Seasonality in the Primary Growth of *Cupressus sempervirens* L. From Western Crete[1])

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Abstract

The primary growth increment of forty eight seedlings from nine natural provenances of *Cupressus sempervirens* L. from Western Crete was measured from January 1994 to August 1995 at 10-day-intervals. On the basis of the collected data, parameters characterizing the seasonal pattern of the apical shoot growth were defined and analyzed. The study showed that the species provenances from Western Crete exhibited height elongation all year around except during the dry summer. In addition, short growth cessation occurred for some of the trees during the winter.

All provenances were consistent in their growth pattern during the two observed spring seasons. The duration of the spring growth period and the date of growth cessation in summer varied significantly among the provenances and the genotypes within them. The results indicate strong genetic control of these parameters and the presence of differential adaptation to the summer drought. On the other hand, the variation in the spring and the autumn growth resumption dates and the durations of the summer and winter rest periods were small and not significantly different among the provenances due to the high variation they contained.

The northern provenances and those located on the northern aspects had shorter cessation in summer, while the provenances from the lower altitudes had a shorter winter rest period. The altitude of the provenance seems to affect the date of the peak in the spring growth. The lower appeared to have it earlier than the higher provenances.

Key words: Cupressus sempervirens, seasonal pattern, primary growth, provenance variation.

FDC: 165.52; 161.4; 181.525; 181.8; 232.12; 174.7 *Cupressus sempervirens;* (495.9).

Introduction

The relative rate of height growth is an important tree characteristic which at the seedling stage affects the successful establishment of a plantation and in later stages is a major determinant of volume increment. There is also periodicity in the leader growth, which is important to be understood because the effectiveness of silvicultural treatments might well vary depending on the timing of application. Except for studies on the morphology of the cypress shoot apex (PILLAI, 1963; GELLINI and GROSSONI, 1980) and the research on the cambial activity of the species (LIPHSCHITZ and LEV-YADUN, 1986), no attempts have been made to investigate the seasonal pattern of the primary growth or the major factors influencing the rate and periodicity of the leader elongation of *Cupressus sempervirens* L. PANETSOS (1967) reports that it was found from height measurements, conducted on two-year-old seedlings growing in a nursery near Athens, that the trees were growing actively in winter. The same author concludes that the growth pattern depends upon the genotype of the plant material used in the experiment and the environmental conditions of the testing site. The subject of the present study is the yearly cycle of the height growth of the species. The variation among and within nine Cretan provenances of *Cupressus sempervirens* concerning some parameters of the primary growth and the influence of the locality variables of the parental provenances on this variation were also investigated.

Materials and Methods

Seeds from nine natural provenances of *Cupressus sempervirens* from Western Crete were sown in the nursery of Mediterranean Agronomic Institute of Chania during the spring of 1991 *(Table 1)*. Six to nine trees were randomly chosen from 5 provenances, Zourva, Prasses, Fress, Omalos and Askifou. The other 4 provenances had limited numbers and so only 2 to 4 trees were sampled. In total 48 seedlings were used for data collection.

Considering the fact that the primary growth takes place in the apical shoot meristem, a constant point on the main stem placed at 20 cm to 50 cm from its top was labelled for each tree at the beginning of the study. Measurements were taken from the labelled point to the top of the terminal shoot with 1 mm accuracy. This was done to avoid the heterogeneity of the soil level around the trees and to get more exact numbers for the current height growth.

The described measurements were obtained from January 1994 to August 1995 at 10 day intervals, i.e. two spring (1994, 1995), one summer and one autumn-winter seasons were covered. The cumulative increment (CI) and the average increment per ten days (AI) for each tree and 10-day period were calculated.

The following growth rhythm parameters were defined and analyzed:

- dates of autumn and spring growth resumption (DAR and DSR, respectively);
- date of spring growth cessation (DSC);
- dates of spring and autumn growth peaks (DSP and DAP, respectively);
- durations of the spring growth period, winter and summer cessations (DrSG, DrWC, DrSC).

Each date was expressed as the number of days from the beginning of the calendar year.

The effect of the provenance and the individual tree on the variation in the spring resumption, cessation and peak dates

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Table 1. – Location of the *Cupressus sempervirens* provenances.

