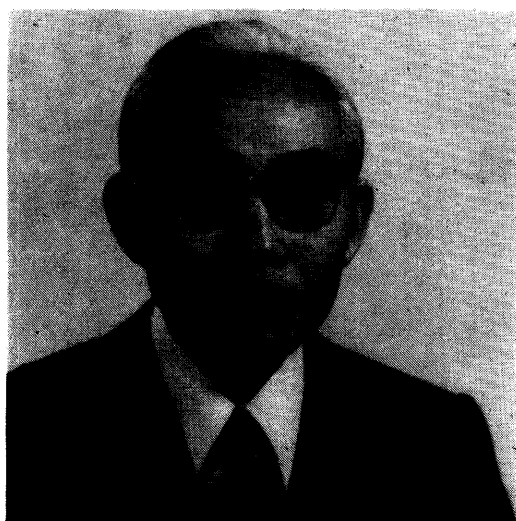# Dr. Sin Kyu Hyun †

1911 — 1986

Dr. S. K. Hyun died on Nov. 21, 1986, following his return home from the XVIII IUFRO Congress in Yugoslavia and a meeting of the International Poplar Council (IPC) in Belgium. It can be truly said that he died of causes related to the pursuit of a better, global climate for scientific forestry.

His early interests in philosophy were diverted into forestry in which he received his Ph.D. in 1949 from Kyushu University. He was an early leader in the rapid development of scientific forestry in the Republic of Korea and, following further study in the United States, began his own genetics research in 1953. While serving as a Professor of forestry at Seoul National University he founded the Institute of Forest Genetics and, with dual appointments, was able to guide the development of students, scientists, and the science itself in Korea and beyond. He served on the executive committee of the IPC, as chairman of the three breeding section of Society for the Advancement of Breeding Researchers in Asia and Oceania (SABRAO), and was active in IUFRO and other professional organizations. He was widely recognized and honored for his contributions, most notably in receiving the Cultural Decoration, the highest civilian award given by the Republic of Korea.

Dr. Hyun's extensive contributions to the practice and science of forestry include teaching, administration, active forest establishments, and research into physiology, silviculture, ecology and genetics. Although he was perhaps most widely known for his daring use of interspecific pine hybrids in the reforestation of Korea, he was eclectic in his breeding methods for other species. He also investigated the basis for understanding gene effects and long term recurrent selection methods. He was enduringly curious about new concepts and technologies, and continued to be both a producer as well as a teacher and user of scientific information.

Dr. Hyun's personal legacy, however, goes beyond these well marked accomplishments. The global community of his students and colleagues will long be influenced by his steadfast faithfulness to the pursuit of truth and his quiet belief in the good of dedicated work in the face of personal difficulties and disappointments. His life was a tale full of adversities overcome by a strength and moral clarity which he demonstrated by quiet example. He was never one to impose his will over others, but he led by supporting and respecting the contributions of others. We are all diminished by the loss of this gentle man.

GENE NAMKOONG, Raleigh, U.S.A.

Origin of Variation in Fir forests of Greece[1])

By D. J. Mitsopoulos and C. P. Panetsos[2])

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Summary

This paper reports on the structure and variation of the Greek fir populations in Greece. The research is based on samples obtained from a provenance-species test, established in central Greece, and two more samples of Bulgarian origin, obtained from a similar test. Fourteen morphological-anatomical and six biochemical (monoterpenes of the cortical oleoresin) traits were examined and scored. Statistical analyses consisted of two types, single variate and multivariate, using Mahalanobis D^2, "generalized distance function".

The pattern of variation of individual traits was generally clinal with a south to north trend, and for populations below Lat. 38°50' N a trend was observed from east to west.

Multivariate analyses of morphological and chemical characters were similar in discriminating groups of populations, the chemical being more efficient. Greek fir consists of populations belonging to the species *Abies cephalonica*, probably introgressed with *A. alba* genes, in the south, hybrid populations more or less intermediate between *A. cephalonica* and *A. alba* in central Greece, and hybrid populations dominated by *A. alba* traits in the north. Populations of Agion Oros and Cephalonia were distinguished from the others in both analyses. Agion Oros, particularly,

cluster closest with *A. equi-trojani*, a fir of Asia Minor, which suggests gene-flow from the east.

Zusammenfassung

In der vorliegenden Studie werden die Ergebnisse eines Versuchs über die Struktur und Variation der Tannenpopulationen in den Naturwäldern Griechenlands aufgezeigt. Der Versuch basiert auf Proben, die einer in Mittelgriechenland angelegten Versuchsfläche entnommen wurden und auf zwei zusätzlichen Proben einer ähnlichen Versuchsfläche in Bulgarien (Proben aus der Ausgangspopulation). Es wurden 14 morphologische und 6 chemische Merkmale (Monoterpene der Rinde) geprüft und gemessen. Die statistische Analyse wurde mit zwei Methoden, nämlich der uni- und der multivariaten Analyse (verallgemeinerte Distanzfunktion-Mahalanobis D²), durchgeführt.

Das Variationsmuster der individuellen Merkmale war generell klinal mit einem Süd-Nord-Trend und zeigte für die Populationen unter 38°50' N einen Ost-West-Trend.

Die multivariaten Analysen der morphologischen und chemischen Merkmale waren in den Diskriminanz-Gruppen der Populationen ähnlich, was bei den chemischen Merkmalen noch deutlicher wurde.

Die griechische Tanne besteht im Süden aus Populationen, die der Species *Abies cephalonica* angehören, bei der wahrscheinlich eine Introgression von *Abies alba*-Genen stattgefunden hat. In Zentralgriechenland bestehen die Tannenwälder aus mehr oder weniger intermediären Populationen *Abies cephalonica* × *Abies alba,* während die Bastardpopulationen im Norden dominierende *Abies alba*-Merkmale aufweisen. Die Populationen von „Agion Oros" (Athos Berg) und „Cephalonia" (Cephalonia Insel) unterschieden sich in den beiden Analysen von den anderen Populationen. Die „Agion Oros" Tanne schließt sich gruppenweise eng an *Abies equi-trojani* an, einer Tanne aus Kleinasien, was einen Genfluß aus dem Osten nahelegt.

Introduction

Fir populations occur in Greece from the most southern mountains of Peloponnesos and the island of Cephalonia, to the northern borders with Albania, Yugoslavia and Bulgaria *(Fig. 1)*. According to MATTFELD (1930) the southern populations up to latitude 38°50' N belong to species *Abies*
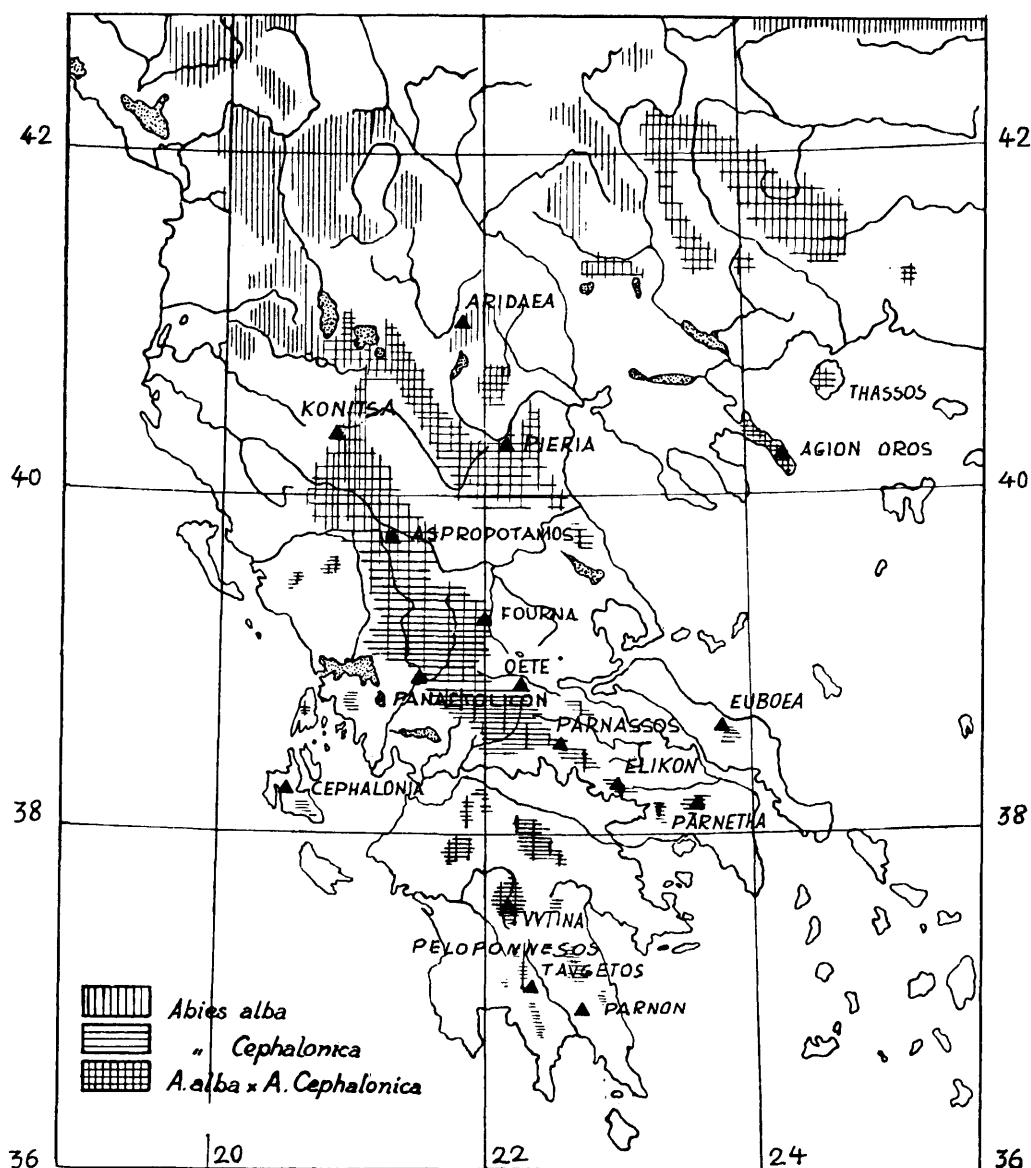

