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The environmental effect on crown shape of common cypress clones in the Mediterranean countries

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Abstract – Crown shape of four different clones planted out in six experimental fields located in five European countries are described and compared using discriminant analysis. The correlations among the considered traits were computed for each clone in each location. The results of the discriminant analysis showed that the locations in which trees have grown have a greater discriminating effect than the clones themselves. It means that the ecological factors that characterize a particular location effectively mould the shape of the tree's crown. The phenotypic correlations between characters were altered when trees grow in different conditions. For one of the clones taken into account these changes are due to the differential phenotypic plasticity of the considered traits. This characteristic may have considerable implications on the breeding programs. A question is whether it is worth the effort to select clones from a particular environment and then use them under very different conditions of habitat.

common cypress / crown shape / discriminant analysis / phenotypic plasticity

Résumé – L'effet du milieu sur la forme des houppiers du cyprès. On décrit ici la forme des houppiers de 4 clones différents plantés dans 6 essais expérimentaux de 5 pays européens et on les compare entre eux par une analyse discriminante. Les corrélations entre les traits considérés ont été calculées pour chaque clone dans chaque localité. Les résultats des analyses discriminantes ont montré que les localités où les clones ont poussé sont plus discriminantes que les clones. Cela signifie que les facteurs écologiques caractéristiques d'une localité sont capables de modeler la forme des houppiers. Les corrélations phénotypiques entre caractères sont altérées si les arbres ont poussé dans des conditions différentes. Pour un des clones étudiés ces changements sont provoqués par la différente plasticité phénotypique des traits considerés. Cette caractéristique peut avoir des profondes implications sur les programmes d'amélioration génétique. La question est de savoir s'il vaut la peine de sélectionner des clones provenant d'un habitat particulier pour les employer dans des conditions très différentes.

cyprès / houppiers / analyse discriminante / plasticité phénotypique

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1. INTRODUCTION

The cypress plays a central role in the Mediterranean basin landscapes. Its uses are three-fold: ornamental tree, afforestation and as a wind-breaking barrier. In recent decades, however, the cortical canker, caused by the deuteromycete *Seiridium cardinale* (Wag.) Sutton and Gibson, caused serious damage throughout Europe causing fears for the future of the existing trees and making new cypress plantations inadvisable. For this reason, cypress improvement programs for resistance were set up with the attempt to cultivate resistant clones throughout wide-reaching territories and areas with highly diverse pedoclimatic conditions. Some patented clones, resistant to the canker, are commercially available [10, 11]. Selection also took into account the shape of the crown because clones have to serve for ornamental use and as wind-breaking barriers. The strong effect of environment and of environment by genotype interaction on cypress clones has been already noted [14], but while the genetic basis for resistance has been studied or is under further investigation, there is little information about the morphological adaptability of the selected clones to different environmental conditions. Two environmental components, climate and soil, determine most of the evolutionary adaptedness of plants, being an immediate source of limiting factors for the growth of plants, as nutrients and energy [5]. Adaptedness, according to Allard [1], is the degree to which an organism is able to live and reproduce in a given set of environments, the state of being adapted, and adaptation is the process of becoming adapted or more adapted. Many studies regard phenotypic adaptadness of plants to the different environment. Recently de la Vega [5] defined that the ecogeographical distribution of species and ecotypes and the existence of different physiological mechanisms and developmental patterns are good evidence of plant adaptedness to soil and climate. Modifications of the phenotype is common for quantitative (polygenic) characters of organisms that inhabit heterogeneous environments [22]. The profile of phenotypes produced by a genotype across environments is called "norm of reaction" [19]; the extent to which the environment modifies the phenotype is termed phenotypic plasticity [3, 8]. Falconer [6] suggested that a character expressed in two environments can be viewed as two characters which are genetically correlated.

Because phenotypic plasticity of a trait can be under genetic control, it has to be considered as a trait itself. Considering this, the plastic response of a trait could evolve independently from the trait itself. Thus, plasticity and reaction norm can follow different evolutive paths [16, 18]. Different traits can show, accordingly, different patterns of response to environmental factors.

