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DIVERSITY AMONG *P. brutia* subsp. *brutia* AND RELATED TAXA - A REVIEW[1]

Dr. Gabriel SCHILLER[1]

Abstract

Several studies on the genetic diversity of *Pinus brutia* Ten. subsp. *brutia* were reviewed. It is concluded that within its natural range, this subspecies can be divided into two groups: a western Anatolian group including the Aegean islands populations, which can be divided into high and low elevation races; and an eastern Anatolian group including the Black Sea populations, which are more closely related to tho subspecies *eldarica, pithyusa* and *stankewiczii*, and the populations at the periphery of the range, such as those, of Crete Cyprus and Iraq. The populations of the second group and those in the periphery are more distinct and homogenous then those of the first group. This is probably due to their isolation, which prevent gene exchange with neigbouring populations. The results confirm that *Pinus alderica, stankewiczii* and *pithyusa* are subspecies of *Pinus brutia*, and that subsp. *stankewiczii* is probably most like an expected progenitor of the entire *P. brutia-P. halepensis* complex.

1. INTRODUCTION

Calabrian pine or red pine (*Pinus brutia* Ten.) was introduced into Israel in the late 1920s (Heth, 1968), but has become widely used in afforestation projects only recently. This tree is clearly superior to the still widely used Aleppo pine (*Pinus halepennis* Mill.), because of the straight shape of its bole, its resistance to snow pressure and to the pine bast scale *Matsucoccus josephi* Bodenh. et Harpaz. This insect, which is endemic on *P. brutia* subsp. *brutia* in Turkey, Crete and Cyprus (Mendel, 1992), is the Major, and often lethal, pest of Aleppo pine (Mendel 1984; Mendel and Liphschitz, 1988; Liphschitz and Mendel, 1989a, 1989b). Owing to the growing importance of *P. brutia* Ten. for afforestation in dry areas outside of its natural range, attention has been given lately to research into the diversity within this species complex.

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As presently understood, *Pinus brutia* Ten. is a complex composed of four subspecies (Nahal, 1982). Subspecies *brutia* has a natural range extending from the Aegean islands, Crete and Cyprus, through Turkey to Lebanon and northern Iraq (Critchfield and Little, 1966). Because of the absence of *M. josephi*, we assume that subsp. *brutia* growing on the island of Thasos, the peninsula of Chalkidiki and westward on mainland Greece is an introduction brought in for the acceleration of honey production with the help of the honeydew secretion by the aphid *Marchalina hellenica* which is collected by the bees (Schiller and Mendel, 1993; Mendel and Schiller, 1993). Subspecies *eldarica* occurs naturally in a very small area in the Caucasus; land races of this subspecies probably extend to part of Iran and possibly Afghanistan. Subspecies *pithyusa* and subspecies *stankewiczii* occur in relict stands on the Black Sea coasts of the Caucasus range and Crimea, respectively.

2. GENETIC DIVERSITY

Despite the great heterogeneity of sites occupied by *P. brutia* Ten. (Arbez, 1974; Mirov, 1967) only few data have been published in international journals, on the geographic patterns of genetic variation of the species. Most of the research done up to now has been based mainly on the seed collection activities carried out within the FAO-IUFRO international project on the identification of provenances of *Pinus halepensis* and *Pinus brutia* suitable for different countries (Table 1). Available information is mainly the result of provenance trials in Argentina, Australia, Greece, Italy, Israel, Mexico (Eccher *et al.*, 1982; Fisher *et. al.*, 1986; Palmberg, 1975; Panetsos, 1981; Spencer, 1985; Weinstein, 1989a, 1989b); and laboratory studies on germination and early root growth under water and temperature stress of seeds of several provenances (Calamassi, 1982; Calamassi *et al.*, 1980; Falusi and Calamassi, 1982; Falusi, 1982; Falusi *et al.*, 1984; Pelizzo and Tocci, 1978).