Figure 1. — Natural range of fir forest in Greece (MATTFELD 1930; BASSIOTIS 1956; PANETSOS 1975) and location of seed collections (black triangles).
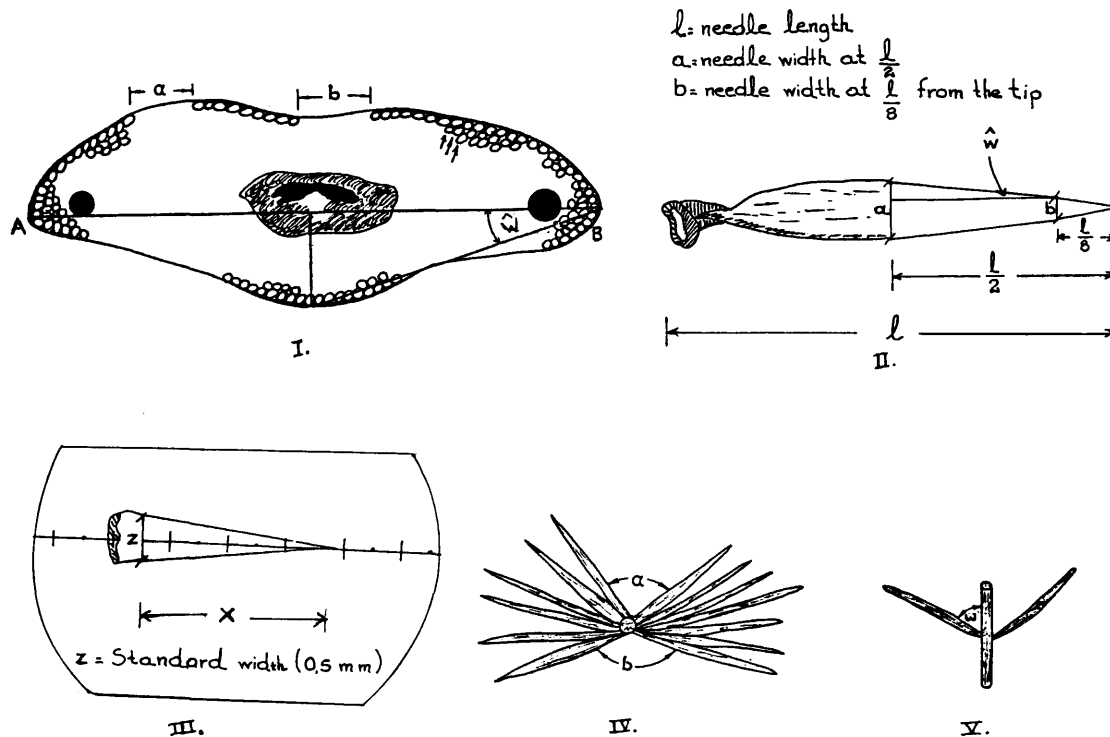
Figure 2. — Diagrammatic representation of eight morphological-anatomical characters.

I. Cross-section of the midpoint of the needle showing: a) the bottom (abaxial) angle $\hat{w}$. b) parts of the upper surface of the needle without hypodermal cells and c) points with double and triple hypodermal cells.

II. A schematic representation of a needle showing how angle $\hat{w}$ is defined.

III. Needle-tip, under stereoscopic microscope with a micrometer.

IV. End-on view of twig showing needle arrangement.

V. Longitudinal view of twig showing needle angle.

cephalonica LOUD., while to the north on the mainland and island of Thassos a series of intermediate forms occurs, which at their northern limit most resembles A. alba MILL., the European silver fir, and grow with trees typical of that species. At the southern limit the intermediate forms resemble and accompany typical A. cephalonica. Only intermediate forms are found on the Athos peninsula (Agion Oros) in north-eastern Greece, and in the Rhodope mountains of Bulgaria. These intermediate forms were designated collectively by MATTFELD as a dinstinct species, namely A. borisii-regis. He also advanced the hypothesis that A. borisii-regis represented a series of products of ancient hybridization between A. alba and A. cephalonica, plus derivatives of segregation and backcrossing.

Further investigations have revealed that A. cephalonica is clearly distinguished from A. alba, by a number of morphological and anatomical characters. A summary of the major taxonomic features of A. cephalonica, as they appear in different floras and botanical descriptions is presented by PANETSOS (1975). The two species, today, are well isolated geographically, since no pure A. alba populations occur within Greece, while the range of A. cephalonica is confined below Lat. 38º50' N in southern Greece. The gap between the species ranges is occupied by trees combining characteristics of the two species. Even in the core of the A. cephalonica distribution, in Peloponnesos, occasional trees bear one or more traits of A. alba (BASSIOTIS 1956, PANAYOTIDIS 1965, PANETSOS 1975). Extensive study of morphological, anatomical, cone and seed characters from samples collected all over the natural distribution of A. ce-

phalonica and in the transitional zone to the north (PANETSOS 1975, 1976), showed the existence of considerable variation in a number of traits, both between and within populations, and a tendency of some traits to vary from south to north and/or east to west. However, the magnitude, the extent, the pattern and the sources of the variation were considered as a subject for more sophisticated investigation, which should include populations from the whole range of fir forests in Greece. Moreover, it was felt that such a study would be more conclusive if it were based on samples obtained from trees tested in a common environment experiment, and included biochemical as well as morphological traits. The monoterpene composition of cortical oleoresin is suited to studies of geographic variation because monoterpenes are strongly inherited and not greatly affected by environmental variation (HANOVER 1966 a, b, c, 1971; SQUILLACE and FISHER 1966; HILTON 1968; ZAVARIN 1968, FRANKLIN and SQUILLACE 1971; BARADAT et al. 1972, ROCKWOOD 1973). In this paper we present results from a provenance/species test to quantify the magnitude, the extent, and the pattern of variation in Greek fir forests.

Materials and Methods

Sampling

In fall 1968, mature cones were collected from each of 30 mother trees in each of 16 populations scattered throughout the range of fir forests in Greece. In addition, seeds of A. alba (two provenances) and A. equi-trojani were provided by Italian and Turkish colleagues, respectively. The localities of seed collections are shown in *Figure 1*.

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Table 1. — Provenance means and standard deviations for morphological-anatomical characteristics.

