Provenance Variation and Provenance-site Interaction in *Pinus brutia* TEN.: Consequences of Defining Breeding Zones

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Abstract

Forty-nine provenances of *Pinus brutia* were tested on 13 sites in Turkey, and 10-year results were evaluated. Provenances did not differ for survival except at two sites. There were highly significant differences among the provenances in height and diameter in all test sites located in the Mediterranean, Marmara and in the southeastern regions of Turkey. However, provenances did not differ in Aegean region sites except for diameter at one site. The fastest growing provenances had up to 55% greater height and 50% greater diameter than the site means, implying considerable gain can be realized if the best provenances were selected for plantations. Provenances from the middle elevation zone (400 m to 900 m) of the Mediterranean region had greater growth than the provenances from peripheral distribution of the species at most sites.

In general, the results did not support seed transfer zoning which was based on geographic and climatic data. Sub zoning of the Aegean region was not justified, as type B provenance correlations were high, well over the threshold value (r_B=0.8). For northern Marmara (Kesan site) and southeast Anatolia regions, a land race should be developed. Provenances were significantly different for stability variances, indicating the potential to select for stable genotypes across sites or for genotypes that are the most productive at specific sites.

Key words: Pinus brutia, provenance variation, genotype-environment interaction, seed transfer zones, stability parameters.

Ozet (Turkish)

Turkiye ve kuzey Kıbrıs orijinli 49 kızılçam orijini 13 deneme alanında test edilmiş ve 10 yıllık sonuclar değerlendirilmiştir. Orijinler, iki deneme alanı hariç, bütün deneme alanlarında yaşama yüzdesi bakımından farklı bulunmamıştır. Boy ve çap büyümesi bakımından Marmara, Akdeniz ve GAP bölgesinde yer alan tüm deneme alanlarında orijinler arasında önemli fark bulunmuştur. Ancak Ege bölgesinde yer alan deneme alanlarında orijinler boy ve çap (Nazilli hariç) için farklı bulunmamıştır. Kızılçamda uygun orijinlerin seçimi ile onuncu yaşta %55'e varan boy ve %50'ye varan daha fazla çap büyümesi elde edilebilir. Genel olarak Akdeniz orta zon (400 m–900 m) orijinli populasyonları daha hızlı büyümektedirler. Kızılçamın asıl doğal yayılışının dışında veya 'kenarında' yer alan populasyonlar ise genel olarak sıralamada en alt sıralarda yer almışlardır.

Araştırma sonuçları, coğrafik ve iklimsel verilere göre düzenlenen tohum transfer zonlarını genel olarak desteklememiştir. Deneme alanları arasındaki B tipi korelasyonları genellikle kritik değer olan r_B=0.8'in üzerinde olan Ege bölgesi iki ayrı alt zon yerine bir zon olarak ele alınmalıdır. Diğer taraftan Akdeniz bölgesinde iki ayrı zonun (yüksek zon ve alçak zon) olması gereği desteklenmiştir. Tarkya ve GAP yöresi için yöreye uyum sağlayan ırklar geliştirilmelidir. Orijinler arasında stabil olma bakımından gözlenen önemli farklar, özel sahalar için hızlı büyüyen orijinleri seçme veya dengeli orijinleri birçok yörede kullanma olanagı olduğunu göstermektedir.

Anahtar Sozcukler: Pinus brutia, orijin denemeleri, genotip-cevre etkilesimi, tohum transfer zonlamasi, stabilite parametreleri.

Introduction

Provenance trials are important particularly at the initial stages of a tree improvement program. They provide information about the genetic architecture of the species that is utilized for gene conservation programs, and for maximizing gain for a given area (ANDREW and WRIGHT, 1976). Provenance trials may also be utilized to determine breeding or seed transfer zones. If proper seed sources within a species are selected, the largest, fastest and cheapest gain in most breeding programs can be realized (ZOBEL and TALBERT, 1984; ZOBEL *et al.*, 1987).

From an economic point of view, Turkish red pine (*Pinus brutia* TEN.) is one of the most important forest tree species for Turkey. The species constitutes about 37% of the annual planting program (GUNAY and TACUNER, 1993). Several pulp and paper mills in the Mediterranean and Aegean regions are dependent on Turkish red pine wood. In the lower elevations, resin is extracted from the natural stands and used for the paint industry. Wood from middle and higher elevation stands is preferred for sawmills and for furniture. Due to tolerance of lower elevation seed sources to the salty soil, the species has been used to stabilize sand dune movements along the Mediterranean coast.

The natural range of Turkish red pine is mainly in Turkey, covering about 15% of Turkey's forestland (about 3 millions hectares). It occurs at elevations of sea level up to 1200 m, and is particularly adapted to calcareous soils. Detailed information on the distribution and ecology of the species were given by SELIK (1958), NAHAL (1962), CRITCHFIELD and LITTLE (1966) and ARBEZ (1974). The species has a clinal variation for several traits from sea level to high elevations (ISIK, 1986; ISIK and KARA, 1997; KAYA and ISIK, 1997; KARA *et al.,* 1997). Crown shape and stem straightness of the population changes gradually as the elevation increases (ISIK *et al.,* 1999). Significant genetic differences in growth, stem straightness, branching and crown traits among and within natural populations were observed (ISIK *et al.,* 1999; ISIK and ISIK, 1999). A high percent (17% to 30%) of the variation for bole straightness was accounted for by genetic differences among the populations, suggesting that considerable genetic gain may be realized if selection is based on the best provenances. Middle elevation populations were superior over the low and high elevation ones (ISIK, 1998; ISIK *et al.,* 1999).

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The increased international interest in the species during the last three decades is due to its relative drought tolerance, adaptation to calcareous soils and fast growth compared to other Mediterranean conifers. The first international Turkish red pine trials were initiated by FAO in 1974. A series of experiments was set up in Australia, New Mexico-US, Israel, and in some other Mediterranean countries (PALMBERG, 1975; WEINSTEIN, 1989; FISHER *et al.,* 1986). Some early results showed that Turkish red pine could have a potential use in Australia and in Israel, but similar results were not found in New Mexico where average rainfall is only 200 mm a year (FISHER *et al.,* 1986). Significant differences for growth were reported among the Turkish red pine seed sources in New Mexico trials. SPENCER (1985) reported the superiority of Turkish red pine provenances over *Pinus halepensis* at age 14 in the same trial established in Jerilderie in southern N. S. W. Australia. Although several provenance trials of the species have been carried out in Turkey, most were local and small scale or were not purposely designed to select the best seed sources for ongoing extensive Turkish red pine plantations programs (GEZER and ASLAN, 1980; IKTUEREN, 1986; TULUKCU *et al.,* 1987; ASLAN, 1991; GURSES, 1993).

Turkish red pine tree improvement programs in Turkey have been partitioned into four main breeding zones according to major climatic and geographic gradients. As a precautionary measure, the Mediterranean and Aegean zones were further sub divided into three and two sub zones, respectively, according to elevational ranges (KOSKI and ANTOLA, 1993). Elevational seed transfer zones have been suggested for Turkish red pine using mainly geographic and climatic data (ATALAY *et al.,* 1999). If this zonation is followed, tree breeders in Turkey will be faced with very costly tree improvement programs. The provisional breeding zones have not yet been tested with genetic material on a large scale. Success of tree improvement programs and sound seed transfer requires information on genotype x site interaction (gei). In addition, knowledge of the responses of genotypes included in the tests and of their relative performances is essential to minimize costs and to develop efficient breeding and deployment zones.

Plant breeders are often interested in the response of genotypes to different environments. If the relative performance of genotypes changes across sites, tree improvement programs can be very complex and costly (LI and MCKEAND, 1989; MCKEAND *et al.,* 1990). A stable genotype performing well over many sites would be desirable to reduce costs and increase efficiency. There are several methods to study stability of plants over a wide range of environments (WRICKE, 1962; FINLAY and WILKINSON, 1963; SHUKLA, 1972). SHUKLA's method has the advantages of quantifying the contribution of each genotype to the genotype-environment interaction and of removing the heterogeneity from the stability variances caused by locations (STONECYPHER *et al.,* 1996).

Comprehensive *Pinus brutia* provenance trials were established in Turkey in 1988 by the Turkish Forest Research Institute to address seed transfer zoning and to determine the best seed sources for reforestation programs. The first five-year results were published as a technical report (CENGIZ *et al.,* 1999). The objectives of this study were (i) to determine the best performing provenances for each geographic zone in Turkey, (ii) to assess the verification of the seed transfer zones that were based on geographic and climatic information by analyzing provenance-site interactions, and (iii) to study stability of the provenances by analyzing ten year results of the provenance trials in Turkey.

