A quantitative study of some agronomic characters in Sulla (Hedysarum coronarium L.)

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Agronomie 20 (2000) 223–231

Original article

A quantitative study of some agronomic characters in Sulla (*Hedysarum coronarium* L.)

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(Received 24 August 1999; accepted 22 December 1999)

Abstract – Eleven populations of *Hedysarum coronarium* L. collected from North Africa and Southern Italy were analyzed using both univariate and multivariate analyses on a data set for 25 quantitative traits. Broad sense heritabilities were estimated and ranged from 0.072 to 0.703. Seven principal components were found to explain 81.5% of the total variation. On the basis of these 7 principal components, populations were clustered at a similarity level estimated by euclidian distances. Three clusters were identified. Genetic divergence between these clusters was quantitatively measured by using Mahalanobis D^2 distances.

cluster analysis / *Hedysarum coronarium* / heritability / morphological variability / multivariate analysis

Résumé – Étude quantitative de quelques caractères agronomiques chez le Sulla (*Hedysarum coronarium* L.). Vingt cinq caractères morphologiques ont été mesurés chez 11 populations de *Hedysarum coronarium* collectées de l'Afrique du Nord et de l'Italie du Sud. Les données obtenues ont été soumises à une analyse univariée et une analyse multivariée. L'héritabilité au sens large a été estimée ; elle varie entre 0,072 et 0,703. L'ACP révèle que 7 composantes principales absorbent 81.5 % de la variance totale. L'application de la méthode de classification hiérarchique sur la matrice des distances euclidiennes a permis de répartir les populations en 3 groupes. L'utilisation de la distance de Mahalanobis D^2 a permis d'estimer la divergence génétique entre ces groupes.

analyse multivariée / classification hiérarchique / *Hedysarum coronarium* / héritabilité / variabilité morphologique

Communicated by Mervyn Humphreys (Aberystwyth, UK)

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1. Introduction

Hedysarum coronarium L. (2n = 2x = 16), often called "Sulla", has value as a forage species and is of considerable agronomic interest. It is characterized by considerable morphological variability [9, 21], and in Tunisia its distribution is limited to the north of the country. Native plants of this annual species are generally prostrate, with a variable number of prostrate branches having short internodes and small leaflets. Plants with an erect growth habit are rarely found in natural populations, although improved varieties originating from Italy have an erect growth habit such as the "Grimaldi" variety recently introduced into Tunisia. However, this cultivar has a woody stem and is not favored by livestock. Also, greenhouse observations indicate that this variety is sensitive to *Podosphaera leucotricha*, the causal agent of Oïdium. Therefore, it would be useful to breed improved varieties with the good agronomic characteristics of "Grimaldi" (such as an erect growth habit, long leaves, large leaflets and good biomass) combined with those of wild populations of Sulla (such as less woody stems and resistance to Oïdium).

Assessment of morphological variability is an important stage in breeding programs. Seed collections of populations from different geographical origins may contain useful genetic variation. Several studies on different plant species for a number of morphological characters indicate significant variability between populations [12, 13, 18, 22], and the application of hierarchical cluster analysis allows estimation of genetic distances separating populations. Our objective was to study morphological variability in *H. coronarium* in terms of a broad range of traits. The heritability of each trait was estimated and a multivariate analysis was applied to classify the populations with the aim of identifying useful material for breeding programs.

2. Materials and methods

The seeds used in this study were collected from 8 wild populations and from 3 Italian cultivars of *H. coronarium*. The sites of origin are indicated in Figure 1.

About 60 seeds from each population were germinated in petri dishes on wet filter paper. They were manually scarified in order to increase their germination percentage. Seedlings were transplanted to pots, 20 cm in diameter, in the greenhouse of