Several different methods have been used to analyze the possible genetic diversity within this species complex, the results of which form the subject of this review.

Isik (1986), investigated 16 seed and seedling characteristics of several populations from different elevations in southern Turkey. These populations belong to the western group of the natural range of the subspecies. He concluded that subsp. *brutia* has locally adapted populations, with predominantly altitudinal variation patterns. He also concluded that there is a high genetic variabilty within populations.

Calamassi *et al.* (1988), investigated 11 morphological and anatomical characters of needles in 14 populations. On the basis of the results of their research, they postulated the division of the Turkish range of subsp. *brutia* into a Mediterranean sector and the Karadeniz population. Their results also reflect the differences among populations of different regions. The cluster from their publication (Figure 1) shows the grouping of the examined populations into two groups with five subgroups; the first group consists of populations from the Mediterranean sector, the second group consists of populations which grow at the borders of the main range of the species. By using also discriminant analysis, Calamassi *et al.* concluded that there is low diversity within populations situated at the edge of the natural area of distribution, whereas, there is high diversity within populations growing in the interior of the main range of the subspecies.

In our experiments (Schiller and Grunwald, 1987; Schiller and Genizi (1993) we used cortex or needle resin monoterpene conposition as a genetic marker (Squillace, 1967) to determine the diversity among subspecies. *brutia*. different provenances planted in Israel. Cluster analysis of cortex resin composition (Figure 2) shows the division of the examined population into mainly two groups, a western and an eastern group. The western group can be divided into low -and high- elevation porvenances. Results which basically confirm those obtained with cortex resin were also obtained by use of needle resin somposition. Cluster analysis of needle resin composition (Figure 3) shows the grouping of the provenances in to seven major groups. Four groups consist each of a single seed source: Cyprus, Iraq and low and high altitude provenances in Crete. The remaining three groups are comprise Turkish seed soures: cluster 4 includes low-elevation provenances from the Taurus range and the Black sea coast; cluster 5 includes hihg-altitude provenances of the Taurus; cluster 6 comprises east Anatolian provenances.

To better analyze the diversity and the possible phylogeny among the *P. halepensis* - *P. brutia* species complex, we also used horizontal starch gel electrophoresis of isozymes extracted from the haploid endosperm of individual germinated seeds from different seed sources (Conkle *et al.* 1988; Grunwald *et al.*, 1986; Schiller *et al.* 1985). The seed sources of the *Pinus brutia* Ten. species complex used in this study are shown in *Table 2*. Genetic diversity values for *Pinus brutia* Ten. complex and *Pinus halepensis* races are summarized in *Table-3* and genetic distance values in *Table 4* (From Conkle *et al.*, 1988). Two phylogenetic trees were produced: one includes unpublished data on *Pinus brutia* subspecies and a hybrid between *P. halepensis* and *P. brutia;* the second which includes *Pinus brutia* subspecies and *Pinus halepensis* races. From the first phylogenetic tree (Figure 4) it can be seen that the first dichotomy from the tree root separates the hybrid and *P brutia* from Greece from the other subspecies; the zawita provenance in Iraq is the first and nearest on the second branch; secondly, provenances of subspecies *eldaria* and Quetta pine are grouped together; and thirdly, subspecies *stankewiczii* and *pithyusa* are on the same branch together with the Black Sea subsp. *brutia* provenance at Çamgölü. The subsp. *brutia* of various provenances show the tendency to associate into altitudinal groups. From the second phylogenetic tree (Figure 5) (from Conkle *et al.* 1988) it can be seen that the first dichotomy from the tree root separates the *P. brutia* group from *P. halepensis*. The 10 subsp. *brutia* provenances used to create this phylogenetic tree are clustered after subsp. *stankewiczi* and *pithyusa;* they have a tendency to associate into three geographic-physiographic groups: low elevation western, mixed-elevation central, and an eastern group. Subspecies *eldarica* and Quetta pine are joined on the same branch, forming the closest association with populations of the eastern group.