Materials and Methods

Materials

In this study, 46 provenances originating from Turkey and three provenances from northern Cyprus were evaluated. Most provenances included in the experiment were phenotypically superior stands and had been designated as seed stands for operational planting programs for a particular region. The original elevation of provenances ranged from 60 m to 1150 m above sea level, representing all natural occurrences of the species in Turkey (*Table 1*). Most provenances (29 out of 49) originated from the Mediterranean region where the species has its widest distribution. Fourteen provenances from Aegean and Marmara, two from Black Sea (provenances #44, #45) and one from southwestern Anatolia (#47) regions were sampled. Provenances #44 and #45 from the Black Sea region and provenance #47 from southeastern Anatolia are somewhat isolated from the main distribution. For each provenance, about 30 trees were sampled. The distance between any two sampled trees was at least 50 m in order to avoid relatedness among them. Cones were bulked for each stand and sun dried to extract seeds.

Bare root seedlings for each test site were raised in the winter of 1988. One-year old seedlings were then transplanted into 26 sites in the late autumn of 1988 and in the winter of 1989. Experimental sites covered a wide geographic area, from the southeast (KZT site, 37° 14'/E) to the west (INY site, 26° 19'/E), and from the north (KSN, 40° 40') to the Mediterranean region of Turkey (*Figure 1, Table 2*). All the test sites were located within the natural distribution of the species, except site KZT, which is located in the semi-arid southeastern Anatolia region of Turkey (northern Mesopotamia). This site may give important information for using Turkish red pine as a wood source in the region where a severe wood shortage is expected in the near future. The elevation of the sites varied from 70 m to 950 m. Number of provenances varied among the sites ranging from 39 to 49.

The sites were cleared of any woody vegetation and then plowed. Randomized complete block designs with three replications were used for all the test sites. Each provenance was initially represented by 16 seedlings in square plots in each block. Spacing was 1.5 m between trees in a row and 3 m between the rows. One growing season after planting (i.e. November to December, 1989), survival was assessed and dead seedlings of each provenance were replaced with two-year-old containerized seedlings. The identity of those replaced seedlings was not available. Data were collected from the experimental sites in the autumn of 1998 and in the winter of 1999 when the trees were 10 years old in the field.

Traits assessed

Survival was assessed as the proportion of surviving trees in each plot. The first two-year seedling mortality was considered due to poor planting (human) quality, seedling conditioning in the nursery, or mismanagement of the planting site. Total height (cm) and diameter at breast height (mm) were measured. Stem straightness was assessed visually using subjective scores from one (most crooked) to six (straightest). Forking and insect damage were assessed based on the present/absent basis.

Statistical analysis

The range and number of observations for stem straightness were considered large enough to approximate a normal distribution. Survival percentages were log transformed before analysis of variance to a normal distribution. Very few trees

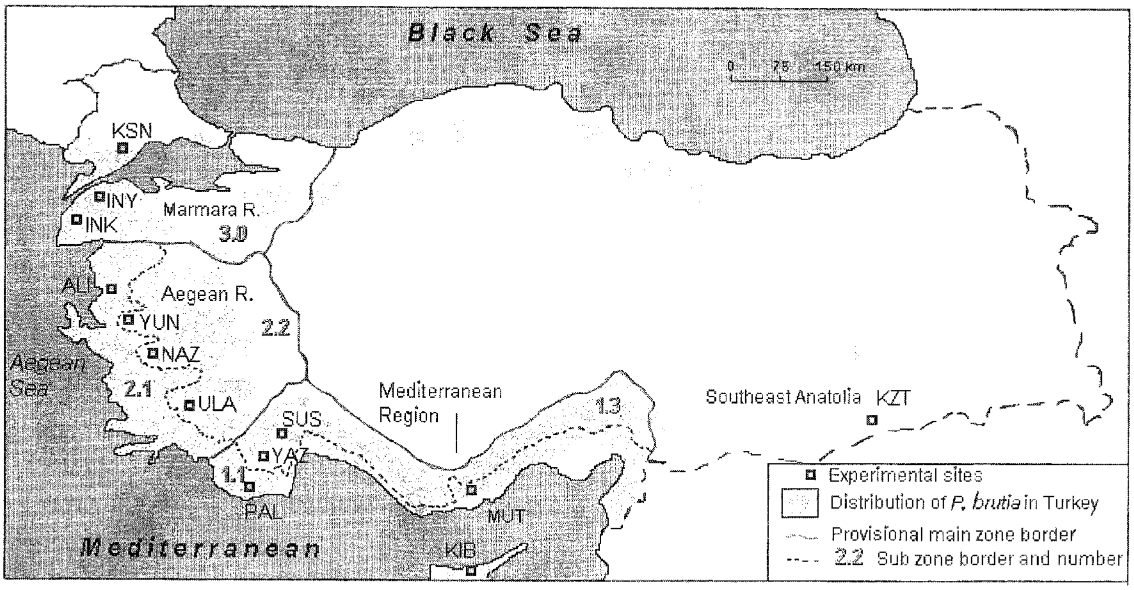

Fig. 1. – Distribution of *Pinus brutia* in Turkey, provisional seed transfer zones and experimental sites assessed.

Table 1. – Geographic information on Turkish red pine (*P. brutia*) provenances.

No	CODE	Provenance Name	Compartment No	Latitude (N)	Long. (E)	Altitude (m)	FAO Code
1	KRST	Pos-Karsanti	37, 38	37° 34'	35° 24'	600	122
2	BUFA	Cyprus-Buffavento	65, 67	35° 17'	33° 24'	500	201
3	KARA	Cyprus-Karaagaç	82	35° 18'	33° 32'	320	301
4	TK68	Tarsus-Karakoyak 68.	68	37° 05'	34° 33'	1000	1327
5	ANGÖ	Anamur-Gökcesu	102	36° 11'	32° 45'	600	1225
6	ANYV	Anamur-Yivil	219	36° 05'	32° 41'	650	–
7	PEMB	Gulnar-Pembecik	49	36° 14'	33° 15'	650	1226
8	TK43	Tarsus-Karakoyak 43.	43	37° 07'	34° 31'	800	–
9	FP88	Mersin-F.pinari 87,88,102	87, 88, 102	36° 55'	34° 26'	750	1230
10	AKDE	Silifke-Akdere	115	36° 13'	33° 43'	125	1132
11	GÜZO	Erdemli-Güzeloluk	87	36° 45'	34° 10'	1150	1333
12	FP46	Mersin-F.pinari 46	46	36° 57'	34° 24'	1150	1343
13	ANCA	Anamur-Caltibükü	79	36° 17'	32° 48'	1000	1344
14	MELL	Bucak-Melli	83, 102	37° 24'	30° 37'	800	124
15	BMER	Bucak-Merkez	159, 160, 161	37° 30'	30° 41'	800	125
16	DZCA	Antalya-Düzlercami	359, 362, 365	36° 59'	30° 33'	275	116
17	GÜZB	Gundogmus-Güzelbag	146, 148	36° 45'	31° 58'	650	127
18	ESKB	Gundogmus-Eskibag	302, 306	36° 42'	32° 10'	1000	138
19	K328	Kas-Karacay 328, 344	328, 344	36° 24'	29° 30'	720	139
20	K355	Kas-Karacay 355, 356	355, 356	36° 24'	29° 32'	830	1310
21	PGÖZ	Serik-Pinargözu	150, 151	37° 16'	31° 58'	750	1242
22	KARG	Alanya-Kargi	607, 628	36° 36'	31° 57'	350	1137
23	KUML	Kumluca	57	36° 26'	30° 15'	250	1339
24	KESC	Antalya-Olimpos	372, 397	36° 35'	30° 28'	350	–
25	SEYD	Sindirgi-Seydan	150	39° 12'	28° 08'	400	3112
26	AYBA	Ayvacik-Baharlar	168	39° 36'	26° 34'	550	3116
27	EZNE	Ayvacik-Ezine	33	39° 53'	26° 25'	300	3117
28	BAKA	Bayramic-Karaköy	74	39° 50'	25° 55'	400	3118
29	BIGA	Bigadic	129, 134, 135	39° 24'	28° 22'	350	–
30	MKCB	M.K.pasa-Caltilibük	31	39° 58'	28° 40'	450	3113
31	OELI	Orhaneli	62	40° 00'	28° 55'	600	3115
32	GÖLH	Gölhisar	258	37° 04'	30° 32'	1100	1319
33	SUKD	Sutculer-Karadag	116, 117, 118	37° 30'	30° 51'	650	1220
34	SUSÖ	Sutculer-Sögütdagi	25, 37	37° 21'	30° 54'	400	1138
35	ULUC	Antakya-Ulucinar	109, 163, 164	36° 21'	35° 57'	385	1121
36	SUCA	K.maras-Sucati	95, 7	37° 46'	36° 42'	800	4223
37	YAYL	Antakya-Yayladag	48	35° 54'	36° 01'	480	1224
38	CETB	Marmaris-Cetibeli	30, 31	37° 00'	28° 19'	60	2134
39	MYAR	Mugla-Yaras	59	37° 06'	28° 32'	750	2235
40	BOYL	Yilanli-Boyali	202	37° 17'	28° 34'	750	2236
41	SKAY	Gordes-Sahinkaya	168	38° 50'	28° 04'	350	2141
42	DLDE	Dursunbey-Delikdere	168, 175	39° 42'	28° 37'	600	–
43	IOZU	Goynuk-Ibrahimözü	80	40° 11'	30° 49'	600	–
44	CAMG	Bafra-Camgölü	9	41° 39'	35° 27'	100	–
45	NIHD	Niksar-Huridagi	3, 4	40° 38'	36° 43'	250	–
47	SIFN	Siirt-Findik	150	37° 29'	42° 00'	700	–
48	IZKD	Izmir-Karacadag	177	38° 06'	27° 05'	400	–
49	KDDE	Kesan-Dokuzdereler	30	40° 44'	26° 43'	175	–
50	KIBG	Cyprus-Güzelyurt	49	35° 18'	33° 03'	200	101

Table 2. – Description of the test sites and their allocation to the main breeding zones and sub zones in Turkey and northern Cyprus.