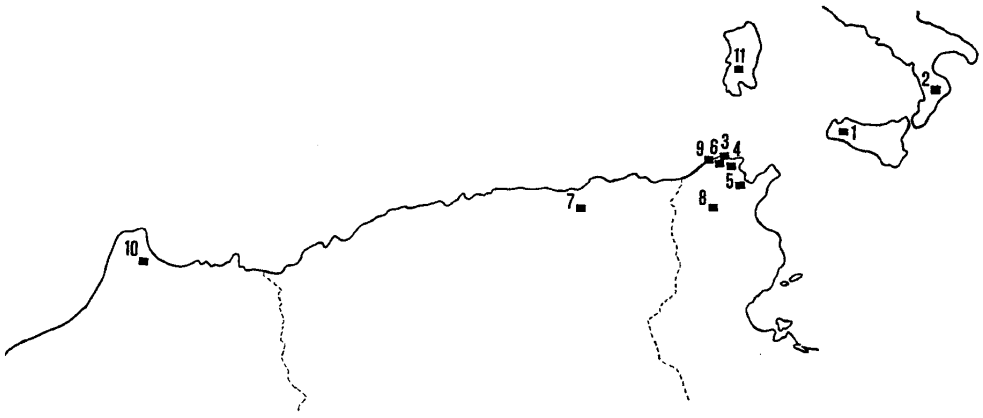

Figure 1. Collection sites of 11 studied *Hedysarum coronarium* populations: 1: Monteroni Sicily (Italy); 2: Vicigliano (Italy); 3: Nadour (Tunisia); 4: El Alia (Tunisia); 5: Tunis (Tunisia); 6: Bougabrine (Tunisia); 7: ALO56 (Algeria); 8: Maktar (Tunisia); 9: Amaïria (Tunisia); 10: Ma 008 (Morocco); 11: Sa 004 Sardinia (Italy).

the Faculté des Sciences de Bizerte, Tunisia. They were arranged in 3 randomized complete blocks with 7 plants per population and per block. Twenty-five morphological characters were recorded. They were divided into 2 categories: vegetative characters and reproductive characters (Tab. I). The data was analyzed by 2-way analysis of variance (ANOVA) with fixed populations and random blocks [6].

Phenotypic variance (p) was divided into environmental (e) and genetic (g) components, since p = g + e. These components were calculated as in [12], with 10 degrees of freedom (d.f.) for between populations, 2 d.f. for between blocks and 20 d.f. for populations × blocks.

Genetic variance was estimated as:

$$g = (MSpop - MSpop \times block) / nb;$$

where: MSpop = population mean square;

MSpop × block = interaction mean square;

n = number of repetitions (= 7);

b = number of blocks (= 3).

Environmental variance was estimated as:

$$e = MSpop \times block.$$

Table I. Quantitative traits measured in *H. coronarium.*

Character	Abbreviation	Signification
Vegetative characters		
C1	FPL	First leaf petiole length
C2	FTL	Total length of the first leaf
C3	FLL	First leaf limb length
C4	FLW	First leaf limb width
C5	NUF	Number of unifoliate leaves
C6	NPL	Total number of prostrate axis
C7	LPA	Length of the axis holding the first inflorescence
C8	NSPA	Number of ramifications of axis in C7
C9	FPA	Number of leaves of axis in C7
C10	LF	Total length of the leaf axilling the first inflorescence
C11	NF	Number of leaflets of C10
C12	FL	Terminal leaflet length of C10
C13	FW	Terminal leaftet width of C10
C14	LOF	Length of the erect axis
C15	PPL	Length of the longest prostrate axis
C16	NEN	Number of internodes of the longest prostrate axis
C17	TSL	Length of all aerial axes
Reproductive characters		
C18	FD	Flowering date
C19	NIF	Number of inflorescences
C20	NMF	Flowers / inflorescence
C21	D1	Total length of the inflorescence (cm)
C22	D2	Insertion level of the first flower on the inflorescence (cm)
C23	EL	Standard petal length (cm)
C24	CL	Keel petal length (cm)
C25	CW	Keel petal width (cm)

For the variables C_{20} to C_{25} which are associated with reproductive characters, each value represents a mean of 5 measures on 5 different flowers (or inflorescences) per plant.

The determination of g and e allowed between-population heritabilities (H^2) to be calculated as [12, 13]:

$$H^2 = \frac{g}{g + e} \cdot$$

Principal components analysis (PCA) was carried out after standardization of the original data to zero means and unit variance. This analysis defined principal components which were synthetic and independent variables representing linear combinations of the original correlated measured variables. Euclidian distances were established from the population means of PCA scores, and a cluster analysis (average linkage method) was performed.

3. Results

The results of the 2-way analysis of variance for each measured trait are shown in Table II. Of the 25 traits measured, 4 failed to show significant differences between-populations and were omitted from further analyses. These included the total length of the first leaf (FTL), the dimensions of the first leaf (FLL and FLW), and the number of ramifications of the axis holding the first inflorescence (NSPA).

