Altitudinal Variation in Pinus brutia Ten.: Seed and Seedling Characteristics

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Summary

A total of 60 wind-pollinated families of *Pinus brutia*, grouped into six populations from different elevations in southern Turkey, were raised in a nursery near Antalya and assessed for 16 seed and seedling characteristics. Nine traits showed significant differences among the populations, and 15 traits were significantly different among families within populations. The high elevation families germinated slowly, were low in germination percentage, and produced smaller seedlings than the middle and low elevation families. There was a general pattern of clinal variation. The altitudes of origin of parent trees explained 69 percent of variation in terminal growth and 44 percent of variation in germination percentage.

The genetic variances among the populations for germination and terminal growth characteristics were larger than both the among- and within-family variations. Most characters showed a very high percentage of within-source variation that indicates a high genetic variability within populations. The Hacibekar population from a high altitude and a somewhat interior locality appears to be the most variable population, whereas centrally located Buk population is phenotypically the least variable.

The narrow sense heritabilities estimated on a single tree basis for terminal growth (0.72) and for root collar diameter (0.30) show that a considerable portion of genetic variance is additive which suggests the possibility of rapid genetic improvement on growth characters at early ages through family and parent tree selection in *P. brutia*.

Key words: Provenance test, clinal variation, germination polymorphism, genetic variability, adaptation, heritability.

Zusammenfassung

Insgesamt wurden 60 frei abgeblühte Familien von *Pinus brutia*, die in 6 Populationen verschiedener Höhenlage aus der Südtürkei eingruppiert wurden, in einer Baumschule in der Nähe von Antalya angezogen und auf 16 Samen- und Sämlingsmerkmale hin untersucht. Bei 9 Merkmalen gab es signifikante Unterschiede zwischen den Populationen, bei 15 Merkmalen signifikante Familienunterschiede innerhalb der Populationen. Die Familien aus Hochlagen keimten nur langsam, hatten geringe Keimprozente und produzierten kleinere Sämlinge als die aus mittleren- und Tieflagen. Es gab ein klinales Variationsmuster. Die Höhenlage der Herkunft der Elternbäume erklärte 69% der Variation im Längenwachstum und 44% bei den Keimprozenten.

Die genetischen Varianzen zwischen den Populationen für die Keimungs- und Längenwachstumsmerkmale waren größer als zwischen und innerhalb von Familien. Die meisten Merkmale zeigten einen sehr hohen Prozentsatz an Variation innerhalb der Herkünfte, der anzeigt, daß innerhalb von Populationen eine hohe genetische Variabilität existiert. Die Hacibekar-Population aus einer Hochlage und eine etwas mehr im Interior gelegene Population zeigten die größte Variabilität, während die zentral gelegene Buk-Population am wenigsten variabel war.

Die Heritabilitäten im engeren Sinn, geschätzt auf Einzelbaum-Basis, für das Höhenwachstum (0.72) und den Wurzelhalsdurchmesser (0.30) zeigten, daß ein beträchtlicher Umfang der genetischen Varianz additiv ist, was die Möglichkeit einer schnellen genetischen Verbesserung der Wachstumsmerkmale in der Jugend durch Familien- und Elternselektion bei *Pinus brutia* nahelegt.

I. Introduction

Pinus brutia Ten., an eastern Mediterranean pine, is distributed mainly in southern and western Turkey with small isolated populations along the Black Sea Coast. Occasional small stands are also found in northeastern Greece, Aegean Islands, Cyprus and western Syria. In its natural range in Turkey, it usually forms pure stands from sea level up to 500 m in the North and up to 1400 m on the Taurus Mountains along the Mediterranean Sea in the South. Natural stands are found on an extremely wide range of soil types and under a variety of climatic conditions (Kayacik 1954, Selik 1958, Critchfield and Little 1966, Panetsos 1981).