Breeding Zone	Code	Site	Rainfall	Lat.	Long.	Alt.	Soil Texture	Main Rock
			mm/yr	North	East	m		
1.1	PAL	Kas Palamut	906	36° 25'	29° 20'	200	Clay	Limestone
1.1	MUT	Mut Distas	418	36° 21'	32° 40'	400	Sandy loam	Limestone
1.1	KIB	G.yurt, Cyprus	418	35° 17'	33° 03'	230	Sandy loam	Limestone
1.3	YAZ	Finike Yazir	933	36°30'	30° 07'	950	Sandy clay L.	Limestone
1.3	SUS	Susuz	473	37° 04'	30° 12'	900	Clayey loam	Limestone
2.2	YUN	Manisa Yuntdagi	747	38° 54'	27° 34'	475	Silt clay L.	Marl
2.1	ALI	Menemen G.hisar	606	38° 50'	26° 59'	70	Clay, salty	Marl
2.2	NAZ	Nazilli	611	37° 41'	28° 48'	650	Sandy loam	Schist
2.2	ULA	Mugla Cicekli	1221	37° 06'	28° 28'	570	Clayey loam	Limestone
3.0	INY	Intepe,Yigincakil	629	39° 55'	26° 19'	240	Sandy clay	Quartz cement
3.0	INK	Intepe, Kayislar	629	39° 55'	26° 19'	240	Sandy loam	Schist
3.0	KSN	Kesan C.dere	627	40° 40'	26° 42'	220	Clayey loam	Sandstone
4.0	KZT	Kiziltepe Nursery	689	40° 38'	37° 14'	540	Clay	Conglomerate

were recorded which suffered from insect approximate damage or had forks. Preliminary analysis of these traits showed that neither forking nor insect damage had any variation at this stage. Thus, these traits were not considered for further analyses. Due to the poor establishment or inadequate maintenance, 13 sites out of 26 were not included in the analyses. Coefficients of variation (CV) obtained by using the plot-to-plot variance and field observations were used as a basis to evaluate the precision of an experiment. In general, coefficients of variation for height ranged from 27 to 50. Higher CV's above 64 such as 71 (Melemez site), 79 (Gazipasa Delikdere) and 93 (Gulmez site) were indicative of very heterogeneous sites, which were not included in the analyses.

The least squares method (LSMEAN) in the GLM procedure of SAS (SAS, 1989) was used to predict provenance means for height, diameter and stem straightness in a given site according to the following linear model:

$$y_{ijk} = \mu + b_i + p_j + bp_{ij} + e_{(ij)k} \qquad \textbf{[Eq. 1]}$$

Where:

y_{ijk} = Observation on k-th tree in j-th provenance in i-th replication;

μ = Overall mean;

b_i = Random effect of i-th block, i=1, 2,...b, $E(b_i) = 0, Var(b_i) = \sigma^2_b$;

p_j = Random effect of j-th provenance, j=1, 2,...p, $E(p_i) = 0, Var(p_i) = \sigma^2_p$;

bp_{ij} = Block x provenance interaction, $E(bp_{ij}) = 0$, $Var(bp_{ij}) = \sigma^2_{bp}$;

$e_{(ij)k}$ = Within plot error, normally and independently distributed random deviation of k-th tree in provenance j in block i, k=1, 2,...n, $E(e_{(ij)k}) = 0$, $Var(e_{(ij)k}) = \sigma^2_e$,

Survival was analysed on a plot means basis (percentage of surviving trees). Thus, for survival, the block x provenance interaction term (bp_{ij}) was the only error term. To predict provenance means across sites, a combined site analysis using the following linear model was used:

[Eq. 2]

$$y_{ijlk} = \mu + s_l + b/s_{li} + p_j + ps_{jl} + (bp)/s_{lij} + e_{(lij)k}$$

Where:

y_{ijlk} = Observation in k-th tree in j-th population in i-th replication in l-th site;

μ = Overall sites mean;

s_l = Random effect of l-th test site, l=1, 2, ...s, $E(s_l) = 0$, $Var(s_l) = \sigma^2_s$;

b/s_{li} = Fixed effect of i-th block nested within l-th site, i=1, 2,...b, $E(b/s_{li}) = 0$, $Var(b/s_{li}) = \sigma^2_{b/s}$;

P_j = Random effect of j-th provenance, j=1, 2,...p, $E(p_j) = 0, Var(p_j) = \sigma^2_p$;

ps_{jl} = Interaction effect of j-th provenance with the l-th test site, $E(ps_{jl}) = 0$, $Var(ps_{jl}) = \sigma^2_{ps}$;

$bp/s_{(lij)}$) = Interaction effect of j-th provenance with i-th block nested in l-th test site; $E((bp/s_{ijl}) = 0$, $Var((bp)/s_{ijl}) = \sigma^2_{(bs)/p}$;

$e_{(ijl)k}$ = Normally and independently distributed random deviation of k-th tree of l-th site in provenance j in block i, k=1, 2, ...n. $E(e_{(ijl)k}) = 0, Var(e_{(ijl)k}) = \sigma^2_e$.

Provenances, sites and their interactions were analyzed as random effects, because the inferences from the analysis will be made about all the provenances of Turkish red pine, and the test sites were considered as samples of the environments where the provenances could be tested. F statistics for provenance effects were based on replication-provenance and site-provenance interaction variances as an error term in a given site and for combined site analysis respectively. If the differences between populations were significant for the traits studied at the 0.05 level on the basis of the F test, then least square means were compared using LSMEANS Adjusted Tukey option (SAS, 1989; SOKAL and ROHLF, 1995). The standard error of a site was calculated as dividing the square root of provenance-replication variance by the number of replications. PEARSON correlation coefficients were estimated between growth traits and straightness and between growth traits and geographic variables of the origin of the provenances.

To test whether the zoning is necessary and to what extent zoning is required for the species, provenance-site interactions (gei) were studied by combined ANOVA using the zones as factors. If gei was significant, then a series of analyses of variance were conducted and variance components were estimated to determine the most interacting site. Each time one site was excluded from the analysis and its contribution to the gei variance component was estimated.

Although, the detection of genotype-environment interaction by analysis of variance is a useful tool, it does not give insight on the behavior of genotypes at different environments. Genotype-environment interaction can also be studied by correlating the same trait in two different environments (ROBERTSON, 1959; BURDON, 1977). When variances in two sites are homogenous, type B provenance correlations (interclass correlations) can be used as approximate indicator of gei among the sites (ROBERTSON, 1959). Type B correlations were utilized to determine breeding zones having similar environments.

Where:

$$r_B = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_{ps}^2} \qquad \textbf{[Eq. 3]}$$

r_B = B type phenotypic correlations at the population level;

σ_p^2 = Variance components due to the populations;

σ_{ps}^2 = Variance components due to the population-site interaction.

Before combined sites analyses, raw observations at each site were divided by their site standard deviations to standardize the data, to eliminate the undue effect of the scale and possible different site variances on the statistics to be estimated. Stability parameters of provenances were estimated by employing WRICKE's (1962) ecovalence, SHUKLA's (1972) 'stability' variances and joint regression analysis (FINLAY and WILKINSON, 1963; EBERHART and RUSSELL, 1966). WRICKE's ecovalence (w_i^2) assesses the contribution of each genotype to the gei sum of squares. The smaller the w_i^2, the more stable the genotype. SHUKLA's stability variances ($\hat{\sigma}_i^2$) are appropriate when the data are balanced and when the error variances are homogeneous across the sites. The joint regression method characterizes interaction by a series of regression coefficients, which are taken as stability of the genotypes (MCKEAND *et al.*, 1990). If the regression coefficient is b=1.0 and residual mean squares is small, then the genotype is considered to have an average stability. Provenances having b>0 coefficients are unstable but responsive to better sites. Provenances with b<0 are stable and do not respond as much to site changes. All the sites (13) were included in the analysis for the regression method to sample a broad environmental range. For SHUKLA's stability parameters, only Mediterranean sites were included in the analysis as gei was significant among the Mediterranean sites. For WRICKE's ecovalence and FINLAY-WILKINSON methods, the sites and provenances were considered fixed effects.