For the 21 characters which demonstrated significant population differences, genetic (g) and environmental (e) components of between-population variation were calculated and are given in Table III together with estimates of between-population heritabilities (H^2). The character "length of the erect axis" (LOF) showed the greatest heritability (0.703). This character was successfully used in selecting the variety Grimaldi (which has a well-developed erect axis). This variety is extensively commercialized and intensively cultivated in Tunisia. The other vegetative characters gave heritabilities which varied between 0.072 (for FPL) and 0.602 (for LF). For the reproductive characters (H^2 = 0.144–0.607), the heritability was distinctly larger for traits associated with floral part dimensions (CL, CW and EL) and inflorescence dimensions (D1 and D2). Higher values of H^2 correspond to characters which show large population differences as it is shown by the strong positive correlation between heritability H^2 and the Fp ratio (r = 0.942).

Table II. Variance components for measured traits in *H. coronarium*.

Character	MSp	MSb	MSpxb	MSe	Fp
FD	14.884	2.0554	1.4046	0.2521	10.53[a]
CL	13.9444	0.2096	0.6408	0.3905	21.76[a]
CW	12.8295	0.2268	0.6066	0.4501	21.15[a]
NMF	12.1957	9.5627	1.3552	0.3122	9.00[a]
LOF	16.35	0.1233	0.3226	0.3020	50.69[a]
NPL	7.0767	4.6896	0.7647	0.6796	9.25[a]
PPL	9.8184	1.3974	0.9133	0.5594	10.75[a]
NEN	9.1721	5.286	0.7401	0.5702	12.39[a]
LPA	11.0592	10.3138	0.5449	0.5363	20.30[a]
NSPA	0.9017	1.0935	1.0448	0.5080	0.86*
FPA	9.8416	21.6	0.8366	0.4964	11.76[a]
LF	13.7467	1.0398	0.4200	0.4144	32.73[a]
NF	8.7784	0.4287	0.6220	0.6165	14.11[a]
FL	7.8532	0.5548	0.6156	0.5341	12.76[a]
FW	7.1025	0.3944	0.8016	0.6946	8.86[a]
FPL	5.2399	0.0388	2.0217	0.6924	2.59[b]
NUF	7.9982	5.3629	1.4131	0.5608	5.66[a]
EL	14.4510	0.1463	0.5888	0.3896	24.54[a]
D1	15.6009	0.1942	0.4665	0.4460	33.44[a]
D2	16.3004	1.5675	0.5559	0.3881	29.32[a]
NIF	6.3649	0.1930	1.4001	0.6819	4.55[a]
TSL	4.9347	4.5704	1.4508	0.6582	3.40[b]
FLL	4.9014	0.1395	2.4070	0.6382	2.04*
FLW	2.8651	4.6357	2.8069	0.6232	1.02*
FTL	6.5460	0.0969	2.8141	0.6701	2.33*

MSp: mean square population; MSb: mean square block; MSpxb: mean square interaction; MSe: residual mean square; Fp: F test of population effect.
[a] Population effect significant at P < 1%; [b] population effect significant at 5%; * population effect not significant at 5%.

Standardization of phenotypic raw data is necessary due to the large differences in the scale of measurement [12, 13, 23]. The data matrix obtained was submitted to various multivariate analyses. PCA was carried out using the correlation matrix for all the 21 characters showing a significant genotype effect, and a hierarchical cluster analysis of populations was performed.

Table III. Genetic (g) and environmental (e) components of variance and between population heritabilities (H^2) for 21 traits.

Character	g	e	H^2
FD	0.6418	1.4046	0.314
CL	0.6335	0.6408	0.497
CW	0.5820	0.6066	0.490
NMF	0.5162	1.3552	0.276
LOF	0.7632	0.3226	0.703
NPL	0.3006	0.7647	0.341
PPL	0.4240	0.9133	0.317
NEN	0.4015	0.7401	0.352
LPA	0.5007	0.5449	0.479
FPA	0.4288	0.8366	0.339
LF	0.6346	0.4200	0.602
NF	0.3884	0.6220	0.384
FL	0.3446	0.6156	0.359
FW	0.3000	0.8016	0.272
FPL	0.1575	2.0217	0.072
NUF	0.3135	1.4131	0.182
EL	0.6601	0.5888	0.529
D1	0.7207	0.4665	0.607
D2	0.7497	0.5559	0.574
NIF	0.2364	1.4001	0.144
TSL	0.1659	1.4508	0.103

Table IV. Eigenvalue, percentage variance accounted for and cumulative variance for the first 7 principal components identified.