Provenance	Altitude (m)	Longitude (E)	Latitude (N)	Aspect
Zourva	550	23°57'30"	35°23'	Northern
Prasses	650	23°51'	35°22'40"	Northern
Fress	175	24°09'	35°22'30"	Northern
Omalos	1100	23°52'20"	35°19'30"	Southern
Askifou	850	24°10'	35°17'	South-western
Agia Irini	700	23°50'20"	35°19'40"	South-eastern
Kalergi	1400	23°56'	35°19'20"	North-western
Anopoli	1650	24°08'	35°15'	Southern
Tavri	1000	24°10'	35°19'	Eastern

and in the duration of the spring growth were analyzed by two-way Analysis of Variance (ANOVA). The among-provenance variations in date of autumn resumption and peak, and duration of summer and winter cessation were subjected to one-way ANOVA. Since the numbers of the trees sampled from each provenance were different, the formulas of ANOVA for samples of unequal sizes were used (SNEDECOR and COCHRAN, 1989). Variance component analyses were performed to locate and apportion the total variation. The difference between the average growth rates in 1994 and 1995 (the overlapping period) was evaluated by WILCOXON rank-sum test.

Correlation coefficients were calculated between the series of 10-day average increments for 1994 and those for 1995 (the overlapping dates), and the growth rhythm parameters in 1994 and 1995. Only the significant correlations (Correlation coefficient > 0.3, probability < 0.05) are presented and discussed.

Stepwise regression analyses (CODY and SMITH, 1987) were performed to study the influence of the provenance location parameters longitude, latitude, altitude and aspect on the growth rhythm variables. The average values for the provenances were used in the analyses and only the best stepwise model is presented. It was defined as that which was statistically significant, produced the lowest residual mean square, and exhibited no relationship between residuals and independent variables (DRAPER and SMITH, 1981).

Results

The correlation analyses between the time sequences of the growth rates (AI) in the two years showed that all provenances are consistent in their growth pattern *(Table 2)*. Correlations between the dates of the spring growth cessation and between the durations of the spring growth period for the two years were also present *(Table 3)*. Despite this fact, the average growth rate in 1994 was significantly higher than those in 1995 when overall data were analyzed *(Table 4)*. When the data by provenances were analyzed, the difference appeared to be significant for Fress and Askifou, while the remaining provenances had comparable growth rates over the two years *(Table 4)*.

Table 2. – Correlation analyses between the growth rates in the years 1994 and 1995 (1. Jan. to 1. Aug.).

Provenance	Correlation Coefficients
Zourva	0.62899 ***
Prasses	0.90867 ***
Fress	0.82934 ***
Askifou	0.75858 ***
Omalos	0.85240 ***
Agia Irini	0.88331 ***
Anopoli	0.96255 ***
Kalergi	0.63394 ***
Tavri	0.81370 ***
AVERAGE	0.78847 ***

*** Probability < 0.001

Table 4. – WILCOXON rank-sum test for comparison of the average growth rates in 1994 and 1995.

Provenance	Average growth rate (cm per 10 days)		Level of
	1994	1995	significance
Zourva	1.471429	1.421176	ns
Prasses	1.230357	1.180878	ns
Fress	0.935979	0.671326	*
Askifou	1.244643	0.850149	*
Omalos	1.062857	0.813988	ns
Agia Irini	1.382143	0.894643	ns
Anopoli	0.82381	0.502381	ns
Kalergi	1.271905	1.108036	ns
Tavri	0.647619	0.285714	ns
AVERAGE	1.118971	0.858699	**

ns Z > 0.05; * Z < 0.05

Table 3. – Correlation analyses between the growth rhythm parameters in 1994 and 1995.

	DSC 1994 - DSC 1995	DrSG 1994 -DrSG 1995
Correlation coefficient	0.43381 **	0.47331 ***

** Pr < 0.01, *** Pr < 0.001
DSC – date of spring growth cessation; DrSG – duration of spring growth period

A. Spring-summer

The growth resumption dates in spring did not differ significantly among the provenances and among the trees within them *(Table 5)*. The spring growth started in the second half of February for almost all provenances in both years (except Kalergi – in the second half of March 1994; Zourva – first half of February 1995; Prasses – first half of January 1995). The provenances Zourva and Prasses showed most intensive initial growth in the two observed spring seasons (*Charts 1* and *2*).

The average growth resumption dates appeared to be affected by the aspect and by the longitude and latitude of the provenances *(Table 6)*.

The differences among and within the provenances in the time of peak growth were not significant *(Table 5)*. Highest spring peaks were achieved consistently by the provenances Agia Irini and Zourva (*Charts 1* and *2*).

The spring peak appeared to be associated with the altitude of the parental provenance *(Table 6)*. The higher provenances reached their peak in the growth later than the lower-ones (data not shown).