Results

Performance of provenances

Survival

Survival was high at all test sites, ranging from 95% to 100%. There were not significant differences among the provenances for survival except at two sites. Provenances differed for survival only at a low elevation Mediterranean site (MUT) at $p \leq 0.05$ level and at one of the most northern sites in the Marmara region (INY) at $p \leq 0.001$ level. The difference in survival at MUT site arose mainly due to the low survival of provenance #28 originating from northwestern Turkey, far from the site. At the northern site (INY), geographically the most distant and isolated provenance (#47) and one of the most southern provenances (#35) had low survival percentages. The reason for these high percentages could be due to the exclusion of the first two-year seedling loss from the analysis. As the trees age, considerable loss may be expected for some 'exotic' provenances in the sites located in peripheral distribution (i.e. KSN and SUS) or out of the natural range (KZT). The trees in those sites may not have faced extreme low temperatures or severe droughts in ten years. ZOBEL and TALBERT (1984) suggested a minimum of half rotation age (25 to 30 years for Turkish red pine) when the species is tested out of its natural range.

Height and diameter and bole straightness

Provenances were significantly different in height and diameter at all test sites located in the Mediterranean (except site SUS) and Marmara regions (*Table 3*) and at the KZT site in southeastern Anatolia region.

The top provenance at each site had 31% to 51% greater diameter than the site mean and 1.4 times to 3.6 times greater diameter than the slowest growing provenances. The best performing provenances in the Mediterranean region test sites originated from various geographic regions and elevational ranges. However, the poorest provenances at Mediterranean sites were generally from the fringes of the species range. In the Aegean region, provenances did not differ for height and diameter (except site NAZ) when sites were analyzed separately (*Tables 3*). However, combined sites analysis taking the sites as replications revealed significant differences among the provenances. Best provenances at a given site had 11% to 28% greater height, and 22% to 35% greater diameter than the site means. In the southeast region of Turkey (KZT site), almost all the best performing provenances originated from the middle to high elevations of the Mediterranean region. The best performing provenance (#7) had 23% greater diameter then the site mean. Middle elevational provenances also seemed to perform better by age 10. The top three provenances (#7, #5 and #9) at age 10 were also highly ranked (first, third and fourth respectively) at age five (CENGIZ *et al.*, 1999). There were highly significant differences ($p \leq 0.001$) among the provenances in height and diameter at three sites of the Marmara region (*Table 3*). The fast growing provenances in site KSN had about 32% greater diameter than site mean. The frequency of high elevational and northern provenances was noticeable among the top groups at the three sites. There were significant differences (mainly at $p \leq 0.001$) among the provenances in bole straightness at 10 sites out of 13 (results are not reported).

Relationships between traits and geographic variables

There were significant relationships between the growth (height and diameter) and geographic variables (elevation, latitude and longitude) at the provenance level at 6 out of 13 sites. Diameter was negatively correlated with latitudes at five sites (ULA, KIB, PAL, KZT and ALI) ranging from –0.31 to –0.52. Similarly bole straightness had negative correlations with the latitude of the provenances at four sites that ranged from –0.31 to –0.37. Correlations obtained for each main zone i.e. combining the sites within each zone were also negative for diameter (range –0.22 to –0.37). Provenances originating from higher elevations of the Mediterranean region had significantly straighter boles at most sites (0.43 to 0.59), whereas relationships between growth traits and original elevation of the provenances were generally weak.

Table 3. – Diameter (mm) and height (cm) least square means of provenances at age 10. Means in bold in a given column are the best performing group.

#	Provenance code	Mediterranean										Aegean								Marmara						GAP	
		PAL		MUT		KIB		YAZ		SUS		ALI		ULA		NAZ		YUN		INY		INK		KSN		KZT	
		HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh	HT	dbh
1	KRST	198	17	**266**	**26**	405	45	**382**	**42**	–	–	448	65	409	52	484	72	446	68	280	35	309	44	**386**	**59**	448	60
2	BUFA	**259**	**23**	208	20	364	38	270	24	**236**	**21**	448	67	409	56	420	**66**	506	80	243	28	244	27	–	–	434	64
3	KARA	**249**	**25**	226	21	386	40	310	32	**232**	19	538	80	435	62	387	57	469	67	243	29	314	45	296	42	457	**70**
4	TK68	–	–	**262**	**27**	348	36	285	27	199	17	**482**	**70**	305	40	419	62	521	86	261	33	**335**	**55**	351	**58**	**468**	**71**
5	ANGÖ	**248**	**22**	248	24	**456**	**50**	**383**	**43**	**282**	**30**	503	74	417	57	403	57	484	74	286	**41**	**348**	**55**	338	50	**536**	**75**
6	ANYV	**268**	**26**	**262**	**25**	**462**	**48**	316	33	**253**	**24**	511	72	398	52	410	62	490	73	**354**	**50**	**366**	**59**	–	–	**514**	**73**
7	PEMB	**257**	**25**	225	23	407	**48**	354	**40**	**268**	**28**	491	70	**427**	61	397	61	496	71	**308**	**44**	318	**51**	346	53	**560**	**84**
8	TK43	232	20	**263**	**28**	**430**	**48**	294	27	**215**	**19**	490	65	363	51	442	**71**	488	76	275	**38**	**360**	**60**	313	42	480	72
9	FP88	**217**	**19**	**260**	**28**	**456**	**53**	318	34	**228**	**22**	460	73	416	60	462	**69**	508	80	297	**43**	291	46	327	49	**538**	**75**
10	AKDE	**250**	**23**	**269**	**29**	**431**	47	321	34	**268**	–	526	76	387	52	463	**72**	532	90	278	**38**	**359**	**58**	294	43	**504**	**75**
11	GÜZO	185	15	**252**	**27**	**434**	45	276	24	**235**	**21**	504	67	391	52	443	63	454	72	281	36	288	41	360	**54**	**499**	67
12	FP46	**214**	**19**	**292**	**32**	**476**	**55**	287	27	**236**	**23**	**465**	65	349	45	399	60	431	61	249	31	**329**	**52**	**354**	**59**	**513**	**74**
13	ANCA	**235**	**18**	213	19	392	42	352	39	**212**	19	432	67	415	54	423	65	460	67	**316**	**49**	321	47	351	53	**491**	**70**
14	MELL	**253**	**21**	191	17	352	37	327	34	**234**	**23**	498	71	391	52	444	63	490	80	**305**	**43**	**356**	**56**	341	52	448	**69**
15	BMER	**249**	**23**	229	21	366	40	**368**	**43**	**241**	**24**	446	61	367	49	386	58	464	72	263	36	**346**	57	**420**	**71**	471	70
16	DZCA	**260**	**25**	191	19	368	37	264	24	**236**	**22**	454	68	387	51	453	**69**	425	61	250	33	285	39	328	**58**	–	–
17	GÜZB	–	–	233	23	**461**	**51**	328	35	**235**	**26**	497	71	415	57	469	**73**	512	80	**305**	**43**	323	**52**	330	51	**489**	68
18	ESKB	**251**	**24**	239	23	396	44	**364**	**40**	**257**	**28**	505	73	360	45	440	62	464	71	283	**38**	**357**	**59**	**397**	**63**	**467**	67
19	K328	210	**18**	190	15	378	41	282	26	**206**	**19**	446	65	326	44	392	59	435	63	243	30	**335**	**53**	**371**	**58**	454	**69**
20	K355	**235**	**18**	220	21	298	29	279	26	176	15	502	**71**	341	49	428	**65**	490	83	297	**45**	283	43	275	41	**517**	**71**
21	PGÖZ	**267**	**24**	246	23	368	38	294	27	**259**	–	445	67	406	56	454	**72**	479	70	**308**	**42**	**344**	**51**	351	54	**488**	**73**
22	KARG	**260**	**24**	**283**	**28**	401	45	266	23	**238**	**21**	474	72	495	70	424	**66**	480	74	**322**	**47**	**347**	**54**	**366**	**58**	**500**	**73**
23	KUML	**263**	**26**	199	**24**	408	45	**372**	**46**	192	16	470	73	426	66	422	65	515	83	293	**44**	283	41	255	37	–	–
24	KESC	**245**	**23**	**271**	**31**	303	33	310	31	**226**	**21**	477	71	457	61	469	**75**	465	68	**311**	**46**	**325**	**48**	**371**	**59**	411	57
25	SEYD	199	**17**	234	21	343	35	327	37	**222**	17	474	71	337	39	447	**68**	490	68	238	28	271	33	346	50	390	55
26	AYBA	196	14	203	17	369	41	319	33	**223**	**21**	418	70	334	39	474	**78**	512	76	252	33	303	**48**	343	52	–	–
27	EZNE	208	**19**	–	–	–	–	–	–	–	–	442	64	396	55	–	–	–	–	**309**	**42**	–	–	–	–	–	–
28	BAKA	210	17	210	21	351	39	283	29	**250**	**27**	462	63	390	50	406	58	454	**66**	269	36	267	39	361	**58**	419	63
29	BIGA	200	16	240	22	390	44	329	33	**262**	**26**	435	63	378	48	450	**70**	443	62	264	35	292	37	331	48	451	66
30	MKCB	**243**	**20**	**265**	**27**	383	38	316	30	210	16	534	67	398	51	413	55	483	77	296	37	**342**	**50**	–	–	**518**	**71**
31	OELI	209	**19**	210	18	373	40	266	25	**236**	**22**	466	63	395	52	409	61	460	65	255	32	307	41	**382**	**58**	384	53
32	GÖLH	203	16	220	20	334	36	285	29	**237**	**25**	502	71	330	42	454	**68**	478	74	270	35	295	42	**364**	54	468	65
33	SUKD	**242**	**21**	**269**	**27**	409	43	**369**	**43**	**276**	**29**	497	71	408	53	444	**69**	483	77	281	37	286	37	309	42	473	64
34	SUSÖ	**262**	**22**	225	20	416	44	320	34	**237**	**25**	510	75	395	53	445	65	518	81	283	**38**	282	38	349	51	416	61
35	ULUC	**229**	**19**	**306**	**33**	**433**	**49**	346	**40**	**230**	**21**	466	66	379	51	416	64	521	82	287	**40**	**340**	**50**	376	**60**	**473**	**79**
36	SUCA	210	15	196	18	389	42	340	36	**209**	18	–	–	–	–	395	58	–	–	–	–	283	38	–	–	474	63
37	YAYL	**232**	**22**	**282**	**30**	415	46	**401**	**48**	**252**	**25**	547	80	431	64	453	**69**	490	89	**316**	**45**	292	42	331	51	349	58
38	CETB	**250**	**24**	**307**	**36**	**429**	**48**	308	31	**244**	**23**	471	70	409	55	440	**68**	507	79	295	**42**	**351**	**57**	–	–	–	–
39	MYAR	**256**	**22**	231	21	**450**	**53**	**407**	**50**	**281**	**29**	533	83	463	69	412	58	513	84	**324**	**46**	**380**	**62**	347	55	–	–
40	BOYL	–	–	**253**	**27**	365	40	**369**	**41**	**283**	**31**	520	71	448	65	481	**72**	485	77	**302**	**42**	317	**48**	282	38	–	–
41	SKAY	202	**17**	**261**	**27**	334	36	297	30	**223**	19	479	73	367	44	403	62	405	59	246	33	259	30	304	41	–	–
42	DLDE	–	16	236	21	**437**	**48**	345	37	**273**	**29**	476	61	383	49	469	**68**	513	80	293	**39**	**343**	**48**	**377**	54	–	–
43	IOZU	192	21	196	18	291	28	253	24	**221**	**21**	470	64	310	37	393	51	515	81	269	34	269	35	322	46	400	55
44	CAMG	**248**	–	235	20	**420**	43	307	29	**287**	**30**	433	57	441	56	406	58	473	72	**317**	**45**	**346**	47	**407**	**61**	485	67
45	NIHD	172	14	214	19	332	33	324	36	**235**	**22**	440	62	307	34	357	47	355	45	215	22	278	34	319	45	401	47
47	SIFN	131	–	231	21	356	35	282	28	**221**	**20**	462	68	332	41	355	47	495	74	273	36	272	34	290	41	484	67
48	IZKD	**256**	**21**	–	–	–	–	–	–	–	–	489	72	399	57	–	–	493	77	**303**	**40**	–	–	–	–	–	–
49	KDDE	**267**	**24**	–	–	–	–	–	–	–	–	496	69	391	52	393	59	515	81	250	32	294	43	353	54	–	–
50	KIBG	**222**	**18**	148	15	376	40	320	31	186	13	460	64	339	42	377	54	462	67	257	32	256	34	–	–	480	67
	Site Mean	230	20	239	25	390	42	321	33	238	23	479	69	388	52	426	64	480	74	282	38	312	47	344	52	478	68
	SE	40.6	5.4	50.4	8.1	68.6	9.3	68.9	12	34.3	6.2	77.3	12	83.4	16	64.8	13	74.7	20	41.2	8.6	52.3	12	51.2	12	42.7	8.5
	CV	53	81	63	98	53	67	64	112	43	80	48	52	64	91	46	54	47	79	44	68	50	78	45	67	27	38
	F (prov)	***	*	**	*	***	***	*	*	***	**	ns	ns	ns	ns	ns	*	ns	ns	***	***	***	***	***	**	***	***

