to the ratio of the expected to actual numbers of ramets of each clone included in the incomplete design.

Once the horizon becomes equal to any of the specified minimum separations, SOD's strategy depends upon the user's specifications. The default is to gradually increase the number of ramets available for each clone, to allow SOD greater flexibility in arranging the design. However, the user may specify that SOD should reduce the separations between related ramets. In any case, once the number of ramets available for each clone becomes large, the separations are reduced progressively until a design is achieved.

SOD will never fail to produce a design. It may need to reduce the nominated separations and increase the number of ramets for certain clones, but it will always produce a design. However, if the design produced is for some reason unsatisfactory, more clones, preferably unrelated to those already in the design, should be included, and the program restarted.

Using SOD

SOD is designed for ease of use. It requires a minimum of input for its succesful operation. The basic input required includes a title, description of the orchard (number of clones, rows and trees in the orchard and numbering system) and the separation to be maintained between related ramets. The user must also specify the relationships between the clones comprising the orchard.

The user may also specify the size and shape of the horizon to be used when searching the vicinity of any position in the orchard for related ramets, and the location of adjacent ramets. This enables the user to take account of rectangular and staggered spacings, and of prevailing winds, etc.

Group identity may be given for two classes of groups. SOD will attempt to maximize panmixis within (and miniminze between) groups of the first class, and thus this class may be used to indicate early or late flowering, etc. SOD maximizes panmixis between (and minimizes within) groups of the second class, and thus this class may be used to indicate coastal or mountain provenances, etc.

If the orchard is not rectangular with every position occupied, a plan may be given to indicate planted positions. If the design to be created adjoins an existing orchard, it may be desirable to take the composition of the existing adjacent section into account when creating the new design by including trees from the adjoining section in the design criteria. The number of trees to be included depends on the horizon.

SOD produces a list of the clones, showing the name, pedigree, related clones and the number of ramets included in the orchard; a table showing links completed between all clones, and a value showing the panmixis achived; a list of grafting (or planting) instructions for each clone sorted by row and tree position; plans of the orchard showing the pedigrees and clone names; and a compact summary of the orchard plan in a computer file for archival purposes.

Discussion

Although SOD was developed independently of COOL (Bell and Fletcher, 1978a), and specifically for Queensland's tree breeding program, they share some similarities. SOD does not provide the systematic thinning facility given in COOL, but tests indicate that systematic thinning in a SOD design rarely alters the clonal composition. The computer costs incurred are similar for both programs. However, SOD does offer some advantages:

- It ensures separation of related clones.
- It employs information on provenance, compatibility, flowering and general combining ability.
- It provides scores to enable the breeder to assess the level of panmixis and inbreeding expected in the orchard.

Copies of the SOD program are available from the author, who can also arrange use of the program on the Queensland Department of Forestry computers.

Acknowledgements

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Variability of Juvenile Greek Firs and Stability of Characteristics with Age

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Summary

Two successive studies on the morphology of the leaf and branch system and on the growth strategy (phenology and height growth) of the Greek Fir (*Abies cephalonica* Loudon) were carried out on the same provenances, one in the nursery five years after germination and the other in a comparative experimental field in the south of France twenty years after germination. They made it possible to characterize intraspecific variability and to evaluate its stability with age.

Morphology varies regularly from the southern to the northern regions of the native area. In the south of the Peloponnesos, a high number of individuals of the pure *Abies cephalonica* type can be found, while in the north, in the Pindos mountains, a mixed stand can be found containing an increasingly important number of hybrid individuals (*Abies borisii regis* MATTFELD). This is the result of the probable superimposition of two opposed phenomena: first, the increasing introgression of *Abies alba* (MILLER) towards the north, and second, the adaption of stands to increasing drought towards the south.

Only a few phenological and morphological characteristics vary little with age, e.g. early flushing of the Pindos stands, stomatal density on the upper side of needles and lateral branch pubescence. These last two morphological characteristics seem to be genetically related: lateral branch pubescence increases from the south to the north, while the number of stomata decreases.

On the other hand, the expression of growth (annual shoots and total height) changes over time and makes early selection for this characteristic difficult. Generally, at twenty years of age, the Pindos and Menalon provenances seem to be the most hardy and those from the Taygetos and Parnassos seem to be the least hardy.

Key words: Abies cephalonica LOUD., *Abies borisii regis* MATTF., morphology, phenology, growth, temporal variability.

Résumé

Deux études successives de la morphologie de l'appareil végétatif (feuilles et rameaux) et de la stratégie de croissance en hauteur du Sapin de Grèce ont été faites sur les mêmes provenances, l'une en pépinière 5 ans après germination et l'autre en plantation comparative dans le sud de la France 20 ans après germination. Elles ont permis de caractériser l'allure de la variabilité intraspécifique et de juger de sa stabilité avec l'âge.

La morphologie varie régulièrement du sud au nord de l'aire naturelle. On passe de populations à forte fréquence d'individus de type pur *Abies cephalonica* (LOUDON) dans le sud du Pèloponnèse, à des populations mélangées, comportant une proportion croissante d'individus de type hybride (*Abies borisii-regis*, MATTFELD) dans le Pinde. Ceci résulte de la superposition probable de deux phénomènes variant en sens opposés: introgression croissante d'*Abies alba* (MILLER) vers le nord, adaptation des populations à la sécheresse croissante vers le sud.

Seuls quelques caractères, phénologiques (débourrement précoce des populations du Pinde) ou morphologiques (densité des stomates à la face supérieure des aiguilles et surtout pubescence du rameau), varient peu avec l'âge. Ces deux derniers caractères morphologiques semblent génétiquement liés: du sud vers le nord, la pubescence du rameau augmente alors que le nombre de stomates diminue.

A l'inverse, l'expression de la croissance (pousses annuelles et hauteurs totales) se modifie avec le temps et rend problématique toute sélection précoce de ce caractère. Globalement, à l'âge de 20 ans, les provenances du Pinde et du Mainalon semblent les plus vigoureuses, celles du Taygète et du Parnasse les moins vigoureuses.

Mots clefs: Abies cephalonica LOUD., *A. borisii regis* MATTF., morphologie, croissance, variabilité temporelle.