Although almost all provenances started their spring growth at the same time, the dates of the growth cessation in summer differed among them. This growth parameter seems to be significantly affected by the provenance as well as by the trees within the provenance *(Table 5)*. The provenance accounted for 19.04% and the trees within the provenance for 22.40% of the total variation in the spring growth cessation date *(Table 5)*.

Duration of the spring growth season varied significantly among the provenances as well as among the trees within them *(Table 5)*. The provenance accounted for 12.43% of the total variation in the spring growth duration, while the trees within

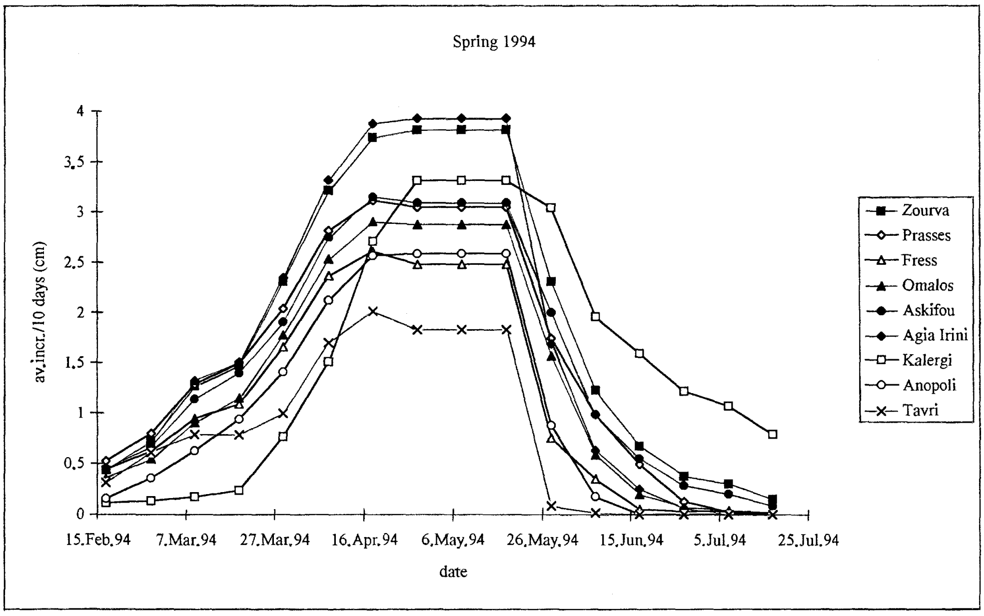

Chart 1. – Growth pattern of the provenances during the spring 1994.

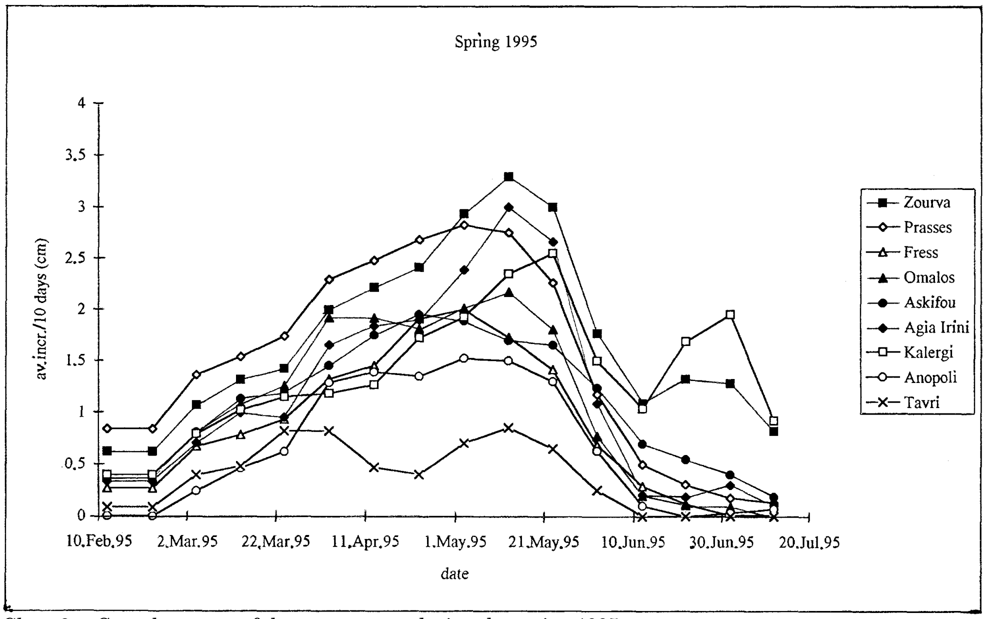

Chart 2. – Growth pattern of the provenances during the spring 1995.