*, **, ***: Probability levels of ANOVA F test which are significant at 0.05, 0.01 and 0.001 levels respectively, ns: not significant. SE: Standard error of the provenances means, CV: plot to plot coefficient of variation.

Provenance-site interactions

Contribution of each site to the provenance-site interaction variance within the main seed transfer zones were presented in *table 4*. Provenance-site interaction (gei) was highly significant in the Mediterranean ($p \leq 0.001$) and Marmara regions ($p \leq 0.01$) but not in the Aegean region (*Table 4*).

In the Mediterranean region, site SUS (900 m) was the major source of gei variance for height, when excluded from the analysis, gei variance decreased from 5.48% to 5.18% (*Table 4*). For diameter, the two higher elevation sites (SUS and YAZ) were the most contributing to the gei variance. When these both sites were dropped from the analysis, gei percentage in

Table 4. – Contribution of sites to GxE interaction within and between main zones, change (%) relative to the overall sites in a region.

Site(s)	Height			Diameter		
	MS_{GxE}	gei %	Change%	MS_{GxE}	gei %	Change%
Mediterranean sites (1)	4.96***	5.48	–	3.76***	2.54	–
KIB excluded	0.347 **	8.47	2.99	0.268 ns	4.59	2.05
MUT excluded	0.353 **	5.88	0.40	0.280 ns	2.48	-0.06
PAL excluded	0.328 *	5.88	0.40	0.285 ns	2.48	-0.06
SUS excluded	0.383 **	5.18	-0.30	0.294 ns	2.36	-0.18
YAZ excluded	2.112 **	6.12	0.64	0.264 ns	2.31	-0.23
SUS and YAZ excluded	0.398 **	5.39	0.09	0.272 ns	1.69	-0.85
Aegean Region (2)	2818 ns	5.10	–	110.7 ns	2.50	–
Med-Aegean (1-2)	0.326 ns	0.80	–	0.272 ns	0.40	–
Marmara (3)	0.251 **	2.60	–	0.237 **	2.70	–
KSN Excluded	0.185 ns	1.50	-1.10	0.196 ns	1.30	-1.40
Aegean-Marmara (2-3)	0.297 ns	5.10	–	0.272 ns	2.50	–

MS_{GxE} Mean square by provenance-site interaction, gei% percentage of gei in total variance, *, **, ***: Probability levels of ANOVA F test which are significant at 0.05, 0.01 and 0.001 levels respectively

the total variance for diameter was the least (1.69%). Combined Mediterranean and Aegean sites analysis did not reveal significant gei variance. In the Marmara region (zone 3.0) when KSN site dropped from the analysis, gei variance decreased substantially for height (from 0.251** to 0.185 non-significant) and for diameter (from 0.237** to 0.196 non-significant). When two southerly sites (INY and INK) were included with the Aegean sites for combined analysis, gei variance was still not significant (*Table 4*).

Type B provenance correlations

Type B provenance correlations for height and diameter among all sites are given in *table 5*. A coefficient of r_B=0.8 is suggested as a threshold to decide whether gei has a practical importance (ROBERTSON, 1959). Coefficients among the lower Mediterranean breeding zone (1.1) sites were not consistent, being high between KIB and MUT, but below the threshold between KIB and PAL. Similarly, coefficients between PAL and MUT were r_B=0.29 and r_B=0.86 for height and diameter, respectively, making it difficult to draw clear conclusions. On the other hand, coefficients between two sites (YAZ and SUS) in the higher Mediterranean breeding zone (1.3) were over the threshold value, suggesting that the two high elevation sites have a myriad of common provenances that perform the same. However, coefficients between the low and high Mediterranean sub-zones were generally lower, thus justifying of two separate breeding zones in the region.

Type B provenance correlation coefficients for height and diameter among the Aegean sites (breeding zone 2.1 and 2.2) were well above the threshold level, suggesting that sub zoning is not necessary in the region (*Table 5*). When the NAZ site was not taken into account, provenance coefficients between the lower Mediterranean zone (MUT, PAL, KIB including YAZ) and Aegean region sites were generally high, implying that seed transfer between the lower elevation Mediterranean sites and Aegean region sites may be reasonable. There was not enough information to explain the different behavior of provenances in the NAZ site. In the Marmara region (3.0), correlations between two southerly sites INY and INK were high, but the KSN site had very low coefficients with INY and moderate coefficients with INK. The KZT site located in the southeastern Turkey had high coefficients with Mediterranean low elevation sites KIB (r_B=0.86 for height, r_B=0.96 for dbh) and with PAL site (r_B=1.00) but not with the MUT site (*Table 5*). The seven best provenances out of 11 at KZT site were also among the best performing at the KIB site and originated from middle and high elevations of the Mediterranean region.

