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Intra- and interspecific variations of polycyclism in young trees of *Cedrus atlantica* (Endl.) Manetti ex. Carrière and *Cedrus libani* A. Rich (Pinaceae)

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Abstract – Growth pattern and polycyclism were studied for three French populations of *Cedrus atlantica*, and ten populations of *Cedrus libani* (seven Turkish and three Lebanese populations). The polycyclism rate and the length of annual shoots and growth units were recorded at two sites in France. There were significant variations in polycyclism rate and annual growth between the Turkish and Lebanese populations. Polycyclism appeared to be linked to the climatic conditions of the current growth year for French and Turkish populations, unlike the Lebanese populations. The Turkish populations have exhibited a greater stability as well at the between-station as at the between-year levels. Polycyclism appears as an adaptive trait of trees to difficult growth conditions. The construction of a dendrogram based on polycyclism and annual shoot length revealed two distinct main clusters corresponding to the different geographical origins. Polycyclism could be used in breeding and genetic improvement programmes of these species.

Cedrus atlantica / *Cedrus libani* / polycyclism / growth pattern / morphological variability

Résumé – Variations intra- et interspécifiques du polycyclisme chez de jeunes arbres de *Cedrus atlantica* (Endl.) Manetti ex. Carrière et *Cedrus libani* A. Rich (Pinaceae). Les variations de croissance et du polycyclisme ont été étudiées pour trois provenances françaises de *Cedrus atlantica* et pour dix provenances de *Cedrus libani* comprenant sept provenances turques et trois provenances libanaises plantées en France. Le taux de polycyclisme et les longueurs des unités de croissance et des pousses annuelles de la tige principale des arbres ont été mesurés sur deux sites différents. Des variations significatives du taux de polycyclisme et de la croissance annuelle ont été observées entre les provenances turques et libanaises de *Cedrus libani*. Le polycyclisme est fortement lié aux conditions climatiques de l'année de croissance pour les provenances françaises et turques contrairement aux provenances libanaises. Les provenances turques ont montré une plus grande stabilité dans l'expression de ce caractère, tant au niveau stationnel qu'au niveau inter-annuel. Le polycyclisme apparaît comme un caractère adaptatif des Cèdres à des conditions de croissance difficiles. La construction d'un dendrogramme basé sur le polycyclisme et la longueur des pousses annuelles fait apparaître deux groupes principaux distincts correspondant à des origines géographiques différentes. Le polycyclisme est un critère morphologique permettant de séparer des provenances de Cèdres et peut être utilisé dans les programmes de sélection et d'amélioration génétique des espèces concernées.

Cedrus atlantica / *Cedrus libani* / polycyclisme / croissance / variabilité morphologique

1. INTRODUCTION

Four species are commonly recognised in the genus *Cedrus* [18]. Wild *Cedrus atlantica* (Endl.) Manetti stands are found in the mountains of Algeria and Morocco [18], while *C. brevifolia* (Hook. F.) Dode originated in Cyprus. The *C. deodora* (D. Don) G. Don natural distribution range stretches from Eastern Afghanistan to Northwestern Pakistan and north-western India [23]. That of *C. libani* A. Rich, which is very patchy, runs through Southern Turkey, the Western Taurus mountains, the Taurus, Antitaurus and Amanos ranges and the Pontic Alps [2], up to Northern Turkey near Black Sea [22].

This species is also found in the mountains of Syria and Lebanon [18, 23]. Recent taxonomic studies using genetic markers demonstrated that the genus *Cedrus* could be organized into three species, *C. deodora*, *C. atlantica* and *C. libani*. This last one is divided into three sub-species: *C. libani* spp. *libani* from Lebanon, *C. libani* spp. *stenocoma* from Turkey and *C. libani* spp. *brevifolia* from Cyprus [22, 42].

In French Mediterranean forests, the plantations set up at the end of the 19th century show that *Cedrus atlantica* present a low inflammability, a high regeneration capacity, a remarkable plasticity, a good tolerance to climatic stress and a higher wood quality than Mediterranean pines [6]. As a result of the

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Table I. Geographical data concerning *Cedrus atlantica* and *Cedrus libani* studied populations (source: Bariteau, INRA, Avignon).

INRA code	Country	Place	Latitude North	Longitude East	Altitude (m)	Exposure	Rainfall (mm)
<i>Cedrus atlantica</i>							
F9201	France	Ventoux	44°07'	5°11'	780-930	South	800
F9202	France	Ventoux	44°07'	5°11'	780-930	South	800
F9204	France	Marcelly	43°19'	2°28'	550-600	East	900
<i>Cedrus libani</i>							
L9203	Lebanon	Hadeth and Jebbe	34°14'	36°55'	1560	North	1 400-1 500
L9204	Lebanon	Barouk	33°36'	35°41'	1 500-1 700	West/Southwest	1 300
L9206	Lebanon	Ain Zhalta	33°39'	35°43'	1 300	West	1 300
T9110	Turkey	Düden	36°29'	32°56'	1 350	North	1 000
T9201	Turkey	Arslankoy	37°00'	34°14'	1 800	Southwest	800
T9203	Turkey	Sütlegen	36°23'	29°26'	1 550	North	1 000
T9204	Turkey	Gülmez	36°21'	30°05'	450-1 200	South/Southeast	1 000
T9210	Turkey	Arpacik	36°49'	29°14'	1 350	South	1 000
T9213	Turkey	Kas-Lengüme Karaçay	36°24'	29°46'	1 550	North	900
T9514	Turkey	Gökyurt	37°40'	32°02'	1500	North	600-800

ecological and economic interests of using this species for afforestation at altitudes from 300 to 800 m above sea level, the Ventoux, Saumon and Ménerbes stands are now recognised as “controlled” artificial seed-stands [6]. The adaptability to drought and growth performances observed for *Cedrus libani* from Turkey led the Mediterranean Forest Research Unit of Inra in Avignon to establish some comparative plantations in the French Mediterranean zone during the winter of 1993–1994. These included Turkish and Lebanese populations of *C. libani* and French populations of *C. atlantica* [2].