Component	Eigenvalues	Percentage variance	Cumulative variance
1	6.9866	33.3	33.3
2	3.7782	18.0	51.3
3	1.5860	7.6	58.8
4	1.5509	7.4	66.2
5	1.3253	6.3	72.5
6	1.0231	4.9	77.4
7	0.8634	4.1	81.5

Based on eigenvalues of the order of 0.8 as was suggested by [20], the PCA grouped the variables into 7 components (Tab. IV). These 7 principal components explained 81.5% of the total variance. The loadings are shown in Table V; correlation coefficients between the original data (standardized matrix) and the PCA scores were also calculated. Table V presents data which allows us to interpret each principal axis by its correlations with the original variables. If we consider the plane defined just by the first 2 principal components, which accounted for 51.3% of the total variation, 2 groups of characters can be distinguished (Fig. 2):

(i) The first group includes variables positively correlated to axis 1. These are the dimensions of floral parts (CW, CL, EL) and of the inflorescence (D_1, D_2), the mean number of inflorescences (NMF) and the length of the erect axis (LOF).

(ii) The second group of variables associated with axis 2 essentially represents the vegetative development of the plant. This axis is negatively correlated to characters NPL, PPL, NEN, TSL and also to the total number of inflorescences (NIF).

In order to improve the hierarchical cluster analysis of populations, we included just the 7 first principal components, accounting for 81.5% of the total variation. For this, we used the matrix of euclidian distances calculated from the population mean PCA scores. The clustering method applied was that of average linkage which is based on the regrouping of populations at similarity level estimated by euclidian distances. The dendrogram obtained is represented in Figure 3. It shows that at a distance of the order of 2.84, the 11 populations are distributed into 3 groups:

Group 1 consists of the 3 Italian populations (Monteroni, Vicigliano and Sa004) and 2 populations of different geographical origin: a Moroccan population (Morocco 008) and a Tunisian population (Nadour).

Group 2 includes only natural populations originating from Tunisia (El Alia, Bougabrine, Maktar and Tunis).

Group 3 associates the Algerian natural population (Al056) with the Grimaldi cultivar originating from the Tunisian population Amairia.

Mahalanobis distances representing the extent of genetic separation between the groups of populations are given in Table VI. This information may be used to determine which interpopulation crosses

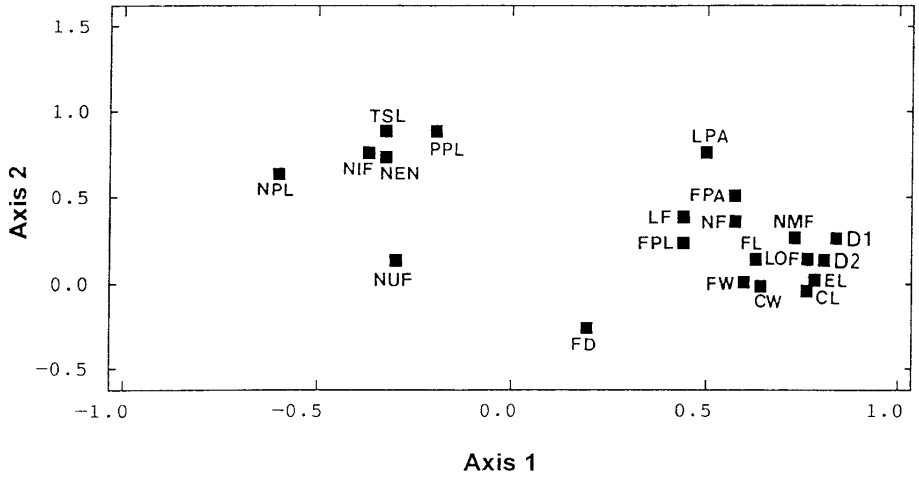

Figure 2. Scatter plot of variables for the first 2 principal components.

Table V. Loadings for the 7 principal components derived from phenotypic correlations between the measured traits.