The main purpose of this research was to measure the influence of the environmental factors on crown shape of cypress clones, and to discuss the current methods for the definition of the crown characteristics.

2. MATERIALS AND METHODS

The data analysed in this study derived from a series of tests carried out in the frame of the EC CAMAR Project and AIR Cypress Project.

Pedoclimatic and topographic characteristics of the experimental sites, are listed in *table I*.

In February 1988 four clones (43F, 47F, 171F, 318F) were grafted onto 1-year old *C. sempervirens* seedlings in Firenze (Italy). Ramets were transplanted in pot (18 × 10 cm) in January 1989, sent to european partners in March and lastly planted out in the experimental plantations in November 1989.

In November 1994, in each experimental field, by each research unit, the following morphological characteristics were measured on 10 ramets for each of the clones:

1) Diameter of the trunk at breast height (cm) (*D*);

Table I. Principal pedo-climatic and topographic characteristics of the sites of the trials in the different countries.

	Mean Maximum Temperature of hottest month (°C)	Mean Minimum Temperature of coldest month (°C)	Rainfall (mm)	Soil	Lat.	Long.	Altitude a.s.l. (m)
Fréjus (France)	29.2	2.8	787.4	sandy	43°26' N	6°44' E	4
Megalopolis (Greece)	22.7	6.2	873.3	silty loam	37°25' N	22°6' E	450
Karistos (Greece)	26.8	10.3	680.2	sandy loam	38°01' N	24°25' E	10
Roselle (Italy)	30.0	4.0	452.0	clayey	42°48' N	11°05' E	5
Lisbon (Portugal)	29.1	7.1	756.4	clayey	38°42' N	9°11' W	150
Jerica (Spain)	16.5	9.3	477.6	clayey	40°10' N	0°10' W	750

2) Total height (m) (H_{tot});
3) Diameter of the crown at 1/3 of the tree's height (cm) ($D_{1/3}$);
4) Diameter of the crown at 1/2 of the tree's height (cm) ($D_{1/2}$);
5) Diameter of the crown at 2/3 of the tree's height (cm) ($D_{2/3}$).

Diameters were obtained by two crossed measures.

In order to describe the differences in crown shape, 3 "thinness" indexes for the crown were derived by calculating the ratio between total height of each cypress and crown width at 1/3; 1/2; 2/3 of tree's height.

6) Index 1 = $H_{tot}/D_{1/3}$;
7) Index 2 = $H_{tot}/D_{1/2}$;
8) Index 3 = $H_{tot}/D_{2/3}$.

In the statistical analysis Diameter of the trunk, Total Height and the three Indexes were considered.

The following linear model was used to analyse original data and indexes:

$$y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijk}$$

where y_{ijk} = individual observation belonging to the kth ramet (k = 1, 2, ..., 10), of the jth clone (j = 1, 2, ..., 4) at the ith location (i = 1, 2,..., 6), μ = overall mean; α_i = effect of the i-th "location"; β_j = effect of the j-th "clone"; $\alpha\beta_{ij}$ = location by clone interaction effect; ε_{ijk} = experimental error.

Homogeneous groups of means for each variable were identified by Tukey test with respect to clones and locations, respectively.

In order to verify whether the hypothesis that trait correlations were independent from environment, Pearson phenotypic product moment correlation matrices were derived within each clone in each location. All correlations were z-transformed and tested for homogeneity across locations [20]. Lack of homogeneity indicates that the correlation is altered by environment [17].

Moreover, the stability of the shape measurements was also assessed by means of a Multiple Discriminant Analysis procedure applied to the 3 thinness indexes. As discriminant factor was considered, separately, clones and locations. The discriminant power, assessed through resubstitution procedure, was considered as an additional index of relative stability of the trait, within clones and within location respectively.

The Statistical Analysis was performed by means of the Statistical Analysis System (SAS) package, Version 6.12.

