PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol 11(2): 149–160
https://doi.org/10.14719/pst.2896

HORIZON
e-Publishing Group
HePG

RESEARCH ARTICLE

Genetic diversity in Algerian diploid and tetraploid oats (*Avena* L.) based on their morphological characters and eco-geographical parameters

Yacer Boudersa[1], Djamila Benouchenne[1,2]*, Ines Bellil[1] & Douadi Khelifi [1,2]

[1]Laboratory of Genetic, Biochemistry and Plants Biotechnology, Faculty of Natural and Life Sciences, University of Mentouri Brothers, Constantine 1, 25000 Constantine, Algeria
[2]Higher National School of Biotechnology Taoufik KHAZNADAR, Nouveau Pôle Universitaire Ali Mendjili, BP. E66, Constantine, 25100, Algeria

*Email: d.benouchenne@ensbiotech.edu.dz

OPEN ACCESS

ARTICLE HISTORY
Received: 26 August 2023
Accepted: 28 December 2023

Available online
Version 1.0 : 29 March 2024
Version 2.0 : 01 April 2024

Check for updates

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (https://creativecommons.org/licenses/by/4.0/)

CITE THIS ARTICLE

Boudersa Y, Benouchenne D, Bellil I, Khelifi D. Genetic diversity in Algerian diploid and tetraploid oats (*Avena* L.) based on their morphological characters and eco-geographical parameters. Plant Science Today. 2024; 11(2): 149–160. https://doi.org/10.14719/pst.2896

Abstract

This study was conducted to determine the different ploidy levels of various species of the genus *Avena*, located in northern Algeria, using different morphological and eco-geographical parameters. The specific objectives of the investigation were to estimate phenotypic diversity for different morphological descriptors. One hundred and thirty-eight populations of the genus *Avena* were collected from 98 different sites in northern Algeria. Harvest sites were determined based on latitude, longitude, and altitude. The pluviothermic Emberger quotient (Q2) was identified by combining three climatic factors (P = annual rainfall, M = average of the maximum temperature of the warmest month, and m = average of the minimum temperature of the coldest month). The interpretation of this quotient required the use of the Emberger climate diagram, which placed each station in one of the 54 combinations of bioclimatic Mediterranean climate. To evaluate intra and inter-specific morphological variations and the extent to which they express genomic variations, the ordination-based Principal Component Analysis was performed. The results showed the presence of the following species: *A. barbata* with 59 accessions, *A. wiesti* with 27 acessions, 21 accessions of *A. hirtula*, 13 accessions of *A. longiglumis*, 9 accessions of *A. macrostachya*, 3 accessions of *A. clauda*, 4 accessions of *A. eriantha* (ex-Pilosa), and 2 accessions of *A. ventricosa*. Quantitative traits were crucial for distinguishing inter and intra-specific individuals. Morphological variations proved largely to express genomic variation among the species studied, especially in distinguishing between species carrying both A and C genomes. The morphological differences could not convey the genomic differences among species that share the C genome.

Keywords

Avena ; morphology; eco-geography; genomic; Mediterranean climate

Introduction

Oats are one of the most important cereal crops in the world. The genus *Avena* L. belongs to the tribe Aveneae Dumort, the subfamily Pooideae Benth, and the family Poaceae (Gramineae). It includes about 28 wild and cultivated species worldwide (1), with different ploidy levels (diploid, tetraploid, and hexaploid), which limits their morphologic differentiation. Wild species reflect a wide range of botanical and ecological diversity, mainly growing in Mediterranean climatic regions.

The diploid species are clearly divided into two distinct lineages with the A and C genomes. Recent developments in molecular cytogenetics, particularly fluorescence in situ hybridization (FISH) and a related technique, genomic in situ hybridization (GISH), have aided research into the genome composition of allopolyploids, the pairing of homologous chromosomes, and the identification of translocations between chromosomes of different genomes (2). Two different probes were used for fluorescence in situ hybridization to distinguish between A- and C-genomes types: A genome-specific pAs120 (3) and C genome-specific AF226063 (4, 5).

It has been reported that the number of *Avena* species found in Algeria varies from 10 to 15 (1, 6, 7). Although these species grew wildly, they mainly occurred in northern regions of Algeria. Wild species of the genus *Avena* are among the most competitive weeds in winter cereals (8) and are of great importance. Many previous studies showed the main morphological (1, 6, 9-13) and cytological (4, 14-19) differences between various species of the *Avena* genus. Algeria, by its geographical position represents a high biodiversity of plant population, due to its climatic conditions. Oats are among the well-known cereal products in Algeria. Despite the importance of this cereal, only few studies have been reported about this plant in Algeria. This study was conducted to examine the different species of the *Avena* genus in northern Algeria. To the best of our knowledge, we reported here for the first time, the influence of several eco-geographical factors on the distribution and morphological traits of different species of the studied *Avena* genus in Algeria. Furthermore, this research was done to check whether morphological differences are expressions of genetic and cytological differences between the species.

Materials and Methods

Plant material and taxa identification

One hundred thirty-eight populations of the genus *Avena* from different bioclimatic and ecological conditions were used for the present study, they were collected from 98 different sites, while the species were classified into the A and C-genome. The *Avena* genus accessions were collected from 98 different sites in Northern Algeria as shown in Fig. 1, including, 59 accessions of *A. barbata*, 27 *A. wiestï*, 21 *A. hirtula*, 13 *A. longiglumis*, 9 *A. macrostachya*, 3 *A. clauda*, 4 *A. eriantha* (ex pilosa) and 2 *A. ventricosa*. Varying number of plants were randomly collected at each sampling site. Identification was verified using the key of Loskutov (7).

Morphological analyses

The variation of 69 morphological characters was analyzed (Supplementary Table 1). Stem, panicle, leaf, spikelet, and seeds characteristics were examined using a microscope, binocular, meter and caliper. Observations were made on three individual plants per population. A total of 414 individuals were examined. Morphological characteristics were selected from species descriptions of different floras and from taxonomic studies (1, 6, 7, 9, 10, 13, 14, 20-22). Leaf and stem characters were measured at the third node. Seeds were observed in the harvested mature spikelet's.

Ecogeographic parameters

A global positioning system (GPS GARMIN eTrex model 30) was used to record the latitude, longitude and altitude of the sampled sites. Each sampling site was characterized by the five ecological factors (Supplementary Table 2) of Mediterranean climate (P = annual rainfall, M = average of the maximum temperature of the warmest month, m = average of the minimum temperature of the coldest month, Q2 = Emberger coefficient and A = altitude). The data submitted to NOM (National Office of Meteorology, Algeria) were used to characterize the climatic parameters of the stud-

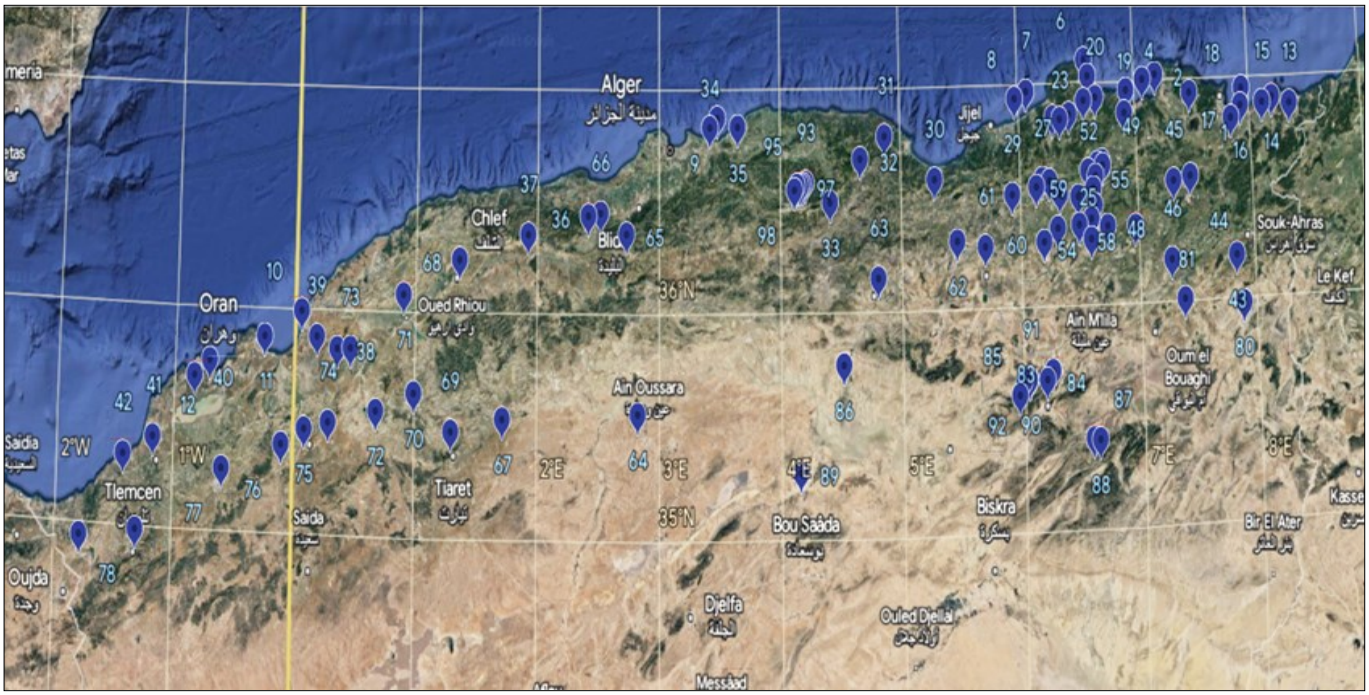


Fig. 1. Map indicating the location of the sampled diploid and tetraploid accessions of the *Avena* genus.

ied sites. However, data from three stations (Mila, AinTemouchent, and Blida) were not available; therefore, data from CLIMATE-DATA.ORG (http://fr.climate-data.org/) was used for these sites.