Allozyme information from Conkle *et al.* (1988) supports many conclusions about species relationships that were previously based on phenotypic characteristics (Debazac and Tomassone, 1965; Mirov, 1955; Mirov *et al.* 1966). Allozymes indicate a highly significant divergence between *P. brutia* and *P. halepensis*. Subsp. *stankewiczii* has allozyme variation much like that to be expected in a genetically variable progenitor of the *P. brutia-P. halepensis* complex. The evolutionary history of these related pines, reconstructed from allozyme evidence, indicates that the center of origin included the regions bordering the Black Sea and easternmost Anatolia, with eastward extensions into lands between the Black and Caspian seas. Early populations there may have been more widespread, larger in size, and more nearly contiguous. Modern subsp. *brutia* around the

Aegean and Mediterranean seas is a widespread taxon that maintains significant levels of allozyme variation throughout its geographic distribution. Eastern populations of subsp. *brutia* are now geographically isolated from the main distribution. Several of the eastern populations resemble subsp. *stankewiczii*, *pithyusa* and *eldarica* by possessing rare alleles and by having allele frequencies that distinguish them from western populations of subsp. *brutia*. The morphologial differentation of subsp. *stankewiczii*, *pithyusa* and *eldarica* has been sufficient for some taxonomists to assign species status to them, but enzyme allele frequencies of these subspecies closely resemble the frequencies for subsp. *brutia*. Furthermore, evidence from allozymes indicates that geographically widespread *P. halepensis* is a geneticaly depauperate derivative from subsp. *stankewiczii*- like progenitors.

3. RESULTS

In conclusion, the existence of diversity within *Pinus brutia* subsp. *brutia* was confirmed by using several methods. All the previous studies which were reviewed concluded that within its natural range, this subspecies can by divided into two groups: a western Anatolian group including the Aegean islands populations, which can be divided into high and low elevation races; and an eastern Anatolian group including the Black Sea populations, which are more closely related to the subspecies *eldarica*, *pithyusa* and *stankewiczii*, and the populations at the periphery of the range, such as those of Crete and Cyprus.

The populations of the second group and those in the periphery are more distinct and homogenous then those of the first group. This is probably due to their isolation, which prevents gene exchange with neigbouring populations.

The results confirm that *Pinus eldarica*, *stankewiczii* and *pithyusa* are subspecies of *Pinus brutia*, and that *subsp. stankewiczii* is probably most like an expected progenitor of the entire *P. brutia*-*P. halepensis* complex.

P. brutia subsp. *brutia* VE İLİŞKİLİ TAXONLAR ARASINDA GENETİK ÇEŞİTLİLİK[1]

Dr. Gabriel SCHILLER[2]

Kısa Özet

Bu makalede, Kızılçam (*Pinus brutia* Ten. subsp. *brutia*)'ın genetik çeşitliliği ile ilgili çalışmalar gözden geçirilmiştir. Çalışmalara göre, bu alt türün, doğal yayılış alanı içerisinde iki gruba ayrılabileceği sonucuna ulaşılmıştır: Bunlardan birincisi; Ege adalarındaki populasyonları da kapsayan ve kendi içinde alçak ve yüksek mıntıka ırklarına bölünebilen Batı Anadolu grubudur. İkincisi ise Karadeniz populasyonlarını kapsayan; *elderica, pithyusa* ve *stankewiczii* alt türleri ve yayılışının sınırlarındaki Girit, Kıbrıs ve Irak'taki populasyonlar ile daha yakın ilişkisi (akrabalığı) olan Doğu Anadolu grubudur. İkinci grup ve sınırdaki populasyonlar birinci gruptakilere göre daha farklı ve homojendirler. Bu durum, muhtemelen, onların komşu populasyonları ile gen alışverişini engelleyen izole yayılışlarının bir sonucudur. Sonuçlar; *Pinus elderica, stankewiczii* ve *pithyusa*'nın Kızılçam'ın birer alt türü olduğunu ve *Pinus brutia* ssp. *stankewiczii*'nin de, büyük bir ihtimalle, *P. brutia-P. halepensis* kompleksinin atası olduğu yolundaki beklentileri teyit etmektedir.

