.49 | 0.56  | −0.01    |
|             | Number of needles per brachyblast: NN/R | 68.90 ± 7.14  | 59.10 | 81.20 | 15.26 | 0.38  | −0.63    |
| *O*         | Needle length (mm): NL        | 10.45 ± 1.94  | 8.00  | 12.13 | 17.43 | −0.77 | −1.90    |
|             | Needle width (μm): NW         | 1133.47 ± 243.91 | 812.00 | 1462.94 | 23.51 | −0.16 | −1.08    |
|             | Cuticle thickness (μm): CT    | 9.59 ± 2.33   | 7.32  | 14.00 | 32.48 | 1.71  | 3.45     |
|             | Number of stomatal lines: NLS | 5.90 ± 1.13   | 5.00  | 7.63  | 32.16 | 0.99  | −1.12    |
|             | Number of facets: NF          | 3.98 ± 0.109  | 3.78  | 4.11  | 20.62 | −1.44 | 3.60     |
|             | Number of needles per brachyblast: NN/R | 60.98 ± 16.07 | 42.00 | 85.78 | 28.62 | 0.68  | −0.51    |

*M, Moudemame; Tazekka; O, Aıt Oufella; A, Aıt Ayach; T, annual mean temperature; T<sub>max</sub> and T<sub>min</sub> stand for mean maximum and mean minimum temperature; P, annual mean precipitation; mean, average values; SD, standard deviation; min, minimum; max, maximum; CV, variation coefficient.*

3.3. Geographical Structure of Morphological and Anatomical Traits Variation. Interactions between traits were analyzed using the Pearson correlation coefficient matrix, which shows that NW is positively correlated with CT (Table 4). That is to say that the cuticle thickness increases with the needle width. The correlation between morphological and anatomical characters, with altitude, latitude, longitude, temperature, and precipitation, is given in Table 5. The NL and NLS are negatively related to altitude and positively related to latitude and precipitation at a 99% threshold, i.e., the longest needles with a high number of stomatal lines were found at low altitudes. The thickest needles with large cuticles were found in the low-longitude populations. The NW, CT, and NN/R correlate negatively with temperature, that is, populations with thick needles with high numbers per rosette are at low temperatures. While the precipitation is positively correlated with NL and negatively with NW, that is, populations located in the areas with significant rainfall have the needles long and thin (Table 5).

Principal component analysis (PCA) was performed on the average values of each tree and environmental factors. This analysis revealed four principal components with eigenvalues >1 (Table 6).

Table 3: Differences between analyzed characters of needles of populations in Tukey’s test and Kruskal–Wallis test.

| Traits                        | M/A | M/T | M/O | T/A | T/O | A/O |
|-------------------------------|-----|-----|-----|-----|-----|-----|
| NL                            | *** | *** | *** | *** | *** | *** |
| NW                            | *** | *** | *** | *** | *** | *** |
| CT                            | *** | *** | *** | *** | *** | *** |
| NF                            | *** | *** | *** | *** | *** | *** |
| NLS                           | *** | *** | *** | *** | *** | *** |
| NN/R                          | *** | *** | *** | *** | *** | *** |

*M, Moudemame; T, Tazekka; O, Aıt Oufella; A, Aıt Ayach; NL, needle length; NW, needle width; CT, cuticle thickness; NF, number of facets; NLS, number of stomatal lines; NN/R, number of needles per brachyblast. *P ≤ 0.01; **P ≤ 0.05.*

The two first canonical variables components account for 58.18% of the total variation and demonstrated three dispersed clouds of single trees, representing four compared populations (Figure 2, Table 6). The first component C<sub>1</sub> was determined primarily by the traits: NW, CT, and factors: longitude and temperature, while component C<sub>2</sub> was determined by altitude, latitude, and precipitation (Figure 2). This dispersion shows that populations: Moudemame and Tazekka are dispersed without overlap with the Aıt Oufella and the Aıt Ayach populations (Figure 2). The individuals of the latter two populations are mostly intermingled with each other.