Provenances	Statistic	Needle length (1)	Needle width (2)	Needle thickness (3)	Bottom needle angle (4)	Needle shape (5)	Hypodermal cell layers (6)	Hypodermal cells (7)	Needle-tip sharpness (8)	Upper vertical needle angle (9)	Lower vertical needle angle (10)	Horizontal needle angle (11)	Pubescence twing density (12)	Needle-tip shape (13)	Stomata needle density (14)
Cephalonia	Mean	18.74	1.84	0.72	0.46	0.056	12.89	1.93	9.62	4.37	46.00	87.37	1.65	1.00	2.70
	S.D.	2.25	0.13	0.05	0.04	0.01	3.35	2.76	1.44	14.03	40.94	5.24	1.12	0.28	1.70
Taygetos	Mean	21.19	1.88	0.69	0.42	0.042	13.32	0.88	9.62	5.25	99.50	84.00	1.03	1.00	1.42
	S.D.	2.54	0.15	0.05	0.04	0.007	3.86	1.88	1.44	14.65	25.87	7.56	0.32	0.24	0.74
Parnon	Mean	20.44	1.87	0.66	0.40	0.040	10.79	3.96	8.79	30.62	118.87	83.12	1.60	1.07	2.05
	S.D.	2.86	0.13	0.07	0.04	0.008	4.96	6.49	2.37	33.07	38.04	8.31	1.18	0.34	1.25
Vytina	Mean	20.45	1.85	0.68	0.42	0.045	9.79	2.48	9.62	5.00	95.00	86.12	1.07	1.03	1.55
	S.D.	3.68	0.17	0.04	0.05	0.01	3.92	3.35	1.92	14.30	39.90	6.03	0.36	0.26	0.90
Parnetha	Mean	20.54	1.79	0.65	0.43	0.040	8.11	6.69	8.74	13.12	90.75	74.87	0.98	1.00	1.06
	S.D.	3.29	0.13	0.04	0.05	0.009	3.49	6.89	1.40	27.16	29.04	8.24	0.24	0.25	0.32
Elicon	Mean	19.49	1.82	0.65	0.42	0.045	9.56	2.80	9.42	14.68	79.06	88.12	1.50	1.00	1.75
	S.D.	3.12	0.13	0.05	0.04	0.01	3.73	4.09	1.98	22.02	36.37	3.52	0.95	0.28	0.79
Parnassos	Mean	20.89	1.82	0.64	0.40	0.040	8.86	3.60	9.69	22.25	100.87	82.00	1.60	0.97	2.12
	S.D.	3.13	0.18	0.05	0.05	0.009	3.54	4.75	1.65	28.04	25.22	8.20	1.26	0.24	1.12
Euboea	Mean	21.23	1.67	0.60	0.44	0.025	7.63	3.08	7.06	11.87	115.75	67.75	1.07	1.35	2.02
	S.D.	3.40	0.13	0.03	0.04	0.006	2.90	3.76	1.41	21.37	33.57	8.13	0.40	0.66	1.01
Panaetolicon	Mean	20.04	1.70	0.59	0.40	0.042	7.84	2.46	10.71	15.75	121.50	70.75	1.62	1.00	1.97
	S.D.	3.21	0.15	0.04	0.04	0.01	3.84	3.03	1.93	31.34	44.96	7.08	1.15	0.26	1.10
Oete	Mean	19.68	1.71	0.61	0.40	0.042	7.25	3.90	11.01	18.60	110.40	77.20	1.56	1.02	1.92
	S.D.	2.16	0.12	0.05	0.04	0.008	2.47	4.68	2.20	22.88	20.98	6.18	1.15	0.27	1.08
Fourna	Mean	19.45	1.77	0.57	0.37	0.043	6.63	6.17	8.48	25.00	127.14	70.87	1.62	1.03	2.47
	S.D.	2.92	0.16	0.03	0.06	0.01	2.72	6.91	1.53	23.75	21.61	8.50	1.09	0.39	1.24
Aspropotamos	Mean	20.46	1.80	0.57	0.35	0.035	5.14	11.03	7.14	28.00	155.00	61.12	2.67	1.26	3.10
	S.D.	2.86	0.16	0.03	0.05	0.01	2.11	9.49	1.71	31.64	21.70	7.33	1.63	0.40	1.15
Konitsa	Mean	21.08	1.85	0.52	0.27	0.026	3.66	21.76	4.28	29.75	158.75	58.62	3.77	2.10	2.72
	S.D.	3.71	0.15	0.04	0.06	0.007	1.87	13.93	1.03	33.32	25.40	7.62	1.28	1.11	1.06
Agion Oros	Mean	27.07	1.78	0.56	0.37	0.012	5.46	9.10	2.79	27.00	151.12	56.87	1.60	3.10	2.32
	S.D.	4.33	0.18	0.04	0.06	0.004	2.29	7.28	1.17	25.92	21.16	5.69	1.12	1.12	1.30
Pieria	Mean	20.57	1.77	0.56	0.36	0.037	3.82	13.29	7.77	42.87	152.50	68.25	3.12	1.08	3.07
	S.D.	3.09	0.16	0.03	0.03	0.01	1.30	7.44	2.25	29.58	21.35	7.51	1.59	0.44	1.35
Aridaea	Mean	21.58	1.96	0.52	0.29	0.020	2.30	32.43	1.62	41.25	184.37	59.50	4.45	4.20	3.32
	S.D.	3.24	0.12	0.04	0.05	0.005	1.40	16.86	0.99	32.59	14.75	5.95	0.76	0.92	0.76
Bulgaria 3	Mean	24.28	1.98	0.48	0.26	0.020	1.55	31.77	1.58	15.25	187.25	55.50	4.92	4.92	2.80
	S.D.	3.40	0.12	0.02	0.05	0.004	0.79	12.07	0.60	19.83	7.49	6.11	0.39	0.30	0.59
Bulgaria 4	Mean	26.07	2.04	0.49	0.25	0.019	0.91	55.65	1.70	59.00	184.50	59.00	4.55	4.47	3.00
	S.D.	2.61	0.14	0.02	0.05	0.006	0.49	16.14	0.78	37.17	5.54	6.49	0.68	0.85	0.84
A.equi Trojani	Mean	24.03	1.76	0.59	0.41	0.011	5.50	11.67	0.93	3.60	178.00	57.20	1.16	4.36	2.28
	S.D.	3.84	0.14	0.04	0.05	0.004	2.31	7.70	0.52	9.97	30.26	9.15	0.37	0.96	1.50
A. alba (Italy)	Mean	20.57	1.99	0.49	0.22	0.019	1.18	42.75	0.83	99.12	178.00	64.75	4.96	5.03	4.90
	S.D.	3.09	0.16	0.04	0.05	0.007	0.72	15.39	0.40	31.72	12.46	7.12	0.30	0.25	0.39

All seeds from each provenance were combined and sown in March 1969 in a nursery on the mountain Parnetha near Athens. The resulting seedlings were field-planted, as 5-0 bare-rooted stock, in February 1974. The plantation is located in central Greece (Lat. 38º57', Long. 21º56', Elev. 950 m) on the mountain Tymphrestos. Seedlings were hand-

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Table 2. — Intra-provenance coefficients of variation for the morphological-anatomical characteristics.

Provinces \ Characteristics	Needle length	Needle width	Needle thickness	Bottom needle angle	Needle shape	Hypodermal cell layers	Hypodermal cells	Needle-tip sharpness	Upper vertical needle angle	Lower vertical needle angle	Horizontal needle angle	Pubescence twing density	Needle-tip shape	Stomata needle density
Cephalonia	0.12	0.07	0.07	0.09	0.25	0.26	1.43	0.15	3.21	0.89	0.06	0.68	0.28	0.63
Taygetos	0.12	0.08	0.07	0.09	0.17	0.29	2.29	0.15	2.79	0.26	0.09	0.31	0.24	0.52
Parnon	0.14	0.07	0.11	0.11	0.22	0.46	1.64	0.27	1.08	0.32	0.10	0.74	0.32	0.61
Vytina	0.18	0.09	0.06	0.12	0.23	0.40	1.35	0.20	2.86	0.42	0.07	0.34	0.25	0.58
Parnetha	0.16	0.07	0.06	0.10	0.24	0.43	1.03	0.16	2.07	0.32	0.11	0.24	0.25	0.30
Elicon	0.16	0.07	0.07	0.12	0.25	0.39	1.46	0.21	1.50	0.46	0.04	0.63	0.28	0.45
Parnassos	0.15	0.10	0.08	0.11	0.24	0.40	1.32	0.17	1.26	0.25	0.10	0.79	0.25	0.53
Euboea	0.16	0.08	0.05	0.10	0.24	0.38	1.22	0.20	1.80	0.29	0.12	0.37	0.49	0.50
Panaetolicon	0.16	0.09	0.07	0.10	0.23	0.49	1.23	0.18	1.99	0.37	0.10	0.71	0.26	0.56
Oete	0.11	0.07	0.08	0.10	0.20	0.34	1.20	0.20	1.23	0.19	0.08	0.74	0.26	0.56
Fourna	0.15	0.09	0.06	0.15	0.27	0.41	1.12	0.18	0.95	0.17	0.12	0.67	0.38	0.50
Aspropotamos	0.14	0.09	0.06	0.13	0.27	0.41	0.86	0.24	1.13	0.14	0.12	0.61	0.32	0.37
Konitsa	0.17	0.08	0.07	0.22	0.27	0.51	0.64	0.24	1.12	0.16	0.13	0.34	0.53	0.39
Agion Oros	0.16	0.10	0.08	0.15	0.41	0.42	0.80	0.42	0.96	0.14	0.10	0.70	0.36	0.56
Pieria	0.15	0.09	0.05	0.09	0.30	0.34	0.56	0.29	0.69	0.14	0.11	0.51	0.41	0.44
Aridaea	0.15	0.06	0.08	0.18	0.28	0.61	0.52	0.61	0.79	0.08	0.10	0.17	0.22	0.23
Bulgaria 3	0.14	0.06	0.04	0.18	0.22	0.51	0.38	0.38	1.30	0.04	0.11	0.08	0.06	0.21
Bulgaria 4	0.10	0.07	0.05	0.19	0.33	0.54	0.29	0.46	0.63	0.03	0.11	0.15	0.19	0.28
A.equi Trojani	0.16	0.08	0.07	0.12	0.37	0.42	0.66	0.56	2.76	0.17	0.16	0.32	0.22	0.46
A.alba (Italy)	0.15	0.08	0.09	0.21	0.36	0.61	0.36	0.48	0.32	0.07	0.11	0.06	0.05	0.08

planted, in randomized complete block design, in 25-tree plots, with 4 replications at 3 m × 3 m spacing. Survival was nearly 99%.

In February 1980, i.e. six growth periods after field planting and eleven from seeding, a branch, with branchlets and needles of the years 1979 and 1978, were sampled from the south side of the trees and at the height of the 1978 node. After cutting, the branches were placed in plastic bags and sealed. In each bag a label was inserted with the number of provenance, replication, and the relevant position of the tree in the plot. From each provenance 40 trees were sampled, 10 from each replication. In total the number of trees sampled was 722, because provenance Oete and A. equi-trojani were represented with only 25 trees and Elicona with 38. In addition two provenances of Bulgarian origin were added, with 20 trees each, from Dr. GAGOF's provenance test experiment in the university forests at Judula, Bulgaria.

All samples were collected on the same day, transferred to the laboratory in Thessaloniki, and stored in a deep freezer at a temperature of −30° C.

Characters Studied

a. Morphological-anatomical

The following characters (see *Fig. 2*) were measured from the two-year-old portion of the branch, except for pubescence, for which the evaluation was made on young twigs:

(1) needle length in mm; (2) needle width in mm; (3) needle thickness in mm; (4) bottom (abaxial) needle angle expressed as tangŵ; (5) needle shape as tangŵ; (6) proportion of the upper surface of the needle cross-section without hypodermal cells in relation (%) to the needle width A-B; (7) number of points on upper surface of the needle with double and triple layers of hypodermal cells, per mm of needle width; (8) needle-tip sharpness in 0.1 mm,

measured by the length "x" from the point where the needle attains 0.5 mm width (Z) up to the tip; (9) vertical needle angle (a) at the upper surface of the branch; (10) vertical needle angle (b) of the lower surface of the branch; (11) angle of the needles with branch axis; (12) density of pubenscence on young twigs, scored as very dense (4), medium (3), few hairs (2), and hairless (1); (13) needle-tip shape, classed as sharply pointed (1), very pointed (2), pointed (3), obtuse (4), and notched (5); (14) density of stomata on upper (abaxial surface of the needle, in relation to the area they occupied along the length of the needle, was classed as without stomata (1), few at the needle-tip (2), area less than 1/2 of the needle length (3), area equal to 1/2 (4), and area equal to more than 1/2 of the needle length (5).