Corrections of climatic data

The reference station data did not reflect the actual ecogeographical and bioclimatic conditions. Namely, we applied a correction to the climate data based on extrapolations for different altitudes. According to the altitudinal gradient of Seltzer in his study of the climate of Algeria (23) the following gradients are advocated: For pluviometry, for every 100 m altitude, there is an increase of 40 mm for continental sites and 80 mm for the coastline. For tempe-rature, every 100 m, there is a decrease of 0.7°C for M and 0.4°C for m. This results in an increasing altitude gradient for pluviometry and a decreasing one for temperature. The correction factors make it possible to obtain more accurate data on the elements under consideration. The rainfall correction is performed as follows:

$$K = (A+P)/P \quad \ldots\ldots(1)$$

Where; K : correction factor, A: rainfall increase calculated as follows (mm):

$$A = d \times 40/100 \text{ for the continental} \quad \ldots\ldots(2)$$

$$A = d \times 80/100 \text{ for coastline} \quad \ldots\ldots(3)$$

d: difference in altitude between the two stations, P: sum of the monthly average rainfall of the reference station.

The correction factor (K) is multiplied by the monthly rainfall data for the reference station. Calculation of Emberger's bioclimatic coefficient and definition of bioclimate (24).

The pluviothermic Emberger quotient (Q2) is determined by the combination of three important climatic factors. This quotient is simple to interpret: The larger Q2 values, the more stations are wet. The formula of Stewart's (25) was used, who transformed the equation and obtained the following formula for the Mediterranean region.

$$Q2 = k \times P/(M-m) \quad \ldots\ldots(4)$$

Where; k: constant equal to 3.43; temperatures in degrees Celsius for M and m; precipitation (P) in millimeter. The interpretation of this quotient requires the use of the Emberger climate diagram which places each station in one of the 54 combinations of bioclimatic Mediterranean climate.

Data analyses

Principal component analysis (PCA) was performed to clarify the correlation between the morphological features used and to identify the features that contribute mostly to the discrimination of the accessions. Furthermore, ordination based on PCA was assessed to determine the effects of PCA axes on the differentiation of harvested communities. The data were analyzed using the software STATISTICA (version 6.1). To determine the correlation between the Euclidean distance matrices of the morphological traits and the ecogeographic parameters, a Mantel test Pearson correlation (26) was used (XLSTAT Pearson edition, version 2014.5.03).

Results

Eco-geographical variation

Ecogeographic characterization parameters revealed the adaptation range of species and showed the most important environmental factors or variables for adaptation. For this reason, the use of environmental information became very important in the collection areas of conserved germplasm (27). The data showed differences in distribution among the studied species, with *A. hirtula* in the foreground and present in all climatic zones. *A. barbata* and *A. longiglumis* followed with four climaxes, including Subhumide (SH), Upper subarid (USA), Low subarid (LSA) and Upper Arid (UA), followed by *A. wiestii*, *A. clauda* and *A. eriantha*. *A. macrostachya* was harvested in only two climatic zones (H and SH). In conclusion, both *A. ventricosa* accessions were found in the same climatic zone (SH) and differed only in that one endured a mild and warm winter while the other encountered a warm winter.

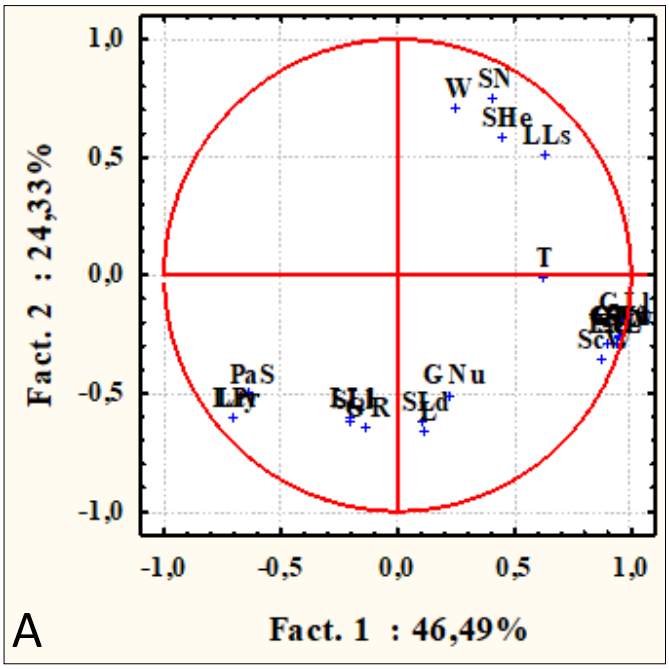
With the exception of *A. macrostachya*, all accessions occurred at elevations above 1500 m, with a limited distribution in the mountainous regions of Djurdjura and Aures. However, some accessions of other species managed to exist at similar altitudes, as in the case of *A. ventricosa* and *A. wiestii* (ven88, wie87 and wie85; 1777 m, 1525 m, and 1446 m, respectively), followed by hir62 (1108 m), bar69 (1062 m), and lon84 (1015 m), but also at very low altitudes as in the case of the following individuals (hir15, bar16 and wie17; 6m, 7m and 17m respectively), or relatively low as in the case of lon12 (181m). In contrast, *A. clauda* and *A. eriantha* (ex *A. pilosa*) occurred at identical altitudes of not more than 200 m in all their growing areas with a minimal spatial distribution (Supplementary Table 2).

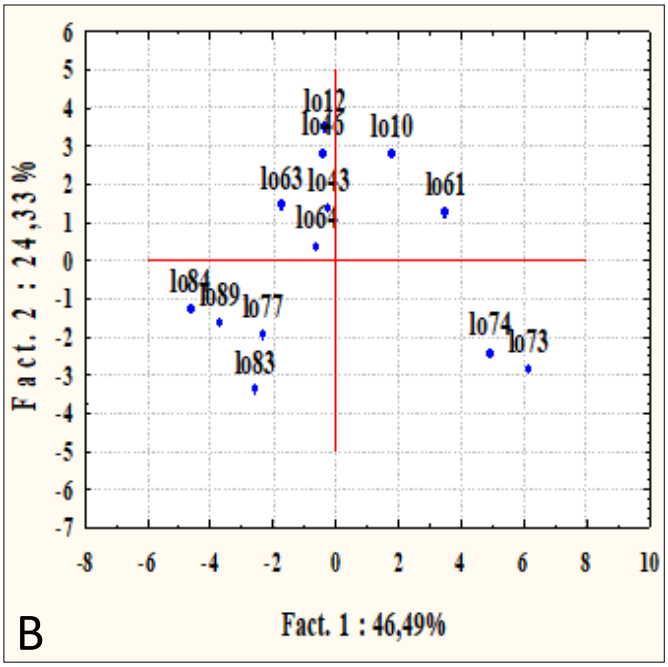
Intraspecific morphology variation

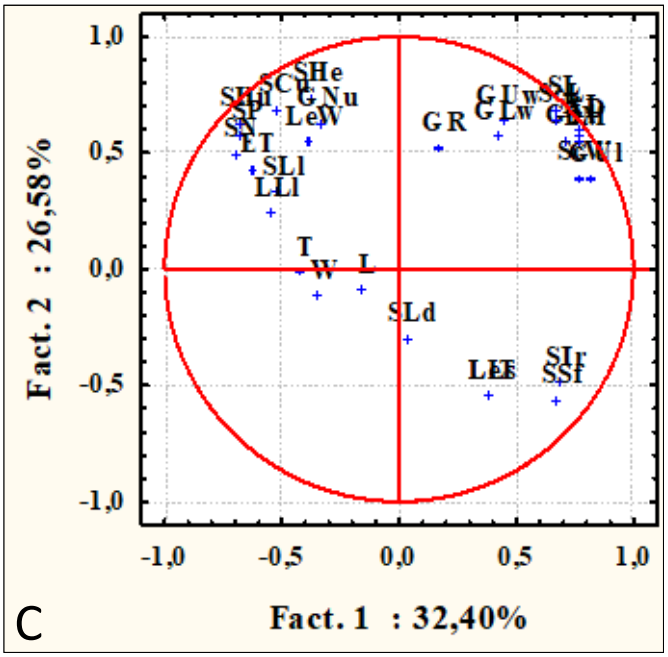
To clarify the relationships among the morphological traits and to identify the traits that contributed most to the separation of the populations, a principal component analysis (PCA) was performed, which yielded the following results:

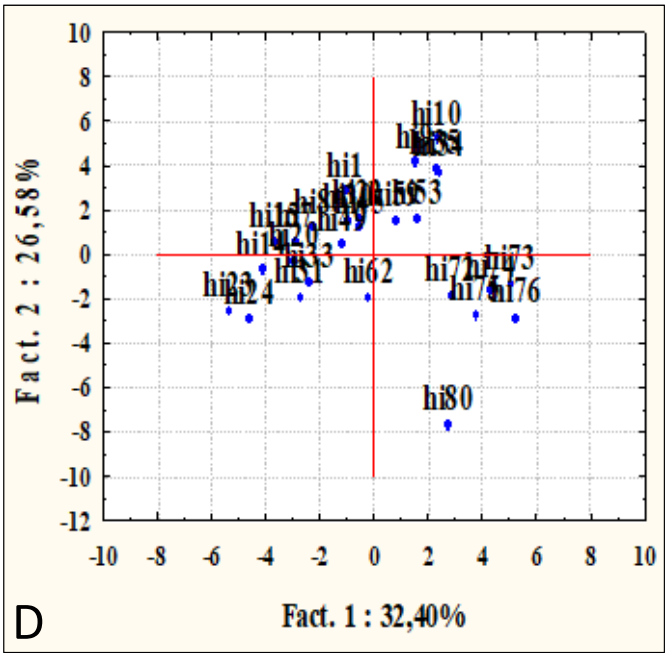
Forty-six morphological traits were excluded because they were 100% identical in all individuals in the *A. longiglumis* collected population. PCA analysis showed that the first two factors represented 70.83% of the total variance. Features like SL-GUl-GLl-GUw-GLw-ScL-ScW-RL, EM, and EM had the highest correlation ($|r| > 0.70$) in the first factor, which made up 46.5% of the whole variance. In the second factor, "SN" and "W" had the highest correlation (Fig. 2A). Through the ordination results based on PCA analysis, we noted that both axes contributed to the separation of the *A. longiglumis* accessions, especially lo73 and lo74 accessions, as the first axis had the strongest influence in separating them from the other populations (Fig. 2B).