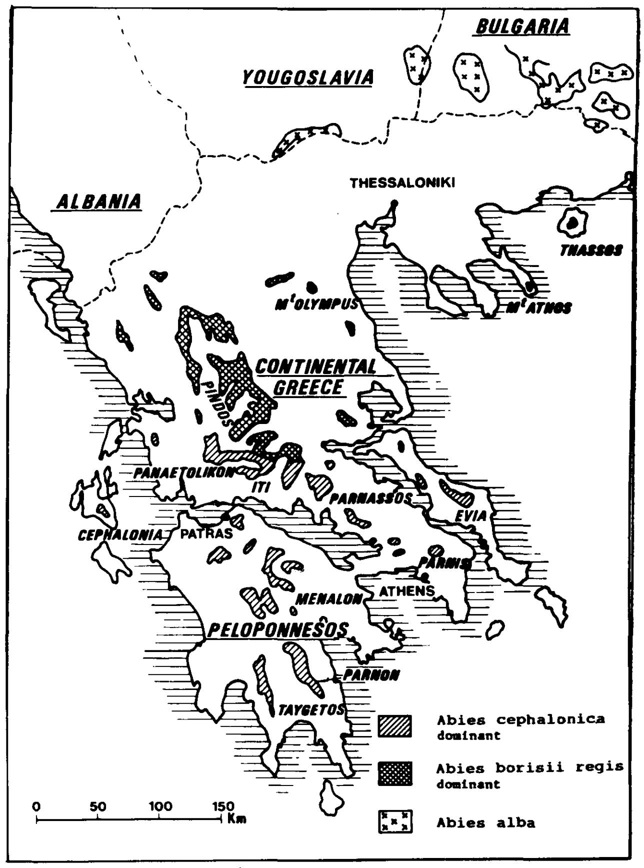

Figure 1. — Natural distribution area of the Greek Fir (from QUÉZEL and BARBERO, 1985).

Introduction

Apart from the island which gave it its name, the range of the Greek Fir, *Abies cephalonica* LOUD. principally covers the Peloponnesos and continental southern Greece. The first pure stands of *Abies alba* MILL. can be found only beyond the northern limits of Greece (MITSOPOULOS and PANETSOS, 1987). It has been supposed (MATTFELD, 1930; MAYER, 1981; PANESOS, 1975) that contact between these two species, during the southern migration of the silver Fir at the time of the last Ice-Age, gave birth to a hybrid population called *Abies borisii regis* by MATTFELD. These hybrids are located in continental Greece, in the Pindos mountains and in association with *Abies cephalonica* in the Peloponnesos. They progressively resemble pure *A. cephalonica* as they extend southwards (*Figure 1*).

The Grecian fir forests have been described by many authors, in particular by BASSIOTIS (1956), PAULY (1962), BARBERO and QUÉZEL (1975, 1976) and PANETSOS (1975). In southern Greece, *A. cephalonica* ranges from 700 m to 2200 m in altitude, with an ecological optimum between 1000 m and 2000 m. It thus completely occupies the supra- and mountain-Mediterranean, as well as the upper portion of the meso-Mediterranean level. It is frequently mixed with the black Pine (*Pinus nigra* ARN.), except in the driest stations of the Peloponnesos. From a climatic perspective, the sites occupied by *A. cephalonica* can be characterized by a sharp summer drought (three months long, on average) and a humid bioclimate (approximately 1000 mm of rainfall per year) with a temperature variation from extremely cold (average minimum of the coldest month: m < —7 °C), to cool (0 < m < 3 °C), which is a wide range for a Mediterranean Fir.

The hybrid fir forests have a wetter and cooler climate with mean annual rainfall of approximately 1500 mm and temperature variation from cold (—3 < m < 0 °C) to extremely cold. Due to this, these fir forests basically occupy only the mountain-Mediterranean level. Throughout the range, many different types of substrates can be found: limestones, dolomites, flysch, schists, etc.

This brief review of the ecology of the Greek Fir in its natural area sufficiently demonstrates the interest that exists in using this species for reforestation in southern France at the level of the pubescent Oak forests and in the upper part of the holly Oak forests.

This study was carried out within the framework of a program in which the aim was to show the ecological requirements and the genetic variability of the Greek Fir ("Mediterranean Fir" program, I.N.R.A.). Its goal was to determine all the morphological and growth characteristics of the Greek Fir provenances planted in France from their juvenile stage of development, to point out their particularities and to study their stability over time.

Material and Methods

1.1 Plant Material

The 11 Greek Fir provenances used were supplied by the Greek Forestry Service. They covered a large part of the species' natural distribution, including the hybrids. *Table 1* shows the information obtained for these trees, as well as that for other Mediterranean Conifers present in the experimental plots (the specific name *Abies cephalonica* should be considered in its broadest sense). In addition, *table 2* summarizes the main characteristics of the experimental design.

Table 1. — Characteristics of Provenances from the experimental design for "mediterrane an firs" program.

Code	Provenance	elevation, aspect and altitudinal zone	substrate	species
PRIL	Profitis Ilias Taygetos, Greece	1450 m, North Supra-mediterranean	Limestone	Abies cephalonica
XERO	Xerovounia Taygetos, Greece	1200 m, North Supra-mediterranean	limestone	Abies cephalonica
KAPO	Kapota Menalon, Greece	1300 m, East Supra-mediterranean	dolomitic limestone	Abies cephalonica
VLAH	Vlahica, Menalon, Greece	1300 m, North Supra-mediterranean	limestone	Abies cephalonica
LAGA	Lagada Menalon, Greece	750 m, North-west Supra-mediterranean	limestone	Abies cephalonica
BROM	Bromopigado Parnassos, Greece	1800 m, North-east Mountain-medit.	limestone	Abies cephalonica
KORO	Koromilies Parnassos, Greece	1500 m, North-east Supra-mediterranean	limestone	Abies cephalonica
KOLO	Kolokithovrissi Parnassos, Greece	1250 m, North Supra-mediterranean	Flysch	Abies cephalonica
MEVR	Megali-Vrissi Parnassos, Greece	1220 m, South-west Supra-mediterranean	Flysch	Abies cephalonica
KRAS	Kerasini Pindos, Greece	1200 m, North Supra-mediterranean	Flysch	Abies cephalonica
PALE	Paleoturnos Pindos, Greece	900 m, North-west Supra-mediterranean	Flysch	Abies cephalonica
ITAL	Italy, arboretum provenance, probably a hybrid			Abies cephalonica
AMAN	Amance, North-east France. Arboretum provenance			A. nordmanniana
KRAN	Krasnodar, Caucasus mountains, USSR			A. nordmanniana
BABO	Babors mountains, Algeria			Abies numidica
PIRO	Pinsapar de Ronda, Andalusia, Spain			Abies pinsapo
SACR	Sangre de Cristo, Colorado, USA			Abies concolor
SEYA	Sehirli-Yayla, Bolu, Turkey			A. bornmuelleriana
VENT	Ventoux, Southern France, planted provenance			Cedrus atlantica

1.2 Measurement and Observation Methods after five years in the Nursery

1.2.1 Morphological Characteristics

Many different morphological characteristics were measured or observed for five year old Greek Firs sampled in two groups of 50 individuals per provenance, one from Ruscas (Var, southern France) and the other from Amance (Meurthe-et-Moselle, northeastern France). The study of

Table 2. — Description of the experimental design.