Works on genetic and morphological variability of the species *C. atlantica* and *C. libani* revealed that needle length, number of needles per short shoot, number of rows of stomata and length of the corneous part of the apex are criteria that could be used to discriminate between species in nursery [3]. The angle of branch insertion and the number of branches per annual shoot can also be used to discriminate between young individuals of certain populations [24]. Variations in height growth, budbreak date and water stress resistance represent criteria that can be used to characterize the degree of adaptability of a species or population and were found significant both between species and between populations of the same species of *Cedrus* [6]. At the moment, no easily observable morphological characters have ever been detected to differentiate populations of *C. atlantica* and *C. libani*. Thus, an architectural analysis [7, 28] of these two species was undertaken in order to evaluate the phenotypic variations within these taxa and to identify discriminant morphological criteria.

In species originating from temperate areas, annual stem growth takes place in one or more successive extension phases. The portion of leafy axis established during a continuous extension phase corresponds to a growth unit [27, 28]. The portion of leafy axis built up over a single growth year corresponds to an annual shoot. Polycyclism refers to the formation of several growth units in the same year [12]. Polycyclic growth has been described in many conifers or broadleaved species [12]. During ontogeny, the rate of polycyclism generally gradually increases during the establishment phase, before

stabilizing when the stationary growth phase occurs and decreasing with tree age [16, 29, 31, 34]. Polycyclism expression also varies according to the species [17, 19] and, for a given species, on general environmental conditions [10, 13, 15, 20, 31, 36] or climatic conditions during the current year of growth [31, 37].

In *Cedrus atlantica*, polycyclic annual shoots are only seen for some years of growth, on young, not very vigorous individuals [39]. Up to now, there has been no study of the diversity of polycyclism expression in the genus *Cedrus*. The aims of our study were to characterize annual shoot structure and to analyse the variations in polycyclism expression according to species, geographical origin and growth conditions.

2. MATERIALS AND METHODS

2.1. Study sites

The study was conducted in South-Eastern France, on two comparative plantations set up by the French agricultural research organization Inra (Mediterranean Forest Research Unit, Avignon). The first stand was located at La Rouvière (latitude 44° N, longitude 4° 40' E) near Rochefort du Gard (Gard). The second stand was located at Puechabon (Hérault; latitude 43° 42' N, longitude 3° 37' E). The Puechabon site is located on a limestone plateau at 290 m above sea level and with an annual rainfall average of 1 000 mm. On this site, a late frost occurred on April 18th 1997. The La Rouvière site faces eastwards and is 115 m above sea level, with an annual rainfall average of 780 mm. The soil is alluvial. This site is the more fertile than the previous one.

2.2. Vegetal material

Two species of *Cedrus* with a total of 13 populations were studied. Observations concerned three French *Cedrus atlantica* populations, seven Turkish and three Lebanese *Cedrus libani* populations. The geographical characteristics of the sites where each population was sampled are shown in table I, and each population is henceforth referred to by its code number (table I).

Table II. Number of analysed trees (nb.) and mean height in cm for each population (pop.) according to study site and year of growth. Newman and Keuls method was used for comparing tree mean height. Non-significant difference at 5% level between values linked by the same letter.

“La Rouvière” site March 1998			“Puechabon” site March 1998			“Puechabon” site September 2000		
pop.	nb.	Height	pop.	nb.	Height	pop.	nb.	Height
T9201	40	178 a	T9110	31	100 a	F9202	43	156 a
T9110	49	165 ab	T9201	30	94 ab	F9204	28	148 ab
F9201	51	162 ab	F9202	39	90 abc	T9110	34	145 ab
F9204	48	162 ab	F9204	20	86 bc	T9201	36	143 abc
F9202	50	160 ab	F9201	35	84 bc	T9203	30	136 abc
T9203	49	151 bc	T9214	32	78 c	F9201	34	131 abcd
T9213	45	138 cd	T9213	38	76 de	T9214	32	128 abcde
T9210	47	138 cd	T9210	34	74 def	T9204	39	125 bcde
T9214	35	133 cde	T9203	20	73 def	T9210	32	119 bcde
T9204	46	127 efg	T9204	30	71 fg	T9213	23	114 efg
L9203	49	117 efg	L9203	44	68 g	L9203	36	110 fgh
L9206	48	113 fg	L9206	30	58 h	L9206	19	101 gh
L9204	51	104 g	L9204	25	56 h	L9204	20	90 h

The trees were grown from seeds taken from noteworthy stands. The plants were grown during a year at the DDAF (departmental agriculture and forestry service) nursery at Aix-les-Milles (Bouches-du-Rhône), and planted in both sites during Autumn 1994. The field design in La Rouvière site was a set of three parcels on which the trees follow a complete random distribution and are planted out at a 3×3 m spacing. The field design in Puechabon site is a set of 86 random incomplete blocks. Each block is generally composed of 30 individuals (one-tree plots) planted out at 5×2 m spacing.

The trees were four-year-old at the time of the first set of measurements, in March 1998, and seven-year-old at the time of the second set, in September 2000. The number of analysed trees per population ranged from 19 to 51, according to population and site (table II). From each sample of trees, it was estimated the total height of the main stem obtained by adding up the lengths of its successive annual shoots. According to the data obtained in March 1998, the mean tree heights of the Turkish populations of *Cedrus libani* (T9201, T9110) and French populations of *Cedrus atlantica* (F9201, F9202, F9204) were greater than that of the Lebanese populations of *Cedrus libani* (L9203, L9206, L9204; table II). The mean height at La Rouvière site was 142 cm, and was significantly greater than the 78 cm observed at the Puechabon site. The September 2000 observations at the Puechabon site confirmed these variations in average tree height between the French, Turkish and Lebanese populations (table II).

2.3. Observed traits

2.3.1. Growth pattern

Growth in Cedar is rhythmic and all the axes are built up by a succession of annual shoots. Each annual shoot may result from one or several successive growth phases. Annual shoots are thus composed of one, two or three growth units, and so called as mono-, bi- or tri-cyclic, respectively.