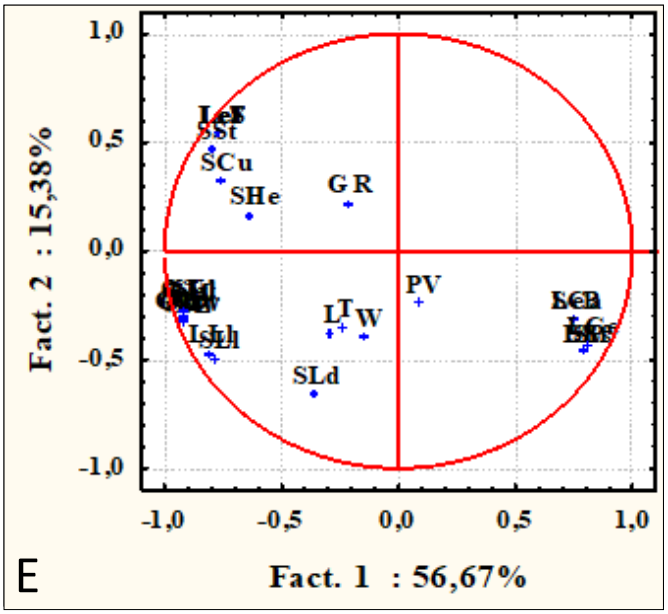
Forty morphological characters were excluded because they were 100% identical in all individuals of the collected population of *A. hirtula*. PCA analysis revealed that the first 3 factors accounted for 72.4% of the total

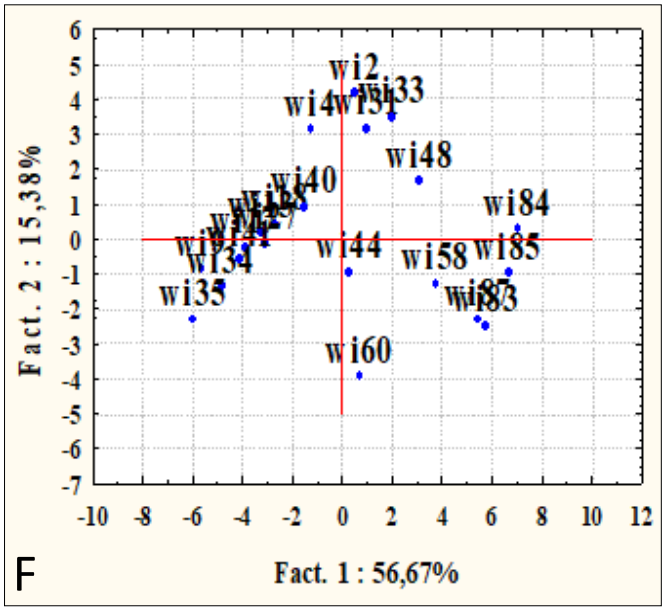

Fact. 2 : 24,33%
Fact. 1 : 46,49%
W
SN
SHe
LLs
T
PaS
GNu
SLd
L
A


Fact. 2 : 24,33%
Fact. 1 : 46,49%
lo12
lo10
lo63
lo43
lo61
lo64
lo84
lo89
lo77
lo74
lo73
lo83
B


Fact. 2 : 26,58%
Fact. 1 : 32,40%
SHe
SCu
GNu
LeW
GR
LT
SLl
LLl
T
W
L
SLd
C


Fact. 2 : 26,58%
Fact. 1 : 32,40%
hi10
hi1
hi53
hi62
hi73
hi80
D


Fact. 2 : 15,38%
Fact. 1 : 56,67%
SCu
SHe
GR
PV
LT
W
SLd
E


Fact. 2 : 15,38%
Fact. 1 : 56,67%
wi2
wi33
wi4
wi48
wi40
wi84
wi44
wi58
wi85
wi35
wi60
F

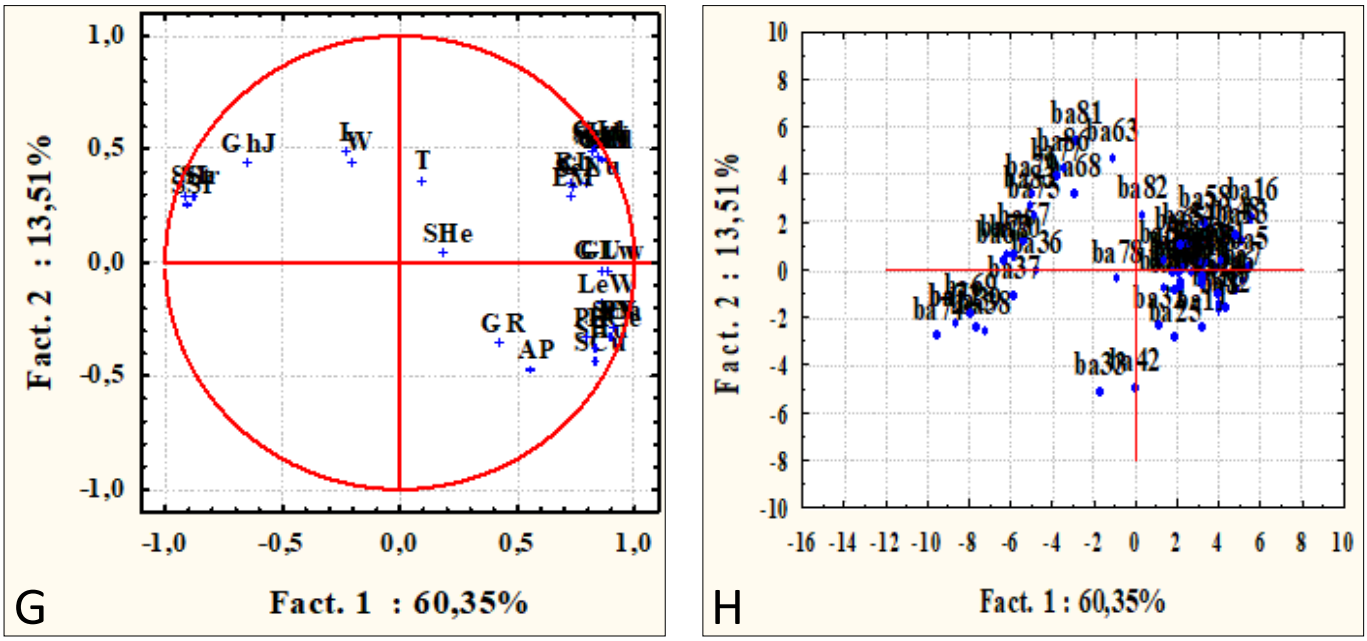


Fig. 2. Principal Component Analysis of morphological characteristics of: (**A**) *A. longiglumis*, (**C**) *A. hirtula*, (**E**) *A. wiestii*, and (**G**) *A. barbata*. Ordination based on PCA of populations of: (**B**) *A. longiglumis*, (**D**) *A. hirtula*, (**F**) *A. wiestii* and (**H**) *A. barbata*.

variance. In the first factor (which accounts for 32.4% of the total variance), traits such as Ghl-GLl-ScW-AD-RL and EM had the highest correlation (|r|> 0.70) in the first factor, while "SHe" had the highest correlation in the second factor and "L, W" in the third factor (Fig. 2C). Based on the results of the PCA analysis-based ordination, we noted that both axes contributed to the separation of the *A. hirtula* acessions, especially hi80, as the second axis had the strongest influence on the separation from the other populations (Fig. 2D).

Thirty-nine morphological characters were excluded because they were 100% identical in all individuals of the *A. wiestii* collected populations. PCA analysis revealed that the first two factors accounted for approximately 72% of the total variance. In the first factor, which made up 56.67% of the whole, characters like SCa-SCu-SLi-LeB-LeS-LeT-LeF-LLs-LLi-SL-Gul-GLl-GUw-GLw-SSf-SSt-SP-ScL-ScW-LCe-AD-RL and EM had the strongest relationships (r> 0.70) in the first factor (Fig. 2E). Using the results of ordination based on PCA analysis, we noted that both axes contributed to the separation of the *A. wiestii* accessions, especially wi44, as the first axis had the strongest influence on separation from the other populations (Fig. 2F).