In total 3610 needles from 722 trees originating from 20 provenances were measured with the use of a projection microscope, binocular dissecting microscope and an eyepiece micrometer.

b. Monoterpenes

After the branch was removed from the freezer, a drop of oleoresin was collected within 2 to 3 minutes from cortical tissue by excising branch buds, at approximately 10 mm or less from the tips. Exuded oleoresin was diluted in 0.1—0.2 ml of pentane (proanalysis). The sample size injected into chromatograph was 0.1—0.5 μl. Quantitative and qualitative analysis of each sample was made with a gas-liquid chromatograph, model TRACOR, on a 3.05 m, 1.6 mm 60/80 mesh chromosorb W column packed with 10 % β, β oxydipropionitrile.

The identification of components from the analysis of monoterpenes was made in two ways. a) Comparison of the relative volume of known and unknown elements under the same analytic conditions. b) Enhancement of the unknown peak, after mixing it with standards. The stand-
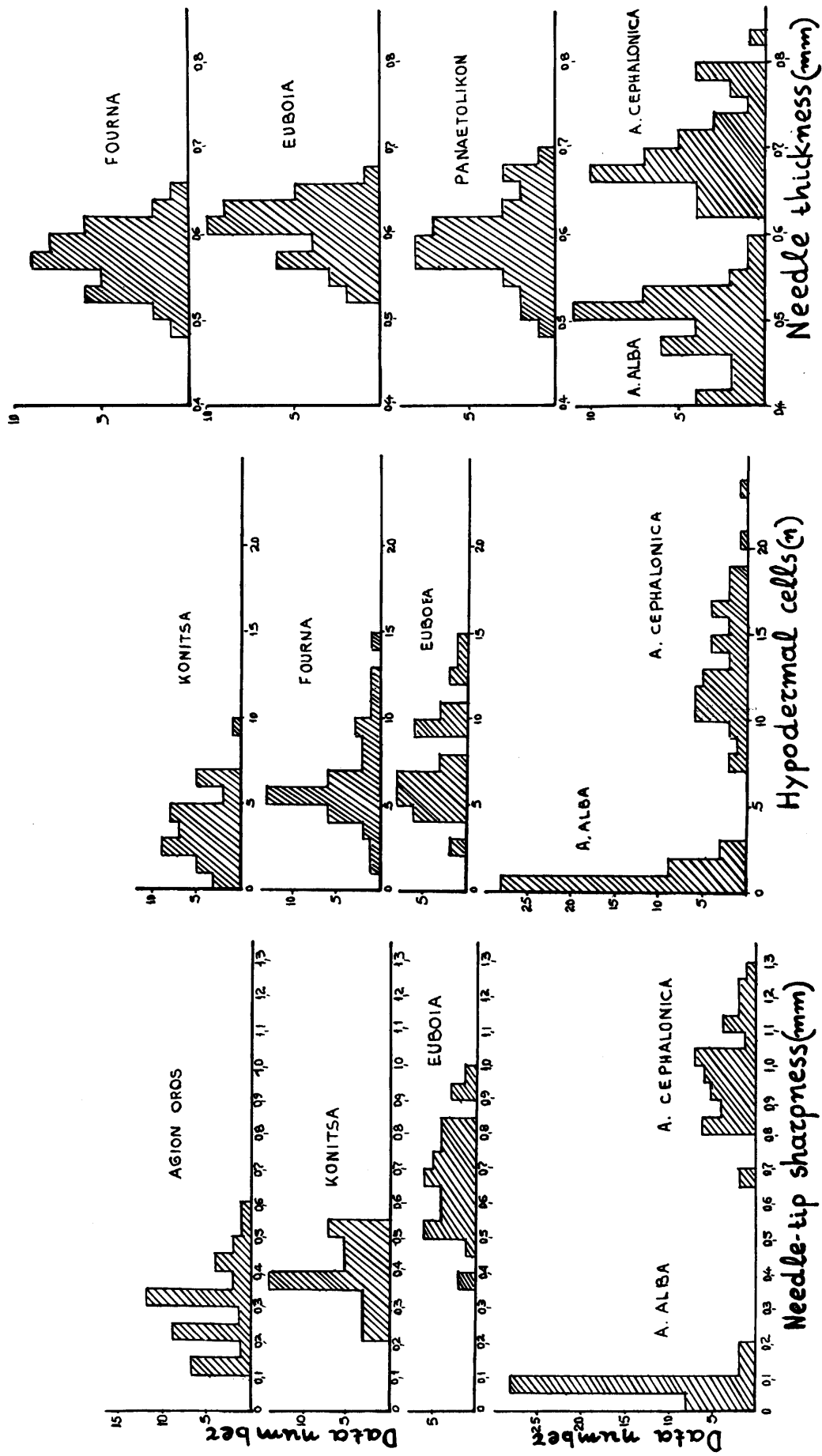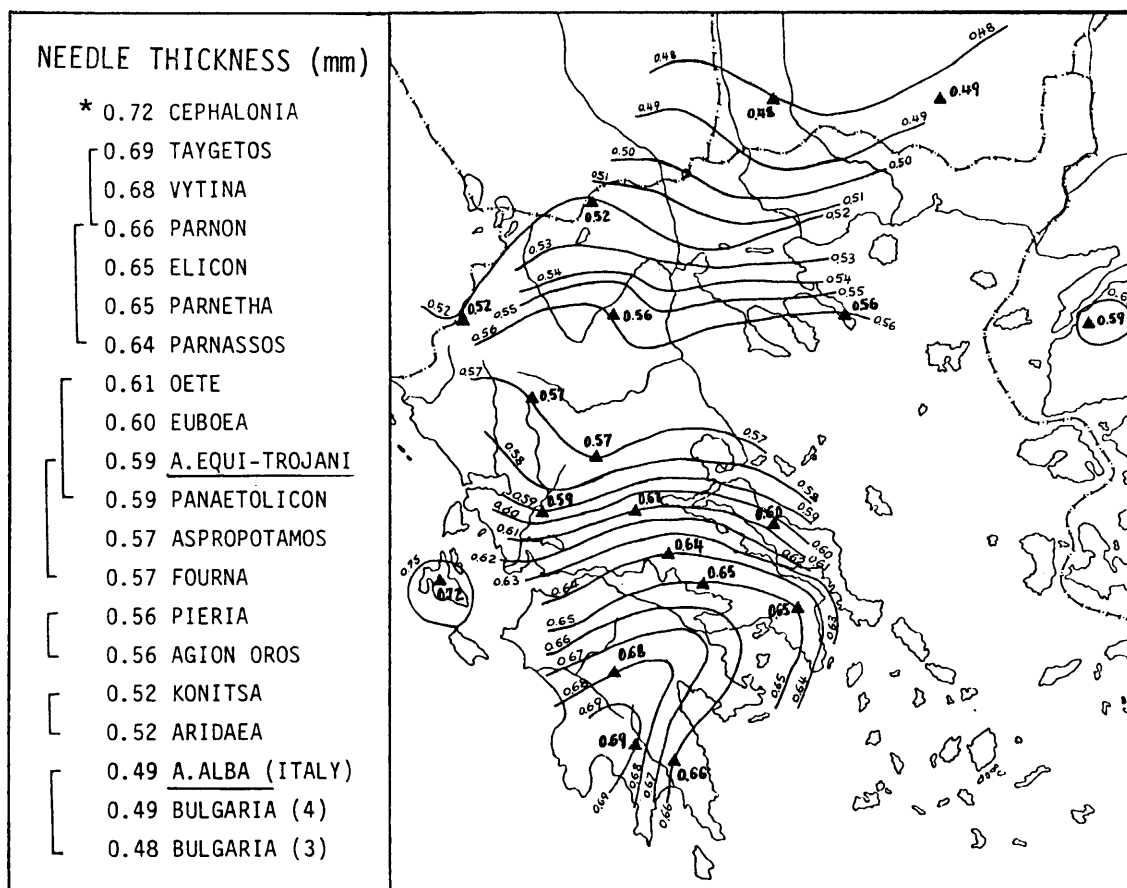
Figure 3. — Frequency distributions of needle length, needle thickness, and hypodermal cell number for A. alba and A. cephalonica and populations exhibiting intermediacy.

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NEEDLE THICKNESS (mm)