Morphological markers can be used to reconstitute tree growth a posteriori. On young *Cedrus* axes, inter-annual or winter and intra-annual stops of growth are clearly shown by the presence of several cataphylls (e.g. scale leaves) associated to very short internodes (figure 1). An intra-annual stop of growth (i.e. growth cessation between two successive growth units produced in the same year) is identified by a smaller number of cataphylls compared to an inter-

annual stop of growth (figure 1b and c). From one polycyclic shoot to another, there may be some variations in the length of internodes between the cataphylls, and in the number of cataphylls, reflecting a more or less marked intra-annual stop of growth (figures 1c and 2). On the oldest parts of the axes, the annual shoot limits are marked off by rings of scars left by the cataphylls that have fallen down. The intra-annual limits between two growth units are sometimes less easy to see on older stems. But the presence of a pseudo-whorl of small branches in the median part of an annual shoots helps in the identification of an intra-annual stop of growth. In our case, the intra-annual limit between two growth units was sometimes difficult to identify on the part of three-year-old axes (e.g. annual shoots produced in 1998) during the set of measurements in September 2000. Intra-annual stops of growth occur at the end of May and/or in mid-summer.

2.3.2. Branch development pattern

Branch development may be delayed or immediate, depending on whether it follows a rest phase after lateral meristem initiation or not [12]. In *Cedrus atlantica* and *C. libani*, the branches, which develop a year after extension of the bearing shoot (i.e. one-year-delayed branches), possess a series of cataphylls associated to short internodes at their base (figure 1b). On polycyclic shoots, branches develop on the first growth unit, at the same time as the second growth unit edifies. These branches have thus a one-flush-delayed development and present a series of cataphylls at their base (figure 1c), although the number of cataphylls is smaller than on one-year-delayed branches. The immediate branches are easily recognizable by a lack of cataphylls and by leaves associated to long internodes at their base.

Combined qualitative analyses of the number of growth units per annual shoot and of the type of branches produced were used to draw up a typology of the annual shoots produced in 1997.

2.3.3. Analysed growth parameters

The length of the successive annual shoots is measured for the main stem of each individual. In March 1998, the number and the length of growth units produced in 1997 were recorded for all individuals of the 13 populations at both sites. In September 2000, the number and the length of growth units of annual shoots produced in 1998, 1999 and 2000 were recorded at the Puechabon site.

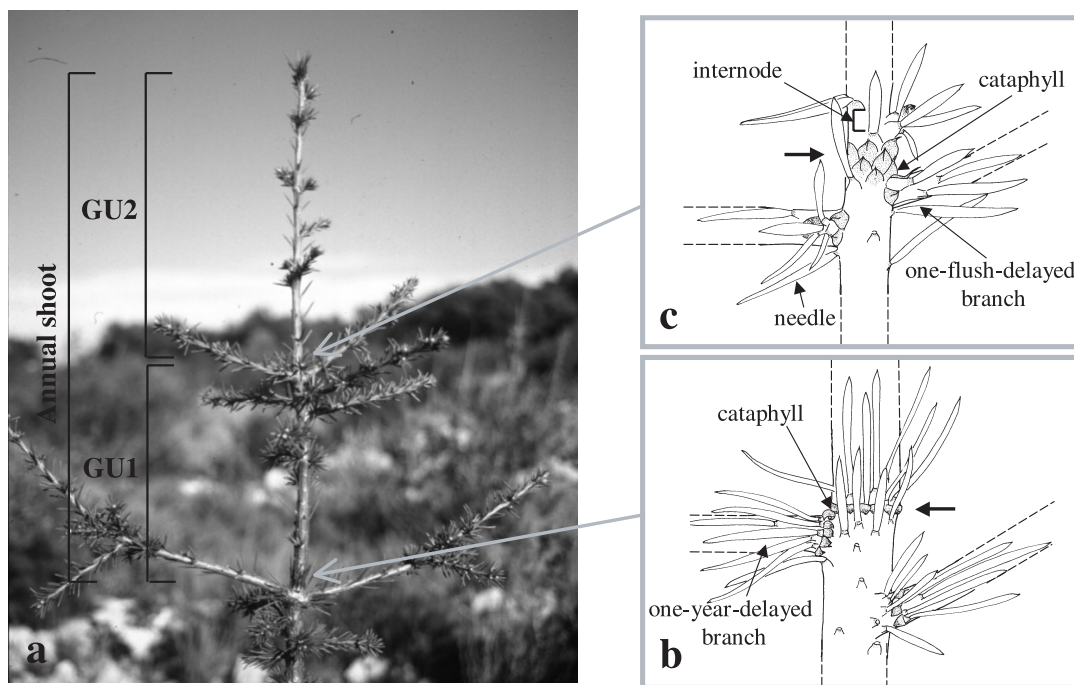


Figure 1. Morphological markers of growth and branching patterns in cedars. **a:** bicyclic annual shoot; **b:** limit between two annual shoots (→) and basal part of one-year-delayed branches; **c:** limit between spring growth unit and summer growth unit (→) and basal part of one-flush-delayed branches. GU 1: first growth unit; GU 2: second growth unit.

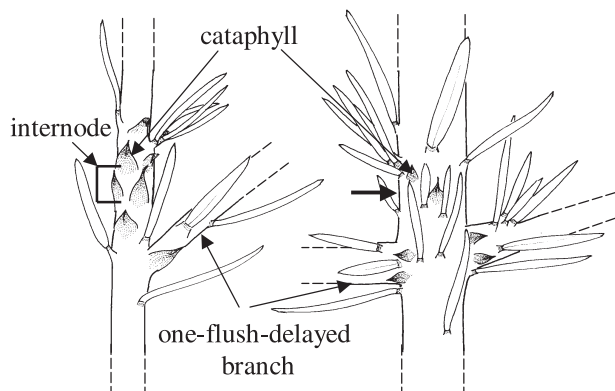


Figure 2. Morphological markers of an intra-annual stop of growth between the first and the second growth unit of a bicyclic shoot, according to the annual shoot diameter (increasing from left to right) in *Cedrus libani*. (→) intra-annual limit.

For each population and for each set of measures, the annual shoots were clustered according to their number of growth units. Mean values were obtained for the annual shoot length and for the lengths of the first and second growth units of bicyclic shoots.

Shoots whose terminal bud had died during the shoot extension were excluded from the analysis. If the terminal bud had died outside the extension period, only trees with a clearly differentiated relay axis were included in the analysis.

2.4. Statistical analysis

Comparisons of length distributions between mono- and bicyclic annual shoots, between monocyclic shoots and the first growth units, and between the first and second growth units of bicyclic shoots, both within the same population and between populations, were carried out with the Wilcoxon-Mann-Witney non-parametric test [41], using a significance level of 0.01.