Stability parameters

Several stability parameters of provenances were estimated (*Table 6*). Regression coefficients of the provenance means on the site means were estimated using all the test sites. Whereas, ecovalence and stability variances of the provenances in the Mediterranean sites are reported, since gei variance seemed to have a practical importance in the region.

The average contribution of each provenance to the gei sum of squares was 2.22%. The contribution of each provenance (w_i^2 %) to the gei sum of squares ranged from the most stable 0.2% (#3), to the most interacting 6.3% (#12). The most stable provenance #3 ranked 16th, 28th, 25th, 26th and 27th at five sites in the Mediterranean region. These kinds of provenances are stable whatever are the site conditions. On the other hand, one of the best performing provenance (#12) changed its ranking considerably across the sites. Four provenances out of 45 explained about 20% of the total gei sum of squares. Among the 45 provenances studied, 20 were significantly unstable. Deployment of those interactive provenances over wide areas may result in genetic loss and poor adaptability. According to an approximate F test, most provenances (25 out of 45) had an average stability ($\hat{\sigma}_i^2$), and their contributions were negligible. Some of the best provenances (i.e. provenances 5, 7, 10, 18) contributed little to the gei, and they were stable over the sites. There was not a significant relationship between the average height of the provenances and their contribution to the gei interaction (correlation coefficient r=0.09). The results also revealed that several fast growing provenances (i.e. #9 and #12) are more responsive to the better site conditions as shown by their higher regression coefficients (*Table 6*). Regression coefficients of provenances ranged from 0.37±.141 to 1.27±.114. Most provenances had an average stability with regression coefficients around 1.0 (*Table 6*) and responded to site quality accordingly.

Table 5. – Type B provenance phenotypic correlations among the paired sites for height (above diagonal) and for diameter (below diagonal, bold).

		Mediterranean (1)					Aegean (2)				Marmara (3)			
		PAL	MUT	KIB	YAZ	SUS	ALI	ULA	NAZ	YUN	INY	INK	KSN	KZT
Mediterranean (1)	PAL (200 m)	–	0.29	0.57	0.57	0.53	1	1	0.48	0.96	0.76	0.74	0.12	1
	MUT (400 m)	**0.86**	–	0.82	0.44	0.59	1	0.90	0.31	0.63	0.65	0.83	0.14	0.44
	KIB (230 m)	**0.57**	**0.84**	–	0.77	0.71	0.68	0.84	0.31	0.63	0.65	0.79	0.21	0.81
	YAZ (950 m)	**0.57**	**0.42**	**0.82**	–	0.89	1	1	0.59	0.64	0.72	0.58	0.04	0.07
	SUS (900 m)	**0.77**	**0.38**	**0.72**	**0.92**	–	1	1	0.57	0.12	0.56	0.65	0.49	0.09
Aegean (2)	ALI (70 m)	1	1	**0.53**	1	**0.31**	–	1	1	1	1	1	0	0.27
	ULA (570 m)	1	1	**0.98**	**0.97**	**0.81**	**1**	–	1	1	1	0.75	0	0.56
	NAZ (650 m)	**0.58**	**0.46**	**0.46**	**0.25**	**0.50**	**1**	**0.92**	–	1	0.72	0.41	0	0
	YUN (475 m)	1	**0.63**	**0.63**	1	**0.52**	**1**	**1**	**1**	–	1	0.73	0	0.56
Marmara (3)	INY (240 m)	**0.86**	**0.69**	**0.61**	**0.62**	**0.55**	**0.84**	**1**	**0.62**	**1**	–	0.92	0.11	0.56
	INK (240 m)	**0.81**	**0.71**	**0.85**	**0.40**	**0.59**	**0.59**	**0.69**	**0.39**	**0.98**	**0.82**	—	0.72	0.65
	KSN (220 m)	**0.12**	**0**	**0.28**	**0**	**0.40**	**0**	**0**	**0**	**0**	**0.05**	**0.72**	—	0
	KZT (540 m)	1	**0.74**	**0.96**	**0.06**	**0.26**	**0.82**	1	**0.41**	1	**0.72**	**1**	**0.17**	–

Discussions

Performance of provenances

Differences among the provenances were expected since they originated from contrasting major geographic regions and elevations. The main reason for not revealing differences among the provenances at Aegean sites may have come from the poor maintenance of the test sites and from the limited number of replications used. It is apparent that poorly managed or established sites (i.e. YAZ, ULA) had the highest coefficients of variation (CV) for diameter (*Table 3*). Whereas site KZT established in a nursery, had the lowest coefficient of variation. In general, at most sites in this study, trees from the middle-higher elevations performed better then other sources, particularly provenances originating from fringe distributions. ISIK *et al.* (1999) also reported superiority of middle elevation range of the populations. The results confirmed the widely accepted theory that fast growing genotypes evolve in the optimum conditions, while genotypes from the peripheral of the distribution or from isolated populations that are more prone to extreme whether conditions tend to grow slower (WELLS, 1983).

Turkish red pine has the reputation of being a rough tree due to its crooked stem form, coarse branches and wide crowns, particularly in lower elevations. Thus, improvement of bole straightness is vital to improve wood quality. ISIK *et al.* (1999) reported that variation for bole straightness in Turkish red pine is mainly due to the genetic variation between the natural populations rather than within populations. The results from this study were parallel to the previous study, indicating it would be fairly efficient to improve bole straightness by applying selection at the provenance level.

Performances of all provenances in a given site can be used to assess the site quality (FINLAY and WILKINSON, 1963). There were highly significant differences among the sites for diameter and height (*Table 3*). The difference between the best (YUN) and the poorest sites (PAL) for diameter tripled, showing the importance of site selections for profitable plantations. However, growth at most sites was far from satisfactory, probably due to poor site quality available at the time of planting. In fact, the species can grow comparatively fast in the dry conditions of the Mediterranean, if planted on favorable sites. USTA (1991) reported a 7 m^3/ha mean annual increment of unimproved Turkish red pine plantations on average sites.

Provenance-site interactions

Provenance-site interactions (gei) among the Mediterranean sites were significant. Significant provenance-site interaction was also confirmed by the low type B provenance correlations among the sites. Site SUS is located in a transition zone between the Mediterranean climate which is characterized with mild winters and the continental climate which has harsh winters. Trees in this site have probably experienced more extreme low temperatures, early and late frosts. In contrast, low elevation sites very rarely experience frost. As elevational difference between the sites increased, coefficients decreased accordingly. The results support the justification of two sub zones in the region, i.e. high zone including SUS and YAZ sites and a low zone including the rest. The upper level of the lower zone should be determined not just by the elevation alone, but also frequency of the frosts and snow should be taken into consideration. For the high elevations and Turkish red pine plantations in the transition zone between the Mediterranean and inland, cold hardiness along with fast growth should be considered when selecting seed sources. Due to lack of experiments in the provisional middle elevation zone of the Mediterranean region, justification of another sub-zone (i.e. middle altitude zone) could not be tested. It may me speculated that type B correlations would be lower between the middle and low sub zones compared to that between low and high sub zones. It is also interesting to note that gei variance was not significant when the Mediterranean and Aegean zones were combined in the analysis. However, type B correlations were not in harmony with the gei variance. Thus interpretation should be done cautiously.

Table 6. – WRICKE's ecovalence contribution (%) to the gei variance, SHUKLA's stability variances, approximate F statistics, significance levels and regression coefficients of each provenance for height (Mediterranean region).