Character	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
FD	0.188	–0.265	0.420	–0.623	–0.355	0.085	0.069
CL	0.772	–0.031	0.120	0.369	–0.328	0.068	0.093
CW	0.649	–0.085	0.100	0.528	–0.367	0.134	0.014
NMF	0.743	0.192	–0.061	–0.279	0.085	0.059	–0.236
LOF	0.779	0.092	–0.338	0.037	0.259	0.002	0.201
NPL	–0.592	0.618	–0.042	0.173	0.019	0.182	0.049
PPL	–0.200	0.779	0.322	–0.069	–0.254	–0.150	–0.213
NEN	–0.329	0.733	0.344	0.070	–0.254	–0.181	–0.001
LPA	0.495	0.666	0.102	–0.353	–0.046	0.087	–0.003
FPA	0.575	0.474	–0.003	–0.220	–0.029	0.203	0.310
LF	0.447	0.285	0.117	0.006	0.201	–0.532	0.488
NF	0.557	0.372	–0.367	–0.055	–0.157	–0.239	0.116
FL	0.642	0.047	0.489	0.216	0.378	–0.015	–0.200
FW	0.598	–0.001	0.407	0.260	0.484	–0.052	–0.219
FPL	0.428	0.164	–0.451	0.060	–0.036	0.397	–0.077
NUF	–0.287	0.008	0.463	–0.013	0.255	0.548	0.446
EL	0.771	–0.086	0.126	0.350	–0.417	0.064	0.041
D1	0.791	0.078	–0.063	–0.241	0.162	0.033	–0.090
D2	0.838	0.196	–0.059	–0.188	0.050	0.059	–0.137
NIF	–0.373	0.696	–0.196	0.343	0.182	0.003	0.086
TSL	–0.317	0.816	–0.076	0.028	0.055	0.207	–0.179

are likely to give the most heterosis through genetic recombination [13]. The highest genetic divergence occurred between clusters 2 and 3 (D^2 = 25.3457).

In order to identify the characters which discriminate between the 3 groups of populations, the means and standard deviations of traits were calculated for each group separately. Comparisons of

Table VI. Matrix of Mahalanobis squared distances between the 3 groups.

Group	1	2	3
1	0.0000	7.0293	20.7824
2		0.0000	25.3457
3			0.0000

trait means between groups using an F test (Tab. VII) show that the means differ significantly for all the characters, at least for 2 of the 3 groups. Group 1 possesses the highest means for 5 traits: date of flowering, length of the longest prostrate axis, number of internodes, length of the axis holding the first inflorescence and total length of all aerial axes. Group 2 possesses the highest means for 3 characters: number of unifoliate leaves, number of prostrate axes and the total number of inflorescences. Group 3 possesses the highest means for the 13 other characters which are associated with flower and inflorescence dimensions, length of the erect axis and leaf dimensions.

4. Discussion

Although the evaluation of heritability by the method of Humphreys [12, 13] is approximate, it provides initial values for decisions on programs of varietal selection [11, 14]. Our study showed that the character "length of the erect axis" (LOF) gave the highest between-population heritability. Estimates of heritability showed considerable differences among the other vegetative traits (H^2 = 0.072–0.602). Reproductive characters maintained by natural selection allows this allogamous species [5] to be adapted to entomophilic pollination. Flowers of large size and bright in color (in the red spectrum) attract pollinators, notably bees [10]. High heritabilities for the flower parts indicate a potential for selection on flower size. Large flowers are considered to be an important component of reproductive success [7]. Heritabilities found in our study are in good agreement with those found for other species [19, 25]. However in our study, we estimated broad sense heritabilities which represent a summary evaluation of the total level of genetic variation. It could be biased upwards by a non-additive genetic variation [15, 16], and is considered to represent the upper limits for narrow-sense heritability [8, 24].

Information obtained through PCA may assist plant breeders to identify a limited number of highly differentiated populations for use in programs of crossing and selection [22]. It can be seen from the clustering pattern shown in Figure 3 that the grouping of populations does not strictly represent the geographic origin, since very distant populations such as the grouping of the Tunisian population Nadour and the Moroccan population Morocco 008

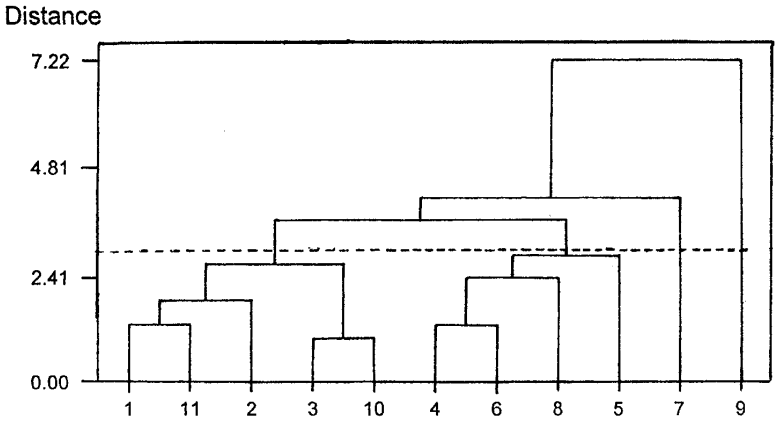

Figure 3. Hierarchical classification of the 11 populations based on euclidian distances.