The others analyses were performed with the DIOGENE software, an extended version of the OPEP software [4, 5]. To estimate the effects of population, station or year of growth on tree height, annual shoot length and polycyclism rate, multivariate analyses of variance in cross classification were carried out. Multiple comparisons of means used Newman and Keuls method at the significance level of 0.05. Individual relative ecovalences modified from Wricke [43] were used to measure, for each character, the contribution of an every population to the overall sum of squares for interaction, with a correction for design inbalanceness. This standardised parameter corresponds to the percentage of the sum of individual weighed ecovalences attributable to a genotype or to an environment. Given a two-way cross fixed ANOVA model in cross classification involving a genetic and an environmental factor, with *A* and *B* modalities, respectively:

$$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + e_{ijk}$$

where μ , α_i , β_j , $(\alpha\beta)_{ij}$ and e_{ijk} are the general mean, the genetic effect, the environmental effect, the interaction effect and the error term, respectively.

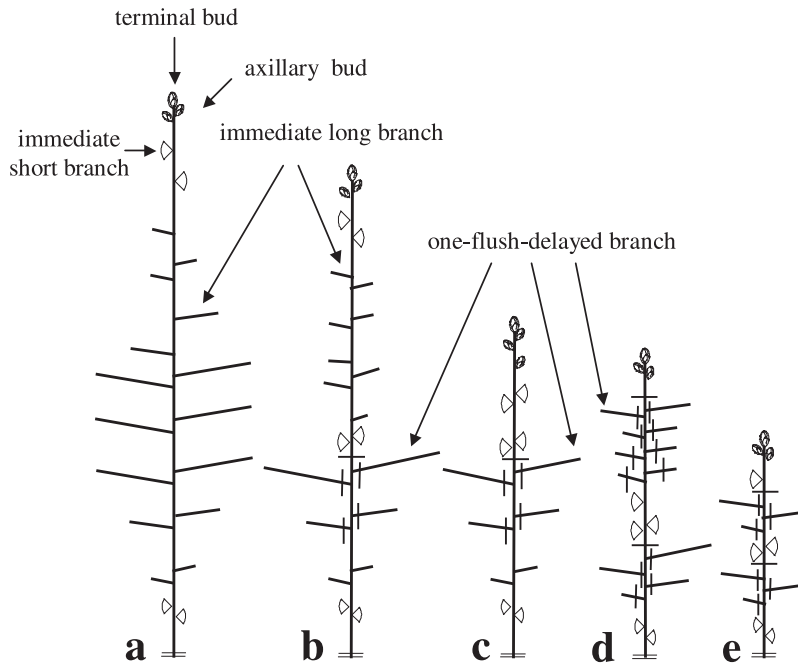


Figure 3. Diagrammatic representation of the different types of annual shoots produced in 1997 for the trees of all studied populations growing at Puechabon. **a:** long monocyclic shoot with immediate branches; **b** and **c:** bicyclic shoots with one-flush-delayed and immediate branches; **d** and **e:** tricyclic shoots with one-flush-delayed and immediate short branches. (=): inter-annual limit; (-): intra-annual limit.

The corresponding individual relative ecovalences are written below:

Ecovalence of the p th genotype Ecovalence of the q th environment

$$w_p = 100 \frac{\frac{1}{n_p} \sum_{j=1}^B n_{ij} (\alpha\beta)_{ij}^2}{\sum_{i=1}^A \sum_{j=1}^B \frac{n_{ij} (\alpha\beta)_{ij}^2}{n_i}} \quad w_q = 100 \frac{\frac{1}{n_q} \sum_{i=1}^A n_{ij} (\alpha\beta)_{ij}^2}{\sum_{i=1}^A \sum_{j=1}^B \frac{n_{ij} (\alpha\beta)_{ij}^2}{n_j}}$$

The weights in the formulas correct for inequality of size among the different levels of each factor: all happens as if the ANOVA would be computed from a design with all cells filled and one individual per cell (the reason to qualify this ecovalence as “individual”). Compared to the Finlay-Wilkinson model for genotype \times environment analysis [21, 25], ecovalence does not assume a linear response of genotype to environment, a strongly limitative condition [30]. Moreover, it is symmetrical and enables to measure the contribution of a particular environment to overall interaction as well as the overall stability of genotypes which decreases with an increasing ecovalence. Of course, the parameter may be computed only if the overall interaction is significant. Because of the lack of analytical expression for standard error of ecovalence, the significance for a given trait of this robust stability parameter was assessed by a Jackknife resampling [41], using the all-but-one procedure which allows the best precision on the sampling variance. We classified each level of factor according to the 95% confidence interval of the parameter by comparison with its expected value in case of null hypothesis (equal contribution of the different levels to the overall interaction sum of squares). Following this principle, “+” means a contribution significantly greater than this expected value, “-” means a significantly lower contribution and “0” was used for a contribution whose confidence interval overlaps the expected value. Ecovalences were computed both for the provenance \times site and provenance \times year interactions; only the last set of results is presented.

For the Puechabon site and for the four years of growth, a discriminant analysis was performed so as to separate the populations

according to annual shoot length and polycyclism rate. The Mahalanobis distance [41] between populations, combined with a Newman and Keuls tests on each axis, was used to study the relationship between population clustering and their geographical origin. Clustering of the n populations by a dendrogram according to the single linkage algorithm [41] used standardised similarities, S_{ij} , derived from

Mahalanobis distances: $S_{ij} = \frac{D_{\max}^2 - D_{ij}^2}{D_{\max}^2}$, where D_{\max}^2 is the

maximum observed distance among the $\frac{n(n-1)}{2}$ combinations and D_{ij}^2 is the distance between populations i and j .