ÖZET

Bu makalade, Kızılçam (*Pinus brutia* Ten. subsp. *brutia*)'ın genetik çeşitliliği ile ilgili birçok çalışma gözden geçirilmiştir. Bu türün, doğal yayılış alanı dışındaki ağaçlandırma çalışmalarının artan önemi nedeniyle, başta Akdeniz çevresindeki ülkeler olmak üzere birçok ülkede, son zamanlarda dikkatler, bu tür kompleksi içindeki uygun orijinlerin seçimine esas teşkil edecek genetik çeşitliliğin araştırılmasına yöneltilmiştir.

Işık (1986), araştırmalarının sonucunda, Kızılçamın yükseltiye bağlı olarak, üstün nitelikte lokal varyasyonlarının örneklerini ortaya çıkarmış, aynı zamanda bu populasyonların içinde de yüksek bir genetik çeşitlilik olduğunu saptamıştır. Calamassi ve arkadaşları (1988), Kızılçam'ın

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[1] Uluslararası Kızılçam Simpozyumu (18-23 Ekim 1993 Marmaris, Türkiye)'na bildiri olarak sunulmuş fakat geç geldiği için bildiriler kitabında yer almamıştır. Özetin Türkçe'ye Çevirisi Prof. Dr. Melih BOYDAK tarafından yapılmıştır.

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Türkiye'deki doğal yayılışının, Akdeniz ve Karadeniz bölümleri olarak ayrılmasını kabul etmişlerdir. Araştırıcılar, bu türün, doğal yayılışının sınırlarındaki populasyonlar içinde düşük, bunun aksine olarak optimumundaki populasyonlar içinde yüksek derecede bir genetik çeşitlilik gösterdiğini bulmuşlardır. Schiller ve Grunwald (1987) ve Schiller ve Genizi (1993), Kızılçamın doğal yayılışının, Batı veDoğu Anadolu grubu olmak üzere iki büyük gruba ayrılabileceğini saptamışlardır. Ayrıca Batı Anadolu grubunun alçak ve yüksek mıntıka populasyonları olarak bölünebileceğini belirlemişlerdir. Girit, Kıbrıs ve Irak'taki populasyonlar Anadolu populasyonlarından farklılık göstermektedirler.

Sonuçlar; *Pinus elderica, stankewiczii* ve *pithyusa*'nın Kızılçamın birer alt türü olduğunu ve *Pinus* brutia ssp. *stankewiczii*'nin de, büyük bir ihtimalle, *P. brutia-P. halepensis* kompleksinin atası olduğu yolundaki beklentileri teyit etmektedir.

Tablo 1: *Pinus brutia* Ten. Subsp *brutia* kompleksinde, reçinedeki monoterpen kompozisyonu ve anatomik-morfolojik karakterleri esas alan çalışmalar için kullanılan tohum örneklerinin alındığı coğrafik orijinler.

Table 1: Geographic origin of *Pinus brutia* Ten. species complex seed samples used in studies based on resin monoterpene composition and anatomical-morphological characters.

IUFRO No.	Country Ülke	Provenance Orijin	Lat. N. Enlem (0')	Long. E. Boylam (0')	Alt. Yük. (m)
B1	Greece	Chania, Crete	35 17	23 57	300-1400
B2	Greece	Kavala	40 48	24 42	–
B3	Greece	Lassithiou, Crete	35 06	25 37	1100
B4	Greece	Alexandropolis	41 08	26 13	–
B5	Cyprus	–	35 08	33 17	100-200
B6	Turkey	Marmaris	37 00	28 18	100-250
B7	Turkey	Isparta	38 04	29 32	1050-1150
B8	Turkey	Düzlerçamı	37 03	30 25	100-250
B9	Turkey	Pamucak	37 40	30 41	750-1250
B10	Turkey	Bozburun	37 21	30 45	200-300
B11	Turkey	Bakara	36 09	32 43	100-200
B12	Turkey	Silifke	36 13	33 43	500
B13	Turkey	Çamgölü	41 50	35 20	70
B14	Turkey	Başpınar	37 48	35 15	1000-1500
B15	Turkey	Kızıldağ	36 21	35 58	300-500
B16	Iraq	Zawita	36 35	44 20	500-1000
E	İran	Karaj	35 56	51 00	–