Germination Date	spring 1966, Caunes (Var, southern France) nursery, in the ground under shade cloth		
Lifting	at 3 years of age at Ruscas (Var) and at Amance (M. et Moselle, north-eastern France), 100 seedlings par m^2 ; planting during winter 1970-1971, 3-2 seedlings		
	LE TREPS	PELENQ	LA LIVINIERE
Localization and aspect	Collobrières (Var) State Forest, Maures mountains, altitude 600 m, north	Pélenq State Forest (Var), Haut-Var region, altitude 520 m, east-north-east	La Livinière State Forest (Hérault), Minervois mountains altitude 450 m., south
Rainfall	1200 mm per year	750 mm per year	650 mm per year
Substrate	micaschists ; shallow, highly filtering soil	limestone ; decarbonated surface soil, argillaceous	micaschists.Relatively deep soil, good retention
Preceding Forest Type	degraded maritime Pine forest. Medit. cork Oak series	holly and pubescent Oak coppices Medit. pubescent Oak series	holly Oak maquis or uncultivated land, supra-Medit pubescent Oak series
Plantation Type	bare roots, full sun 2m X 2m spacing, undersoil preparation	bare roots, protective rows, 2m X 2m spacing, undersoil preparation	same as Le Treps
Experimental Design	16 provenances, 20 blocks, 4 prov. per block, 72 seedlings per unit plot 5 replications	same	same, but 64 seedlings per unit plot
Plant material	12 provenances of Greek Fir, plus PIRO, VENT, AMAN et SACR	12 provenances of Greek Fir, plus KRAN, VENT, AMAN et SACR	12 provenances of Greek Fir, plus SEYA, VENT, AMAN et SACR

each individual was focused on the lateral branch of the last whorl:

-shape of needle apex located in the middle of the lateral branch (by magnifying glass) using the following notation scale:

1: bilobular or emarginate
2: rounded, simple or mucronate
3: bifid acuate
4: blunt acuate (conical)
5: sharp acuate (acuminate)

-length of lines of stomata (stomatal density) on the upper side of needle near the apex (magnifying glass with micrometer: 100 graduations = 3 mm);

-number of lines of stomata on the underside in the needle mid-section;

-number of stomata per 3 mm of line on the underside in the needle mid-section (magnifying glass and micrometer);

-pubescence on the lower generative organs of the lateral branch using the following scale:

0: glabrous
1: low pubescence
2: average pubescence
3: high pubescence

1.2.2 Phenological Characteristics

Vegetative Flushing

The relative earliness of terminal bud flushing in young four-year old saplings was evaluated in two different ways:

-at Amance: four successive observations were made one week apart on 36 individuals per provenance using the following scale (Debazac, 1965 and 1967):

0: dormant bud
1: swollen bud, scales more or less spread apart
2: young needles appearing through the transparent cap
3: flushed bud, free needles in a fine brush still covered by the cap
4: needles in a brush with separated ends, free of the cap, the young shoot beginning growth.

-at Ruscas, the exact date of bud break was determined: 300 individuals per provenance were systematically observed every 2 days or 3 days for 3 weeks.

End of Elongation

During the fifth year of growth, elongation of 16 to 20 individuals per provenance was followed at Ruscas every 2 days or 3 days using reference marks cut into attached metal poles. The date of the end of elongation was conventionally set at the moment when 95% of the length of the annual shoot had been reached.

1.2.3 Growth Characteristics

Total height, diameter at the collar and the number of lateral branches of the last whorl were measured at Ruscas at the end of the fifth year of growth on 200 individuals per provenance (five replications).

The same measurements were made at Amance on 256 individuals per provenance (four replications). They went with the measurement of the tap root length for 144 three year old saplings per provenance (four replications).

1.3 Measurement and Observation Methods at 20 years of age in the Experimental Field

1.3.1 Morphological Characteristics

At Le Treps (*Table 2*), three provenances of comparable vigor were chosen: PALE from the Pindos Mountains, KOLO from Parnassos and KAPO from Menalon. Each was represented by 120 individuals distributed in two blocks. All the samples were taken from the lateral branch of the fifth whorl oriented towards the south. The measurement scales were similar to those used in the nursery. Characteristics which showed no significant differences between provenances in the nursery were not considered. Two supplemental characteristics were added:

-position of needles on the laternal branch:

1: in a bottle brush-shape (radial)
2: 3/4 bottle brush-shaped (V on the underside)
3: brush-shaped (absence of needles on underside)
4: comb-shaped

-amount of resin on buds

0: none
1: present at base of bud
2: abundant all over bud

1.3.2 Phenological Characteristics

The observation of bud break was made for the three above provenances with the same accuracy as before following the identical five-point scale. For the same individuals, the duration of elongation was evaluated by weekly measurements using a telescopic pole graduated in cm. As before, the date of the end of elongation corresponded to the moment when 95% of the length of the annual shoot was reached.

1.3.3 Growth Characteristics

Total height was measured using a telescopic pole graduated in cm. for all of the 11 provenances in the experimental design (see *Table 2*) over several growing seasons (an average of 300 individuals with five replications per provenance). Diameter at the collar was measured for each of the 3 provenances: PALE, KOLO and KAPO.

Variability Observed at 5 Years of Age (Nursery)

2.1 Seed Size and Number of Cotyledons

The weight of 1000 seeds, calculated from four replications of 50 seeds, varied between 50.1 g and 71.4 g *(Table 3)*. This variation did not follow any geographical gradient, although the provenances from the same mountain range had good cohesion: thus, for example, the Menalon provenances had a lower seed weight than that of the other provenances without it being possible to find a satisfactory adaptational explanation for this fact. The average number of cotyledons varied between 5.8 and 6.4 and did not seem to be correlated with seed weight (non-significant correlation coefficient).

2.2 Needle and Lateral Branch Morphology

2.2.1 Variability Between Provenances

All the F tests were significant at the 1% level in the two experimental sites.