Table 5. – *F*-test significance of two-way ANOVA for the growth rhythm parameters.

Source of variation	Dependent variable					
	DSR	DSP	DSC		DrSG	
			Level of significance	Variance Component (%)	Level of significance	Variance Component (%)
Provenance	ns	ns	***	19.04	***	12.43
Tree (Provenance)	ns	ns	*	22.40	**	32.74

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$
DSR – date of spring growth resumption; DSP – date of spring growth peak;
DSC – date of spring growth cessation; DrSG – duration of spring growth period.

Table 6. – Stepwise regression analyses for the growth rhythm parameters (best model)*).

Environmental parameters- *F*-value in the best model	Dependent variable			
	DSR	DSP	DrSC	DrWC
Latitude	10.48*	–	13.17*	–
Longitude	7.24*	–	0.40^{ns}	21.98**
Altitude	–	6.43*	3.52^{ns}	18.64**
Aspect	19.87**	–	21.97**	–
R^2	0.8097	0.4789	0.8768	0.8766

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$
DSR – date of spring growth resumption; DSP – date of spring growth peak;
DrSG – duration of summer cessation; DrWC – duration of winter cessation;
*) The results of regression analysis for those growth rhythm variables that appeared to be affected by none of the provenance location parameters are omitted.

the provenance contributed 32.74 % to the variance *(Table 5)*.

The date of the spring growth cessation and the duration of the spring growth period did not seem to be significantly affected by the location variables of the parental provenances as it was shown by the regression analyses.

The duration of the summer rest period varied from 0 to 120 days among the measured trees *(Table 8)*, but the provenance did not appear to be a significant source of variation *(Table 7)*.

The latitude and the aspect of the original provenances affected significantly the duration of the summer rest period *(Table 6)*. The northern provenances of the species and those with a northern or a north-western aspect had shorter summer cessation than the southern provenances and those situated on southern or south-eastern slopes.

B. Autumn-winter

The second growth season for all provenances (except Kalergi) started at the same time, in mid-September *(Chart 3)*, and no significant difference among the provenances was found concerning the date of autumn growth resumption *(Table 7)*.

The primary growth had its peak earlier for some provenances (the end of October, the beginning of November) and later for other (the first half of November), while the provenances in the third group had a double peak *(Chart 3)*. Significant differences among the provenances were found concerning the time of the maximum growth in autumn. In this parameter, the provenance accounted for 20.14 % of the variation *(Table 7)*.

All provenances continued to grow during the winter *(Chart 3)* except Tavri and Anopoli. In fact, most observed trees ceased their growth at least for 10 days *(Table 9)*. The trees within the provenances, however, did not stop growing at the same time, so that the average growth rates for the provenances were always over zero. The differences among the provenances in the average duration of the winter cessation (based on the growth cessation duration of the individual trees) were not significant *(Table 7)*. Minimum winter growth for all prove-

Table 7. – *F*-test significance of one-way ANOVA for the growth rhythm parameters.

Source of variation	Dependent variable				
	DrSC	DAR	DAP		DrWC
			Level of significance	Variance Component (%)	
Provenance	ns	ns	*	20.14	ns

ns $P > 0.05$, * $P < 0.05$
DrSC – duration of summer cessation; DrWC – duration of winter cessation; DAR – date of autumn growth resumption; DAP – date of autumn growth peak.

Table 8. – Periods of summer growth cessation.