3. RESULTS

Figure 1 shows the virtual images derived from the means of the measurements taken of ten ramets on clone 318 F in each of the six locations. As may be seen, there exist not only differences in size from one location to the next, but also differences in shape, that is, in the appearance of the crown.

The analysis of variance, applied to the original observations and to the indexes, allowed us to refute - in most of the cases - the hypotheses of equality of clone means, sites and interaction effects. The results are reported in *table II*.

The main results related to the proposed indexes are shown in *table III*, in particular with respect to the equality test on the means of the various clones in the various locations. As is clear from the Tukey test, the indexes differ significantly from site to site, even though they refer to plants belonging to the same genotype (clone).

The qualitative differences in correlation structure among locations is apparent from the correlation networks of the significant intercorrelations in each treatment *(figure 2)*. In the analysis of heterogeneity of

Table II. Relevant results from the ANOVA model (Analysis III) applied to the data of 4 clones of Cypress grown in 6 different locations. [MS = Mean Squares: ** = Null Hypothesis rejected at the $P \leq 0.01$ level; ns = Null Hypothesis accepted; Df = Degrees of Freedom; R^2 = Coefficient of Determination].

		Total height		Diameter		Index 1		Index 2		Index 3	
Items	Df	MS	R^2	MS	R^2	MS	R^2	MS	R^2	MS	R^2
Locations (L)	5	221714.4 **	0.46	13986.9 **	0.07	13.3337 **	0.46	12.7999 **	0.32	92.0399 **	0.37
Clones (C)	3	23328.4 **	0.03	2007.4 *ns*	0.01	5.8030 **	0.12	4.9439 **	0.07	6.9810 *ns*	0.02
L × C Interaction	15	15309.4 **	0.10	5441.2 *ns*	0.08	1.3369 **	0.14	1.5069 **	0.11	8.7470 **	0.10
Error	204	4853.9		3911.72		0.1950		0.4859		3.0961	
R^2 (full model)			0.59		0.16		0.72		0.51		0.50

Table III. Means, standard deviation and results of the Tukey test on individual means for each clone in each site. Indexes 1 ÷ 3 are derived variables of the shape of the crown (thinness indexes) as described in the text. Homogeneous means of the considered index are indicated by the same letter. STD = standard deviation.