The taxonomic records indicate that *P. brutia*, in addition to its variants such as *elderica*, *pithysua*, etc., is an extremely variable species (Mirov 1967, Palmberg 1975). It exhibits considerable variation both in form and growth characters in its natural range in Turkey. Trees in the coastal regions usually have forms inclusive of relatively wide and thin crowns, crooked stems, and coarse and long branches with acute angels. Trees at middle and higher elevations, however, generally have distinctly narrow, dense crowns and straight stems with small branches (Alemdag 1962, Arbez 1974). Similar variation patterns have been reported in the Aegean Islands populations (Panetsos 1981). Most of the variation seems to be a function of altitude and associated climatic factors in the region. However, some portion of this variation is of adaptive importance and seems to be under genetic control. If genetically controlled, such a variation pattern presents ample opportunities for genetic improvement of *P. brutia* in the summer-dry eastern Mediterranean basin where it plays an inportant role both as a timber and as an amenity species.

This study reports the genetic variability found in nursery growth of *P. brutia* seedlings from 60 open-pollinated parents sampled from six populations. Specific objectives of the study were to: 1) Determine patterns of genetic variation within and among families and populations, 2) describe patterns of variation in association with altitude in the region, and 3) assemble seedling material to be used in common garden experiments to be established on various elevations for future selection and breeding studies.

II. Materials and Methods

1. *Seed Collection and origin*

Two altitudinal transects extending from the Mediterranean coast to the Taurus Mountains were established, one located on the east and the other on the west side of

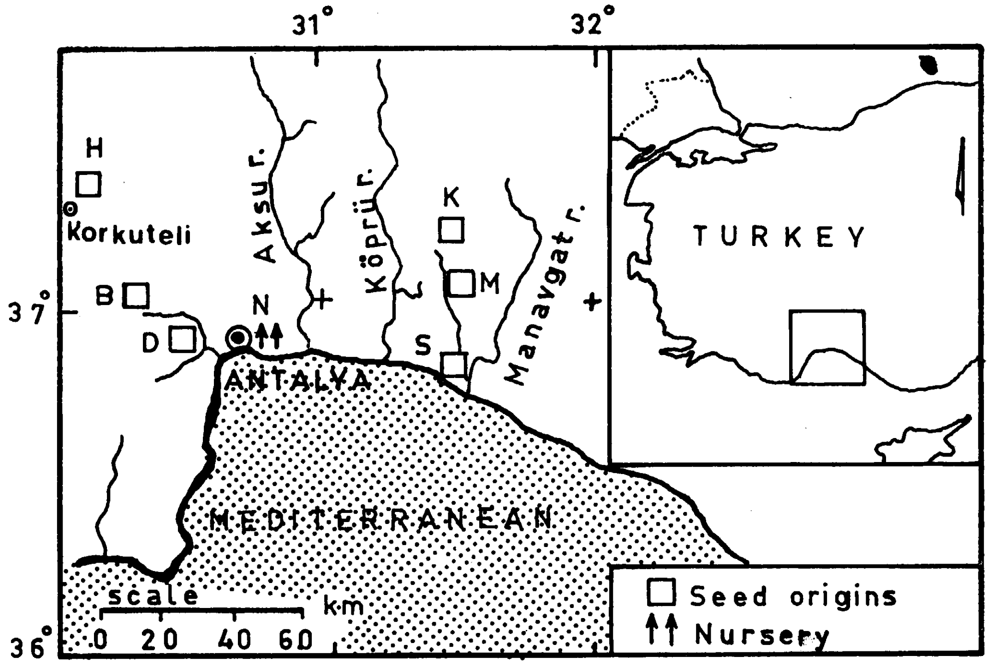

Figure 1. — Geographic locations of *Pinus brutia* population samples (D:Doyran, elev. 61 m; S:Sarilar, 92 m; B:Buk, 481 m; M:Murtbeli, 486 m; K:Kapan, 932 m; H:Hacibekar, 1033 m; N:Nursery, 40 m).

the mainly alluvial Antalya plain in southern Turkey. One coastal, one middle and one high elevation population were chosen from each transect, with corresponding populations being at comparable altitudes *(Figure 1, Table 1).* At least 10 parent trees from each population were randomly selected with at least 100 m distance between any two trees. Open pollinated cones from trees containing at least 30 to 70 cones were collected and labeled separately by tree in May and June 1977. The cones were sun dried for three weeks in August, and seeds were extracted manually, cleaned and stored at 3° C ± 1.