Tablo 2: *Pinus brutia* Ten. subsp. *brutia* kompleksinde, isozym elektroforezis tekniğine dayanılarak yapılan çalışmalarda kullanılan tohum örneklerinin alındığı coğrafik orijinler.

Table 2: Geographic origin of *Pinus brutia* Ten. species complex seed samples used in studies based on the isozyme electrophoresis technique.

Seed lot No.	Country Ülke	Provenance Orijin	Lat. N. Enlem (0')	Long. E. Boylam (0')	Alt. Yük. (m)
Subsp. brutia					
a	Greece	Chalkidiki	–	–	–
b	Turkey	Ayvacık	39 30	26 30	250
c	Greece	Samos (Ak)	37 45	26 53	750
d	Greece	Samos (Ak)	37 47	26 57	150
e	Greece	Chios (Am)	38 46	28 08	200
f	Greece	Chios (An)	38 36	28 08	1100
g	Turkey	Marmaris (B6)	37 00	28 18	100-200
h	Turkey	Düzlerçamı (B8)	37 03	30 25	100-250
i	Turkey	Pamucak (B9)	37 40	30 41	750-1250
j	Turkey	Silifke (B12)	36 13	33 43	500
k	Turkey	Çamgölü (B13)	41 50	35 20	70
l	Cypruss	– (B5)	35 08	33 17	100-200
m	Cypruss	– (T)	35 05	32 30	800
n	Cypruss	–	–	–	–
o	Cypruss	–	–	–	–
p	Iraq	Zawita (B16)	36 35	44 20	500-1000
Subsp. *stankewiczii and pithyusa*					
q	USSR	Georgia (C)	43 10	40 30	–
r	SSR	Yalta (D)	44 30	34 09	–
s	USSR	Sudak (G)	44 45	35 00	–
Subsp. *eldarica*					
t	Pakistan	Quetta (S)	67 00	30.00	1700
u	USSR	Azerbaijan (Z)	41 00	45 00	400
v	Iran	Elbrus Mt.	–	–	–
w	USA	Afghan pine	–	–	
x	USA	Afghan pine	–	–	–

hybrid between P. halepensis and P. brutia

Tablo 3: Genetic diversity values for *P. brutia* subspecies and *P. halepensis* races; from 30 loci with standard errors in parentheses. (Adapted from Conkle et al., 1988).

Table 3: Kızılçam alt türleri ve Halepçamı ırklarının 30 lokustaki genetik çeşitlilik değerleri (Standart sapmalar parantez içindedir) (Conkle ve ark. 1988'den adapte edilmiştir).

Subspecies and races Alt türler ve Irklar	Sample size Örnek Büyüklüğü	Mean alleles per locus Her lokustaki ortalama alleller	Mean effective alleles per locus Her lokustaki ortalama etkili alleller	Percent of loci polymorphic Polimorfik lokusların yüzdesi	Mean expected heterozygosity İstenen ortalama heterozigotluk
Pinus brutia					
Subsp. brutia	480	1.53 (0.12)	1.23 (0.06)	43	0.118 (0.034)
Subsp. stankewiczii	60	1.43 (0.10)	1.17 (0.05)	40	0.118 (0.029)
Subsp. pithyusa	50	1.30 (0.09)	1.16 (0.05)	30	0.097 (0.031)
Subsp. eldarica	50	1.37 (0.09)	1.12 (0.05)	37	0.075 (0.027)
Quetta pine	50	1.30 (0.09)	1.15 (0.06)	30	0.082 (0.030)
P. halepensis					
Eastern race	480	1.23 (0.07)	1.10 (0.05)	23	0.055 (0.026)
Western race	820	1.23 (0.08)	1.06 (0.03)	23	0.035 (0.017)

1) Sample size : Number of megagametophytes analyzed.