  * 0.72  CEPHALONIA
  ┌ 0.69  TAYGETOS
  │ 0.68  VYTINA
  └ 0.66  PARNON
  ┌ 0.65  ELICON
  │ 0.65  PARNETHA
  └ 0.64  PARNASSOS
  ┌ 0.61  OETE
  │ 0.60  EUBOEA
  │ 0.59  A.EQUI-TROJANI
  │ 0.59  PANAETOLICON
  │ 0.57  ASPROPOTAMOS
  └ 0.57  FOURNA
  ┌ 0.56  PIERIA
  └ 0.56  AGION OROS
  ┌ 0.52  KONITSA
  └ 0.52  ARIDAEA
  ┌ 0.49  A.ALBA (ITALY)
  │ 0.49  BULGARIA (4)
  └ 0.48  BULGARIA (3)
```

* Provenance not connected by the same line are significantly different at P ≤ 0.05.

Figure 4. — Test of means and contour diagram of provenance variation in needle thickness.

ards were kindly offered by DRAGOCO C/O GmbH Holzminden - W. Germany.

Quantitative calculations were made by normalizing disc integrator values of peak areas; i.e. each monoterpene was calculated as a percentage of the total amount of monoterpenes. In total 660 trees were analysed from 20 provenances. Fifteen provenances were represented with 36 trees each, provenance Oete and A. equi-trojani with 25, Eliconas with 30, and each of the two Bulgarian provenances with 20 trees.

Statistical Analysis

Statistical analyses consisted of two types, single variate and multivariate for both groups of traits, morphological and biochemical. Due to the fact that various kinds of units were employed to measure the characters, standard errors and deviations could not be used for purposes of comparison. Instead, we used the coefficient of variation (CV).

For many characters the mean and median were found to be different, and also the values of percentiles were in many instances asymmetric, which indicated a lack of normality. Test of goodness of fit with X^2 criterion, and calculations of skewness and kurtosis for all characters demonstrated a significant derivation from the normal distribution. Lack of normality makes the analysis of variance doubtful, so the application of nonparametric statistics was used as an alternative. The technique called KRUSKAL-WALLIS one-way analysis of variance, or the H-test, was considered the most appropriate. The H-statistic is calculated from the formula:

$$H = \frac{12}{n(n+1)} \sum_{i=1}^{K} \frac{R_i^2}{n_i} - 3(n+1),$$

where n_i is the number of observations in the ith sample, $i = 1 \ldots\ldots\ldots k$. $n = \Sigma n_i$, and R_i is the sum of the ranks for the ith sample.

Multivariate analysis was employed to examine the pattern of geographic variation considering groups of traits simultaneously. For this purpose Mahalanobis "generalized distance function", D^2, was chosen (for discussions of this and other multivariate techniques, see RAO 1948, 1952; HOTTELING 1954; HUGHES and LINDLEY 1955; SQUILLACE 1966; NAMKOONG 1966; LEE and KALTSIKES 1973). D^2 values were computed for 14 morphological-anatomical, and 5 biochemical traits separately. Finally an attempt was made to find relations among morphological-anatomical characteristics by simple correlation and partial correlation coefficients. The data analysis was done with an 1106 electronic computer at the University of Thessaloniki Computing Center, using the programme STATJOB (Acad. computing Center-Univ. of Wisconsin, Madison U.S.A. 1975) kindly offered by the Institute of Forest Policy of our Department.

Results

Morphological-anatomical traits

The means and CVs for each trait for each provenance appear in *Tables 1* and *2*. Except for needle length and width, almost all traits were efficient in dicriminating A. cephalonica from A. alba and in identifying hybrid forms (e.g., *Figure 3*).

7

NEEDLE SHAPE (tang ŵ)

* 0.056 CEPHALONIA
  0.045 ELICON
  0.045 VYTINA
  0.043 FOURNA
  0.042 PANAETOLICON
  0.042 TAYGETOS
  0.042 OETE
  0.040 PARNON
  0.040 PARNETHA
  0.040 PARNASSOS
  0.037 PIERIA
  0.035 ASPROPOTAMOS
  0.026 KONITSA
  0.025 EUBOEA
  0.020 ARIDAEA
  0.020 BULGARIA (3)
  0.019 BULGARIA (4)
  0.019 A.ALBA (ITALY)
  0.012 AGION OROS
  0.011 A.EQUI-TROJANI
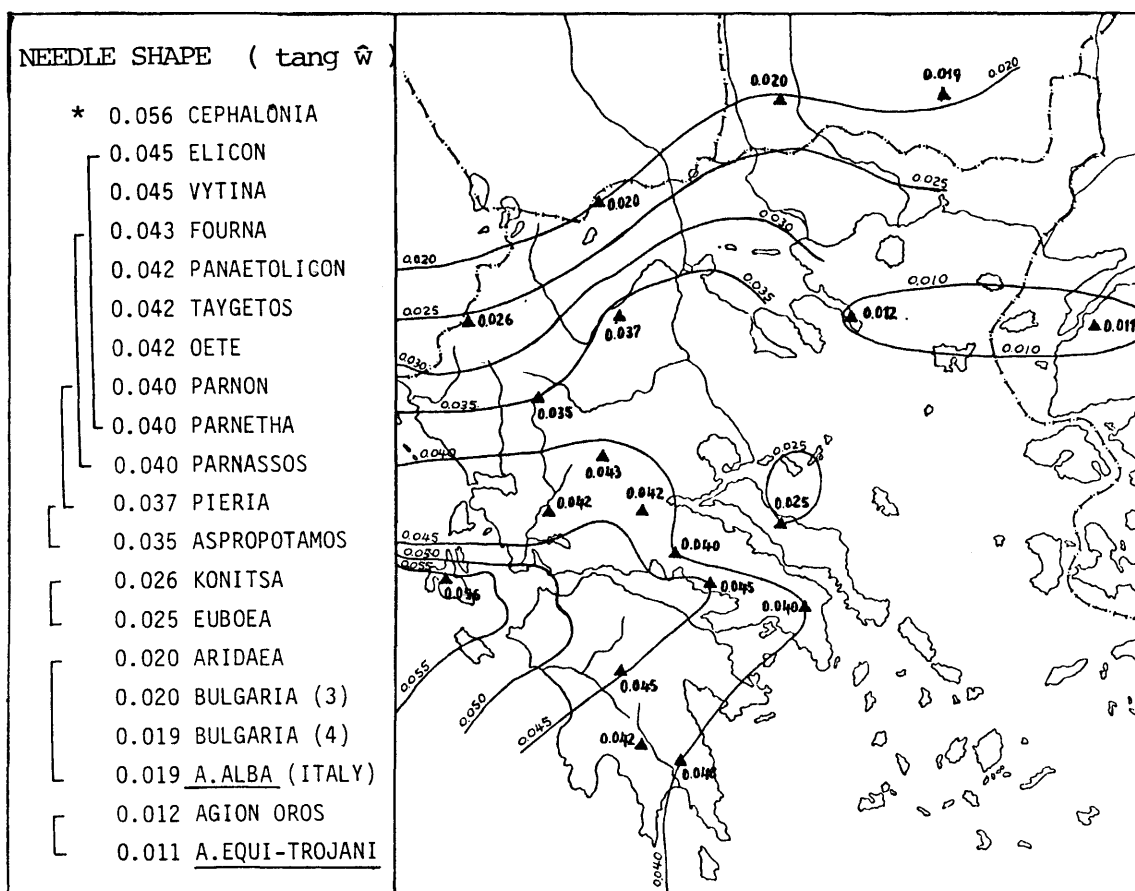
* Provenance not connected by the same line are significantly different at P ≤ 0.05.

Figure 5. — Test of means and contour diagram of provenance variation in needle shape.

When comparing all twenty provenances, results show highly significant differences among provenances for each characteristics (KRUSKAL-WALLIS test, P = 0.99). To test all possible pairs of provenances for each character, the MANN-WHITNEY test (a test equivalent to KRUSKAL-WALLIS for two provenances, (CONOVER 1971; STEEL and TORRIE 1980) was employed. In general all traits exhibited a clinal type of variation from north to south. Four examples appear in *Figures 4, 5, 6,* and *7.* In eight traits, however, in the range of *A. cephalonica* and in the transitional zone, the pattern tended to be from east to west. Finally, each one of the traits 1, 3, 4, 5, 6 ,12, 14, showed discontinuous variation for only one or two provenances (MANN-WHITNEY test e.g., *Figures 4, 5).*

In spite of the fact that each character was able, to some extent, do discriminate the provenance, the complex or contradictory patterns of variation and relationships among provenances call for the application of a more effective method of analysis.

Multivariate analysis

Multivariate analysis was employed to examine the patterns of geographic variation considering the group of traits simultaneously. *Table 3* gives the D^2 values obtained from the Mahalanobis distance function analysis. A low D^2 between two provenances indicates a high degree of similarity, while a high D^2 indicates dissimilarity. The "cluster technique" described by RAO (1952) was used in order to examine relationships among provenances, in various portions of the range of firs included in this study.

The process began with the selection of pairs of adjacent provenances which showed relatively small D^2 values. These pairs formed the nuclei for clusters. Additional provenances were added to each, the requirement for acceptance being that the proposed addition did not greatly increase the average D^2 and that it fitted better with that cluster than with other clusters.