3. RESULTS

3.1. Annual shoot structure

In young trees, the monocyclic annual shoots of the main stem produced immediate branches that are distributed along the growth unit according to a mesotonic vigour gradient [39]. Polycyclic shoots of the current year have branches with one-flush-delayed development located towards the tip of the first growth unit. In our case, at a given station and for a given growing season, we were able to characterize on young trees of every population of each species five morphological main types of main stem annual shoots, according to the number of growth units:

(1) monocyclic shoots with branches with immediate development (figure 3a);

(2) bicyclic shoots. The first growth unit had immediate branches in its median part and one-flush-delayed branches towards the tip. The second growth unit had long and/or short shoots (i.e. short axes with a rosette of leaves) with immediate development (figure 3b and c);

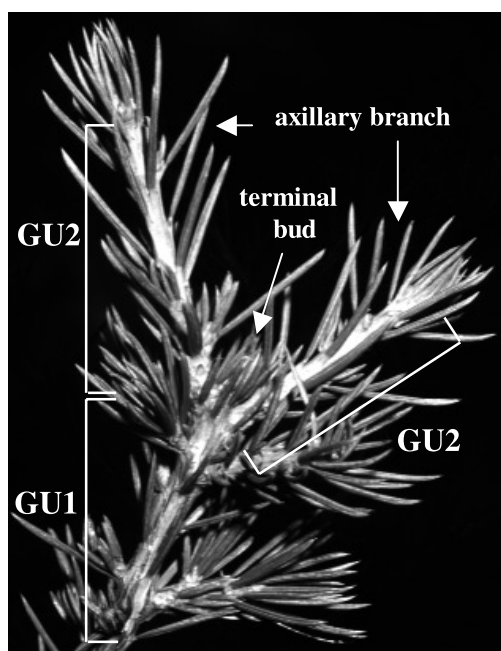


Figure 4. Morphology of the distal part of an annual shoot composed of a first growth unit (GU1) followed by a second growth unit (GU2) resulting from the development of apical axillary buds in *Cedrus libani*.

(3) tricyclic shoots. The first growth unit bore immediate short shoots in its proximal part, and one-flush-delayed long shoots in its distal part. The second growth unit sometimes had immediate short and long shoots and one-flush-delayed long shoots. The third growth unit had only latent buds and/or immediate short shoots (figure 3d and e).

In some cases, during the second or third growth flush, the axillary buds below the apical bud of the shoot gave rise to a growth unit, with the apical bud of the main stem not developing until the following spring (figure 4). One or two, or very scarcely, three, axillary buds were involved. The length of the resulting growth unit was systematically small. The frequency of shoots with a second or third growth unit from apical axillary buds was generally low, but was higher for the Turkish than for the French and Lebanese populations (figure 5a and b).

At La Rouvière site (figure 5a), the frequency of bicyclic shoots was lower than that of monocyclic shoots for populations T9203, T9213, T9210, T9110 and T9201. It was higher than or equal to that of monocyclic shoots for populations T9204, T9214, L9203, L9206, L9204. At Puechabon site (figure 5b), the frequency of bicyclic shoots was higher than that of monocyclic ones for all the populations except T9203. Tricyclic shoot frequency was low for all the populations at both sites.

3.2. Annual shoot length according to its number of constitutive growth units

At La Rouvière site, the mean length of monocyclic annual shoots produced in 1997 was significantly greater than that of

the bicyclic shoots, for all the populations except T9201, T9214 and L9204, for which the differences in length were not significant (figure 6a). At Puechabon site, the mean length of the monocyclic shoots was significantly smaller than that of the bicyclic shoots for populations T9210, T9204, L9203 and L9204, whereas differences in length between monocyclic and bicyclic shoots were not significant for populations F9202, T9213, T9203, T9110, T9214 and L9206 (figure 6b).

At La Rouvière site, the monocyclic shoots were significantly longer than the first growth units of the bicyclic shoots for all the populations, whereas at Puechabon site there was no significant difference for any of the populations except F9202, for which the monocyclic shoots were significantly longer than the first growth unit of bicyclic shoots.

As far as years are concerned, the differences between monocyclic and bicyclic shoot length were not significant (figure 7) except in 1997 for population L9203 (figure 7a) and in 1999 and 2000 for population L9204 (figure 7c). In these cases, the monocyclic shoots were shorter than the bicyclic ones. The mean length was not significantly different between the monocyclic shoots and the first growth units of the bicyclic shoots in 1997, 1998 and 1999 except, in 2000, for populations L9203 and L9204 (figure 7). The monocyclic shoots were significantly longer than the first growth units of the bicyclic shoots for population L9203 and shorter for population L9204 (figure 7c).

3.3. Growth unit length in bicyclic annual shoots

The differences in mean length between the first and second growth units of the bicyclic shoots produced in 1997 were generally not significant. But the first growth units were significantly shorter than the second for population L9206 at La Rouvière site and for populations F9201, F9202, F9204 and T9214 at Puechabon site (table III).

At Puechabon site, the mean length of the first growth units was similar in 1997 and significantly greater in the following years compared to that of the second growth units of the bicyclic shoots for polycyclic populations L9203, L9204 and L9206, except in 1999 for population L9203, for which the first growth units were shorter than the second (figure 7).

3.4. Polycyclism and sites

For the 1997 growing season, the mean length of the annual shoots was significantly greater at the 0.05 level at La Rouvière (44 cm) than at Puechabon (13 cm). The frequency of polycyclic annual shoots (bi- and tricyclic shoots analysed together) was significantly higher at the 0.05 level at Puechabon (0.74) than at La Rouvière (0.31).

The difference in polycyclic shoot frequency between the two sites was less marked for populations T9204, T9214, L9203, L9204 and L9206 than for the others (figure 8). The relative individual ecovalences of the populations (results not shown) displayed a greater stability of the seven Turkish populations, which exhibited an ecovalence lower, than the expected value with an equal contribution of genotypes (7.69%).

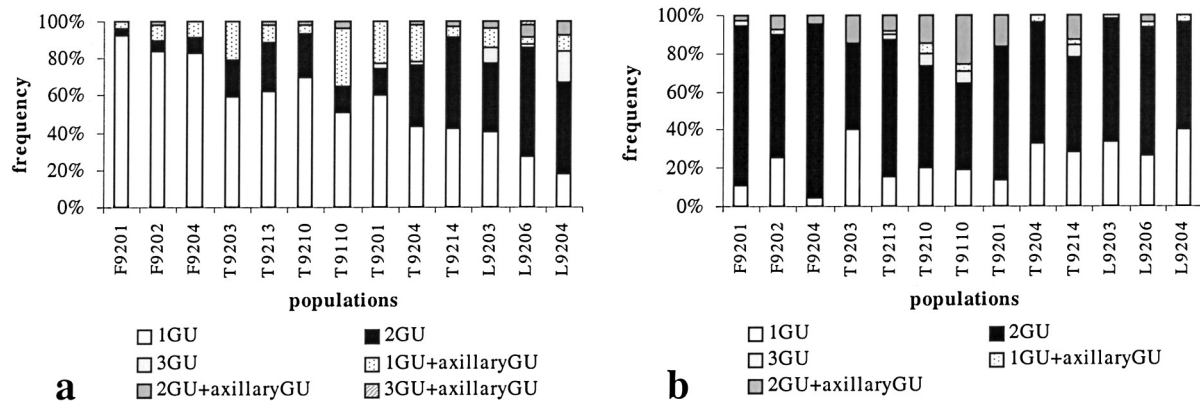


Figure 5. Observation frequency of the different types of annual shoots produced in 1997 according to population and site: La Rouvière (a) or Puechabon (b). Annual shoots composed of one (1GU), two (2GU) or three (3GU) growth units. 1GU + axillary GU: monocyclic annual shoot with one axillary growth unit; 2GU + axillary GU: bicyclic annual shoot with one axillary growth unit; 3GU + axillary GU: tricyclic annual shoot with axillary growth unit.