The established transects fall within the optimum growth range of the species' distribution (Alemdag 1962). The lowermost sites (elev. 30—100 m.) are on rolling foothills where trees are mixed with shrubby and evergreen maqui elements. Ages of seed trees ranged from 20 to 70 years and heights from 8 to 18 meters. The middle elevation sites (elev. 440—545 m.) consist of usually dense, pure stands with relatively straight trees having thinner and shorter branches. Ages of seed trees ranged from 30 to 80 years, and heights from 10 to 23 meters. The uppermiddle and

Table 1. — Geographic locations and sampling data for *Pinus brutia* elevational population samples.

Locality and Popn. Code	Avg. Elev. (m.)	Avg. Lat. (N)	Avg. Long (E)	Original Parent Trees 1)	
				Total Number	Distribution Range (ha)
Doyran D	61	36°52'	30°62'	16	250
Sarilar S	92	31°48'	31°26'	11	150
Buk B	481	36°58'	30°36'	15	250
Murtbeli M	486	37°01'	31°24'	14	200
Kapan K	932	37°06'	31°24'	14	250
Hacibekar H	1033	37°19'	30°11'	15	250

1) For location indices of individual parent trees see Isik *et al.* (1985).

higher elevation stands (750—1150 m.) form occasional mixtures with *Cedrus libani* in Kapan, and with *Pinus nigra* in Hacibekar. The parent trees ranged in age from 21 to 46 years and in height from 11 to 29 meters.

All sample populations except Hacibekar are on the south facing slopes of the Taurus ranges. The Hacibekar population is located on an inland extension of the Taurus massives, somewhat affected by steppe climate with occasional summer rains. The coastal localities are under the influence of severe summer drought (36 mm rainfall from April to Sept.) of typical Mediterranean climate with ample rain in winter (1266 mm. from Oct. to March near Antalya). Precipitation during the growing season (April—Sept.) increases as the elevation rises (36 mm on the Coast, Antalya, to 100 mm on the mountains, Korkuteli).

2. *Experimental design and nursery treatment*

The seeds were sown by family in a randomized complete block design with three replications in April, 1978. Seeds were not pretreated except soaking in tap water for 48 hours prior to sowing. Seeds from the same families were also sown on separate nursery beds to provide seedlings for outplantings.

Seedlings were grown in a Forest Service nursery near Antalya *(Figure 1).* Aside from the labelling required by the experiment, nursery production methods were used in growing the stock. These included green manuring of the nursery in the previous season, pretreatment of nursery beds with herbicide (cobex) against weed seeds, the applications of water and fertilizer, and occasional hand weeding. The roots were undercut only on the seedlings grown on beds for outplanting purposes.

3. *Characters and Measurements*

Seed Characters: To determine percent sound seed, three subsamples each of 100 seeds were taken from each seedlot and floated in water. Seeds that sunk were subjected to cutting test which showed that at least 92 percent of the seeds were full. Weights of 1000 full seeds were calculated from three subsamples each with 100 full seeds.

To determine germination percentage, the seeds were stratified for 45 days in moist and cold sand, an then placed in three replicates each with 50 seeds in Jacobsen germination chambers for a 28-day observation. Germination percentage in the nursery was determined from the nursery plots (in 3 reps, each with 80 seeds).

Seedling Characters: Number of germinating seedlings were counted twice a week, starting on the 15th day and continuing through the 71st day after sowing. The number of days was recorded to reach 50 percent germination. Where 50 percent germination was never reached, the latest observation date on which the last germination occurred was taken as the number of days until 50 percent germination.

At the completion of germination, 10 seedlings per plot (seedlot) from the outplanting nursery bed were uprooted to study the number of cotyledons and hypocotyl length.

Pinus brutia makes more than one annual growth flush and keeps growing when conditions are favorable. Thus, to determine the proportion of seedlings growing on a given date, percent seedlings with visible terminal buds were observed on two different dates: The first measurement was in early winter (Dec. 18, 1978) and the second was in mid-winter (Feb. 10, 1979) on each plot within each replication. The same observer did all terminal bud evaluations to eliminate observer bias. Percent plantable seedlings (PPS) of the seedlots was determined on Dec. 18, 1978. This date was chosen to determine PPS because it is in the middle of the *P. brutia* planting season that starts in late autumn and lasts until early spring.