	43F	**Height**	**Diameter**	**Index1**	**Index2**	**Index3**
Frejus (F)	Mean	415	75.4	2.54ab	3.03	4.30ab
	STD	64.03	15.07	0.67	0.90	1.58
Roselle (I)	Mean	328.8	46.1	2.13 a	2.27	3.32 a
	STD	27.85	5.27	0.37	0.38	1.15
Megalopolis (GR)	Mean	345.5	44	3.35 b	3.73	4.56 ab
	STD	13.43	3.65	0.39	0.39	0.59
Karistos (GR)	Mean	230	25.1	2.41 ab	3.31	3.59 ab
	STD	23.01	5.05	0.38	0.55	0.85
Jerica (SP)	Mean	366.9	50.8	1.73 a	2.36	6.18 b
	STD	46.29	10.96	0.37	0.81	3.11
Lisbon (P)	Mean	418.6	53.9	2.65 a	3.85	4.70 a
	STD	63.94	11.14	0.74	1.38	0.90
	47F	**Height**	**Diameter**	**Index1**	**Index2**	**Index3**
Frejus (F)	Mean	342.5	54.8	2.99 a	3.28 a	5.73 ab
	STD	18.74	10.10	0.53	0.47	1.41
Roselle (I)	Mean	308.2	44.4	2.25 b	2.60 b	3.34 ac
	STD	30.54	8.18	0.20	0.26	0.61
Megalopolis (GR)	Mean	365.5	52.8	4.13 d	4.42 d	5.05 ac
	STD	17.39	4.76	0.28	0.22	0.29
Karistos (GR)	Mean	247	34.1	2.41 b	2.94 d	3.31 c
	STD	17.08	6.02	0.19	0.43	0.34
Jerica (SP)	Mean	329	46.5	1.75 c	2.18 c	7.03 b
	STD	17.61	8.66	0.14	0.25	2.95
Lisbon (P)	Mean	408	58.4	2.18 b	2.97 b	5.08 ac
	STD	22.51	6.93	0.18	0.54	0.92
	171F	**Height**	**Diameter**	**Index1**	**Index2**	**Index3**
Frejus (F)	Mean	369.5	51.8	2.32 a	3.07 a	5.71 a
	STD	47.81	10.37	0.54	0.97	1.61
Roselle (I)	Mean	298.25	33.9	1.68 bc	2.05 bc	3.99 a
	STD	44.66	9.09	0.19	0.36	0.72
Megalopolis (GR)	Mean	316.8	42.4	1.98 ab	2.28 bc	3.06 a
	STD	12.30	4.06	0.16	0.20	0.35
Karistos (GR)	Mean	251.5	31.7	2.11 ab	2.79 ac	3.22 a
	STD	15.99	3.04	0.32	0.33	0.50
Jerica (SP)	Mean	346.7	47.3	1.23 c	1.63 b	10.25 b
	STD	59.58	12.94	0.27	0.60	4.63
Lisbon (P)	Mean	474	68.5	2.09 ab	2.46 ac	3.63 a
	STD	50.15	12.37	0.22	0.43	0.65
	318F	**Height**	**Diameter**	**Index1**	**Index2**	**Index3**
Frejus (F)	Mean	445.2	80.4	2.33 ad	2.77 ab	4.74 a
	STD	43.01	16.99	0.37	0.85	1.53
Roselle (I)	Mean	298.5	40.5	2.31 ad	2.25 ab	2.90 a
	STD	37.75	10.93	0.09	0.11	0.18
Megalopolis (GR)	Mean	364.5	48	4.01 c	4.32 c	4.92 ab
	STD	17.23	4.59	0.21	0.21	0.26
Karistos (GR)	Mean	293.5	42.4	2.52 d	3.03 b	3.94 a
	STD	29.06	9.00	0.37	0.60	0.59
Jerica (SP)	Mean	320	37.78	1.83 b	2.13 a	7.24 b
	STD	61.24	14.58	0.34	0.87	4.06
Lisbon (P)	Mean	439	66.8	2.15 ab	2.46 ab	3.76 a
	STD	41.69	8.06	0.13	0.30	0.37