Prov.	Tree	Date *															
		07.06	17.06	27.06	07.07	17.07	27.07	06.08	16.08	26.08	05.09	15.09	25.09	05.10	15.10	04.11	14.11
Zourva	1						■	■	■	■	■	■	■	■			
	2							■	■	■	■	■	■	■	■	■	
	7					■	■	■	■	■	■						
	8						■	■	■	■	■						
	32			■	■	■	■	■	■	■	■						
	33		■	■	■	■	■	■	■	■	■						
Prasses	3					■	■	■	■	■	■						
	4					■	■	■	■	■	■	■	■	■			
	5			■	■	■	■	■	■	■	■	■	■	■			
	6						■	■	■	■	■						
	27					■	■	■	■	■	■						
	28			■	■	■	■					■					
	29			■	■	■	■	■	■	■	■						
	30		■	■	■	■	■	■	■	■	■						
Fress	9					■	■	■	■	■	■						
	10					■	■	■	■	■	■						
	11					■	■	■	■	■	■						
	12		■	■	■	■	■	■	■	■	■						
	31		■	■	■	■	■	■	■	■	■						
	47			■	■	■	■	■	■	■	■						
	48	■	■	■	■	■	■	■	■	■	■						
	49					■	■	■	■	■	■						
	50					■	■	■	■	■	■						
Omalos	13					■	■	■	■	■	■						
	14		■	■	■	■	■	■	■	■	■						
	15	■	■	■	■	■	■	■	■	■	■						
	16	■	■	■	■	■	■	■	■	■	■						
	23					■	■	■	■	■	■						
	24					■	■	■	■	■	■						
	25		■	■	■	■	■	■	■	■	■						
	26					■				■	■						
Askifou	17		■	■	■	■	■	■	■	■	■						
	18					■	■	■	■	■	■	■	■	■			
	19					■	■	■	■	■	■						
	20					■	■	■	■	■	■						
	42		■	■	■	■	■	■	■	■	■	■	■	■			
	43			■	■	■	■	■	■	■	■	■	■	■			
	44								■	■	■	■	■	■			
	46					■	■	■	■	■	■						
Agia Irini	22			■	■	■	■	■	■	■	■						
	35			■	■	■	■	■	■	■	■	■	■	■			
	37		■	■	■	■	■	■	■	■	■						
	38			■					■	■	■						
Kalergi	21																
	34			■	■	■	■	■	■	■	■						
Anopoli	39	■	■	■	■	■	■	■	■	■	■						
	41	■	■	■	■	■	■	■	■	■	■						
Tavri	36	■	■	■	■	■	■	■	■	■	■						

*) The dark fields indicate the periods of growth cessation

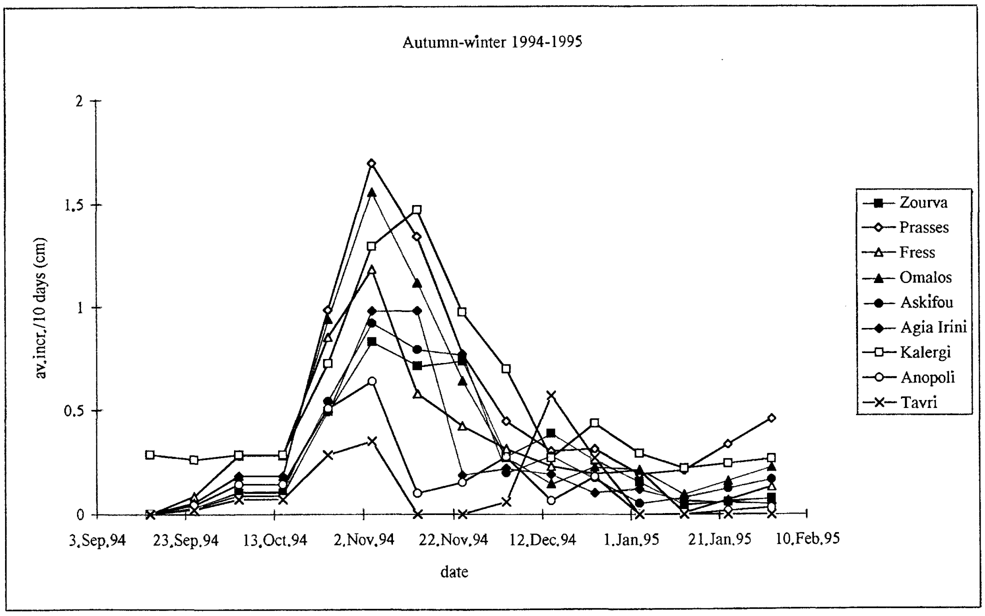

Chart 3. – Growth pattern of the provenances during the autumn-winter 1994 to 1995.

nances was recorded in the period of 24 December to 23 January *(Chart 3)*.

The period of the winter growth cessation was influenced by the altitude and the longitude of the provenance *(Table 6),* while the time of the growth resumption in autumn and the period of the maximum autumn growth were not significantly affected by the location variables of the parental provenances. The western provenances as well as those with higher altitude had longer winter cessation.