The number of lines of stomata on the under side and the density of stomata on each line did not appear to follow any specific geographic variation. However, there was a north-south variation gradient for the other three characteristics (*Figure 2*). Rounded and particularly conical apexes were well-represented in the two Pindos provenances. Outside this zone, which is thought to be characterized by a hybrid stand (*Abies borisii-regis*), the apexes have a single sharp point (acuminate), particu-

Table 3. — **Growth characteristics of 12 *Abies cephalonica* provenances at 5 years of age.**

Provenances	Weight of 1000 seeds	Nb. of cotyledons	Height at 3 years	Height at 5 years (Ruscas)	Height at 5 years (Amance)
PRIL	67,0	5,95	9,1	11,05	14,73
XERO	62,0	5,94	8,9	11,31	13,60
Taygetos mean	64,5	5,94	9,0	11,18	14,17
KAPO	58,5	6,06	9,1	11,55	13,96
VLAH	57,4	6,03	8,8	12,17	14,07
LAGA	50,1	6,10	9,2	12,66	14,43
Menalon mean	55,33	6,06	9,03	12,13	14,15
BROM	67,8	5,89	8,2	10,98	13,76
KORO	69,0	6,43	9,2	11,58	15,63
KOLO	71,4	6,08	8,2	12,15	14,50
MEVR	60,7	5,78	8,1	11,60	12,66
Parnassos mean	67,23	6,05	8,43	11,58	14,14
KRAS	64,4	6,06	10,6	13,50	17,16
PALE	63,0	6,12	9,3	12,43	15,12
Pindos mean	63,7	6,09	9,95	12,97	16,14
ITAL	58,3	5,91			

For all these characteristics, Duncan tests were non-significant at 5% level, except for the KRAS provenance which is clearly superior for height growth characteristics at 3 and 5 years of age at Amance.

larly in the Peloponnesos. The artificial Italian provenance ITAL alone has bilobate, or even bifid apexes, which strongly suggests a fortuitous hybridization (probably with neighboring silver Firs), an inherent problem to growth outside the native environment. The same can be observed for lateral branch pubescence: present in the hybrid Pindos stands, it decreased from north to south, until it almost disappeared in the Taygetos (particularly in the PRIL provenance). However, the comparison of the average by a Duncan test did not make it possible to separate the groups of provenances by their native region in a statistically significant way. The gradation was even clearer for the length of lines of stomata on the upper side of the needle. It increased regularly from the hybrid Pindos Firs, which were statistically isolated from the other provenances for this characteristic, to the Parnassos and Peloponnesos Firs.

The morphological characteristics studied are not transmitted independently; a covariation law can be demonstrated. Thus, as one heads southwards, pubescence decreases while stomatal density on the upper side increases and the apexes become more pointed and acuminate (*Figure 3*).

2.2.2 Variability Within Provenances

The coefficients of variation from the comparable data of the two experimental sites are shown in *Figure 4*.

Provenance variability increases from the south towards the north, towards the hybrid stands, for all characteristics except pubescence. It seems that this characteristic had a simple genetic determinism and was fixed in introgressed stands from the north of the distribution area, demonstrating its taxonomic value.

The simultaneous consideration of all of these characteristics and the existence of relatively large individual variability all the way into the Menalon and even the Taygetos regions, confirms the hypothesis that individuals having hybrid characteristics are present to a significant

Apex Form		Length of Stomata on the upperside		Lateral Branch pubescence	
4,88	PRIL	2,23	LAGA	1,38	ITAL
4,88	LAGA	1,99	PRIL	1,02	PALE
4,84	XERO	1,98	KAPO	0,98	KOLO
4,83	KORO	1,88	VLAH	0,80	KRAS
4,72	VLAH	1,81	KORO	0,76	LAGA
4,72	MEVR	1,73	KOLO	0,65	BROM
4,71	KAPO	1,64	XERO	0,44	MEVR
4,53	BROM	1,60	BROM	0,36	VLAH
4,44	KOLO	1,40	MEVR	0,35	KAPO
4,34	PALE	1,09	KRAS	0,27	KORO
4,20	KRAS	0,98	ITAL	0,26	XERO
3,12	ITAL	0,91	PALE	0,08	PRIL

Regional Averages :

apex :	stomata:	pubescence:
Pindos = 4,27	Pindos = 1,00	Pindos = 0,91
Parnassos = 4,63	Parnassos = 1,65	Parnassos = 0,59
Menalon = 4,77	Menalon = 2,03	Menalon = 0,49
Taygetos = 4,86	Taygetos = 1,80	Taygetos = 0,17

Figure 2. — **Comparison of the variability of 3 morphological characteristics of the Greek Fir at Ruscas 5 years after germination. Duncan test at 5 % level.**

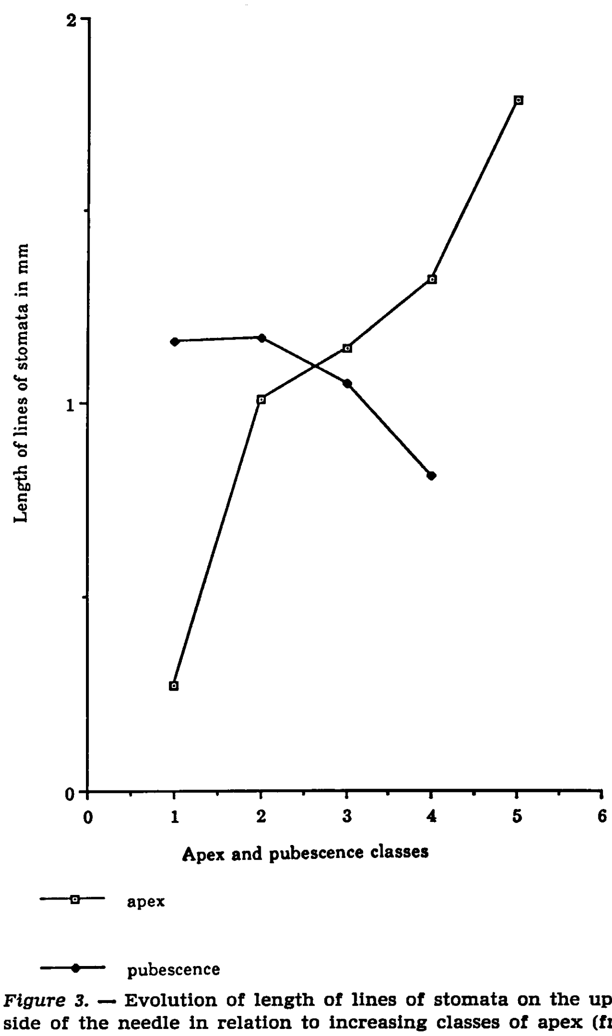

Figure 3. — **Evolution of length of lines of stomata on the upper side of the needle in relation to increasing classes of apex (from rounded to acuminate and pubescence (from glabrous to highly pubescent.**