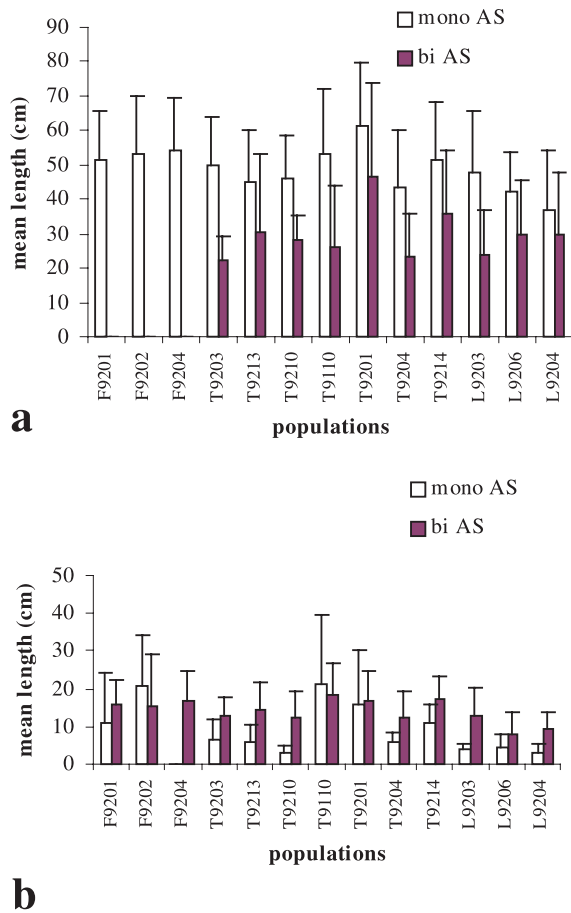


Figure 6. Mean length (\pm standard deviation) of 97-produced mono- (mono AS) and bi-cyclic annual shoots (bi AS), according to population, at La Rouvière (a) or Puechabon (b) sites.

3.5. Polycyclism and year of growth at the Puechabon site

Mean length of annual shoots was the same for years 1997 and 2000 (16 cm). The annual shoots were significantly longer in 1998 (18 cm) and shorter in 1999 (12 cm) at the 0.05 level.

Polycyclic shoot frequency varied considerably according to the year of growth for the French (figure 9a) and Turkish populations (figure 9b), while it remained more or less constant for the Lebanese populations (figure 9c).

For this trait, figure 10 displays the distribution of the relative ecovalences for the four growing seasons and the 13 populations. The contribution of year 1997 to the population \times year interaction was significantly greater than the 25% value expected in case of equal contributions of the four years. At the opposite side, years 1998 and 1999 exhibited an ecovalence significantly lower than the expected value. Among the Turkish populations, five of them exhibited a stability greater than the expected value of 7.9% (T9201, T9203, T9204, T9210 and T9213), as the three Lebanese populations were far the most interactive, but with a 95% confidence overlapping the expected value. These results confirm the greater average stability of the Turkish populations observed at the site level.

3.6. Classification of populations according to polycyclism rate and annual shoot length at Puechabon site

The analysis of similarities between populations for the two morphological features observed revealed two main clusters. The first corresponds to the French and Turkish populations and the other one to the Lebanese populations (figure 11).

4. DISCUSSION

Our results show significant variations in the values of different growth parameters such as polycyclism rate and annual shoot and growth unit lengths according to the site, growth year, population and species for individuals of the same age.

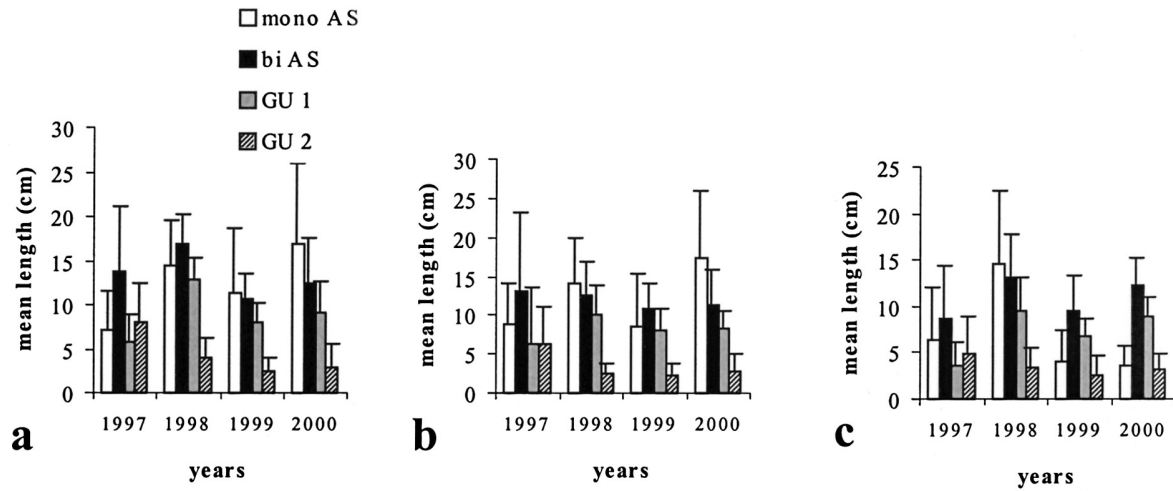


Figure 7. Mean length (\pm standard deviation) of mono- (mono AS) and bicyclic annual shoots (bi AS), and of the first (GU1) and second (GU2) growth unit of bicyclic shoots, according to year of growth, for populations L9203 (a), L9206 (b) and L9204 (c) at Puechabon site.