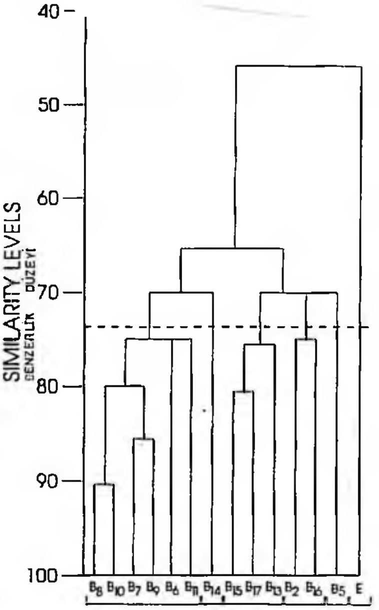
2) Effective number of alleles per locus equals 1/sum allele frequencies squared (Hiebert and Hammrick, 1983)

Tablo 4: Kızılçam (*Pinus brutia* Ten.)'in alt türleri ve *P. halepensis* ırklarında genetik uzaklık değerleri. (Conkle ve ark. 1988'den adapte edilmiştir.)

Table 4: Genetic distance values for *Pinus brutia* subspecies and *P. halepensis* race. (Adapted form Conkle et al., 1988).

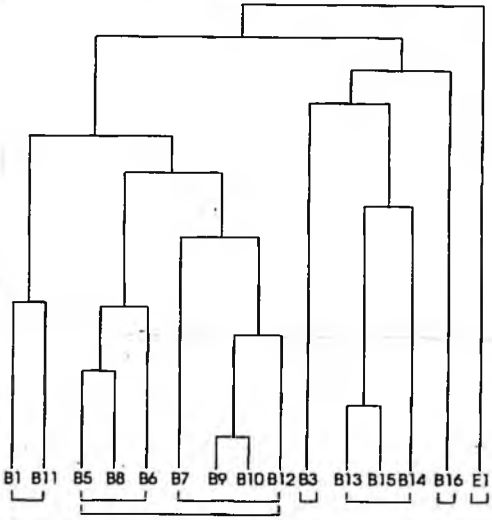
Taxa Taksonlar	Bru.	Sta.	Pit.	Eld.	Que.	Hal.-e	Halw.-
Pinus brutia Ten.							
Subsp. brutia (Bru.)	0.14a	0.19	0.17	0.17	0.16	0.47	0.46
	0.02						
Subsp. stankewiczii (Sta.)	0.06	–	0.18	0.22	0.22	0.43	0.42
Subsp. pithyusa (Pit.)	0.04	0.04	–	0.18	0.17	0.48	0.47
Subsp. eldarica (Eld.)	0.04	0.09	0.06	–	0.15	0.48	0.46
Quetta pine (Que.)	0.04	0.08	0.05	0.03	–	0.051	0.49
P. halepensis Mill.							
Eastern (Hal. -e.)	0.36	0.28	0.36	0.36	0.43	–	0.12
Western (Hal. -e.)	0.34	0.27	0.35	0.34	0.41	0.02	–

a) Cavalli-Sforza and Edwards (1967) chord dstances are above the diagonal, Nei's (1978) unbiased genetic distances are below diagonal.