Ten months after sowing, random bunches of seedlings per plot within each replication were uprooted by hand and prepared for study. Ten plants were randomly chosen to study the following seedling characters: First year terminal growth, root length, seedling diameter at root collar, fresh weight, percent water, number of lateral branchlets, percent seedlings with secondary needles, and percent seedlings having occasional three needle fascicles. Because the observed root lengths may not reflect the actual lengths, no attempt was made to analyze root/shoot ratios.

4. *Biostatistical Analyses*

Basis statistical parameters such as means, standard deviations, 95% confidence intervals, coefficients of variation, and components of variance were calculated using computer programs presented by SOKAL and ROHLF (1969). For characters based on counts (ie. Days until 50 percent germination, number of cotyledons, number of lateral branchlets), the data were first transformed into square root values to make the variances independent of means in analyses of variances (ANOVA). The arcsine (angular) transformation was applied for the characters based on percentage values. Untransformed data were used for the other characters.

A two level ANOVA model with populations fixed and families within populations random was applied for the following characters: Percent sound seed, percent germination in laboratory, percent germination in nursery, days until 50 percent germination, number of cotyledons, hypocotyl length, number of lateral branchlets, percent plantable seedlings, percent seedlings with secondary needles and percent seedlings with tertiary needles. The data were balanced with six populations, and 10 families per population. There were 10 repetitions per family for number of cotyledons, hypocotyl length and number of lateral branchlets, and three repetitions per family for the other characters.

The analysis of variance model for seedling growth characters (terminal growth, root length, root collar diameter, seedling fresh weight) are presented in *Table 2.*

Table 2. — Analyses of variance model for seedling growth of *Pinus brutia* from six localities on the elevational transects in southern Turkey.

Source of Variation	d.f.	Expected Mean Squares 1/
Replications, R	2	$V^2_w + 10\ V^2_{rf(p)} + 600\ V^2_r$
Populations, P	5	$V^2_w + 10\ V^2_{rf(p)} + 30\ V^2_{f(p)} + 100\ V_{rp} + 300\ V^2_p$
R x P	10	$V^2_w + 10\ V^2_{rf(p)} + 100\ V^2_{rp}$
Families, F(P)	54	$V^2_w + 10\ V^2_{rf(p)} + 30\ V^2_{f(p)}$
R x F(P)	108	$V^2_w + 10\ V^2_{rf(p)}$
Within Families (error)	1620	V^2_w
Total	1799	

[1]) Model $Y_{ijkl} = \mu + R_i + P_j + F_{k(j)} + Rxp_{ij} + RxF_{ik(j)} + e_{ijkl}$
where: $i = 1 \rightarrow 3$, $j = 1 \rightarrow 6$, $k = 1 \rightarrow 10$, $1 = 1 \rightarrow 10$.
In testing population variation, an approximate F test (quasi F ratio) was used as discussed in STEEL and TORRIE (1980, p. 357).

DUNCAN's Multiple Range test was used to determine specific differences among populations. A simple correlation matrix was calculated to find the degree of association between the family means of the characters assessed, and between the characters and altitude, latitude and longitude of population origin. Linear regressions were calculated between each trait and the altitude of origins.

Narrow sense heritabilities for terminal growth, root collar diameter and root length were estimated on a single tree basis by the following equation:

$$h^2 = \frac{4\ V^2_{f(p)}}{V^2_{tp}}$$

where: $V^2_{tp} = V^2_{f(p)} + V^2_{rxf(p)} + V^2_w$

Standard errors of $V^2_{f(p)}$ and heritability was computed usings the equation given by BECKER (1975, pp. 45, 68).

III. Results

1. *Correlations between characters*

Of the 120 coefficients, 48 were significant at the 5% level *(Table 3).* Some of these relationships were expected because of interdependence of some characters and others have some biological significance. Families with a high percent of sound seed had a high laboratory germination rate. Seed weight and cotyledon number, both of which are expression of embryo size, were highly correlated. Significant correlations between one thousand full seed weight and root characters (root length and root collar diameter) and between number of cotyledons and root characters were also obtained.