Table III. Mean length (\pm standard deviation) in cm and number (nb.) of first (GU1) and second (GU2) growth unit of bicyclic annual shoots for each population, according to site. Mann-Whitney-Wilcoxon test for populations of which there were more than five individuals. n.s.: test non-significant; x: test significant, $P < 0.01$; xx: test significant, $P < 0.05$.

	La Rouvière				Puechabon			
	nb.	length GU1	length GU2	test	nb.	length GU1	length GU2	test
F9201	-	-	-	-	29	5.41 \pm 2.37	10.24 \pm 5.26	ns
F9202	-	-	-	-	25	5.48 \pm 4.77	9.40 \pm 5.90	ns
F9204	-	-	-	-	18	5.55 \pm 3.38	10.89 \pm 6.19	ns
T9210	7	16.14 \pm 16.17	9.57 \pm 9.07	xx	18	4.83 \pm 3.57	7.33 \pm 4.38	xx
T9213	13	11.52 \pm 4.89	17.46 \pm 18.98	xx	27	4.96 \pm 2.98	8.96 \pm 6.32	x
T9201	-	-	-	-	19	6.63 \pm 3.99	9.47 \pm 5.27	xx
T9203	10	12.30 \pm 4.71	9.80 \pm 5.99	xx	9	3.77 \pm 2.77	8.33 \pm 5.22	x
T9110	7	16.14 \pm 16.17	9.57 \pm 9.07	xx	14	8.93 \pm 7.06	9.21 \pm 5.25	xx
T9204	15	10.73 \pm 8.25	12.33 \pm 7.89	xx	19	5.05 \pm 3.50	6.90 \pm 4.43	xx
T9214	16	18.94 \pm 14.60	18.00 \pm 14.69	xx	16	5.93 \pm 3.73	10.69 \pm 4.92	ns
L9203	18	10.00 \pm 5.21	13.72 \pm 9.48	xx	28	5.21 \pm 3.36	7.03 \pm 4.74	xx
L9206	28	11.46 \pm 9.60	17.82 \pm 11.69	ns	19	3.31 \pm 2.11	4.21 \pm 4.12	xx
L9204	21	11.14 \pm 8.70	17.70 \pm 14.34	xx	14	3.57 \pm 1.60	5.28 \pm 3.83	xx

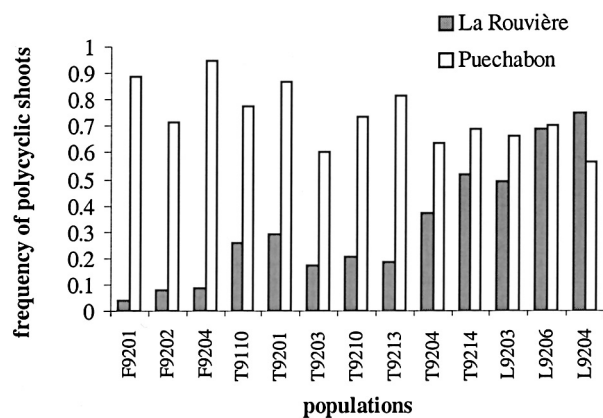


Figure 8. Observation frequency of polycyclic annual shoots according to site and populations.

Overall, La Rouvière site differed from Puechabon site by a greater increase in height for all populations. The environmental factor that account for this difference between the two sites is soil fertility.

4.1. Variations in length of annual shoots and growth units

For most of the populations studied, monocyclic annual shoots were generally longer than bicyclic shoots on the individuals at the more fertile site, and presented the same length on those at the less fertile site. Polycyclism thus does not systematically have a positive effect on the total annual growth of *Cedrus atlantica* and *C. libani* individuals of different populations. This result differs from those obtained with *Quercus rubra* [14, 26, 38], *Quercus petraea*, *Pinus contorta* [37], *Pinus pinaster* [16, 31], *Pinus brutia* [33], and *Pinus halepensis* [34] for which polycyclism generally leads to an increase in annual shoot length.

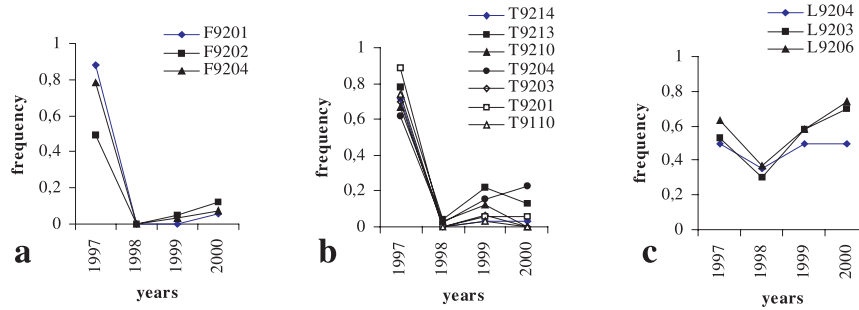


Figure 9. Observation frequency of polycyclic shoots, according to year of growth for the French (a), Turkish (b) and Lebanese (c) populations at the Puechabon site.

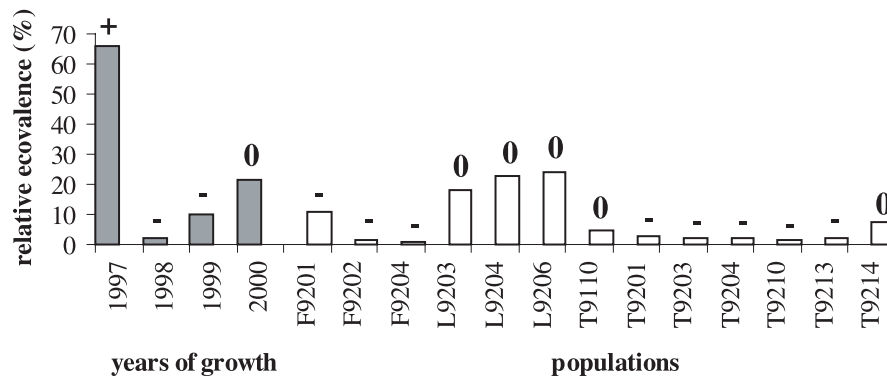


Figure 10. Distribution of relative ecovalences concerning the population × year interaction for percentage of polycyclism rate. (-): ecovalence significantly lower than the expected value; (0): ecovalence overlapping the expected value; (+): ecovalence significantly greater than the expected value.