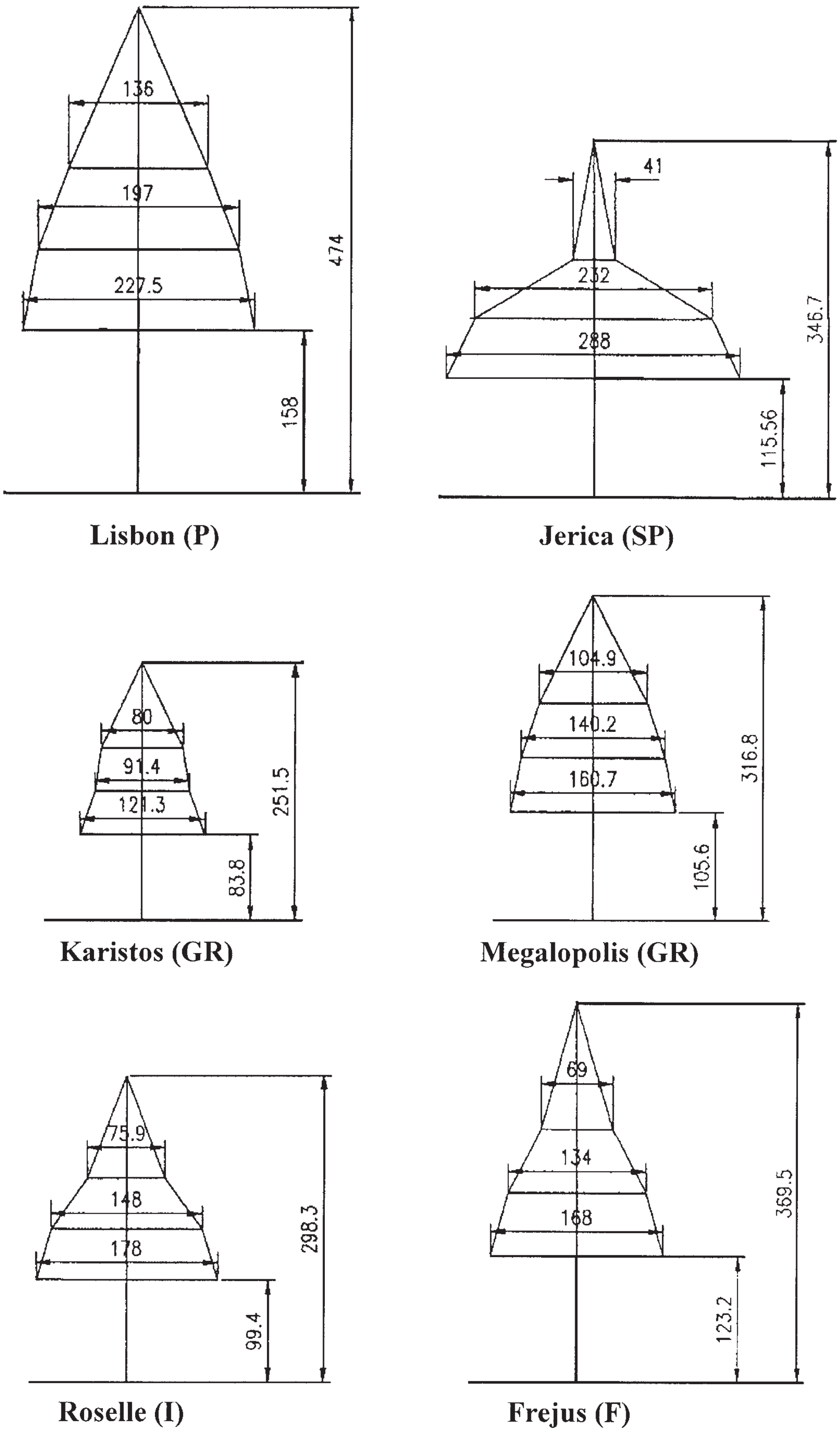

Figure 1. Virtual images of the crown of clone 318F, obtained from the mean of the measurements made on 10 ramets in each of the six locations.