Thirty-six morphological characters were excluded because they were 100% identical in all individuals of the *A. barbata* collected populations. PCA analysis revealed that the first two factors comprised 73.86% of the total variance. In the first factor (accounting about 60.35% of the total variance), characters as SCa-SCu-SHe-SHu-SLd-SLi-SLr-LeW-LLi-SL-SN-Gul-GLl-GUw-GLw-GNu-SSf-SSt-ScL-ScW-LCe-AN-AD-PV-RL and EM possessed the highest correlation (|r|> 0.70) in the first factor (Fig. 2G). The first axis helped divide the *A. barbata* accessions into two big groups based on the results of the PCA analysis (Fig. 2H).

Thirty-eight morphological characters were not considered for the reason that they were 100% identical in all individuals of *A. macrostachya* collected populations. PCA analysis revealed that the first two factors involved 94.29% of the total variance. In the first factor (accounting 68.97% of the total variance), characters such as SCu-SLd-SLi-LeI-LeB-LeS-LeT-LeF-LeW-LLi-PaS-SL-SN-Gul-GLl-GUw-GLw-SSt-ScL-ScW-LPa-AD-AP-PR-RL-EM and L owned the highest correlation (|r|> 0.70) in the first factor, while "T" presented the highest correlation in the second factor (Fig. 3A). The PCA analysis results of ordination disclosed that the first axis contributed to the separation of *A. macrostachya* populations among the groups' mac90, mac91 and mac92 that were harvested in the Aurès Mountains from the other group harvested from the Djurdjura Mountains (Fig. 3B).

Fifty-one morphological characters were kept out because they were 100% identical in all individuals of collected populations of *A. eriantha*. PCA analysis revealed that the first two factors comprise 91.47% of the total variance. Characters like SHe-SLd-SLi-LLi-SN-GUl-GLl-ScW-LPa-AD-RL and L had the highest correlation (|r|> 0.70) in the first factor, which makes up 65.76% of the whole variance. Characters like SL-GUw-GLw-EM and W had the highest correlation in the second factor (Fig. 3C). PCA analysis outcomes showed that both axes contributed to the separation of the *A. eriantha* accessions (Fig. 3D).

Fifty-two morphological characters were excluded because they were 100% identical in all the individuals of the *A. clauda* populations. PCA analysis revealed that the two first factors comprise 100% of the total variance. In the first factor (which formed 63.97% of the total variance), characters as SHe-SLd-SLi-LLi-SL-Gul-GUw-GLw-ScL-ScW-AD-RL and EM owned the highest correlation (|r|> 0.70) in the first factor, while L-W and T possessed the highest correlation in the second factor (Fig. 3E). Ordination PCA analysis results stated that both axes contributed to the separation of the *A. clauda* accessions (Fig. 3F).

Interspecific morphology variation

In this section we made a comparison between the species that had the genome-A, between the species that had the

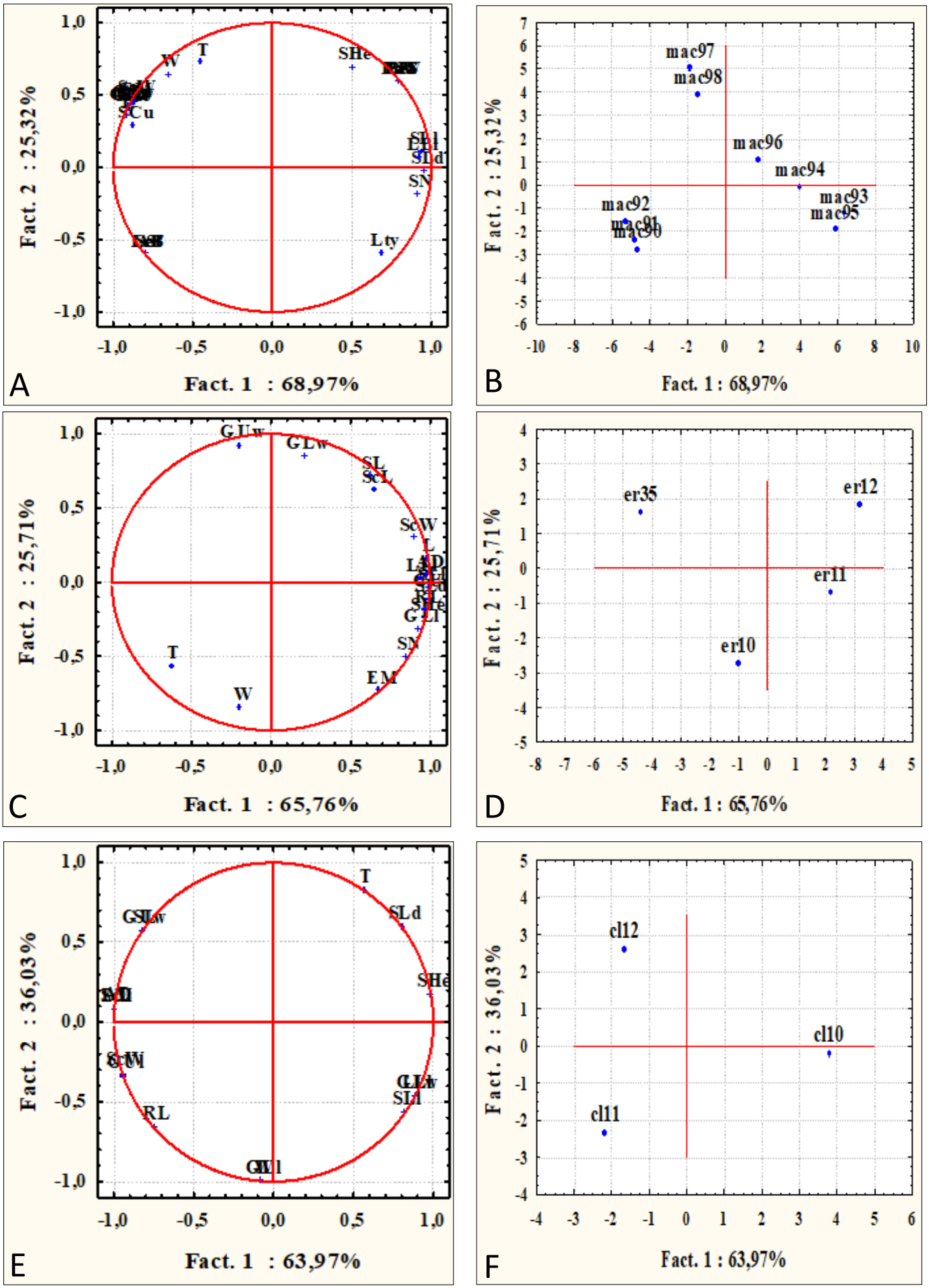


Fig. 3. Principal Component Analysis of morphological characteristics of: (**A**) *A. machrostachya*, (**C**) *A. eriantha* and (**E**) *A. clauda*. Ordination based on PCA of populations of: (**B**) *A. macrostachya*, (**D**) *A. eriantha* and (**F**) *A. clauda*.

genome-C and finally a comparison between the two

groups of genome A and C.

When comparing the accessions of *A. barbata*, *A. longiglumis*, *A. hirtula*, and *A. wiestii*, PCA excluded 19 morphological characters. The results showed that the first two factors accounted for 61.8% of the total variance. In the first factor (comprising 38.24% of the total variance), traits such as SHe-SLd-LeT-LLi-PaD-PaL-SL-Gul-GLl-GUw-GLw-LCe-LPa and AN demonstrated the highest correlation (|r| > 0.70) in the first factor, while SCa-LeI-LeB-LeF-SSf -ScL- CS -LHa-L-W and T possessed the highest correlation in the second factor and SHu-SLr and EM in the third factor (Fig. 4A). Based on the results of PCA analysis ordination findings, the first axis contributed to the separation of the species *A. hirtula*, *A. wiestii*, and *A. barbata*. At the same time, the second axis was effective in separating *A. longiglumis* from the other species with A genome (Fig. 4B).

During the comparison of *A. eriantha*, *A. clauda*, *A. ventricosa*, and *A. macrostachya* accessions, PCA analysis excluded 13 morphological characters. The results revealed that the first two factors accounted for 72.09% of the total variance. In the first factor (comprising 50.8% of the total variance), traits such as GhL –GhJ –Sca –SLd –Lel –LeT –LeF –Lli –PaD – SL –SN –GS -Gul –Guw –GLw –FMd – SSf-SP-ScW –AN –AD –AP –AV –PI –PV –RL –ET-EM –L –W and T exceeded the highest correlation (|r| > 0.70) in the first factor, whereas GLl-LPr-SSt- RT -ScL-RP-LCe and LTt had the highest correlation in the second factor (Fig. 5A). Using the results of ordination based on PCA analysis, the second axis contributed to the separation of the three diploid species with the C genome. At the same time, the first axis was crucial to separate *A. macrostachya* from the other three diploid species with C genome (Fig. 5B).