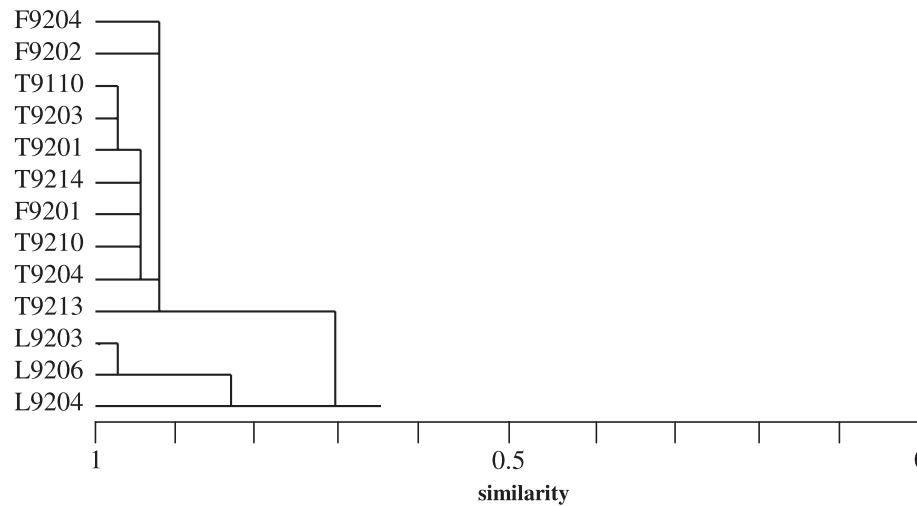


Figure 11. Dendrogram based on the similarities computed from Mahalanobis distance matrix, taking into account the annual shoot length and polycyclism rate, between the 13 populations. The data analysed were obtained over four successive years at the Puechabon site.

In *Cedrus libani*, monocyclic annual shoots were longer than the first growth units of bicyclic annual shoots for the individuals at the more fertile site, and similar for those at the less fertile site. For a same station, the differences in length between the first and second growth units related with year of growth. The differences in growth unit length according to type varied according to environmental conditions, unlike what was seen with young *Quercus rubra* [26] and *Q. petraea* [29, 36], in which monocyclic annual shoots are generally the same length as the first growth units, which in turn are almost always shorter than the second growth units of bicyclic shoots.

4.2. Variations in polycyclism rate according to environmental conditions

The polycyclism rate was higher at Puechabon site compared to La Rouvière site for *Cedrus atlantica* and for the Turkish *Cedrus libani* populations except T9204 and T9214. For these populations, the polycyclism rate was high in 1997, where a spring frost occurred. The polycyclism rate of the French and Turkish populations varied considerably depending on the year of growth. In this case, the polycyclism observed thus resulted from the adverse climatic conditions at

the beginning of the growing season, which temporarily involved a growth stop. In *Pinus pinaster* [31] or in *Pinus contorta* [37], climatic conditions like as a year with dry summer increase polycyclism expression. Unlike for the Lebanese *Cedrus libani* populations, for which better soil fertility did not result in increasing polycyclism, an increase in the number of growth units per annual shoot has been observed with increasing soil resource availability in *Quercus petraea* [13, 15], in *Quercus rubra* [10] or in *Pinus pinaster* [1, 31] individuals. Variations of polycyclism rate have also been observed according to light conditions during the growth [35, 36].

4.3. Variations in polycyclism rate according to population

Within the species *Cedrus libani*, polycyclic shoot frequency varies according to geographical origins of populations. A similar result was obtained for *Pinus contorta* [37] and *P. pinaster* [32]. In *Quercus petraea*, there is a positive relation between polycyclism rate and low original latitude of the populations (Ducouso, personal communication). The results obtained for *Cedrus libani* suggest a similar relation.

According to our results, polycyclism expression is occasional and may be related to difficult climatic conditions during the growing period for the French *Cedrus atlantica* and Turkish *Cedrus libani* populations. A strong link between polycyclism expression and climatic factors has also been described in several species [8, 9, 11, 35]. This behaviour of young trees with respect to polycyclism differs from that of Lebanese *Cedrus libani* populations for which the polycyclism rate remained relatively constant irrespective of station and year of growth. The Turkish populations were less interactive in relation with station and growing season. There is thus a strong genetic determinism of this trait as observed for pines [18, 31] and oaks [20].

In *Cedrus*, polycyclism expression was not linked to an increase in the size of the resulting annual shoot or in the total height of trees. In the event of favourable growing conditions, as at La Rouvière site, bicyclic shoot frequency tends to decrease. In *Cedrus*, annual shoot extension is normally continuous throughout a long growth period [40]. In the event of adverse climatic conditions, as at Puechabon site for French and Turkish populations, extension is stopped momentarily, and resumes once conditions are more favourable. These results suggest that in the Lebanese populations, in which the polycyclism rate is systematically high, polycyclism is a way of adaptation to adverse climatic conditions during the tree growth period.

5. CONCLUSIONS

The results of our study show that polycyclism is observed in the genus *Cedrus* and more particularly in *Cedrus libani*. Unpublished qualitative observations also revealed the extent of polycyclism in *Cedrus brevifolia*. Among the *Cedrus libani* populations studied, two sub-groups were identified according to polycyclism expression and annual shoot length: one of Turkish and the other of Lebanese populations. The differences in polycyclism rate between the two sub-groups of pop-

ulations were more marked for the better growing conditions. This fact could be quantified by there relative contribution to the interaction sum of squares at the between-site or at the between-year level (relative individual ecovalence). Moreover, the two sub-groups were separated by genetic markers, and can be classed as sub-species of *Cedrus libani* [22]. Given its high genetic determinism, this morphological criterion is appropriate for distinguishing between *Cedrus libani* genotypes from different geographical origins, and is a character that should be taken into account in the morphological description of populations. Furthermore, polycyclism leads to modifications in terms of annual shoot structure, particularly in respect to branch pattern. Hence it is important to take this trait into account in genetic improvement programmes.

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