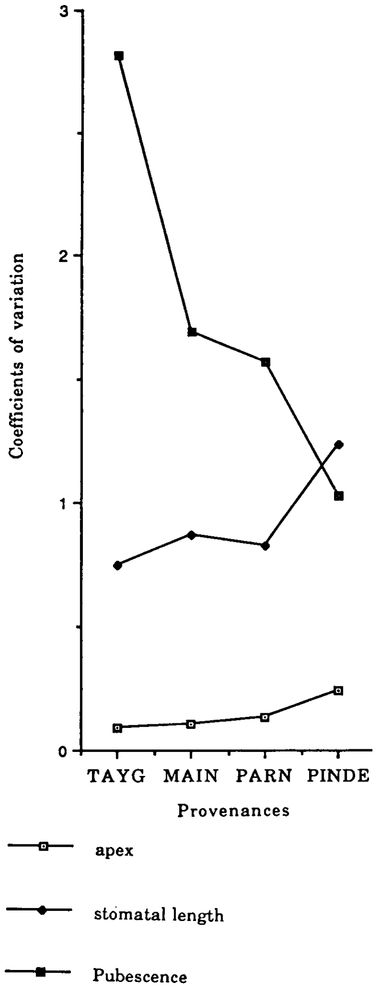

Figure 4. — Evolution of coefficients of variation for 3 morphological characteristics in relation to provenance origin. Average between the 2 nurseries (Ruscas, southern France and Amance, north-eastern France) 5 years after germination.

extent at least in the northern Peloponnesos and that the migration wave of the silver Fir, which caused this to occur, reached far into this region.

2.2.3 Correspondence analysis

In order better to identify the value and importance of each morphological characteristic to make a distinction between provenances, a correspondence analysis was carried out for each of the two study nurseries. The two analyses concurred and only the results from Ruscas are shown.

The main area of variation is found in the first two factors: F1 = 90.59% and F2 = 7.13%. The eigenvalues are low, as is often the case for botanical data.

The characteristics with the greatest importance in the distribution of individuals are: on axis 1, pubescence and length of lines of stomata on the upper side of the needle and, on axis 2, pubescence and apex shape.

Figure 5, which was made using the average coordinates of individuals from the same provenance, clearly shows the separation which exists between Pindos provenances (and the ITAL provenance) and the other provenances of the species, which have a relatively good cohesion. This representation confirms the particular place of the Pindos provenances which contain a much higher number of hybrids than the others without, however, making it possible to place them in another taxonomic group (non-significant Duncan tests, *Figure 2*).

2.3 Phenology

2.3.1 Vegetative Flushing

The results obtained in the two nurseries were highly concordant (r = 0.96) showing that, despite important ecological differences which exist between the north-east and the south-east of France, a remarkable stability of expression can be found for flushing.

Considering the wide spread of bud break dates between the species, the analysis of variance showed highly significant differences (F = 111 at Ruscas for 18 and 69 DF: significant at 1%). The species used as references for this experiment all had later flushing than the Greek Fir (*Figure 6*). Thus, bud break for the *Abies bornmuelleriana* (MATTFELD) provenance occurred more than two weeks later than the average of the Greek Fir provenances and bud break for the *A. nordmanniana* (LINK), *A. pinsapo* (BOISSIER) and *A. concolor* (PARRY) provenances occurred an average of one week later. Although always significantly different from the Greek Fir, bud break for the silver Fir provenance was not, however, much later than that for the Pindos provenances.

The interspecific distinctions are by far the most important ones and tend to hide the variability existing within the *A cephalonica* complex. Thus the Greek Fir has a relatively noticeable specific cohesion compared to other Mediterranean firs, although in the year 1969 there was a one-week spread between flushing for the earliest and latest provenances. The individuals from Parnassos and Menalon were the earliest and those from Taygetos and Pindos were the latest. No apparent geographic or

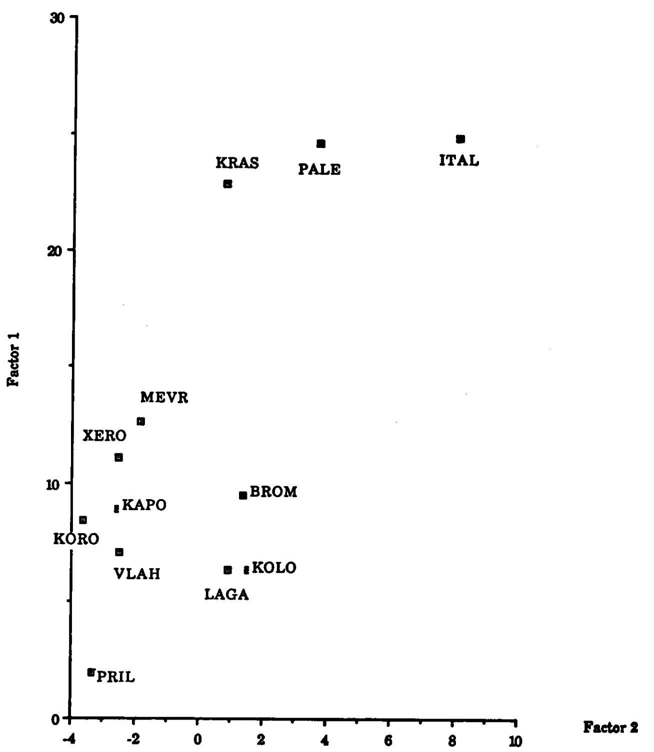

Figure 5. — Factorial plane 1 to 2 of the correspondance analysis for 5 morphological characteristics: needle apex shape; length of lines of stomata on upper side of needle; number of lines of stomata on under side of needle; number of stomata per 3 mm. of line on under side of needle; annual lateral branch pubescence.