When comparing all accessions of the species, PCA excluded 13 morphological traits. The results revealed that the first four factors account for 72.1% of the total variance. In the first, second, third and fourth factors (which has 25.28%, 24.48%, 11.70% and 10.64% of the total variance, respectively), characters such as SLd-SLi-LLi-PaD-PaL-SL-SP-LCe-AN-AC and RL exhibited the highest correlation (|r|> 0.70) in the first factor, while GhL-LeS-PaS-SS-GR-ScL-LHa-PI-RT and RP displayed the highest correlation in the second factor, FMd and AV in the third factor, LeF in

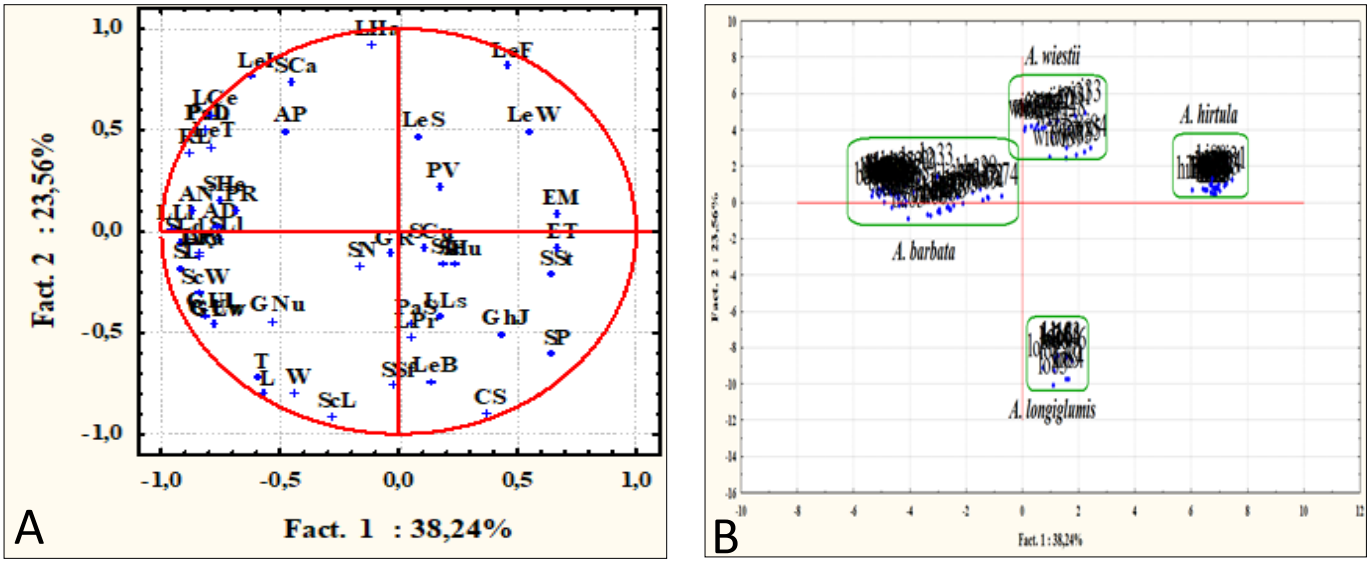


Fig. 4. (**A**) Principal Component Analysis of morphological characteristics, (**B**) Ordination based on PCA of populations of species carrying A-genome.

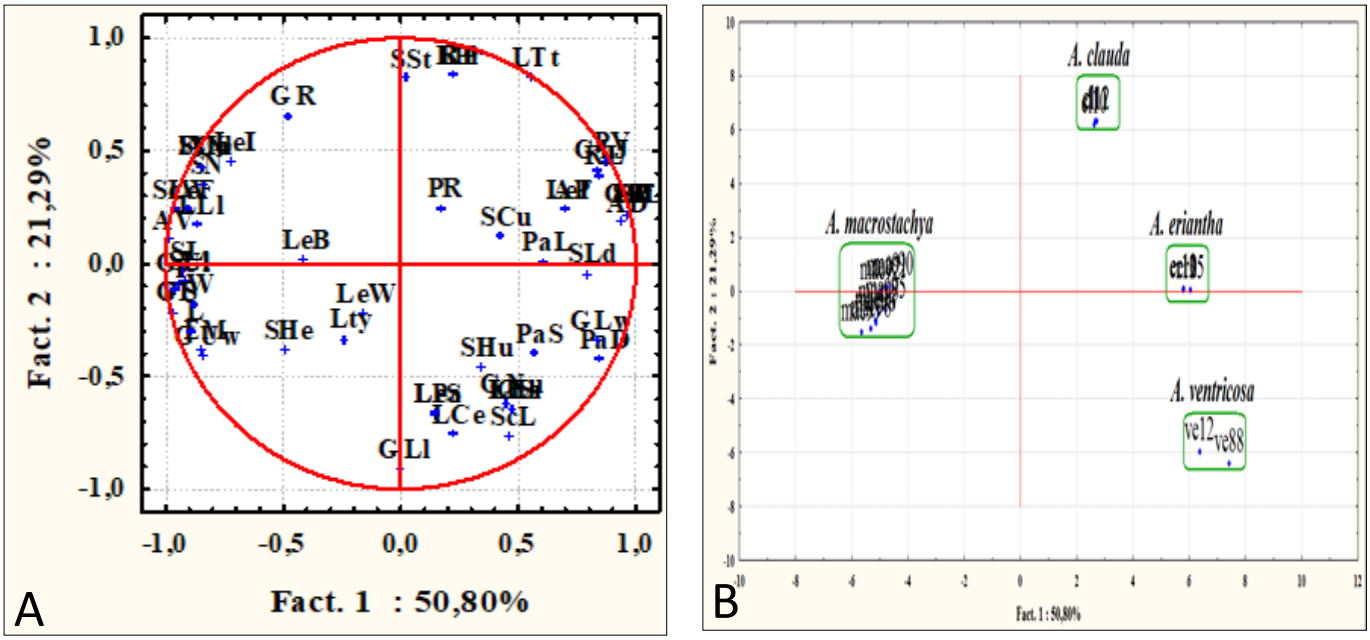


Fig. 5. (**A**) Principal Component Analysis of morphological characteristics, (**B**) Ordination based on PCA of populations of species carrying C-genome.

the fourth factor and SCu in the fifth factor (Fig. 6A). According to the PCA analysis data, the studied species were divided into two groups, as the species with the C genome took their place below the species with the A genome, confirming that the second axis (PC2) had the decisive word in this distinction between the two groups (Fig. 6B). On this basis, the relationship of the species to each other is examined separately for each group.

Correlation between morphology and eco-geography

To determine the relationship between the climatic changes and the morphological changes of the studied oats species, the correlation between the two Euclidean distance matrices of the morphological characters (matrix A) and the eco-geographical parameters (matrix B) was carried out with the Mantel test based on the Pearson correlation of each species according to its own distribution. The results obtained with this test showed that the correlation between morphology and eco-geography was statistically significant for *A. longiglumus, A. hirtula*, *A. wiestii* and *A. macrostachya* ($p > 0.05$), but not significant ($p > 0.05$) for *A. barbata* and *A. eriantha* (Table 1). It should be noted that this test was not applicable for the following two species: *A. ventricosa* and *A. clauda*, because the number of populations required to perform this test was insufficient for both species.

Discussion

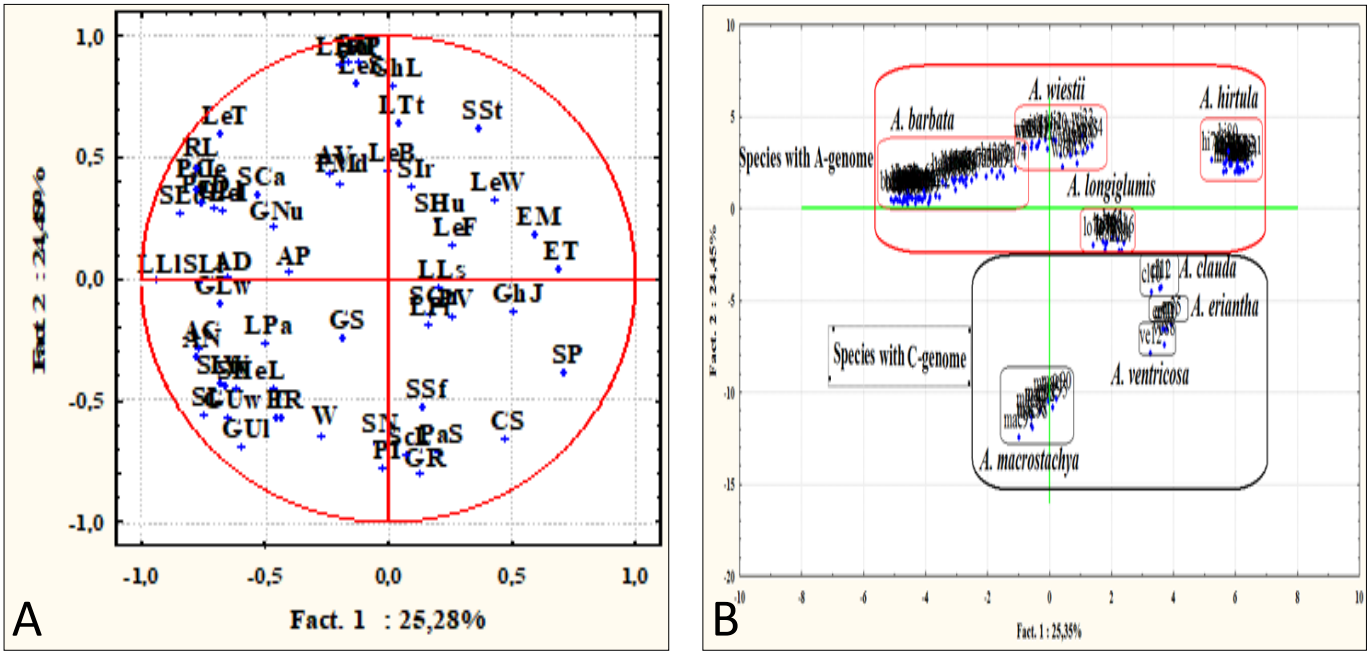


Fig. 6. (**A**) Principal Component Analysis of morphological characteristics, (**B**) Ordination based on PCA of populations of all species.