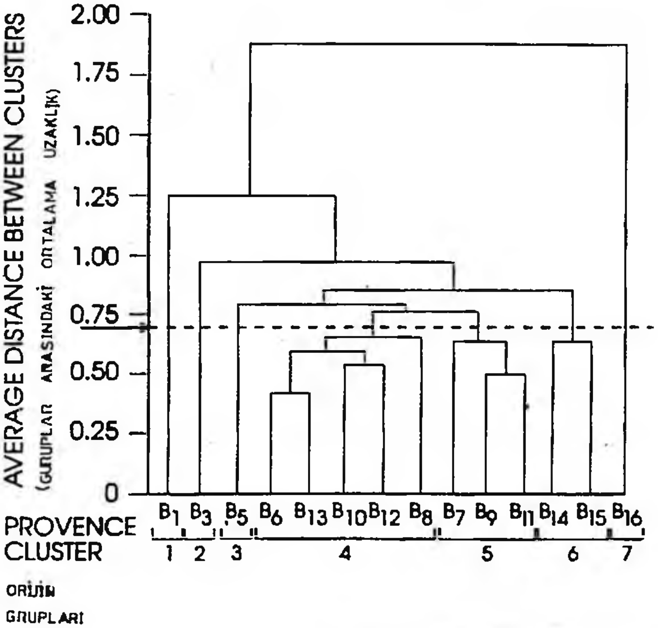
Şekil 1 : 11 adet iğne yaprak özelliğine dayanılarak kümeleme analizleri ile oluşturulmuş, populasyon örneklerinin gruplaşmasını gösteren fenogram (Calamassi ve ark. 1988'den uyarlanmıştır).

Figure 1: Phenogram, by cluster analysis, showing the grouping patterns of populations examined, calculated from 11 needle traits (Adapted from Calamassi et al 1988).



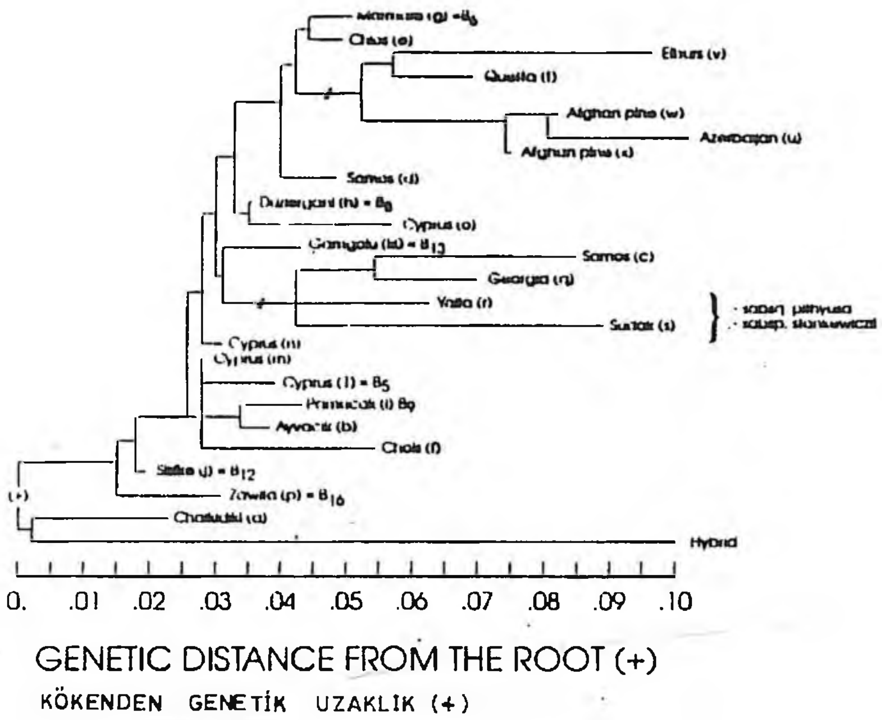
Şekil 2 : Korteksteki reçine kompozisyonuna dayanılarak kümeleme analizleri ile oluşturulmuş, populasyon örneklerinin gruplaşmasını gösteren fenogram (Schiller ve Grunwald 1987'den uyarlanmıştır).