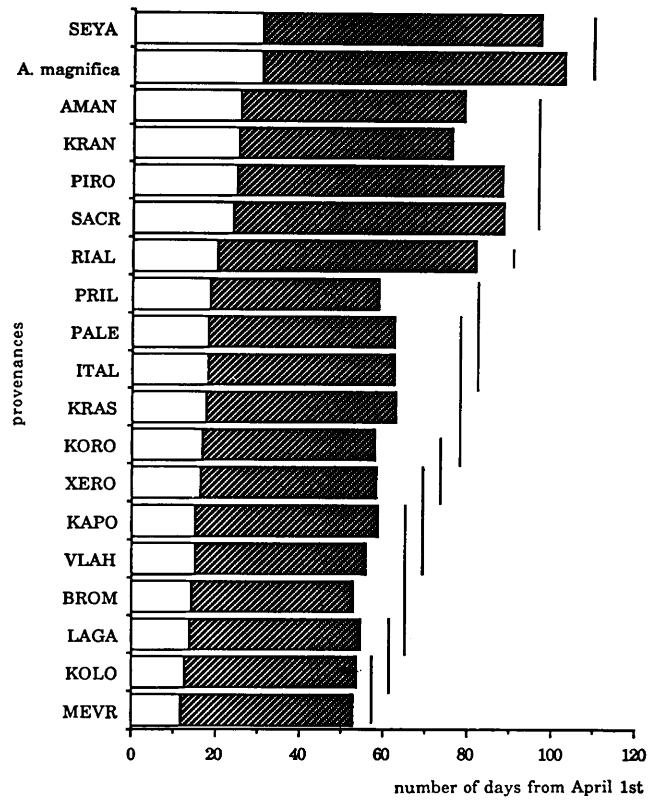

Figure 6. — Comparison of duration and beginning and end dates of elongation for several Mediterranean Fir provenances at Ruscas (southern France 5 years after germination. Duncan test at 5% level.

altitudinal gradient existed in relation to the phenology.

2.3.2 End of Elongation

Large differences were recorded between species (almost one month between the average for Greek firs and *Abies magnifica* MURRAY, and 22 and 24 days respectively for *A. concolor* and *A. bornmuelleriana*) which were highly significant (F = 39.1 for 15 and 95 DF, significant at 1%). The Greek Fir stops its elongation very early *(Figure 6)* and the differences between provenances remains slight. Nonetheless, there is a certain parallel which can be drawn with bud break, as the Parnassos provenances were among the earliest to stop growth and the Pindos (and Italian) Firs were among the latest.

The average duration of elongation did not make it possible to differentiate between the Greek fir provenances. However, the Greek Fir had the shortest elongation period (26.7 days on average) compared to other species whose elongation period averaged from 36 days to 41 days. Only *Abies nordmanniana* had a comparable elongation period (26 days to 28 days). This strategy, among others, provides this species with a remarkably high capacity to respond to large water deficiencies (AUSSENAC, 1980; BOUACHRINE, 1985).

The duration of elongation is not well-correlated with annual growth :it can only account for 25% (r = 0.51 for 17 DF and 0.50 for 10 DF, Greek fir alone) of the size of the annual shoot.

As before, there does not appear to be any geographic or altitudinal gradient in the duration of elongation for the Greek Fir provenances.

2.4 Size and Organization

The results of measurement of total height were fairly comparable in both environments (r = 0.64 for 9 DF, Greek Fir provenances), although the two nurseries had a very different fertility. The Pindos firs in particular (especially KRAS) were quite hardy. The Parnassos provenances seemed to be generally less hardy than those from the Menalon. The Taygetos provenances were the least hardy. With two notable exceptions (PRIL and KORO), which have an increased hardiness in more fertile environments (*Table 3*), the compared performance of each of the Greek Fir provenances was a stable function of the environment (no significant genotype X site interaction). On the contrary, species such as *A. pinsapo* and *A. concolor* showed a greater environmental sensitivity.

It should be noted that seed weight does not appear to have an important influence on the ranking of heights at five years of age.

The simultaneous measurement of the length of the tap root and total height of the above-ground structures at Amance demonstrates a predictable allometric relationship (r = 0.86). However, it was not possible to establish a correlation between increase in tap root length and summer drought conditions in the seed's native environment.

There was also an allometric relationship between total height and diameter at the collar. But neither total height, nor diameter at the collar, nor even the ratio between the two ("form index") made it possible to distinguish significantly between species and provenances.

The number of lateral branches of the last whorl at five years of age shows the organizational level of the tree. This is not entirely independent of hardiness, but it provides additional information related to future leaf biomass and thus to later growth. The comparison of differences between size and organization is particularly noticeable at the interspecific level and therefore has little value in discriminating Greek fir provenances among themselves. However, the Pindos firs have more lateral branches per whorl, despite their greater height, which is similar to the juvenile structure of the Silver fir and once again emphasizes the hybrid morphology of the Pindos firs.

3. Variability observed at 15 years of age (comparative experimental fields) and evolution of the variability with age

The preceding analyses pointed out a certain number of morphological and growth characteristics which made it possible to discriminate between provenances of five year old Greek Firs;

The same type of study was carried out 15 years later (1985) to attempt to individualize those preceding characteristics which had remained significantly discriminative.

3.1 Morphology

3.1.1 Varability Between Provenances

The differences between provenance means were not significant for all the studied characteristics. Apex shape and position of needles on the lateral branch did not make it possible to distinguish between provenances at the 5% level. The apex shape was generally acuminate or occasionally conical and the position of needles was usually radial. However, there was a geographic variation gradient for the other characteristics (*Figure 7*). The quantity of resin on the buds increased noticeably from