General habit: Longevity (GhL), Juvenile growth (GhJ), **Stem:** Color appearance (SCa), **Culm:** (SCu), Height (SHe), Hairiness of upper most node (SHu), Lower internode diameter (SLd), Lower internode length (SLl), Internodes (roughness) (SIr), Culm consistency (SCc), Peduncle (SPe), **Leaf:** Lobes (LeL), Intensity of green color (LeI), Blade hairiness of margins (LeB), Lowest leaves: hairiness of sheaths (LeS), Total length of longest green leaf (including petiole) (LeT), **Flag leaf**: glaucosity of sheath (LeF), Width at widest point (LeW), Ligules shape at younger (LLs), Ligules length on culm leaves (LLl), **Panicle:** Shape (PaS), Density (PaD), Length (PaL), **Spikelets:** Length without awns (SL), Number of florets (SN), Separating from peduncle (SS), Glumes shape (GS), Glumes relative length (GR), Upper glume length (GUl), Lower glume length (GLl), Upper Glume width (GUw), Lower glume width (GLw), Number of nervs of upper glume (GNu), Presence of keels (GP), Florets dispersal unit: Florets: disarticulation (FDd), Florets mode of disarticulation (FMd), Separate (FSd), Scars Shape of first floret scar (SSf), Shape of third floret scar (SSt), Periphery ring (SP), Length (ScL), Width (ScW), **Callus:** Shape (CS), **Lemma:** Color (LCe), Hairiness (LHa), Place of awn insertion (LPa), Structure (LSt), Shape of tip (LTt), Grain husk (LGh), **Awns:** Number of awns (AN), Dorsal awn length (AD), Color (AC), Pubescence (AP), Vestiture below awn insertion (AV), **Palea:** Presence (PP), Apex (incision) (PI), apex (presence of awn) (PA), Rows of cilia along edges of keels (PR), Vestiture of back (PV), Lodicule: Type (LTy), Prickles (LPr), **Rachilla:** Type presence (RT), Length (RL), Pubescence (RP), **Epiblast:** Type (ET), Median range (EM), **Grain:** Length (L), Wide (W), Thickness (T).

Table 1. Correlation results between morphologic and eco-geographic characteristics of collected *Avena* L. species.

Avena species	N	R	p
Avena barbata	10000	0.3806	0.0129
Avena longiglumis	10000	0.4170	0.0026
Avena hirtula	10000	0.5101	0.0073
Avena wiestii	10000	0.0421	0.189
Avena macrostachya	10000	0.5995	0.0059
Avena eriantha	10000	0.8732	0.2149
Avena clauda	10000	-	-
Avena ventricosa	10000	-	-

N= Permutations number, **R**= Pearson correlation coefficient, ***p***-value of Pearson test.

The majority of wild oat species originate in the Mediterranean region (between 20- and 40-degrees north latitude), which stretches north of Algeria (27). The results summarized in Supplementary Table 1 are in the line with the findings of Loskutov *et al.* (27), which reported that this region has the richest and highest genetic diversity of wild oats in the world. The presence of two tetraploid species (*A. barbata* and *A. macrostachya*) and six diploid species (*A. clauda, A. eriantha, A. hirtula, A. longiglumis, A. ventricosa,* and *A. wiestii*) explains this. The current study was achieved using 138 accessions collected from 98 different areas. The harvest area included five of the six bioclimatic stages based on Emberger's pluviothermic quotient (28). As shown in Supplementary Table 1, there is a clear dis-

crepancy in the distribution of the different species studied among the different bio-climatic regions. According to the findings, all species with the A genome were widely spread, except for the *A. wiestii* which presented a limited distribution similar to that of *A. clauda, A. eriantha, A. ventricosa,* and *A. macrostachya* with C genome. Constandinou *et al.* stated that the main important climatic variable that determines the distribution of *A. ventricosa* is the mean daily temperature (29), which was translated by the presence of the two accessions of this species in the climate "SH", but with the only difference that the first has a mild winter and the second a cold winter. The distribution differences between species of the genus *Avena* might be due to the variation in evolution and interaction with bioclimatic changes.

The Mediterranean climate is characterized by changing temperatures and an increase in precipitation. Therefore, the harvesting stations coordinates showed great importance in determining the quality of the climate prevailing in the area and, from this, the manner of its impact on the presence and distribution of the species, as well as the extent of their response and adaptation to all these variables (30). It is known that temperature is one of the most important climatic elements that directly affect the phases of the growth cycle and the vegetation period of oats (31, 32). In addition, plant height, number of seeds per plant, dry weight of seeds and moisture content, all morphological quantitative traits of oats are directly affected by decreases and increases in temperature (33). Our outcomes were in accordance with those studies done by Klink *et al.* (34) and Peltonen-Sainio (35), which found that plants phenology and grain production and quality are influenced by climatic factors such as precipitation.

In addition, drought stress reduced the number of fertile flowers in the panicle because the more severe the drought, the higher the rate of flower death (36). Soil moisture results from the interaction between temperature and precipitation. Although oats have a vigorous root system that makes good use of the soil, their transpiration rates at elevation, and thus their water requirements, are higher than those of other small-grain cereals (37). Therefore, the soil moisture degree is an important factor in the growth and development of oats, especially for the total quantitative characteristics. The most important traits affected by soil moisture are plant height, leaf area production, and biomass productivity, with different responses at different stages of plant growth and among different species (38). From all this, it is clear that climatic factors have a significant influence on quantitative traits of oat growth.

At this point, it should be noted that quantitative traits are important not only for distinguishing between plant populations, but also for how these plants cope with climatic and biotic conditions; the latter has shown that oats with improved organs such as the thickness of the straw and the height of the plant have a high resistance to storage (33).

All studied species showed various differences among themselves and even among their accessions for most quantitative traits. The quantitative traits showed a high correlation ($|r| > 0.7$) with the PC1 and/or PC2 axes, confirming their effective contribution in discriminating between accessions of the same species. The results presented previously, all qualitative traits in diploid species (*A. clauda* and *A. eriantha*) were excluded because they were completely identical with in populations of the same species. This stability in qualitative traits can be attributed to the presence of different populations of these two species in very similar climatic environments.

In contrast, *A. ventricosa* showed variance in the two qualitative characters in the vegetative part: young growth and pubescence of the uppermost node. The vegetative traits (culm, pubescence of the uppermost node, roughness of the internodes, and shape of the ligule at anthesis) showed differences among the accessions of the following species: *A. longiglumis*, *A. hirtula*, *A. wiestii*, and *A. barbata*, the variance can be attributed to changes in abiotic factors such as temperature, rainfall, lighting, and wind strength. With the exception of the last trait, more detailed studies are needed to show what factors control the change in this trait. The previous species populations showed differences in the shape of first floret scar "SSf", the epiblast type "ET" between *A. longiglumis* and *A. wiestii* populations, which are two characteristics at the reproductive system that also need more accurate studies to show factors controlling their differences.

The most qualitative differences appeared between auto-tetraploid *A. macrostachya* accessions that affected the different organs of the vegetative and reproductive systems. From the above observations the qualitative traits among accessions of *A. clauda*, *A. eiantha* and *A. ventricosa* species, which together constitute the diploid species with the C genome, and they were more stable than the accessions of *A. longiglumis*, *A. hirtula* and *A. wiestii* species with A genome. Several reports disclosed that morphological characters are associated with a relatively small number of loci (39-41). The stability of these genes between accessions of the same species resulted in the stability of the whole genome. From the results, it can be concluded that the C genome was more stable than the A genome. This is fully consistent with the fact that A genome was found in several types as Ac, Ad, Al, Ap and As, while the C genome exists only in two types (Cp and Cv) in the diploid species of the genus *Avena* **(**42).

The diploid species with the A genome (*A. hirtula*, *A. longiglumis*, *A. wiestii* and *A. barbata*) showed remarkable differences in quantitative traits (Table 2). These differences appeared between *A. longiglumis* and the two other diploid species. They varied significantly with respect to the vegetative part or the components of spikelets, as shown in Table 1. This makes it easy to observe the possibility of the presence of some species by simple visual observation only. Also, there are important qualitative characteristics in differentiating between these species, as they recorded an absolute correlation coefficient higher than |0.7|. Whereas, the differentiation between the three species was decisive by four qualitative traits: SCa, SSt, CS and LCe. We mention, for example that the shape of the callus

Table 2. Means of quantitative traits.