Figure 2: Phenogram, by cluster analyses, showing the grouping patterns of populations examined, calculated from the cortex resin composition (Adapted from Schiler and Grunwald, 1987).



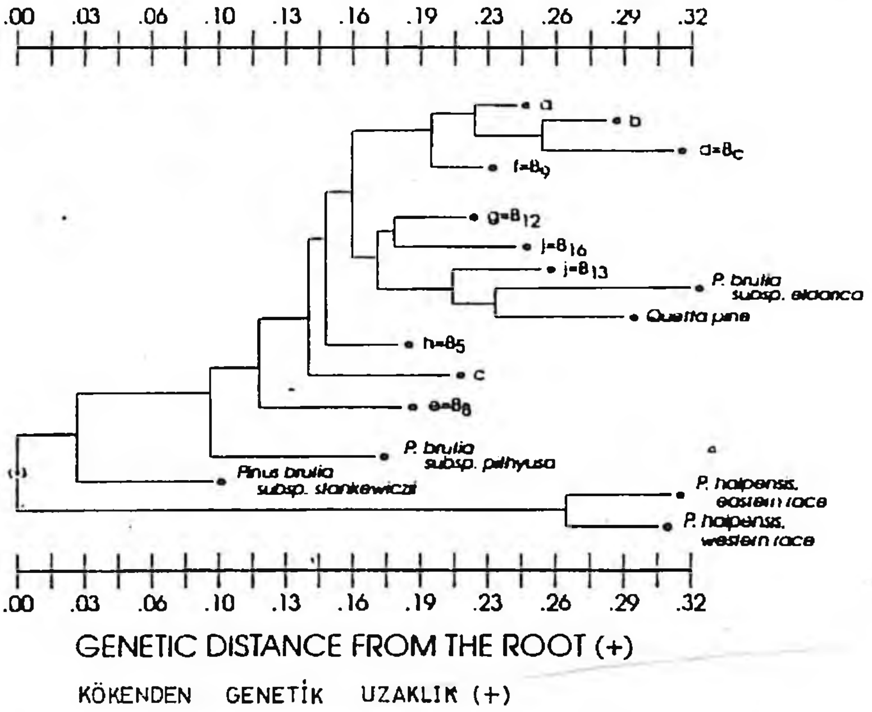
Şekil 3 : İğne yapraklardaki reçine kompozisyonuna dayanılarak kümeleme analizleri ile oluşturulmuş, populasyon örneklerinin gruplaşmasını gösteren fenogram (Schiller ve Genizi 1993'den uyarlanmıştır).

Figure 3: Phenogram, by cluster analysis, showing the grouping patterns of population examined, calculated from the needle resin composition (Adapted from Schiller and Genizi, 1993).



Şekil 4 : Wagner'in Uzaklık Yöntemi ve Cavalli-Sforza ve Edwards'ın "chord distances" yöntemine dayanılarak Pinus brutia Ten. subsp. brutia kompleksi için hazırlanmış soyağacı. (Swofford ve Selander. 1981) (Conkle ve ark. 1989'dan uyarlanmıştır).

Figure 4: Phylogenetic tree for the Pinus brutia Ten. species complex produced using the Wagner distance procedure and Cavalli-Sforza and Edwards chord distances (Swofford and Selander, 1981) (Adapted from Conkle et al. 1989).



Şekil 5 : Wagner'in Uzaklık Yöntemi ve Cavalli-Sforza ve Edwards'ın "chord distances" yöntemine dayanılarak *P. brutia-P. halepensis* kompleksine giren Akdeniz çamları için hazırlanmış soyağacı. (Swofford ve Selander. 1981) (Conkle ve ark. 1989'dan uyarlanmıştır).

Figure 5: Phylogenetic tree for Mediterranean pines of the *Pinus brutia-P. halepensis* species complex produced using the Wagner distance procedure and Cavalli-Sforza and Edwards chord distances (Swofford and Selander, 1981) (Adapted from Conkle et al. 1989).

KAYNAKLAR

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