Provenance		Ecovalence		Stability variance			Regression coefficient	
No	Code	(W_i^2)	%	($\hat{\sigma}_i^2$)	F	p ≤ 0.05	b_i ± stderr	R^2
1	KRST	7847	4.7	6092	3.36	***	0.86 ± .167	.79
2	BUFA	3067	1.8	2340	1.29	ns	0.85 ± .123	.87
3	KARA	371	0.2	225	0.12	ns	0.92 ± .090	.94
4	TK68	5938	3.5	4594	2.54	***	0.87 ± .138	.85
5	ANGÖ	2948	1.8	2247	1.24	ns	1.16 ± .104	.95
6	ANYV	3183	1.9	2431	1.34	ns	1.07 ± .115	.93
7	PEMB	1360	0.8	1001	0.55	ns	1.20 ± .100	.95
8	TK43	3457	2.1	2647	1.46	ns	1.04 ± .133	.90
9	FP88	4735	2.8	3650	2.01	***	1.27 ± .114	.95
10	AKDE	975	0.6	699	0.39	ns	0.99 ± .138	.88
11	GÜZO	6330	3.8	4902	2.71	***	1.19 ± .121	.93
12	FP46	10534	6.3	8201	4.53	***	1.20 ± .169	.88
13	ANCA	2371	1.4	1795	0.99	ns	1.09 ± .091	.95
14	MELL	3144	1.9	2401	1.33	ns	0.87 ± .135	.86
15	BMER	2957	1.8	2254	1.24	ns	0.98 ± .156	.85
16	DZCA	4199	2.5	3229	1.78	ns	0.53 ± .153 *	.61
17	GÜZB	6890	4.1	5341	2.95	***	0.99 ± .159	.85
18	ESKB	1167	0.7	850	0.47	ns	0.94 ± .104	.92
19	K328	719	0.4	498	0.27	ns	1.09 ± .120	.92
20	K355	5195	3.1	4011	2.21	***	1.05 ± .198	.80
21	PGÖZ	2530	1.5	1919	1.06	ns	0.88 ± .094	.93
22	KARG	5421	3.2	4188	2.31	***	0.95 ± .139	.87
23	KUML	7528	4.5	5842	3.22	***	0.63 ± .244	.49
24	KESC	7988	4.8	6203	3.42	***	0.61 ± .137 *	.74
25	SEYD	2017	1.2	1516	0.84	ns	0.77 ± .109	.88
26	AYBA	1006	0.6	723	0.40	ns	0.66 ± .167	.69
28	BAKA	1905	1.1	1429	0.79	ns	0.84 ± .101	.91
29	BIGA	1646	1.0	1226	0.68	ns	0.94 ± .079	.95
30	MKCB	1382	0.8	1018	0.56	ns	1.10 ± .092	.95
31	OELI	1604	1.0	1193	0.66	ns	0.80 ± .151	.80
32	GÖLH	1132	0.7	822	0.45	ns	0.98 ± .099	.93
33	SUKD	1253	0.7	917	0.51	ns	0.88 ± .123	.88
34	SUSÖ	4374	2.6	3366	1.86	**	0.82 ± .113	.88
35	ULUC	4265	2.5	3281	1.81	**	0.98 ± .116	.91
36	SUCA	3985	2.4	3061	1.69	**	–	–
37	YAYL	5310	3.2	4101	2.26	***	0.53 ± .207	.49
38	CETB	6423	3.8	4975	2.75	***	0.57 ± .173 **	.61
39	MYAR	3371	2.0	2579	1.42	ns	0.68 ± .220	.58
40	BOYL	4278	2.5	3291	1.82	**	0.37 ± .141 **	.50
41	SKAY	3643	2.2	2793	1.54	*	0.46 ± .111 **	.71
42	DLDE	2409	1.4	1824	1.01	ns	0.57 ± .181 *	.59
43	IOZU	3901	2.3	2995	1.65	**	0.76 ± .101 *	.89
44	CAMG	5904	3.5	4567	2.52	***	0.98 ± .115	.91
45	NIHD	5479	3.3	4234	2.34	***	0.84 ± .118	.88

R^2: Coefficient of determination;*, **, ***SHUKLA's stability F statistic and regression coefficient is significant at 0.05, 0.01 and 0.001 level, respectively; ns not significant.

High type B provenance correlations among the Aegean sites and lack of provenance-site interaction clearly showed that the Aegean region should not be divided into two sub zones. In contrast, the Aegean zone may be extended further to the north to include the southern Marmara region, because type B provenance correlations between the Aegean and the southern Marmara sites (INK and INY) were high. On the other hand, the northern Marmara region (Site KSN) had different characteristics than the southern part as indicated by low type B correlations and significant provenance-site interactions. This site was the major source of gei variance. This is expected, because KSN is located in the most northern natural occurrence of the species where early and late frosts are more common. Although INY and INK were geographically located in the Marmara region, they share more similar climatic characteristics with the Aegean region sites (*Table 2*). This is also reflected in the high type B provenance correlations between these two sites and the Aegean sites. The results suggest that the KSN site should be considered as a separate sub-zone rather than being incorporated with INY and INK sites. For the northern Marmara region, cold hardiness is probably one of the most important criteria to select genotypes. Slow growth of some low elevation Mediterranean provenances (i.e. #10, #23) may be explained by the undue effect of lower minimum temperatures they normally experience at the test site. Extreme caution should be considered when selecting provenances for the northern Marmara region. A minimum of half-rotation age of the species (25 to 30 years) should be considered before making any definite decision. Sites similar to KSN are subject to early and late frost and this site should be considered the northern extremity for Turkish red pine plantations.

The KZT site in the Southeast of Turkey (northern Mesopotamia) is characterized by long, dry, hot summers and cool, rainy winters. Soil and air humidity in the summer are the major limitations for growth. Studies on *Pinus taeda* showed that movement of seed becomes more critical near the extremities of the natural area of a species (WELLS, 1983; LAMBETH *et al.*, 1984). Significant effect of minimum temperature difference between the local source and planting location on height and survival was reported for *Pinus taeda* and *Picea abies* (SCHMIDTLING, 1994). Although high type B provenance correlations were observed between the lower elevation sites of the Mediterranean region and KZT site, seed movement to the southeastern Anatolia region should be considered cautiously until trees at this site complete at least half rotation age i.e. 25 to 30 years. Drought is the major factor limiting the growth of Turkish red pine in these two regions in contrast to the Marmara region. As Turkish red pine is not native to the region, except a local isolated stand near Siirt that is far from the site, the species needs to be handled as an 'exotic' one. Maybe development of a dry tolerant land race for the area should be considered before starting an extensive plantation and tree improvement program.

The seed transfer guidelines and outlining of the breeding zones based on climatic and geographic variables for Turkish red pine have served as a useful tool in Turkey (KOSKI and ANTOLA, 1993; ATALAY *et al.*, 1999). However, the results of this study indicated that the seed movement should not be constrained within the provisional zones. Similar results were reported for Douglas-fir (*Pseudotsuga menziesii*) in the Pacific Northwest of USA (WHITE and CHING, 1985) where genetic tests did not confirm the necessity of breeding zones in the region, in contrast, seed movement based on the parental performance and stability of the genotypes was suggested (STONECYPHER *et al.*, 1996).

Seed source movement is a very complex issue, related to geographic and climatic factors as well as to the survival and growth of the material tested for at least a half of the rotation period of the species (ZOBEL and TALBERT, 1984). In extremely diverse geography as in the Mediterranean and Aegean regions of Turkey, the problem becomes even more complex. Maybe a sample of material included in the breeding population of the species needs to be tested targeting the major plantation areas. Also, experimental studies showed that genetically heterogeneous diverse populations, such as provenances, are more stable, buffering different environments, compared to populations having a narrow genetic base (OWINO, 1977; WHITE and CHING, 1985; ZOBEL *et al.*, 1987).

Conclusions

There were significant growth differences among the provenances. Up to 55% greater height and 50% greater diameter can be realized at age of 10, if the best provenances were selected for plantations. Provenances from the fringe distribution of Turkish red pine should be avoided, but high and middle-elevation provenances of the Mediterranean region should be preferred at most sites. In general, the results did not confirm seed transfer guidelines based on climatic and geographic variables. The Aegean region did not warrant two separate sub zones. On the contrary, the region may be extended to the north including the southern Marmara region. Northern Marmara should be a separate breeding zone, where cold hardiness along with superior growth should be the selection criteria. Although there are some indications suggesting possible seed movement between the Aegean and Mediterranean regions, further research is needed to confirm our findings. Two sub-zones based on arbitrarily determined elevation gradients in the Mediterranean region are justified. Seed transfer between the low Mediterranean sites and semi-arid southeastern Turkey seems feasible. However, our findings need to be tested with long-term test results. A land race development should be considered for southeast Anatolia where severe drought is the major limitation to grow trees. Provenances were significantly different for stability variances, suggesting possibility of genotype selection for an average performance across the sites and for particular sites.