	ven	cla	eri	lon	wie	hir	mac	bar
SHe (cm)	62.5±7.3	67.15±1.75	67.4±2.7	55.55±19.95	53.7±15.5	42.05±13.55	82.25±6.95	79.25±18.85
SLd (mm)	2.07±0.01	1.84±0.03	2.215±0.045	3.91±0.17	2.555±0.385	2.445±0.065	1.545±0.415	7.08±1.25
SLl (cm)	12.4±0.2	13.9±0.4	13.6±0.5	18.9±3.1	21.6±2	10.35±0.95	17.7±2	17.5±3.1
LLl (mm)	1.775±0.015	2.915±0.025	1.76±0.08	3.11±0.51	3.55±0.33	1.7±0.16	3.59±0.84	3.74±0.66
SL (mm)	21.735±0.85	23.52±0.04	21.32±0.09	22.865±0.675	20.255±3.435	16.46±0.67	27.645±2.475	22.105±3.905
SN	2	4	2 or 3	2 or 3	2	2 or 3	4 or 5	2 or 3
GUl (mm)	23.25±0.09	24.82±0.06	22.64±0.18	26.07±0.77	20.46±3.47	17.155±0.925	30.685±2.745	22.4±3.96
GLl (mm)	18.02±0.05	11.24±0.04	15.705±0.025	25.975±0.765	20.435±3.445	17.135±0.945	15.35±1.33	22.24±3.8
GUw (mm)	4.96±0.02	4.09±0.03	5.045±0.005	5.675±0.165	3.25±0.24	3.735±0.145	6.68±0.6	5.705±0.825
GLw (mm)	4.965±0.025	3.985±0.025	5.03±0.01	5.675±0.165	3.24±0.24	3.7±0.12	3.82±0.33	5.695±0.825
GNu	8 or 9	7	7	9 to 11	7	7 or 9	7	9 or 10
ScL (mm)	4.49±0.02	1.45±0.01	2.02±0.01	1.61±0.05	0.865±0.065	1.055±0.045	1.81±0.16	1.195±0.085
ScW (mm)	0.18±0.01	0.515±0.025	0.225±0.005	0.445±0.015	0.27±0.02	0.315±0.015	0.67±0.06	0.5±0.09
AN	2	3 or up	2	2	2	2	3 or up	2 or 3
AD (mm)	55.25±0.56	54.36±1.75	58.64±0.52	52.47±1.55	58.09±4.27	34.375±1.025	43.33±0.8	48.84±8.63
PR	1 or 2	2	2	1	1	1	1 or 3	1 or 2
RL (mm)	1.575±0.065	2.41±0.02	2.91±0.17	1.59±0.05	2.895±0.215	2.05±0.06	0.96±0.08	4.045±0.295
EM (mm)	0.345±0.015	0.295±0.015	0.315±0.015	0.34±0.01	0.295±0.025	0.69±0.02	0.42±0.04	0.395±0.025
L (mm)	4.77±0.01	4.01±0.01	4.065±0.015	7.255±0.135	4.91±0.07	4.75±0.08	7.11±1.08	5.99±0.19
W (mm)	0.74±0.01	0.76±0.01	0.715±0.005	1.04±0.05	0.795±0.045	0.765±0.055	1.325±0.305	0.88±0.07
T (mm)	0.6±0.01	0.705±0.005	0.685±0.005	1.04±0.03	0.73±0.06	0.66±0.05	1.215±0.155	0.89±0.1

ven=*Avena ventricosa*, **cla**=*Avena clauda*, **eri**=*Avena eriantha*, **lon**=*Avena longiglumis*, **wie**=*Avena wiestii*, **hir**=*Avena hirtula*, **mac**=*Avena macrostachya*, **bar**=*Avena barbata*, **Stem:** Height (**SHe**), Lower internode diameter (**SLd**), Lower internode length (**SLl**), **Leaf:** Ligules length on culm leaves (**LLl**), **Spikelets:** Length without awns (**SL**), Number of florets (**SN**), Upper glume length (**GUl**), Lower glume length (**GLl**), Upper Glume width (**GUw**), Lower glume width (**GLw**), Number of nervs of upper glume (**GNu**), **Scars:** Length (**ScL**), Width (**ScW**), Number of awns (**AN**), Dorsal awn length (**AD**), **Palea** Rows of cilia along edges of keels (**PR**), **Rachilla** length (**RL**), Epiblast median range (**EM**), **Grain:** Length (**L**), Wide (**W**), Thickness (**T**).

in *A. longiglumis* is very primitive compared to that of the other two species (43). These distinct differences between *A. longiglumis* and both species can be considered as an explanation for the slight divergence between the genomes of these species "Al and As" respectively. According to the results shown in (Fig. 4B), we noted that the *A. longiglumis* accessions were clearly separate from the other three closely related species accessions, which is consistent with previously mentioned that *A. longiglumis* carries a genome "Al'' different from the genomes of the other two diploid species "As" (43). When comparing the diploid species carrying the A-genome and the tetraploid species carrying the AB-genome "*A. barbata*" (14), we found many slight differences in quantitative traits. However, the difference was very clear in a limited number of quantitative traits, namely: SHe and RL (Table 1). As for the difference by qualitative traits, it was not much different for quantitative traits. This slight difference can be traced back to the fact that the A-genome of the tetraploid species *A. barbata* was similar to the As-genome (*A. hirtula* and *A. wiestii*) of the diploid species (44).

These results supported what some researchers believe that *A. barbata* is an auto-tetraploid of a diploid species (45), as a result of which the genome of this species can consist of two identical or very close genomes (AA') (45, 46). The number of identical morphological traits (Fig. 6A) and the percentage of differentiation obtained by the two first axes (Fig. 6B) confirmed that the species carrying the A-genome are closer to each other compared to those with the C-genome.

In addition to the differences in the quantitative traits that exist between the species carrying the C-genome, the obtained results also recorded decisive qualitative differences in differentiating between these species distributed between the vegetative and reproductive parts (Table 2), the most important of which are: LLi-LPa-LTt were also crucial to distinguishing each pair of these species. But in a special way, the following morphological characters SCa-AN-AD-AV-RT-FMd and SSt, were decisive in distinguishing between *A. clauda* and *A. eriantha*. As for, the following morphological traits LLs-GR-GNu-CS-LCe-LHa and PV, were crucial in distinguishing between *A. ventricosa* and each of the two following species, *A. clauda* and *A. eriantha*. Also, through the results, we notice that the differences between *A. clauda* and *A. eriantha* were embodied by qualitative and quantitative traits with a slight superiority for quantitative traits. In contrast, qualitative traits were largely decisive in distinguishing between the two former species and *A. ventricosa*. Although *A. clauda* and *A. eriantha* are classified un-

der one biological species, which means that they carry the same type of genome "Cp" (14), but *A. ventricosa* with the different genome "Cv" (4). But, the results of ordination based on PCA analysis, in this study (Fig. 5B), did not clearly agree with this classification, which makes the morphological difference between these species incompatible with the difference at the cytological level, especially between the two species *A. clauda* and *A. eriantha*. The same results shown in Fig. 5B show a relative affinity between *A. clauda* and *A. macrostachya* compared to the other two species, but the relationship between *A. clauda* and *A. macrostachya* needs further deeper studies to prove this convergence.

Conclusion

The morphological intraspecific variation is largely due to quantitative traits, especially in *A. clauda* and *A. eriantha*. This variation is reinforced by qualitative differences in the other remaining studied species to varying degrees. Through the results of this study, it can be highly trusted that the difference in morphological traits is largely expressive of the difference at the genomic level, especially between species carrying the A-genome and species with the C-genome as well as species carrying the A-genome between them. Despite this, species with the C-genome among themselves were not subject to this rule. Quantitative variations had a greater impact on inter-specific differences among species carrying the C-genome; on the contrary, the qualitative morphological traits played the most important role in separating species carrying the A-genome between them. The wider distribution of the studied *Avena* species carrying the A-genome compared to the species with the C-genome may be related to the elasticity of the A-genome and its ability to adapt to eco-geographic conditions, compared to the C-genome which appears to be more stable than the A-genome.

Acknowledgements

The authors gratefully thank the Algerian Ministry of Higher Education and Scientific Research, the General Directorate of Scientific Research and Technological Development, Algeria.

Authors' contributions

YB carried out the molecular genetic studies, drafted the manuscript. DB carried out the revision of the manuscript. IB participated in the design of the study and performed the statistical analysis as well as validated and supervised the work. DK validated and supervised the work. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None.

Supplementary data

Supplementary Table 1**.** Morphological characters state and code used for PCA.

Supplementary Table 2. Eco-geographic characteristics and Emberger quotient calculation of sampling sites of Algeria *Avena* L. species.

References

1. Baum BR. Oats: wild and cultivated: a monograph of the genus *Avena* L. (Poaceae). Biosystematics Research Institute: Canada Department of Agriculture, Research Branch. Ottawa, Ontario, Canada. 1977. Available from: http://publications.gc.ca/site/archivee-archived.html?url=https://publications.gc.ca/collections/collection_2015/aac-aafc/A54-3-14-1977-eng.pdf
2. Raina SN, Rani V. GISH technology in plant genome research. Methods Cell Sci. 2001;23:83-104. https://doi.org/10.1023/A:1013197705523
3. Linares C, Ferrer E, Fominaya A. Discrimination of the closely related a and d genomes of the hexaploid oat *Avena sativa* L. Proc Natl Acad Sci. 1998;95(21):12450-455. https://doi.org/10.1073/pnas.95.21.12450
4. Ananiev EV, Vales MI, Phillips RL, Howard W, Rines HW. Isolation of A/D and C genome specific dispersed and clustered repetitive DNA sequences from *Avena sativa*. Genome. 2002;45(2):431-41. https://doi.org/10.1139/g01-148
5. Liu Q, Li X, Zhou X, Li M, Zhang F, Schwarzacher T *et al*. The repetitive DNA landscape in *Avena* (Poaceae): chromosome and genome evolution defined by major repeat classes in whole-genome sequence reads. BMC Plant Biol. 2019;19:226. https://doi.org/ 10.1186/s12870-019-1769-z
6. Quezel P, Santa S. New flora of Algeria and the southern desert regions. Volume 1 : National Center for Scientific Research, Paris7, France. 1962 ;120-22. [cited 16 April 2023]. Available from: http://ecologia-mediterranea.univ-avignon.fr/wp-content/uploads/sites/25/2019/01/ecologia-mediterranean-442-2018-LR.pdf
7. Loskutov IG. On evolutionary pathways of *Avena* species. Genet Resour Crop Evol. 2007;55(2):211-20. https://doi.org/10.1007/s10722-007-9229-2
8. Kirkland KJ. Spring wheat (*Triticum aestivum*) growth and yield as influenced by duration of Wild Oat (*Avena fatua*) competition. Weed Technology. 1993;7(4):890-93. https://doi.org/10.1017/S0890037X00037945
9. Cosson ME. Classification of species of the *Avena* genus of the *Avena Sativa* group (*Avena*, Sect. Arenalypus). Considerations on the composition and structure of the spikelet in the Gramineae family. Bulletin of the Botanical Society of France. 1854;1(1):11-18. http://dx.doi.org/10.1080/00378941.1854.10825398
10. Battandier JA, Trabut L. Flora of Algiers and Catalog of plants of Algeria, or systematic enumeration of all the plants reported to date as spontaneous in Algeria, with description of the species found in the Algiers region: Monocotyledons. Algiers, Algeria: Adolphe Jourdan 1884;60-63. Available from : https://gallica.bnf.fr/ark:/12148/bpt6k64369281/f23.item.texteImage#
11. Stanton TR. Oat identification and classification: Technical bulletin N° 1100. United States Department of Agriculture, AgEcon. Washington, D.C., USA. 1955. Available from: https://ageconsearch.umn.edu/record/156755/files/tb1100.pdf
12. Coffman FA. Oat history, identification and classification: Technical bulletin N° 1516. United States Department of Agriculture,