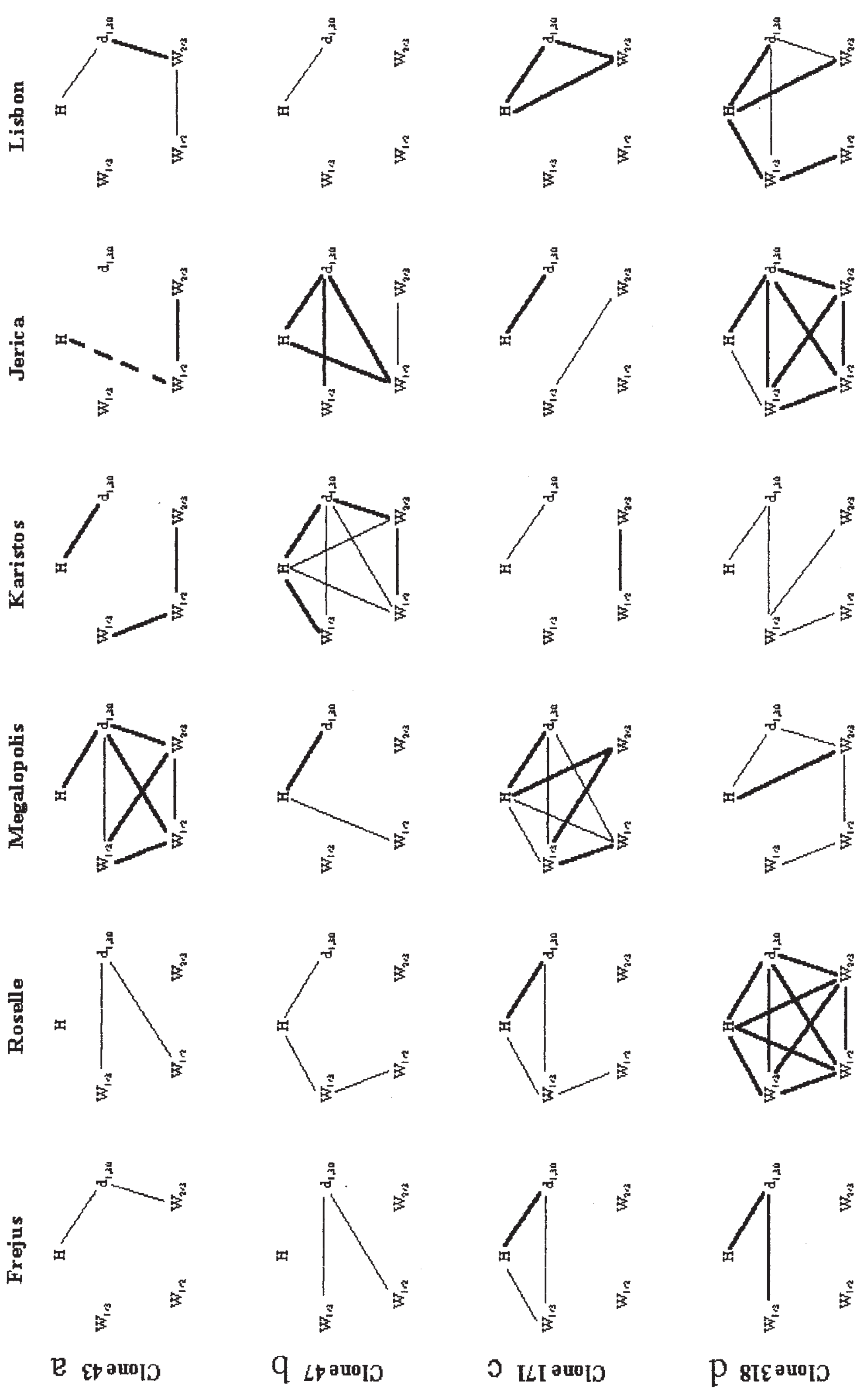

Figure 2. (a-d). Correlation networks of phenotypic correlations within locations for clone 43 (a), clone 47 (b), clone 171 (c) and clone 318 (d). The significant correlations among traits within each location are represented by lines connecting the traits. Solid lines indicate positive correlation, dashed negative. Thick lines indicate a correlation significant at $P < 0.001$, thin lines $P < 0.05$.

individual correlations, only 5% of 10 correlations are expected by chance to show significant heterogeneity at the $P < 0.05$. Clone 43 and clone 171 (*figures 2A* and *2C* respectively) have only one significant correlation respect to the 0.5 expected by chance ($\chi^2 = 0.53$, NS). Clone 47 *(figure 2B)* does not show any significant change across locations ($\chi^2 = 0.53$, NS). On the other hand, there are 3 character correlations in clone 318 *(figure 2D)* which exhibits significant changes across locations ($\chi^2 = 13.16$, $P < 0.001$). The correlations of clone 318 were altered by environmental factors.

An alternative analysis of the stability of the genotypes was therefore carried out by means of discriminant analysis, with the discriminating factors being the clone and the location, respectively. It was expected that the highest discriminant power would be found when the genotype was used as discriminating factor, given that the clones are expected to preserve their crown characteristics whatever the locations in which they are planted. The discriminant analysis allowed this hypothesis to be tested; the belonging of individuals ramets to a specific clone in a location was noted "*a priori*" known. Thus, by means of the "resubstitution procedure" it was possible to estimate just how many of the individuals were correctly reclassified into the classes to which they belong on the basis of the variables measured and on the basis of the discriminant function that was estimated as a result of such measurements. The principal results are reported in *table IV*.