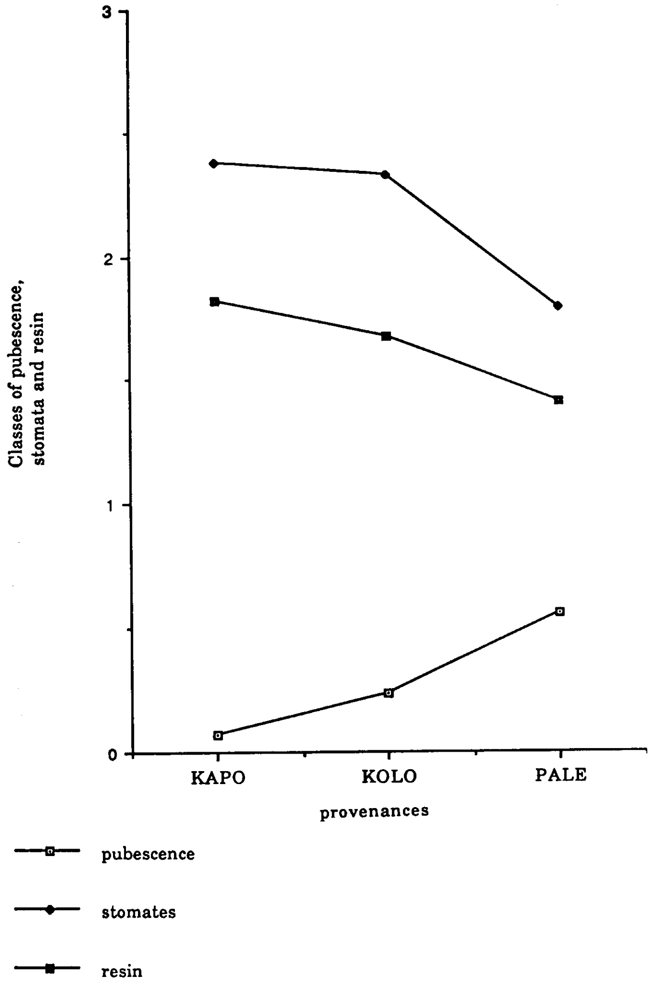

Figure 7. — Evolution of 3 morphological characteristics in relation to provenance geographic origin at Le Trep (Maures mountains, southern France 20 years after germination.

the north to the south (F = 12.96 for 2 and 280 DF, significant at 1%). The buds from the Menalon individuals were coated with resin. The length of the lines of stomata on the upper side (F = 10.04 for 2 and 280 DF, significant at 1%) mainly distinguished the Pindos individuals from the other two provenances. Individuals from the PALE provenance had few stomata which were always localized at the apex, while the KOLO and KAPO provenances had numerous individuals with abundant stomata at the apex or even spread out over the entire upper side. The north-south gradient was particularly clear for pubescence (F = 11.59 for 2 and 280 DF, significant at 1%). Pubescence was frequent in the Pindos (33% pubescent individuals, half of which are highly pubescent), but low in the Peloponnesos (6% pubescent individuals) and even in the Parnassos (17% pubescent individuals, 1/4 of which are highly pubescent).

3.1.2 Variability Within Provenances

The coefficients of variation showed the greatest variability in the PALE provenance for resin and stomata. Pubescence, however, revealed an increased stability in this provenance (*Figure 8*).

3.1.3 Relationship Between Characteristics

The three significant characteristics are not independent of each other. Further towards the north, pubescence increased while the length of the lines of stomata on the upper side of the needle decreased and resin no longer covered most of the bud, only the bud base (*Figure 7*).

3.1.4 Evolution of Discriminating Power of Characteristics With Age

All the morphological characteristics observed, which were thought to be interesting according to the descriptions of different authors (Debazac, 1964; Panetsos, 1975; Viguié and Gaussen, 1929), do not have the same taxonomic value or even the same stability with age. If the apex shape is a good descriptive characteristic for five-year old saplings, no bilobate apex was observed for 20 year olds and all the apexes were acuminate or ogival at this age. The presence of stomata on the upper side of the needle is less noticable in the young adult stage than in the juvenile stage, but makes it possible to distinguish Pindos individuals from others. The presence of resin on the bud is an inaccurate characteristic, but significant at the young adult stage. Lateral branch pubescence remains an excellent distinguishing characteristic and is visible both in the young sapling and later. A recent study on the morphology of the Greek fir (Mitsopoulos and Panetsos, 1987) illustrates the same point.

Some characteristics are lost with age and there seems to be a passage to an adult morphology which is quite different from the juvenile one.

The variation within provenances was comparable in the two studies. That of the Pindos stands was particularly important for most of the characteristics and

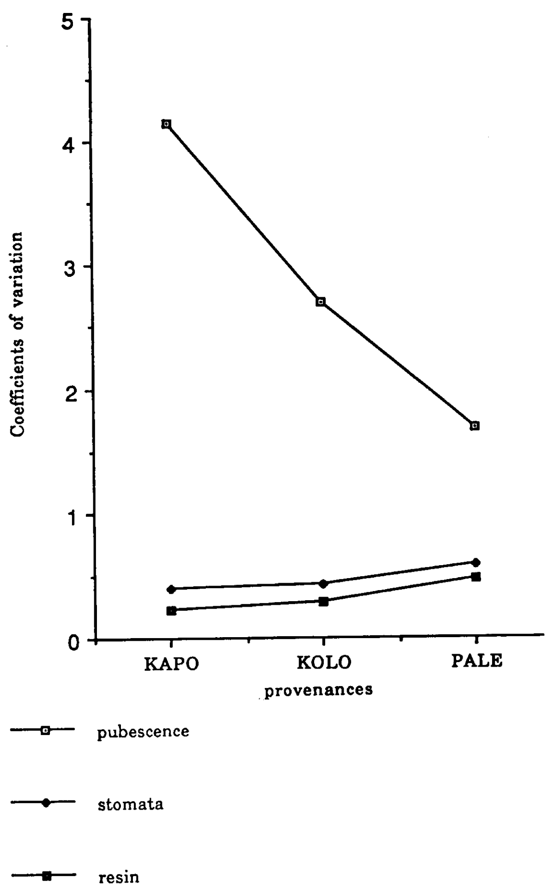

Figure 8. — Evolution of coefficients of variation for 3 morphological characteristics in relation to provenance geographic origin at Le Treps (Maures mountains, southern France) 20 years after germination.

recalls its hybrid origin (MATTFELD's hybrid "swarm"). The high frequency of pubescent individuals observed also signals the introgression of *Abies alba.* Laternal branch pubescence seems to behave like a simple Mendelian and probably dominant characteristic, and presents therefore a high taxonomic value. If the frequency of pubescent individuals decreases southwards, it still remains important (6%) in the Menalon provenances, which shows the presence of hybrid individuals even in this southern part of the Greek Fir's range.

3.2 Phenology

All flushing occurred between May 7th and 10th, with a maximum of 1 day to 2 days difference between provenances, which is very slight. However, the Parnassos provenance was significantly earlier (DUNCAN test, 5% level) than the others (2 days difference with KAPO). The Pindos individuals were later and those from the Menalon were between the two. These differences do not appear to confirm the existence of a geographical gradient of the same type as the morphological gradient.