Finally, all morphological and anatomical traits were used in a hierarchical group analysis (Figure 3). Three groups of populations could be distinguished in the dendrograms. The first group is composed of the populations of
and which show very close relationship between them. The second is composed of the populations $T$, $A$ and $O$ and shows rather close relationship. The third group is formed by populations of $M$, which is the most distinct of all the others (Figure 3).

4. Discussion

4.1. Environmental Effects on the Traits of the Needle of Cedrus atlantica Populations. Studies of leaf variation based on geographic locations and environmental changes are common in trees, especially those with a long life span [52]. In this study, we found a high level of morphological and anatomical variabilities of needles among and within the Moroccan populations of Cedrus atlantica. The results of the correlation of the Spearman analysis show that the majority of cedar needle traits correlated with environmental factors. The NL character was positively correlated with latitude and longitude and negatively with altitude. This relation of NL with the altitude is in agreement with those obtained at P. roxburghii [27] and P. pinaster [52]. While in these last two species, NL does not depend on latitude as was found in Pinus yunnanensis [17]. On the other hand, it was found that NL in Pinus yunnanensis [17] and Pinus uncinata [53] is negatively related to rainfalls; whereas in our study, this trait is positively related to this factor, suggesting that this change of needle is species-related. Moreover, it well known that cell elongation induced by auxin needs more water and carbohydrate; this process is more water consuming in cedar, which was reported more sensitive to hydric deficit, adapting its shape to water availability [40, 54, 55]. In Pinus mugo and Pinus yunnanensis, NL was found to depend on the

| Components | Total | % of variance | Cumulative% | Extraction sums of squared loadings | Total | % of variance | Cumulative% | Rotation sums of squared loadings | Total | % of variance | Cumulative% |
|------------|-------|---------------|-------------|------------------------------------|-------|---------------|-------------|-----------------------------------|-------|---------------|-------------|
| 1          | 3.648 | 33.166        | 33.166      | 3.648                              | 33.166| 33.166        | 3.604       | 32.762                            | 32.762|               |             |
| 2          | 2.752 | 25.016        | 58.182      | 2.752                              | 25.016| 58.182        | 2.796       | 58.182                            | 25.421|               |             |
| 3          | 1.633 | 14.847        | 73.029      |                                    |       |               |            |                                   |       |               |             |
| 4          | 1.144 | 10.400        | 83.429      |                                    |       |               |            |                                   |       |               |             |

Table 6: Total variance explained.
temperature [17, 56]. This ascertainment is in agreement with our results where NL was found to be significantly correlated with the temperature. This different response of NL to environmental conditions, compared to other morphological conifer studies, was supported by intraspecific variation of NL between genetically different C. atlantica populations in the Middle Atlas of Morocco [22].

It has been reported that the stomatal parameters are specific to a particular species but are affected by multiple ecological factors [57, 58]. In our study, the NLS trait varies positively with latitude but negatively with altitude and longitude in cedar populations. On the convex side of the needles of Pinus yunnanensis, NLS is positively correlated with the longitude [17], and at Pinus roxburghii, Tiwari et al. [27] found that stomatal density, stomatal index, and length of guard cells are positively correlated with altitude. In Pinus sylvestris, the number of stomata on needles depends on geographical latitude [59, 60]. Otherwise, the NLS character found in this study varies negatively with temperature and positively with precipitation at a significant threshold, whereas it increases with increasing temperature at Pinus sylvestris [61] and varies negatively with rainfall in Pinus pinaster [52]. Huang et al. [17] found that the average density of stomata per needle in Pinus yunnanensis is positively related to precipitation and that the number of stomata on the needles also depends on rainfall in Pinus sylvestris and Pinus uncinata [53, 62].