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Literature

ANDREW, I. A. and WRIGHT, H. L.: Evaluation. In: A manual on species and provenance research with particular reference to the tropics. Compiled by J. BURLEY and P. J. WOOD. Tropical Forestry Papers No: 10. Oxford Forestry Institute: 103–143 (1976). — ARBEZ, M.: Distribution, ecology and variation of *Pinus brutia* in Turkey. FAO Forest. Gen. Res. Infor. No. 3: 21–33 (1974). — ASLAN, S.: Studies on the selection of some of the best growing coniferous trees in southeastern Anatolia. Technical Bulletin No. 216, 40 pp. (Turkish with English summary) (1991). — ATALAY, I., SEZER, I. and ÇUKUR, H.: The Ecological Properties of Red Pine (*Pinus brutia* TEN.) Forests and Their Regioning in Terms of Seed Transfer. Ministry of Forestry of Turkey, Tree Seeds and Improvement Research Institute publication No. 6, 108 pp. (Turkish with English summary) (1999). — BURDON, R. D.: Genetic correlation as concept for studying genotype-environment interaction in forest tree breeding. Silvae Genetica **26**: 168–175 (1977). — CENGIZ, Y., ISIK, F., KESKIN, S., GENC, A., DODAN, B., TOSUN, S., OZPAY, Z., AKSOY, C., ORTEL, E., GURGEN, D., DAGDAS, S. and UGURLU, S.: Provenance variation in *Pinus brutia* TEN.: Fifth year results. S/W Anatolia Forest Research Institute, Technical Bulletin No. 7, Antalya, Turkey. 43 pp. (Turkish with English Summary) (1999). — CRITCHFIELD, W. B. and LITTLE jr., E. L.: Geographic Distribution of the Pines of the World. USDA Forest Service Miscellaneous publications 991, 41 pp. (1966). — EBERHART, S. A. and RUSSEL, W. A.: Stability parameters for comparing varieties. Crop Sci. **6**: 36–40 (1966). — FINLAY, K. W. and WILKINSON, G. N.: The analysis of adaptation in plant-breeding programme. Aust. J. Agric. Res. **14**: 742–754 (1963). — FISHER, T. J., NEUMANN, R.W. and MEXAL, J. G.: Performance of *Pinus halepensis/brutia* group pines in southern New Mexico. Forest Ecology and Management **16** (1–4): 403–410 (1986). — GEZER, A. and ASLAN, S.: Selection of best performing conifers in the Southwest Anatolia region. Turkish Forest Research Institute Technical Bulletin No. 100. (Turkish with English summary) (1980). — GUNAY, T. and TACUNER, Y. A.: Türkiyede Mevcut Kizilcam (*Pinus brutia* TEN.) Fidanlarinin Genel Ekolojik Özellikleri ve Üretilen Fidanlarin Fizyomorfolojik Kaliteleri. In: Proceedings of international Symp. on *Pinus brutia*. October 18 to 23, Marmaris, Turkiye: 243–253 (1993). — GURSES, K.: *Pinus brutia* TEN. provenance trials in the eastern Mediterranean region of Turkey. International Symposium on *Pinus brutia* proceedings, Ministry of Forestry of Turkey: 314–323. (Turkish with English summary) (1993). — IKTUEREN, S.: *Pinus brutia* and *Pinus halepensis* provenance trials in the eastern Mediterranean region of Turkey. Turkish Forest Research Institute Technical Bulletin no. 167, 29 pp. (Turkish with English summary) (1986). — ISIK, K.: Altitudinal variation in *Pinus brutia* TEN: Seed and seedling characteristics. Silvae Genetica **33** (2–3): 58–66 (1986). — ISIK, F.: Estimation of Genetic Variation, Heritabilities and Genetic Gain in *Pinus brutia* TEN. PhD thesis, Graduate School of Applied Sciences, Akdeniz University, Antalya, Turkey. 231 pp. (Turkish with English summary) (1998). — ISIK, K. and

KARA, N.: Altitudinal variation in *Pinus brutia* TEN. and its implication in genetic conservation and seed transfer in southern Turkey. Silvae Genetica **46**: 113–120 (1997). — ISIK, K. and ISIK, F.: Genetic variation in *Pinus brutia* in Turkey: Branching and crown traits. Silvae Genetica **48**: 293–302 (1999). — ISIK, F., ISIK, K. and LEE, S. L.: Genetic variation in *Pinus brutia* in Turkey: Growth biomass and stem quality traits. Forest Genetics **6** (2): 89–99 (1999). — KARA, N., KOROL, L., ISIK, K. and SCHILLER, G.: Genetic diversity in *Pinus brutia* TEN: Altitudinal variation. Silvae Genetica **46** (2–3): 155–161 (1997). — KAYA, Z. and ISIK, F.: The pattern of genetic variation in shoot growth of *Pinus brutia* TEN. Populations sampled from the Taurus Mountains in Turkey. Silvae Genetica **46** (2–3): 73–81 (1997). — KOSKI, V. and ANTOLA, J.: National tree breeding and seed production programme for Turkey, 1994 to 2003. 52 pp. (1993). — LAMBETH, C. C., DOUGHERTY, P. M., GLADSTONE, W. I., MCCULLOUGH, R. B. and WELLS, O. O.: Large scale planting of North Carolina loblolly pine in Arkansas and Oklahoma: A case of gain versus risk. Journal of Forestry **82** (12): 736–741 (1984). — LI, B. and MCKEAND, S. E.: Stability of loblolly pine families in the southern U.S. Silvae Genetica **38** (3–4): 96–101 (1989). — MCKEAND, S. E., LI, B., HATCHER, A. V. and WEIR, R. J.: Stability parameter estimates for stem volume for loblolly pine families growing in different regions in the southeastern United States. Forest Science **36** (1): 10–17 (1990). — NAHAL, I.: Le pin d'Alep. (*Pinus halepensis* MILL.) (The Aleppo pine). Annls. Ec. Natn. Eaux Forets **19**: 479–686 (French) (1962). — OWINO, F.: Genotype-environment interaction and genotypic stability in loblolly pine. II. Genotypic stability comparisons. Silvae Genetica **26** (1): 21–26 (1977). — PALMBERG, C.: Geographic variation and early growth in south-eastern semi-arid Australia of *Pinus halepensis* MILL. and the *P. brutia* TEN. species complex. Silvae Genetica **24** (5–6): 150–160 (1975). — ROBERTSON, A.: The sampling variance of genetic correlation coefficient. Biometrics **15**: 428–469 (1959). — SAS/STAT User's Guide: Version 6, Fourth Edition, Volume 1. Cary, NC: SAS Institute Inc. 943 pp. (1989). — SAS/STAT User's Guide: Version 6, Fourth Edition, Volume 2. Cary, NC: SAS Institute Inc. 846 pp. (1989). — SCHMIDTLING, R. C.: Use of provenance tests to predict response to climatic change: Loblolly pine and Norway spruce. Tree Physiology **14**: 805–817 (1994). — SELIK, M.: Botanical investigation on *Pinus brutia* especially in comparison with *Pinus halepensis*. Istanbul University, Faculty of Forestry Journal 8a: 161–198 (1958). — SHUKLA, G. K.: Some statistical aspects of partitioning genotype-environmental components of variability. Heredity **29**: 237–245 (1972). — SOKAL, R. R. and ROHLF, F. J.: Biometry. Third edition. W. H. Freeman and Company, New York. 887 pp. (1995). — SPENCER, D.: Dry country pines: Provenance evaluation of the *Pinus halepensis-brutia* complex in the semi-arid region of southeast Australia. Australian Forests Research **15**: 263–279 (1985.). — STONECYPHER, R. W., PIESCH, R. F., HELLAND, G. G., CHAPMAN, J. G. and RENO, H. J.: Results from genetic tests of selected parents of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) in an applied tree improvement program. Forest Science Monograph **32**, volume 42, Number 2, 35 pp. (1996). — TULUKCU, T., TUNCTANER, K. and TOPLU, F.: Investigations on comparisons of some Aleppo pine (*Pinus halepensis* MILL.) and Turkish red pine (*Pinus brutia* TEN.) origins in Marmara and Black Sea regions. Poplar and Fast Growing Exotic Forest Trees Research Institute, Izmit, Turkey. Annual Bulletin No. **23**: 1–12 (1987). — USTA, H. Z.: Yield studies in *Pinus brutia* plantations. S/W Anatolia Forest Research Institute Technical Bulletin No. 219, 138 pp. (Turkish with English Summary) (1991). — WEINSTEIN, A.: Provenance evaluation of *Pinus halepensis, P. brutia* and *P. elderica* in Israel. Forest Ecology and Management **26** (3): 215–225 (1989). — WELLS, O. O.: Southwide pine seed sources study. Loblolly pine at 25 years. Southern Journal of Applied Forestry **7** (2): 63–71 (1983). — WHITE, T. L. and CHING, K. K.: Provenance study of Douglas fir in the Pacific Northwest region. IV. Field performance at age 25 years. Silvae Genetica **34**: 84–89 (1985). — WRICKE, G.: Über eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen. Z. Planzenzucht **47**: 82–92 (1962). — ZOBEL, B. and TALBERT, J.: Applied Forest Tree Improvement. John Wiley Sons, Inc. 505 pp. (1984). — ZOBEL, B., VAN WYK, G. and STAHL, P.: Growing Exotic Forests. John Wiley Sons, Inc. 508 pp. (1987).

Linkage Maps of *Eucalyptus globulus* Using RAPD and Microsatellite Markers

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Abstract

The construction of linkage maps based on RAPD markers using an F_1 intraprovenance cross in *Eucalyptus globulus* subsp. *globulus* is reported. Twenty-one microsatellite loci originating from *E. globulus* and four other *Eucalyptus* species were added to the RAPD maps. Linkages between microsatellites previously reported for *E. grandis/E. urophylla* were found to be conserved in *E. globulus* allowing confident assignment of homology for several linkage groups between maps of these species. Homology was also identifiable between most linkage groups of the two *E. globulus* parents based on microsatellites and RAPD loci segregating from both parents. At a LOD score threshold of 4.9 the male parent has 13 linkage groups covering 1013 cM with 101 framework markers ordered at LOD 3.0. The female parent has 11 linkage groups covering 701 cM with 97 framework markers. On the female map there were more regions of segregation distortion than expected and genetic mechanisms to explain distorted segregation are discussed. Several linkages that arise between pairs of *E. globulus* linkage groups as the LOD score is reduced are supported by interspecific homologies identified using microsatellite loci.

Key words: SSR, blue gum, genomic map, genetic map, segregation distortion.

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