The result of the clustering process is shown in *Table 4* and *Figure 8.* A total of 9 clusters were formed containing 1 to 7 provenances each.

Chemical traits

Monoterpenes that appeared in relatively large amounts were: α-pinene, β-pinene, myrcene, limonene, and β-phelandrene. A minor constituent was camphene, and for this reason it was not considered. Each of the 5 major monoterpenes was expressed as a percentage of the total. Much variation for the main constituents was found, especially between trees in the same provenance. Limonene was the most variable component among the 5 analysed, and was also the only one to show clear bimodality, a strong indication that mendelian inheritance is involved. As far as β-pinene is concerned, there was no clear evidence of bimodality *(Figure 9).*

In *Table 5* the means obtained for each one of the 5 monoterpenes are given, their range, C.V.s, and "H" values. When comparing all twenty provenances together, "H" values obtained from the application of KRUSKAL-WALLIS test (after transformation of proportions with an arcsin-square root function) were highly significant (P = 0.99)

8

HYPODERMAL CELLS (n)

*

13.3 TAYGETOS
12.8 CEPHALONIA
10.7 PARNON
9.7 VYTINA
9.5 ELICON
8.8 PARNASSOS
8.1 PARNETHA
7.8 PANAETOLICON
7.6 EUBOEA
7.2 OETE
6.6 FOURNA
5.5 A. EQUI-TROJANI
5.4 AGION OROS
5.1 ASPROPOTAMOS
3.8 PIERIA
3.6 KONITSA
2.3 ARIDAEA
1.6 BULGARIA (3)
1.2 A. ALBA (ITALY)
0.9 BULGARIA (4)

* Provenances not connected by the same line are significantly different at $P \leqslant 0.05$.

Figure 6. — Test of means and contour diagram of provenance variation in hypodermal cells.

for all 5 monoterpenes. However, when the MANN-WHITNEY test was applied to test all possible pairs of provenances for each character separately, the discrimination obtained was not satisfactory for some of the pairs.

Thus, provenances discriminated by morphological characters, when the MANN-WHITNEY test applied, were not distinguishable on the basis of relative proportions of monoterpenes. These findings showed that the availability of information on the relative proportions of monoterpenes only would limit both the interpretation and the statistical testing of experimental results, probably because of correlations among individual monoterpenes (SQUILLACE 1976; HILTUNEN 1975; SHAW et al. 1982).

Therefore it was necessary to take another approach. All provenances were classified according to the percentage of trees with limonene content higher than 50% of total monoterpene constituents. Limonene was chosen because it was the only terpene to give clear evidence of mendelian inheritance. The results obtained by this technique can be seen in Figure 10. The pattern showed a definite east to west gradient which was not expected, considering the low limonene content of both parental species. It is also interesting to note the high occurence of trees with more than 50% limonene in certain populations, such as Agion Oros and Pieria, while most A. cephalonica and A. alba have very low proportions of limonene (Figure 11).

The complexity of monoterpene data sets can be greatly reduced with multivariate methods (SHAW and ALLARD 1982). Thus, multivariate analysis was employed on transformed

chemical data (arcsinsquare root) to examine the patterns of geographic variation. The result of the clustering is shown in Figure 12. A total of 12 clusters each containing 1 to 4 provenances, were formed.

The two cluster analyses on morphological and biochemical data look very similar. Vytina, Taygetos and Parnon populations, on one hand, and Aspropotamos, Pieria and Fourna on the other belong to the same cluster with regard to both the morphological and biochemical data; Cephalonia, Agion Oros, A. equi-trojani and A. alba stand alone in both analyses. The populations of Parnetha, Elicon, Euboea, Parnassos, Oete, Panaetolicon, and Konitsa, shift between contiguous clusters that are discriminated by very low average D^2 values, indicating relatively similar composition.

Discussion

Fir populations in Greece, as already mentioned, have been classified into two entities (MATTFELD 1930). STEBBINS (1950) adopted MATTFELD's reasoning and advanced the hypothesis that A. cephalonica and A. alba as well as their hybrids (A. X borisii regis) should be taxonomically treated as races of a polytypic species. A number of other botanists and taxonomists, as cited by LIU (1971), recognized and described various species within the range of A. cephalonica forests in Greece. However, one of us (PANETSOS 1975) concluded that recognition of other species or varieties than A. cephalonica is not justifiable based on a large number of needle and cone traits, measured in populations
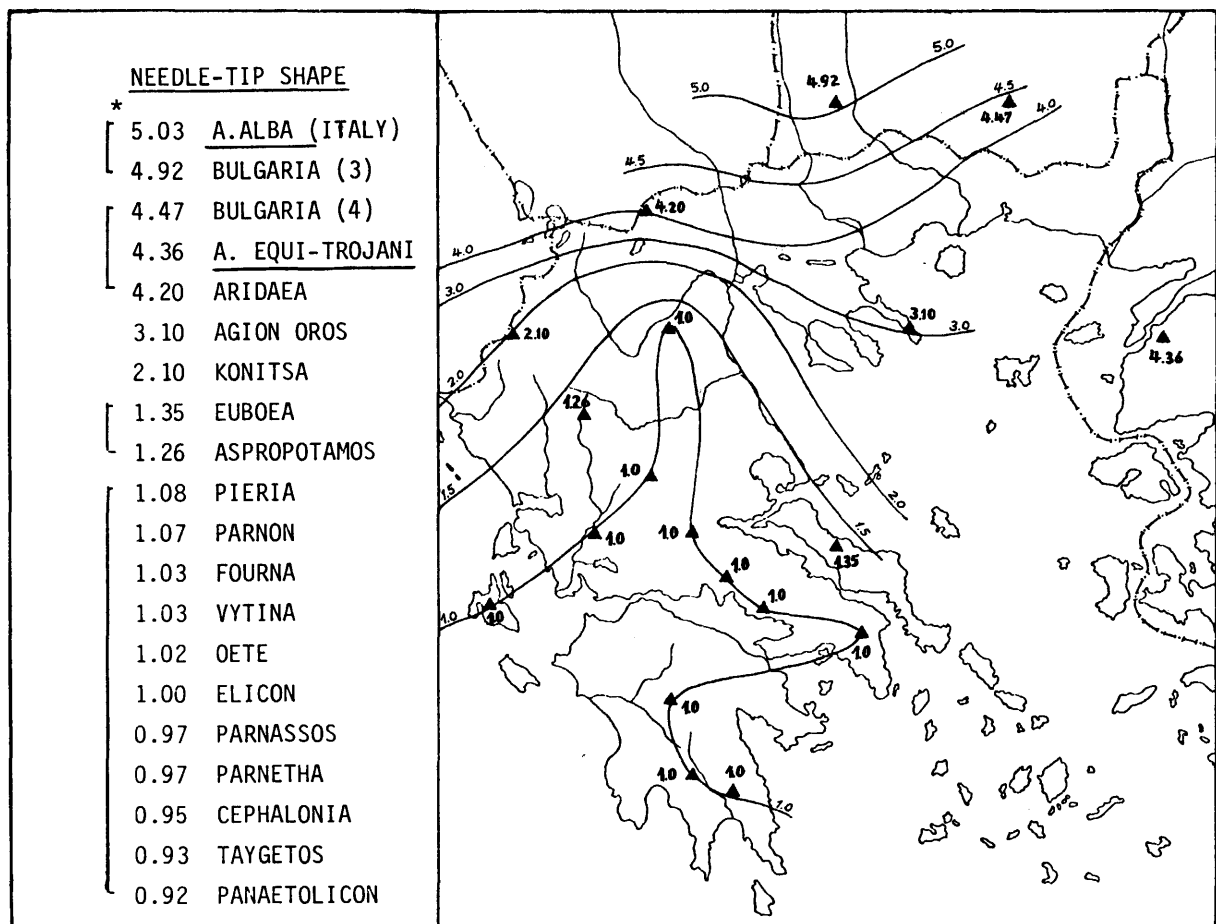
9

throughout the range of *A. cephalonica.* Nevertheless, it was pointed out that considerable variation existed between and within populations.

The question, however, arises whether the intergradation found is primary or secondary. In other words, whether there was a primary population of *Abies,* and as it enlarged its range by dispersing northward after the melting of glaciers, it diverged genetically, evolving into the two extreme forms, *A. alba* and *A. cephalonica,* or whether there were two distinct taxa which came together and hybridized during glaciation. In the first case, the intergradation is the outcome of polymorphic response to a broad array of ecological gradients, while in the second case it is the result of natural hybridization.