Discussion

The observation of 48 sampled genotypes of *Cupressus sempervirens* of Cretan origin showed that the species exhibits primary growth all year around except during the dry summer. There were even trees that continued to grow through late summer or did not have a rest period at all (Kalergi, tree 21). Short cessation in growth was observed also in winter, mainly in January. The results from the study are similar to those obtained by LIPHSCHITZ and LEV-YADUN (1986) about the cambial activity of the species. They found that *Cupressus sempervirens* starts its secondary growth in October when temperatures drop and water is less limiting. The cambium enters dormancy at the beginning of the dry summer and a short cessation of its activity occurs during the winter, especially in cold years. The results presented conflict with the observation by MOONEY and KUMMEROW (1981) that the growth of the deeper-rooted evergreen shrubs around the Mediterranean does not begin until spring. According to those authors, although moisture becomes available to the deeply rooted shrubs by midwinter, stem elongation does not start until spring when the danger of low temperature damage to new tissue is reduced.

Although *Cupressus sempervirens* possesses a central root system that penetrates deep into the soil some morphological peculiarities of its shoot apex have to be considered, as far as the primary growth is concerned. Observations by PILLAI (1963) on the structure and seasonality of the vegetative apex of three cypresses *(Cupressus sempervirens, Cupressus torulosa* and *Cupressus macrocarpa)* showed that there is no period of complete dormancy in shoot apices of *Cupressus sempervirens* during the yearly growth cycle. Despite this fact, the apical initials show greater frequency of periclinal divisions during the spring and summer months than during the autumn-winter period and no periclines are found in January. Furthermore, the genus *Cupressus* exhibits the characteristic of having no real buds (GELLINI and GROSSONI, 1980). Instead of producing in summer a bud with protective scales that will grow the following year, the cypresses simply stop the growth of the apex during the unfavourable season, starting to grow again when conditions are good. According to the classification of the shoot growth (DANIEL et al., 1979) *Cupressus sempervirens* possesses free (indeterminate) type of growth. It has been postulated that this kind of stem elongation, unlike the other two (fixed and fixed-free) is not predetermined and depends on the environmental conditions of the current year.

For this reason a definite date of resumption of the primary growth in spring can not be determined for this species. However, the observations of the annual growth rhythm of the tree showed that the growth has two peak periods (autumn and spring) followed by drops or full growth cessation (in winter and summer, respectively). A similar tendency for having two flushes has been observed for Douglas-fir seedlings (LOOPSTRA and ADAMS, 1989) and has been explained by the intermittent moisture availability during the growth season. For all observed trees in the present study it was noticed that after some date, at the beginning of the spring, the curve of their growth rate becomes steeper, i.e. the growth rate icreases rapidly (*Charts 1* and *2*). This date was assumed to be the date of initiation of the new growth in spring.

It was noticed in the present study that almost all trees started intensive growth at the same time in spring (Mid-February) during the two observed years, and the variation among and within the provenances concerning this growth parameter was not significant. Small variation and non-significant difference in the flushing date were found also for provenances of *Sequiadendron giganteum* (DU and FINS, 1989) and *Pinus armandii* (CHANG-GENG, 1989).

Although the date of spring growth resumption appeared to be significantly affected by the latitude, longitude and the aspect of the parental provenances, general tendencies were not distinguished towards earlier or later resumption date with

Table 9. – Periods of winter growth cessation.

Prov.	Tree	Date *														
		04.11	14.11	24.11	4.12	14.12	24.12	03.01	13.01	23.01	02.02	12.02	22.02	04.03	14.03	24.03
Zourva	1				■	■	■	■	■	■						
	2									■						
	7									■						
	8															
	32							■	■	■						
	33			■	■											
Prasses	3							■								
	4			■						■						
	5					■				■						
	6															
	27															
	28		■	■			■	■	■	■						
	29															
	30															
Fress	9						■	■	■	■						
	10															
	11	■	■					■	■	■	■	■	■	■	■	
	12							■								
	31							■	■	■						
	47					■	■	■	■	■						
	48							■	■	■	■	■				
	49						■	■								
	50				■	■	■	■								
Omalos	13						■	■	■	■	■	■	■			
	14															
	15			■	■	■	■	■	■	■	■	■	■			
	16							■								
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	25									■						
	26															
Askifou	17						■	■	■	■						
	18			■	■	■	■	■	■	■						
	19															
	20			■	■	■	■	■								
	42						■	■	■	■	■	■				
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	38						■	■	■	■						
Kalergi	21															
	34				■	■	■	■	■	■	■	■	■			
Anopoli	39	■					■	■	■	■	■	■				
	41				■	■	■	■			■	■	■			
Tavri	36	■	■				■	■	■	■						

*) The dark fields indicate the periods of growth cessation

the continuous change of each of the above factors. Early- as well as late-flushing provenances were situated on northern aspect. This fact and the lack of correlation between the resumption dates in the two observed years lead us to believe that the results may have been biased.