In this study, the NW trait was negatively correlated with longitude, temperature, and precipitation, but no correlation was observed with altitude and latitude. In Pinus pinaster, NW is negatively related to altitude and positively to latitude, but no significant correlation was reported between NW, longitude, and precipitation [52]. In Asteraceae, Yuliani et al. [63] showed that the leaves of species belonging to this family and located at a low altitude are the largest. While in Pinus yunnanensis, this trait does not correlate with any environmental factors [17]. Our study showed that NF of cedar needles is independent of all environmental factors, whereas NN/R is negatively related to temperature and CT to temperature and longitude. In provenances of the Moroccan High Atlas, NN/R was found maximum but reached the lowest values in the eastern part of the area in Cedrus libani and Cedrus deodora in Algeria [40]. In several studies, NN/R is not taken into account [14, 64–68] due to the leaf life span intraspecific variation which is largely explained as an environmentally determined phenotypic acclimation [69, 70]. These data are in accordance with the negative correlation found here between NN/R and temperature. However, even if the intraspecific variation in leaf life span is much less than the interspecific variation [71], it may be taken into account for such studies. Moreover, we recently found NN/R discriminates between genetically different populations in the Middle Atlas Morocco [22]. The study of the needles of the cedar populations by Jasinska et al. [14] shows that CT does not discriminate between cedar species, while distinguishing C. atlantica populations from the Moroccan Middle Atlas, with a CV from 12.29 to 21.64% in the Rif and the Middle Atlas and a CV of 14.65 to 28.66% for the Cedrus libani. These data are in agreement with our results from which we suggest a classification of the cedar habitats according to CT values: it is low in the Rif region (12.29%) and much more elevated in the High Atlas region (32.48%). Similarly, it has been reported that due to the heterogeneity and independence of habitats, directional selection may play a major role during the differentiation process in individual habitats, as was detected in the case of Abies pinsapo–A. maroccana [72].

Several studies have shown differences between the traits of cedar needles in Morocco [14, 22, 23, 41, 42, 66], but for the first time, our results showed highly significant intraspecific variations in needle traits between and within populations that covered a wide range of latitude and longitude from 32°31′N 4°10′W to 34°08′N 5°11′W, displaying remarkable differences, which depend on the climatic conditions. The largest differences among populations were observed in the studied needles of the T and A populations. These phenotypic variations presented by the cedar tree in comparison with those found in the bibliography in various coniferous species are in agreement with previous studies [14, 27, 52, 17, 73–75] and highlight the most determinant needle traits for acclimation to environmental factors in C. atlantica natural populations.

4.2. Environmental Effects on the Evolution of Cedrus atlantica Populations. Environmental factors in areas of origin had significant impacts on plant growth [28, 77]. Schlichting [78] found that phenotype changes were consistent with changes in environmental gradients, particularly in high altitude habitats where the climate was more complex and dynamic [28]. In this study, the analysis of the Euclidean distance shows that the populations A of the High Atlas and T of the Middle Eastern Atlas have been gathered in the same group, although they are very distant geographically. Whereas for the other two populations, the grouping is in line with their geographical positions.

5. Conclusion

The results of this study showed the plastic adaptation of C. atlantica needle shape to diverse environments.
They show for the first time that the needle length with number of stomatal lines and needle width with cuticle thickness are negatively sensitive to altitude and longitude, respectively. The populations at low temperatures are characterized by thick needles with a high number of rosettes. While, populations placed in areas with high rainfall have long, thin needles. All these results require that the geographical position and the climatic conditions of the populations change the structure of the needles of C. atlantica from Morocco. However, more in-depth studies (including several species and leading to different regions) are needed to determine the other anatomical, biochemical, and genetic parameters controlling tree structure for efficient cedar forest conservation.

Data Availability

The data used to support this study are included within the article.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

The authors acknowledge that this study was made in the Research Unit “Environment Plant Interaction” of the Laboratory of Biotechnology, Environment, Food, and Health (LBEFH), based in Faculty of Science Dhar El Mehraz, Sidi Mohammed Ben Abdellah University, and funded by Sidi Mohammed Ben Abdellah University (Morocco).

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