AgEcon. Washington, D.C., USA. 1977. Available from : https://ageconsearch.umn.edu/record/156755/files/tb1100.pdf

13. Bory MM, Durieu DM. Scientific exploration of Algeria during the years 1840, 1841, 1842, Physical sciences "Botany": Paris, France. 1846;1:44. https://bibdigital.rjb.csic.es/en/records/item/12937-exploration-scientifique-de-l-algerie-atlas
14. Ladizinsky G. Genome relationships in the diploid oats. Chromosoma. 1974;47(1):109-17. https://doi.org/10.1007/BF00326275
15. Fominaya A, Vega C, Ferrer E. Giemsa C-banded karyotypes of *Avena* species. Genome. 1988;30(5):627-32. https://doi.org/10.1139/g88-106
16. Thomas H. Cytogenetics of *Avena*. In: Marshall HG, Sorrells ME, editors. Oat science and technology-Agronomy monograph N° 33 [e-Book]. Madison: American Society of Agronomy and Crop Science Society of America, 677 S. Segoe Rd., USA. 1992;33:473-507. Available from: https://doi.org/10.2134/agronmonogr33.c14
17. Diederichsen A. Assessments of genetic diversity within a world collection of cultivated hexaploid oat (*Avena sativa* L.) based on qualitative morphological characters. Genet Resour Crop Evol. 2008;55(3):419-40. https://doi.org/10.1007/s10722-007-9249-y
18. Badaeva ED, Shelukhina OY, Diederichsen A, Loskutov IG, Pukhalskiy VA. Comparative cytogenetic analysis of *Avena macrostachya* and diploid C-genome *Avena* species. Genome. 2010;53(2):125-37. https://doi.org/10.1139/G09-089
19. Aissat A, Amirouche R, Amirouche N. Cytotaxonomic investigation and meiotic behavior of natural populations of genus *Avena* in Algeria. Euphytica. 2019;215(10). https://doi.org/10.1007/s10681-019-2490-6
20. Malzew AI. Wild and cultivated oats, section *Euavenagriseb.* Supplement no 38, VIR institute: Leningrad, Russian; 1930.
21. Ladizinsky G. Studies in oat evolution. Briefs in Agriculture. 2012. https://doi.org/10.1007/978-3-642-30547-4_1
22. Seltzer P, Auberty E, Seltzer P, Fourey A, Queney P, Grandjean A, Lasser A. The Algerian Climat. impr. The Typo-Lithoet of J Carbonelreunites Algiers, Algeria. 1946. http://catalogue.bnf.fr/ark:/12148/cb326256944
23. Emberger L. A biogeographic classification of climates. Collection, geolo-zoological laboratory work, Faculty of Sciences. Botanical Service. Montpellier. 1955;7:3-43
24. Stewart P. Pluviothermal quotient and biospheric degradation. Bulletin of the National History Society of North Africa. 1969;59:23-36.
25. Mantel N. Adaptation of karber's method for estimating the exponential parameter from quantal data and its relationship to birth, death and branching processes. Biometrics. 1967;23(4):739-46. https://doi.org/10.2307/2528425
26. Parra-Quijano M, Iriondo JM, Torres E. Applications of ecogeography and geographic information systems in conservation and utilization of plant genetic resources. Span J Agric Re. 2012;10(2):419-29. https://doi.org/10.5424/sjar/2012102-303-11
27. Loskutov IG, Melnikova SV, Bagmet LV. Eco-geographical assessment of *Avena* L. wild species at the VIR herbarium and genebank collection. Genet Resour Crop Evol. 2015;64(1):177-88. https://doi.org/10.1007/s10722-015-0344-1
28. Daget P. The Mediterranean bioclimate: Analysis of climatic forms using the Emberger system. Vegetatio. 1977;34(2):87-103. https://doi.org/10.1007/BF00054477
29. Constandinou S, Nikoloudakis N, Kyratzis AC, Katsiotis A. Genetic diversity of *Avena ventricosa* populations along an ecogeographical transect in Cyprus is correlated to environmental variables. Plos One. 2018;13(3):e0193885. https://doi.org/10.1371/journal.pone.0193885
30. Loskutov IG. The collection of wild oat species of C.I.S. as a source of diversity in agricultural traits. Genet Resour Crop Evol. 1998;45(4):291-95. https://doi.org/10.1023/A:1008643705223
31. Mantai RD, Da Silva JAG, Marolli A, de Mamann ÂTW, Sawicki S, Krüger CAMB. Simulation of oat development cycle by photoperiod and temperature. R Bras de Eng Agríc Ambiental. 2017;21(1):3-8. https://doi.org/10.1590/1807-1929/agriambi.v21n1p3-8
32. Adkins SW, Loewen M, Symons SJ. Variation within pure lines of wild oats (*Avena fatua*) in relation to temperature of development. Weed Science. 1987;35(2):169-72. https://doi.org/10.1017/S0043174500078991
33. Olivares A, Johnston M, Calderón C. Effect of rainfall regimes on seed production and quality of *Avena barbata*. Cien Inv Agr. 2009;36(1). https://doi.org/10.4067/S0718-16202009000100006
34. Klink K, Wiersma JJ, Christopher J, Crawford CJ, Stuthman DD. Impacts of temperature and precipitation variability in the Northern plains of the United States and Canada on the productivity of spring barley and oat. Int J Climatol. 2013;34:2805-18. https://doi.org/10.1002/joc.3877
35. Peltonen-Sainio P. Effect of moderate and severe drought stress on the pre-anthesis development and yield formation of oats. AF Sci. 1991;63(5):379-89. https://journal.fi/afs/article/view/72417/34213
36. Ehlers W. Transpiration efficiency of oat. J Agron. 1989;81:810-17. https://doi.org/10.2134/agronj1989.00021962008100050023x
37. Pandey HC, Baig MJ, Shahid A, Kumar V, Singh P. Plant height and tiller production in *Avena* species under water stress and non stress at vegetative and flowering stage. Afr J Biotechnol. 2013. https://www.ajol.info/index.php/ajb/article/view/130586/12016
38. Diederichsen A. Duplication assessments in Nordic *Avena sativa* accessions at the Canadian national gene bank. Genet Resour Crop Evol. 2008;56(4):587-97. https://doi.org/10.1007/s10722-008-9388-9
39. Boczkowska M, Nowosielski J, Nowosielska D, Podyma W. Assessing genetic diversity in 23 early Polish oat cultivars based on molecular and morphological studies. Genet Resour Crop Evol. 2014;61(5):927-41. https://doi.org/10.1007/s10722-014-0087-4
40. Sheikhehpour S, Bahraminejad S, Cheghamirza K. Morphological and molecular genetic variations of oat genotypes grown in Kermanshah, Iran. Mol Biol Rep. 2014;41(6):4023-30. https://doi.org/10.1007/s11033-014-3271-x
41. Bell GDH. The comparative phylogeny of the temperate cereals. In: Sir J Huchinson, edithors. Essays in crop plant evolution [e-Book]. Cambridge UK: Cambridge University Press, United Kingdom. 1965;70-102.
42. Rajhathy T. Chromosomal differentiation and speciation in diploid *Avena*. Can J Genet Cytol. 1961;3(4):372-77. https://doi.org/10.1139/g61-044
43. Ladizinsky G, Zohary D. Genetic relationships between diploids and tetraploids in series eubarbatae of *Avena*. Can J Genet Cytol. 1968;10(1):68-81. https://doi.org/10.1139/g68-010
44. Shepeleva EM. Karyological research of cultivated and wild species of oat. Doklady AN SSSR. 1939;25(3):215-18.
45. Nishiyama I. The genetics and cytology of certain cereals. Jpn J Genet. 1929;5(1-2):1-48. https://doi.org/10.1266/jjg.5.1
46. Fabijanski S, Fedak G, Armstrong K, Altosaar I. A repeated sequence probe for the C genome in *Avena* (Oats). Theor Appl Genet. 1990;79:1-7. https://doi:10.1007/bf00223778