Table VII. Comparison of means for each group by the Fisher test.

Variable	Group 1 (n = 105)		Group 2 (n = 84)		Group 3 (n = 42)		
	Mean	SD	Mean	SD	Mean	SD	SDc
DF	152.42 (a)	19.17	149.93 (a)	9.36	141.69 (b)	17.68	15.99
CL	1.4334 (a)	0.0777	1.3134 (b)	0.1232	1.5495 (c)	0.0846	0.0978
CW	0.67572 (a)	0.05989	0.63285 (b)	0.05515	0.76964 (c)	0.04144	0.05525
NMF	30.624 (a)	7.156	23.845 (b)	5.112	33.524 (a)	13.772	8.184
LOF	18.34 (a)	22.39	2.83 (b)	5.80	64.20 (c)	41.06	23.33
NPL	5.638 (a)	2.122	6.583 (b)	2.396	3.595 (c)	2.285	2.254
PPL	90.74 (a)	22.97	68.01 (b)	16.63	45.79 (c)	29.98	22.43
NEN	13.743 (a)	3.217	11.274 (b)	2.175	8.167 (c)	4.818	3.258
LPA	73.36 (a)	16.84	54.35 (b)	16.16	63.25 (c)	28.56	19.27
FPA	10.924 (a)	1.965	9.179 (b)	2.340	12.310 (c)	4.199	2.631
LF	10.630 (a)	2.163	6.940 (b)	1.507	12.657 (c)	5.831	3.012
NF	8.905 (a)	1.355	7.250 (b)	1.307	9.262 (a)	1.822	1.434
FL	3.239 (a)	0.5141	2.8202 (b)	0.5222	3.5857 (c)	0.6547	0.5449
FW	2.1524 (a)	0.3153	1.9143 (b)	0.3687	2.4357 (c)	0.3925	0.3501
FPL	3.0867 (a)	0.8846	2.8464 (a)	0.7911	3.9167 (b)	1.457	0.9831
NUF	3.695 (a)	0.748	4.750 (b)	1.472	3.548 (a)	0.670	1.06
EL	1.6031 (a)	0.1342	1.4610 (b)	0.152	1.7965 (c)	0.1152	0.1379
D1	9.467 (a)	2.012	7.148 (b)	1.614	10.668 (c)	4.881	2.661
D2	5.082 (a)	1.676	3.123 (b)	0.838	6.284 (c)	3.371	1.892
NIF	31.50 (a)	16.94	31.86 (a)	14.79	24.40 (b)	14.36	15.73
TSL	451.0 (a)	224.2	388.2 (b)	210.0	241.4 (c)	137.1	205.8

SD: Standard deviation; SD_c: cumulated standard deviation.
a, b, c : The means followed by the same letter are not significantly different at the 5% probability level.

were found to be associating with Italian populations. In other studies, it was also found that populations clustered in different groups irrespective of their countries of origin [2, 4]. On the other hand, it has been determined that origin can be a simple means of partitioning variation in germplasm collections. There is more relatedness between entries from a given country than between countries, even when they are neighboring countries [17].

It is important to consider the practical significance of grouping the populations into different clusters and estimating the genetic distance between them, which represents an index of genetic diversity among clusters [2]. It may be useful to produce crosses between genotypes belonging to the clusters separated by large estimated distances [2]. Success might therefore be expected through making crosses between the Tunisian natural populations in cluster 2 and the Amairia population or Algerian population (ALO56) in cluster 3. However, in selecting parental material, important characteristics such as pest and disease resistance, quality of produce, stability of performance and cross-compatibility should also be considered [1, 2]. It seems that the combined effects of genetic drift and selection could have more influence on genetic diversity than geographical distance [2].

Traits discriminating the 3 groups obtained in this study can be identified via an F test (Tab. VII). The results reflect a certain “gigantism” for morphological traits suitable for agronomic purposes: large leaflets and erect habit in group 3. It has been shown that alien plants of *Lotus corniculatus* L. could be characterized by such vegetative characters [3].

In conclusion, the multivariate approach allowed a detailed characterization of populations of *H. coronarium* in terms of traits of agronomic interest. Valuable material, potentially useful in future breeding programs, has been identified such as the

Algerian population (AL056) characterized by its erect growth habit and the Tunisian population (Maktar) which produces more inflorescences and prostrate axes. These populations may be crossed to combine desirable attributes, including resistance to Oïdium, thereby providing an advantage over Italian cultivars.

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