3.3 Search for Best Discriminating Characteristics

The phenological and morphological characteristics were compared using a correspondence analysis. The points on the factorial planes are widely scattered (low eigenvalues). The variance proportion of the axes is also low. However, the scattering on axes 1 and 2 is due to small number of factors, mostly pubescence and early flushing. These two characteristics can explain up to 55% of the variance proportion of the swarm of points. The other characteristics are not sufficiently discriminative before the fifth axis (cumulative variance of the first four axes = 82%).

Flushing and pubescence remain the main distinguishing characteristics between provenances and make it possible to characterize the hybrid individuals from the Pindos mountains. These two characteristics do not change with age as did the other characteristics studied.

3.4 Duration of Elongation

As for five-year old individuals, neither the duration of the elongation period, nor its end date made it possible to separate significantly the Greek Fir provenances. On the other hand, the duration of elongation went from approximately 26 days at five years of age to 50 days at 20 years of age.

In addition, the duration of elongation in the young adult stage no longer had any relationship to the size reached by the shoot during the same growing season (r = 0.04 for 11 DF). At the juvenile stage, 25% of the height of the annual shoot was due to the duration of the elongation period. This suggests that as the tree ages and increases the size of its annual shoots, it changes its growth strategy. The initiation of stem units, which extends over a longer period of the year than elongation (OWENS, 1984, for *Abies grandis*; KREMER and ROUSSEL, 1982 and 1986, for *Pinus pinaster*) could become more important and thus free the tree from environmental conditions existing at the time of elongation. However, growth in year n, although partially determined by the number of stem units preformed in the year n—1 (fixed growth type according to CANNELL, THOMPSON and LINES, 1976), is also influenced by the availability of water and the temperatures during the elongation period (FADY, 1986). The stem units initiated represent a growth potential modulated by the climatic conditions in the year of elongation.

Total Height at 5 years in cm Le Ruscas		Total Height at 7 years in cm Le Treps		Total Height at 20 ans in cm Le Treps	
13,5	KRAS	29,7	PALE	276,9	KOLO
12,7	LAGA	29,1	KAPO	264,0	KAPO
12,4	PALE	28,1	KOLO	263,5	VLAH
12,2	VLAH	27,9	ITAL	261,0	ITAL
12,1	KOLO	27,6	KRAS	244,1	KRAS
11,6	MEVR	27,3	LAGA	243,0	PALE
11,6	KORO	26,4	VLAH	242,6	LAGA
11,5	ITAL	25,3	BROM	239,0	XERO
11,5	KAPO	25,0	XERO	230,8	BROM
11,3	XERO	24,9	KORO	220,2	PRIL
11,1	PRIL	24,7	PRIL	215,9	KORO
10,9	BROM	24,2	MEVR	188,0	MEVR

Regional Averages in cm:

5 years:	7 years:	20 years:
Pindos = 12,97	Pindos = 28,65	Pindos = 243,55
Parnassos = 11,58	Parnassos = 25,63	Parnassos = 227,89
Menalon = 12,13	Menalon = 27,60	Menalon = 256,69
Taygetos = 11,18	Taygetos = 24,86	Taygetos = 229,56

Figure 9. — Comparison of rankings of height growth of Greek Fir provenances at different ages. Duncan Test at 5% level.

3.5 Growth

Total heights were significantly different between provenances, no matter which experimental site was considered (FADY, 1988), as shown by the study of ecovalence (according to WRICKE in FREEMAN, 1973).

The comparison of average heights of provenances by a DUNCAN test at Le Treps showed no evidence of difference between the young adult stage and the nursery (*Figure 9*). However, correlations of heights between these two stages were low. The correlation improved (r = 0.72 for 11 DF) when the heights were compared two years after planting (seven years after germination), once the transplantation trauma is over, and 15 years after planting (20 years after germination).

4. Conclusion

Compared to other Mediterranean firs, *Abies cephalonica* is characterized by early flushing and a very short elongation period; these phenological characteristics allow the tree to begin its annual growth early in the season and probably to profit best from the soil water reserves accumulated over the winter. This is undoubtedly an adaptational advantage. Although these characteristics vary irregularly from the northern to the southern part of its distribution area, the Taygetos provenances (the southernmost) have the shortest elongation period.

The duration of the elongation period only imperfectly explains the length of the shoot formed, particularly with increasing age. This seems to indicate that the genetic control of growth, which is of a fixed type even when the tree is young, depends more on the number of stem units formed than on their individual elongation potential.

The growth potential's geographic variation is significant: 20 years after germination, it is stronger for the provenances from the Menalon and the Pindos and less strong for those from the Taygetos and the Parnassos in general.

Several morphological characteristics of the needles, lateral branch and buds were studied. They were chosen in relation to their potential value as indicators of drought adaptation (stomata on the upper side of the needle, apex shape indicative of cuticular thickness, etc.) or of hybridization with *Abies alba* (pubescence of annual lateral branch). All do not have the same value. The frequency of individuals with pointed apexes is higher in the south of the native region, but does not show a regular geographical evolution. However, the frequency of individuals with a low stomatal density on the upper side of the needle increases regularly from the southern to the northern part of the range; in the same way the frequency of pubescent individuals passes from 6% in the Menalon stands (Peloponnesos) to 33% in those from the southern Pindos.

Flushing, pubescence of lateral branch and stomatal density on the upper side of the needle are stable characteristics with age. Notable in the juvenile stage, the variability in apex shape seems to disappear over time. Height growth, measured at the juvenile stage in nursery, gives little information on later growth. The search for early selection criteria for firs remains a problem of primary importance.

Individual variation and the frequency of pubescent individuals makes it possible to measure the degree *Abies alba* has introgressed into different stands. Although much more noticeable in the northern part of the region studied (Pindos mountains), which is traditionally recognized as the southern limit of the chosen area of the hybrid fir *Abies borisii-regis*, this introgression remains visible to a lesser extent all the way into the southern Peloponnesos.

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Sources of Allozymic Variation in Thuja occidentalis in Southern Ontario, Canada

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Summary

Allozyme variation at 11 loci for seven enzyme systems was studied in three swamp and three cliff populations of *Thuja occidentalis* L. in southern Ontario. Overall genetic variability was extremely small, with 82% of loci monomorphic for all samples. Inbreeding coefficients indicated that no significant inbreeding occured at any site. χ^2-tests showed no significant differences in allele frequencies among the six stands; unbiased genetic distances among all stands were very small (average 0.0015), and no correlation between genetic and geographic distance was found. Of the total variability, 96.9% was among trees within stands, 1.9% among stands from the same habitat, and only 1.2% between habitat types. No variability was found when several branches from the same tree were compared. The number of effective migrants between