Although the difference among the provenances in the time of the spring peak did not seem to be significant, their altitude showed significant influence on the variation of this character. The higher provenances showed a tendency to have a later peak in their growth that could be ascribed to the selection pressure from the more severe temperature conditions at the place of their origin. Significant differences up to one month in the time of the growth peak were found in a study on *Pinus armandii* provenances (CHANG-GENG, 1989). The latitude, rather than the altitude, however, appeared to be the major geographical factor influencing the period of maximum growth of this species. The latitudinal and the longitudinal ranges of the cypress provenances concerned, were both limited which most probably resulted in the small variation in the time of the growth peak and in lack of geographical pattern of the variation.

Most of the studies involving research on the tree growth cessation variation and its factors concern the temperate woody species which cease their growth in autumn, rather than in summer. The only comparable results found were for *Pinus brutia* provenances (CALAMASSI et al., 1987) from the Mediterranean region. An interesting conclusion from this study is that the two Cretan provenances of *Pinus brutia* stopped growing in June unlike the other four which continued their growth through summer. The Cretan provenances of *Cupressus sempervirens* in the present study also ceased their growth during the summer. It has to be noted, however, that the trees continued growing in the months following the last rainfall. This fact confirms that *Cupressus sempervirens* is one of the tree species that is best adapted to the Mediterranean climate since, through its deep root system, it can provide for long periods the water necessary for accumulation of growth increment.

The date of growth cessation is associated with the adaptation of plants to drought. In the present study it was found that there are significant differences among the provenances and the trees within them concerning the date of cessation of the spring growth and the duration of the spring growth period. The results also agree with the statement of ZOBEL and TALBERT (1984) that although much of the genetic variability related to adaptability is a function of a provenance or population, there is still considerable tree-to-tree variability. The examined location variables of the provenances (longitude, latitude, altitude and aspect), however, did not appear to influence the date of growth cessation in summer and the duration of the spring growth period. However, the duration of the summer rest period which seems to be a more precise criterion for the plant adaptation to drought, was significantly affected by the latitude and the aspect of the parental provenance. The northern provenances and those situated on the northern slopes stopped their growth for a shorter period than the others. It seems logical that the longer growing provenances, because of their latitude and orientation on the terrain, have been subjected and adapted to milder conditions, concerning the water stress, at the place of their origin.

Most of the trees started growing again in autumn in the period between the 15 of September to 15 of October *(Chart 3)*. The variation in the autumn resumption date appeared to be low and not significantly different between the provenances; neither was it affected by the location variables studied.

For many conifers growing mainly in the temperate climatic region, significant variation in the flushing date has been found and early and late flushing provenances as well as families within them have been distinguished and directed for selection. It needs to be pointed out, however, that the development of natural selection in this direction has been induced by the existing danger to the buds from late frosts in the particular climatic conditions. In this sense, the late flushing is considered an adaptive characteristic to the late frosts. The temperatures in the region of our study (representative of the Mediterranean climatic region) are milder than temperate zones and thus the danger from late frost is little. Therefore, the flushing date either in spring or in autumn does not seem to be under strong adaptation pressure and the lack of variation in it is logical. Furthermore, the capability of the cypress shoot apex to produce primary growth all year round has most probably reflected the long term evolution and adaptation of the species to the milder climatic conditions of the region.

The primary growth reached its peak in November. None of the location variables seems to affect the date of the autumn growth peak although significant differences among the provenances concerning this phenological parameter were found. These results are difficult to explain especially because data were collected only in one autumn growth season. Some locality factors that were not evaluated could have been involved or the competition of the root systems in the nursery may have played a role.

The average period of the growth cessation in winter, however, was related to the altitude and the longitude of the parental provenances. The trees from the higher altitudes stayed dormant for a longer time than those from the lower altitudes. Although meteorological data about the places of origin of the provenances are absent, could be supposed that the higher-altitude-provenances have been exposed to more severe temperature conditions and the longer winter dormancy is the response to them. It appeared that the eastern provenances have longer winter rest period than the western ones. In our case, it has not been verified that the difference of 10 to 20 minutes in the longitude of the studied provenances makes any difference concerning the pattern and the amount of precipitation and their corresponding growth limitation. Some non-analyzed factors, such as the presence of cold wind, characteristic of the provenances Anopoli, Kalergi and Omalos, and poor dry soil in Kalergi, Askifou, Anopoli and Omalos (PAPAGEORGIOU, 1994), could have played a role.