The first hypothesis should be rejected mainly for two reasons: (a) It cannot explain the occurrence of polymorphic genotypes in a homogeneous environment. In all provenances, especially in those of central and northern Greece, adjacent trees were very different in morphological and biochemical traits. One tree could be typical *A. cephalonica* while that next to it was an intermediate form between the two species. The occurence of intermediate phenotypes between two species and the high degree of individual variation are positive evidences of introgressive hybridization (ANDERSON 1949; MAYR 1963). Continued crossing among F_1 progeny and parental types produces a broad range of genotypes within a limited area, which appears to be the case in the fir forest of central and northern Greece. (b) Species in the genus *Abies,* as can be inferred

by fossil records, originated during the Miocene and thereafter (LIU 1971). Furthermore in the late Pliocene and during the Pleistocene, species like *A. pinsapo, A. nordmanninana, A. cilicica, A. cephalonica* and *A. alba* became distinct and recognizable in Europe (MATTFELD 1930; STEBBINS 1950; LIU 1971; MAYER 1980, 1984). According to STEBBINS (1950), *A. alba* and its close relative of Asia Minor, *A. nordmanniana,* are characteristic elements of the Colchian flora, which, as the fossil remains indicate, were widespread throughout central Europe in Pleistocene. On the other hand. *A. cephalonica* is not only strikingly different morphologically from *A. alba* and *A. nordmanniana* but in addition it occupies a different floristic province, that of the Grecian-Asia Minor Mediterranean flora. This flora appears to have developed in isolation from the Colchian flora during the Pleistocene, since the two have very little in common. It seems to be clear, that during the glacial period the advancing ice sheet forced several species, like *A. alba,* to move southward and into lower elevations (KRAL 1979; ZOLLER 1960). Palynological studies verify that *A. alba* survived in two refugia, in northwest Greece and Calabria (BOTTEMA 1974; GRUGER 1977).

Multivariate analysis, taking into acount simultaneously the 14 morphological-anatomical traits, divided the population into three main groups. *A. cephalonica* in the south, intermediate hybrid populations in central Greece, and a third group of hybrid populations in the north, where *A. alba* characters dominated. Populations not included in any of the above groups differed among themselves, (i.e.,

NEEDLE-TIP SHAPE *	
5.03	A.ALBA (ITALY)
4.92	BULGARIA (3)
4.47	BULGARIA (4)
4.36	A. EQUI-TROJANI
4.20	ARIDAEA
3.10	AGION OROS
2.10	KONITSA
1.35	EUBOEA
1.26	ASPROPOTAMOS
1.08	PIERIA
1.07	PARNON
1.03	FOURNA
1.03	VYTINA
1.02	OETE
1.00	ELICON
0.97	PARNASSOS
0.97	PARNETHA
0.95	CEPHALONIA
0.93	TAYGETOS
0.92	PANAETOLICON

* Provenances not connected by the same line are significantly different at $P \leqslant 0.05$.

Figure 7. — Test of means and contour diagram of provenance variation in needle-tip shape.

Table 3. — D² values, obtained from Mahalanobis distance function analysis, for morphological-anatomical characteristics.

PROVENANCES	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)
1. ARIDAEA																			
2. FOURNA	76																		
3. PARNASSOS	97	8																	
4. PANAETOLICON	90	3	6																
5. PIERIA	34	5	17	10															
6. CEPHALONIA	182	47	14	38	76														
7. PARNETHA	139	15	7	18	25	14													
8. VYTINA	151	23	4	17	37	8	7												
9. PARNON	49	9	2	9	9	11	9	3											
10. KONITSA	16	23	42	35	10	102	49	65	18										
11. ASPROPOTAMOS	34	5	17	12	3	78	21	37	11	10									
12. EUBOEA	88	10	13	14	17	41	12	24	14	31	12								
13. TAYGETOS	194	20	5	14	40	10	8	2	2	74	36	24							
14. AGION OROS	33	43	68	64	26	177	58	98	37	18	25	33	104						
15. ABIES ALBA	15	229	371	414	199	426	521	497	255	35	240	231	544	74					
16. ELICON	124	17	2	18	28	5	7	2	3	43	31	18	3	93	365				
17. OETE	149	8	3	3	20	21	9	8	5	42	17	11	8	72	243	7			
18. ABIES EQUI-TROJANI	41	74	73	73	36	132	87	105	49	34	34	42	125	11	190	84	69		
19. BULGARIA 3	6	157	182	213	89	244	266	239	128	16	105	118	267	29	33	214	195	71	
20. BULGARIA 4	5	85	102	96	48	205	119	151	59	14	46	125	192	38	21	107	109	65	3

the three isolated populations, Cephalonia, Euboea and Agion Oros). Agion Oros appears to be closer, with respect to D² value (3.36), to *A. equi-trojani* than to any other population of pure species or hybrids *(Figure 8)*.

With respect to morphological characters, almost all were useful in discriminating populations. Anumber of trait pairs were closely correlated (3—4, 6—7, 8—13) as shown by partial correlation analysis, while 4 others (3, 8, 10, 12) were independent and more efficient in discriminating *A. alba* from *A. cephalonica* and, therefore, in identifying intermediate forms (Mann-Whitney test, see *Figure 4* in comparison with *Figure 7*).

Table 4. — Average within and between cluster D² values for morphological-anatomical characteristics. Clusters formed according to Rao (1952).

Cluster	A	B	C	D	E	F	G	H	I
A. Parnon-Taygetos-Vytina-Parnetha-Elicon-Parnassos-Oete	4.30								
B. Cephalonia	11.87	-							
C. Euboea	16.53	41.2	-						
D. Pieria-Aspropotamos-Panaetolicon-Fourna	18.90	59.75	13.25	8.53					
E. Konitsa	47.51	102.3	31.40	19.5	-				
F. Agion Oros	75.67	177.0	32.90	39.48	18.00	-			
G. Abies Equi-trojani	84.37	131.90	41.9	54.15	33.90	11.30	-		
H. Bulgaria (3)-Bulgaria (4)-Aridaea	151.95	210.07	110.23	89.54	15.30	33.20	59.00	4.7	
I. Abies alba	399.63	426.00	231.2	270.25	34.60	74.30	190.10	22.93	-

It is extremely interesting to note the existence of *A. alba* characters within the range of *A. cephalonica*, especially in southern populations and even on the island of Cephalonia. Two possible explanations of these findings are that introgression is on — going along a north to south axis or that the observable patterns are remnants of ancient hybridization. Since the two species are not in contact today, hybridization must be ancient. According to the latter scenario, as the glaciers melted and the climate warmed, *A. alba* and hybrid forms could no longer maintain themselves in the south. *A. cephalonica* genotypes, which were better adapted to the new environments, dominated the area. According to Philipson (1958), early in the Pleistocene a landbridge connected Greece and the Ionian islands