It became clear that the individuals that were correctly classified on the basis of the "clone" criterion ranged from a minimum of 23.33% (47 F) to a maximum of 43.86% (171 F). The "location" criterion classified - more effectively - from 25.00% (Lisbon, P) to 72.50% (Megalopolis, GR). This contradicts the expected result and underlines how environmental characteristics influence the development of individuals. It was therefore possible to test the average characteristics of the "shape" taken on in the various locations, classifying it on the basis of the thinness indexes.

4. DISCUSSION

From the analysis of variance, and from the Tukey test, it emerged that the element that distinguishes the greatest number of groups is index 1, which reports the thinness of the tree at 1/3 of its total height. In fact, the differences in the cypress crown shapes were most pronounced near the base of the trees and it is here that is found the distinguishing element between trees with a "flame" shape and those with a "pencil" shape. The analysis of heterogeneity of individual correlations revealed clone 318 as more plastic than the other taken in exam, according to Schlichtling [17]. The correlation networks revealed, even if not statistically significant, marked differences in correlation structure of the other three clones. The phenotypic correlation between two characters is the net result of the influences of both genetic and environmental correlations between those characters [7]. Changes in phenotypic correlations between characters will result when the change in environment produces different types of plastic responses by characters. The manner in which changes in correlations structure across environments affect fitness, and alter the intensity of and response to selection could have a significant impact on the evolutionary potential of populations [16].

If the location has a greater discriminating effect than has the clone itself, as emerged from the results of the discriminant analysis, it means that cypress clones take on different shapes in accordance with variations in environmental conditions and that the ecological factors that characterize a particular location effectively mould the shape of the tree's crown. This fact may have negative consequences on the use of clones for ornamental purposes, where the shape of the crown is of central importance and, to a lesser degree, in agricultural usage where cypresses serve as wind-breaking hedges.

As the results revealed, the shape of the crown, and the correlationships among its components could be altered by environmental factors. Thus, it is possible that the change from the selection site to another could lead to different shaped trees. The results here discussed are comparable to those reported for Australian cotton aphid where the morphology of the aphid is affected by host plant far more strongly than by genetic differences among means of local populations [23]. Morphological adaptedness is, therefore, an evolutive mechanism shared in other kingdoms.

Distinct environmental conditions could lead to different development in apex and lateral branches growth and, therefore, to a different crown architecture of cypress clones. It seems that the effect of alternative environments is variable for the various crown levels leading to a change in phenotypic correlations existing among the considered characters. Plasticity in growth rate of apex and lateral branches increases the variety in crown architecture within the *C. sempervirens* species.

The cypress clones under examination in this study, though growing in completely different habitats, adapted morphologically, thanks to their phenotypic plasticity. Plasticity is an important characteristic because allowed selected clones to be used in a wide range of different pedo-climatic environments. Alternative phenotypes allow a species to exploit a broader range of

Table IV. Discriminant analysis. Resubstitution summary using linear discriminant function. The number of observations and percentage classified of correctly items into location and classified into clone are respectively reported.

a) Number of observation and percent classified into location.

SITE		**Frejus (F)**	**Roselle (I)**	**Megalo-polis (GR)**	**Karistos (GR)**	**Jerica (SP)**	**Lisbon (P)**	**TOTAL**
Frejus	**nb.**	**11**	7	7	6	3	6	40
(F)	**%**	**27.50**	17.50	17.50	15.00	7.50	15.00	100.00
Roselle	**nb.**	1	**25**	0	2	0	7	35
(I)	**%**	2.86	**71.43**	0.00	5.71	0.00	20.00	100.00
Megalopolis	**nb.**	0	10	**29**	1	0	0	40
(GR)	**%**	0.00	25.00	**72.50**	2.50	0.00	0.00	100.00
Karistos	**nb.**	1	8	3	**18**	0	7	37
(GR)	**%**	2.70	21.62	8.11	**48.65**	0.00	18.92	100.00
Jerica	**nb.**	0	5	0	0	**24**	7	36
(SP)	**%**	0.00	13.89	0.00	0.00	**66.67**	19.44	100.00
Lisbon	**nb.**	3	18	3	5	1	**10**	40
(P)	**%**	7.50	45.00	7.50	12.50	2.50	**25.00**	100.00
TOTAL	**nb.**	16	73	42	32	28	37	228
PERCENT	**%**	7.02	32.02	18.42	14.04	12.28	16.23	100.00
PRIORS		0.1667	0.1667	0.1667	0.1667	0.1667	0.1667	