The Analysis of variance did not show the differences to be significant in the winter rest duration among the provenances. This could be ascribed to the high variation within the provenances concerning the duration of the winter dormancy. During this time of the year the soil moisture is not a factor limiting growth and competition for water resources does not play a very important role. On the other hand, the different degree to which the particular trees are able to tolerate the low temperatures could be the reason for the variation among trees. This is in agreement with the statement of ZOBEL and TALBERT (1984) that there is still significant variation within the provenances concerning the adaptability characteristics.

It could be noticed that statistically significant variation was found among the provenances for some growth rhythm parameters, while the same parameters were not affected by any of the location variables. As was mentioned before, although indirect indicators for the natural environments of the provenances, the studied location variables did not describe completely the growth conditions. Other variables such as: the presence of strong wind, the soil quality, the average temperature and rainfall for the different seasons, the slope etc., could be more representative descriptors of the specific growth environment, as is also suggested by studies of other investigators (HATTEMER and KÖNIG, 1975; KHALIL and DOUGLAS, 1979; CHANG-GENG, 1989). On the other hand, the variation among the provenances did not seem to be significant for the primary growth parameters of the other group, and at the same time they were significantly affected by some of the location variables. The main reason for the non-significant difference among the provenances was the significant variation within them, as well as the different environmental conditions in the two years observed. The average values for the provenances, however, were used for the stepwise regression analyses, as was suggested in studies by other investigators (KHALIS and DOUGLAS, 1979; LOOPSTRA and ADAMS, 1989), and the use of the provenance means ignored the intra-provenance and environmental variations.

Finally, it can be concluded that the distinct variation patterns in some phenological characteristics of *Cupressus sempervirens* (duration of summer and winter rest periods, time of the spring growth peak) imply that the natural selection of the species is directed to favour genotypes resistant to drought and low temperatures. On the other hand, the non-systematic variation of other group characteristics of the primary growth (date of winter peak, date of growth cessation in summer, duration of spring growth period) suggests that other factors in addition to natural selection also are involved. In this sense, it has to be considered that the natural forests around the Mediterranean have been generally disrupted by man and for centuries have been subjected to dysgenic selection. The discontinuous natural range of the species and the relatively small population could mean that genetic drift has also played a role in the pattern of provenance variation of growth rhythm.

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Allozyme Differentiation and Phylogeny of Cedar Species

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Summary

The isozyme variation patterns of 21 populations belonging to four Cedar species *(Cedrus libani, C. atlantica, C. deodara, C. brevifolia)* were studied at six loci (6PGD-B, LAP-A, LAP-B, IDH-A, DIA-A, PGI-B) by horizontal starch and polyacrylamide gel electrophoresis. Species specific alleles (DIA-A1 and LAP-A1 for *C. deodara,* IDH-A1 for *C. atlantica,* LAP-A3 for *C. libani* and *C. brevifolia*) and alleles with a particular geographic variation pattern (6PGD-B4 for *C. libani*) were detected in most of the species. Great variation was observed in heterozygosity levels among species which ranged from 0.136 *(C. deodara)* to 0.316 *(C. brevifolia)*. The construction of a dendrogram revealed five distinct clusters corresponding to the following taxa: i) *C. libani* ssp. *libani,* ii) *C. libani* ssp. *stenocoma,* iii) *C. libani* ssp. *brevifolia,* iv) *C. deodara,* v) *C. atlantica.*

Key words: Isozyme variation, phylogeny, *C. libani, C. brevifolia, C. atlantica, C. deodara.*

Introduction

The genus *Cedrus* includes coniferous evergreen species and is distributed in four geographically separated regions: a) Algeria and Morocco, b) Cyprus, c) Lebanon, Syria and Turkey and d) Afghanistan and the Himalayas (ARBEZ *et al.,* 1978; ARBEZ, 1987; M'HIRIT, 1987; VIDAKOVIC, 1991). According to TOTH (1980) and M'HIRIT (1987), *Cedrus* has an exceptional ability to perform well in a variety of soil and climatic conditions and to offer a considerable resistance to pests and fires.

Due to its exceptional adaptation in a variety of environmental conditions, *Cedrus* has been successfully introduced in many countries out of its natural distribution, firstly as an ornamental and secondly as a reforestation species.

Today, in spite of its ecological and economic importance, limited information concerning the amount and pattern of its genetic variability is available (FAO, 1989). According to a