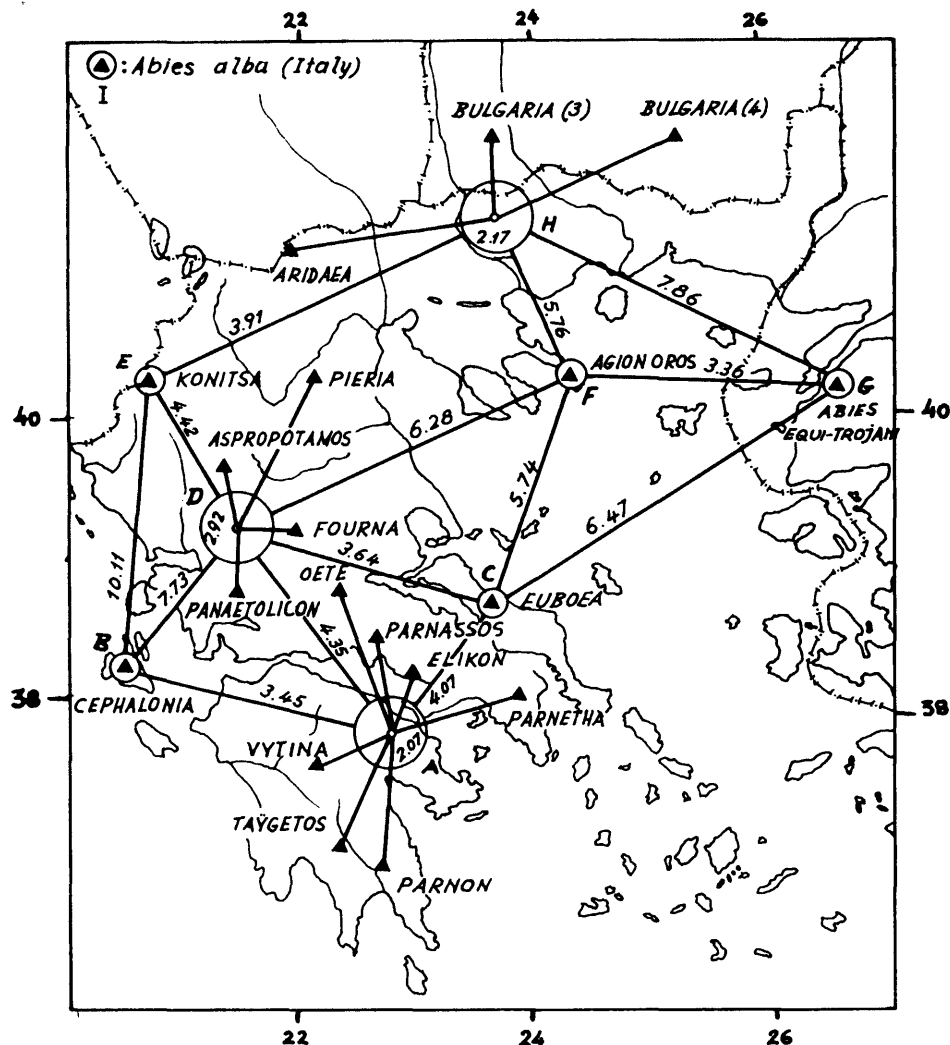
Figure 8. — Diagrammatic representation of the approximate degree of similarity among provenances according to average between cluster D² values for morphological-anatomical characteristics.
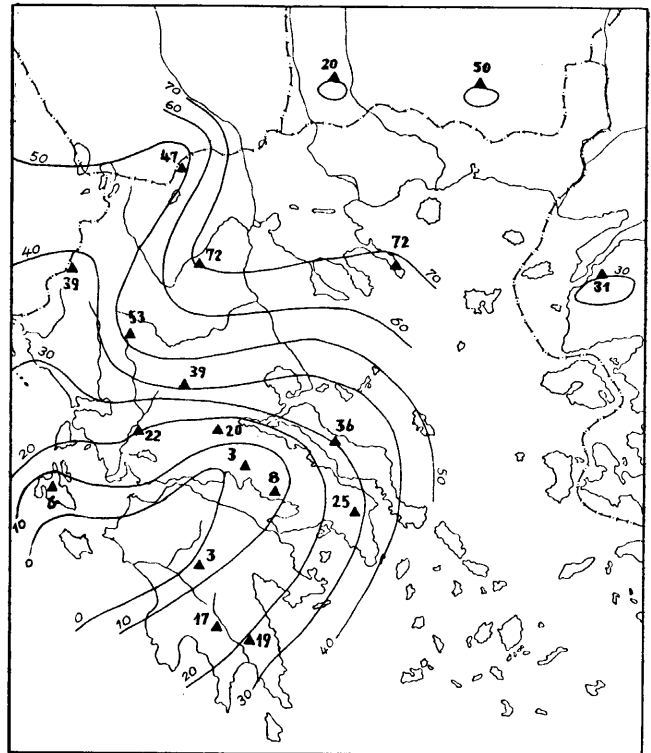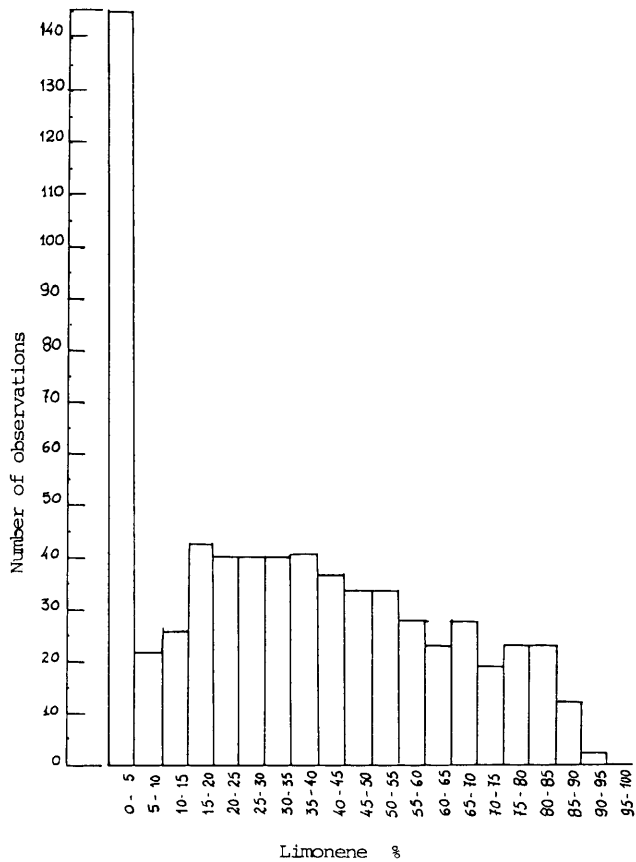
Limonene %

Figure 10. — Contour diagram of percent of trees having limonene content > 50%.

which submerged gradually. During the late Pleistocene the Peloponnesos and especially the island of Cephalonia were isolated by geographic barriers from the rest of the fir
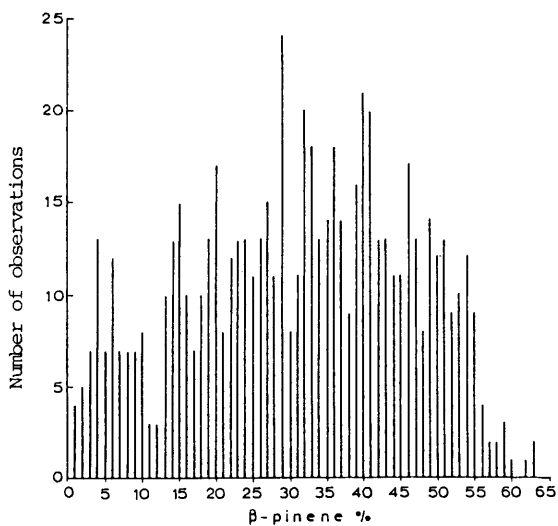

Figure 9. — Frequency distribution for limonene and β-pinene (660 trees).

Table 5. — Mean, range, coefficient of variation (C.V.), and "H" values of monoterpene composition of cortical oleoresin.

Component	X̄ %	Range %	C.V.	"H" value
α-pinene	26.91	2.48-79.41	54	141.7**
β-pinene	30.61	0.34-62.95	9	116.6**
myrcene	2.42	0.27-24.48	74	118.0**
limonene	34.00	0.06-94.09	77	141.7**
β-phellandrene	5.92	0.11-26.26	67	97.1**
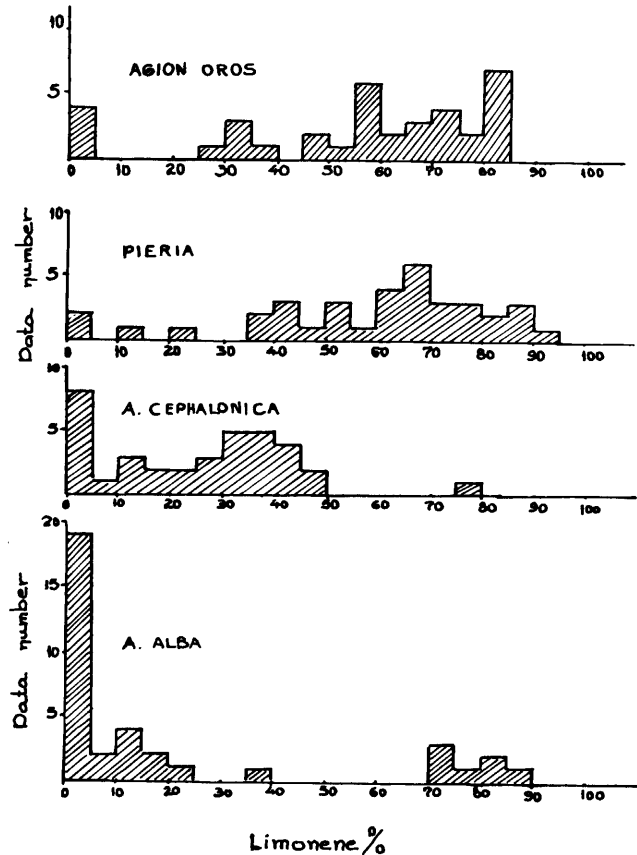
Limonene %

Figure 11. — Frequency distribution of percent limonene for A. alba, A. cephalonica, Pieria and Agion Oros, provenances.
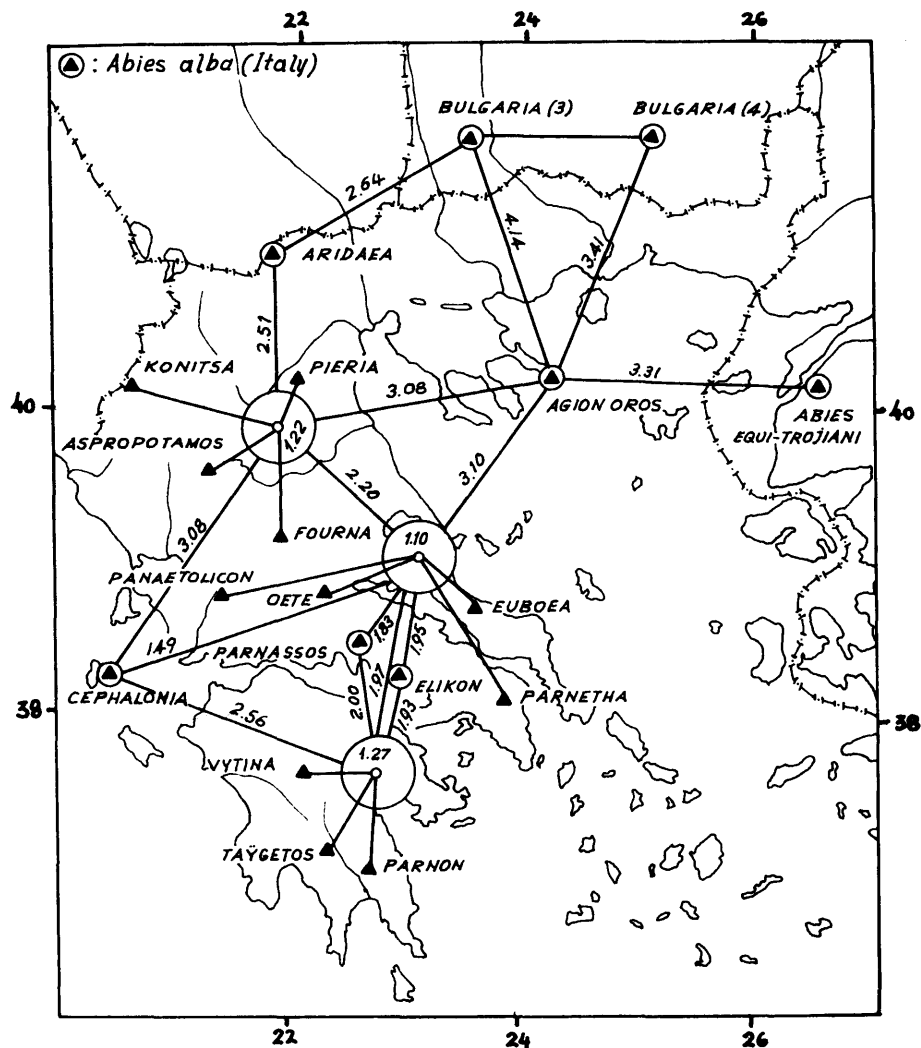
Figure 12. — Diagrammatic representation of the approximate degree of similarity among clusters of provenance according to average between-cluster D² values for monoterpenes.

populations on the mainland of Greece. Geological studies conducted by MARINOS and SAKELLARIOU-MANE (1964) have shown that the Ionian Sea emerged recently.

Statistical analyses revealed high intra-population variation, which may be a result of an adaptation of individuals to particular microecological niches or to hybridization.

Interprovenance variation was found to be negligible among provenances within the *A. cephalonica* range (except for Cephalonia and Euboea) but for populations north of Lat 38°50' N, differences were significant for many traits. The latter can be explained by the hybrid origin of northern populations and their interactions with habitat diversity.

The pattern of variation for individual characters was in general clinal with a trend from north to south, while for southern populations (below Lat. 38°50' N) there appeared to be a change in this trend for a number of traits, from east to west. The clines can be attributed to the gradual climatic changes from north to south and east to west which prevail in Greece. In the same area some traits appear to be discontinuous, (Euboea and Cephalonia) perhaps due to genetic drift.

The Agion Oros provenance was unique. It differs from all others in 4 traits (1, 5, 8, 13) and was separated from other populations by an abrupt discontinuity in 4 more

traits. These findings reinforce the hypothesis advanced by PANETSOS (1975), that the firs of Agion Oros have been influenced by gene flow of oriental origin. *(A. equi-trojani* and/or *A. cilicia).* It could also be the outcome of long isolation combined with either adaptation to a novel environment or genetic drift, not excluding the oriental influence.

Differentiation of the Agion Oros provenance, designated on the basis of morphological characters, was even more distinct when chemical traits were analysed. In this particular provenance 72% of the trees possessed concentrations of limonene > 50%, while the corresponding frequency in *A. alba* was 19% and in *A. cephalonica* only 6% *(Figure 11).*

Multivariate analysis on chemical data appeared to be in agreement with the results based on morphological characters, but more efficient, since it discriminated the Peloponnesos populations, which form the core of *A. cephalonica,* from the transitional zone and the intermediate hybrid populations.

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Scots Pine Resistance to Pine Twist Rust-Conformity between the resistance found in an artificial environment and field trials

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Abstract

The resistance to pine twist rust (Melampsora pinitorqua) was tested in progenies from 4 different Scots pine seed orchards. The progenies were tested as 2-year-old seedlings with artificial inoculation in greenhouses and in forest habitats as 8-11-year-old saplings. The genetic influence on the resistance was identified in the artificial environment as well as in the forest habitat. A correlation between the two tests was found.

Key words: Scots pine, progeny test, pine twist rust, field resistance, artificial inoculation.

Zusammenfassung

Die Widerstandsfähigkeit gegen Kieferndrehrost (Melampsora pinitorqua) wurde in den Nachkommenschaften von 4 verschiedenen Kiefernsamenplantagen untersucht.

Die Nachkommenschaften wurden als zweijährige Samenpflanzen nach künstlicher Inokulation in Gewächshäusern und in Waldbeständen als acht- bis elfjährige Pflanzen geprüft. Der genetische Einfluß auf die Widerstandsfähigkeit war sowohl in den Gewächshäusern als auch in den Waldbeständen erkennbar. Es bestand eine Übereinstimmung zwischen den beiden Prüfungen.

Introduction

The pathogenic fungi of Scandinavian forests are natural parts of their ecosystems. The natural coevolution of the trees and their pathogens has resulted in a relatively stable ecologic balance. Epidemic outbreaks of pathogens have been of a relatively small economic impact so far. Tree breeding for maximum growth may limit the genetic variation in other respects. In this situation it is important to main-