b) Number of observation and percent classified into clone.

CLONE	**43F**	**47F**	**171F**	**318F**	**TOTAL**	
43F	**nb.**	**17**	10	16	11	54
	%	**31.48**	18.52	29.63	20.37	100.00
47F	**nb.**	19	**14**	14	13	60
	%	31.67	**23.33**	23.33	21.67	100.00
171F	**nb.**	22	1	**25**	9	57
	%	38.60	1.75	**43.86**	15.79	100.00
318F	**nb.**	13	12	13	**19**	57
	%	22.81	21.05	22.81	**33.33**	100.00
TOTAL	**nb.**	71	37	68	52	228
PERCENT	**%**	31.14	16.23	29.82	22.81	100.00
PRIORS		0.2500	0.2500	0.2500	0.2500	0.2500

environmental conditions [21]. The relative advantages of fixed *versus* plastic clonal characteristics depend upon the spatial and temporal patterns of resource heterogeneity in the habitat. Failure to respond to environmental conditions or cues may reflect, not merely the constraints of unsophisticated physiology, but selection for conservatism [2]. However, plasticity may be adaptive or may simply result from developmental instability [21].

On the basis of such results, waiting for trials that will have to be based on a wider number of clones and take in account qualitative characters too, cypress seem to be a plastic species. Thanks to plasticity, common cypress has been artificially spreaded since the Phoenicians and Etruscans started to sail all along the Mediterranean sea carrying with them their goods and their culture. Such a spread of cypress is still in act, not only in the

Mediterranean countries, but in every climatically similar area too, where the cypress is able to fit to the local environmental conditions. Unfortunately, this adaptability implies consequences on its resistance to pathogens, or the possible contact with pathogens not present in its natural range, making harder the genetic improvement work for resistance.

A question as to whether it is worth the effort to select clones from a particular environment and then use them under very different conditions of habitat. In fact, if the phenotype is not an aggregate of morphological and physiological characters programmed from individual genes, but rather emerges from the interaction between a particular development program and the particular environments in which it grows, involving the alteration of a suite of characters, then it is worth considering whether, at least as regards the shape of the crown, the clones to use should perhaps be selected locally, instead of aiming the entire research effort at finding a universal clone, that is adaptable to all environments mantaining its own shape. Similar conclusions are also being reached in works involving stability in the resistance to cypress canker disease [15] and this should prove a further impetus for the selection of clones with morpho-physiological characteristics that are suitable for use in a very restricted and determined environment. Now, it is interesting to investigate which are the environmental characteristics that interact most strongly with the genotype and which are the consequences on cypress physiological processes - so much so as to change its crown architecture. The problem is now to define what is environment. If it is accepted that climate and soil conditions play a major role in adaptedness of plants, being the source of nutrients and energy, nevertheless many other influencing factors have to be considered. The man made habitats are clearly correlated to differentiation patterns in *Capsella bursa-pastoris* [9]; the potential effect of endophytic fungi on phenotypic plasticity has not often been recognised, but their clandestine effect on the plasticity of host genotype could have a strong impact [4], the light variation [13] and quality: for instance, red/far red ratios are important environmental signals affecting both individual plant behaviour and organization of whole communities [12]. Also the effect of topography, mycorrhizae, etc. could lead, maybe, to different phenotypes. Now it necessary to break up the source of variance "environment" and to study the single components and their interactions. Such a research is in progress.

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