Germination percentage in the laboratory was significantly correlated with nursery germination, percent plantable seedlings, terminal growth and root length. Families with high germination rates were more vigorous both in terminal and root growth in the nursery. As expected, seedling growth characters (terminal growth, fresh weight, root length, and root collar diameter) were highly correlated among themselves. Hypocotyl length was significantly correlated with terminal growth in the first year.

Families with a high percentage of terminal buds in winter and with a high number of side branchlets had low water content in their seedlings. Thus, those seedlings with

Table 3. — Correlation matrix for family mean values of 16 seed and seedling characters.

Character[1]	PW	NLB	FW	RCD	RL	TG	PPS	PSBF	PSBD	HL	CN	DFPG	PGN	PGL	TFSW
PSS	.14	.14	.05	.07	.10	-.07	-.14	.34	.27	.07	.23	.23	-.22	.51	.21
TFSW	-.32	.41	.36	.25	.49	.12	.12	.28	.24	.20	.56	-.13	.05	.13	
PGL	.13	.07	.13	.11	.25	.29	.33	.13	.12	-.01	.20	-.29	.39		
PGN	.05	.15	.41	.35	.32	.69	.90	-.18	-.04	-.03	.19	-.89			
DFPG	.01	-.14	-.34	-.24	-.38	-.64	-.89	.18	-.00	-.03	-.18				
CN	-.16	.14	.30	.34	.31	.23	.21	.31	.38	.13					
HL	.04	.01	.20	.13	.22	.29	-.05	.04	.05						
PSBD	-.34	.03	.08	.09	.05	-.09	.01	.90							
PSBF	-.27	.08	-.03	-.02	-.03	-.26	-.13								
PPS	.07	.21	.43	.36	.43	.71									
TG	.05	.15	.75	.68	.47										
RL	-.23	.24	.45	.33											
RCD	-.11	.38	.90												
FW	-.20	.49													
NLB	-.33														

Critical r values: $r_{.05} = \pm 0.25$, $r_{.01} = \pm 0.33$, $r_{.001}$ ± 0.41 with d.f. = 58.

[1]) PSS: % sound seed, TFSW: 1000 full seed wt., PGL: % germination in lab., PGN = % germ. in nursery, DFPG: Days until 50% germination, CN: Cotyledon number, HL = Hypocotyl length, PSBD and PSBD: Percent seedlings with terminal buds in Dec. and Feb. respectively, PPS: Percent plantable seedlings, TG: Terminal growth, RL: Root length, RCD: Root collar diameter, FW: Fresh weight, NLB: Number of lateral branchlets, PW: percent water.

buds and lateral branchlets might have a large percentage of woody tissues (thus less water) in their structure. Families with heavy seeds tend to have a high number of lateral branchlets in the first year. It was also apparent from the correlations that seedlings with a high number of lateral branchlets were thicker at root collar and heavier than those with a low number of lateral branchlets.

2. *Variance Analyses, and Correlations Between Geographic Variables and Plant Characters*

Seed and seed related characters: These include percent sound seed, seed weight, germination percentage in laboratory and in nursery, days until 50 percent germination, number of cotyledons, hypocotyl length and percent plantable seedlings. Six of these (except percent sound seed and percent germination in laboratory) showed significant among population differences *(Table 4, Figure 2)*. Percent sound seed, although not significantly different among populations, showed a significant positive correlation with altitude of origins at the 5% level *(Table 5)*.

Populations B from middle and K from upper-middle elevations had the heaviest seeds and were different from all others in this character *(Figure 2)*. Upper-middle (Kapan) and high (Hacibekar) elevation populations had low germination in the nursery, 61 and 46 percent respectively, while germination was at least 83 percent for all other populations. The Kapan and Hacibekar populations were also slow in their germination rate. Seeds from coastal and middle elevations families germinated within 25 days after sowing, while only about 50 percent of seeds from families of Kapan and Hacibekar germinated within 36 to 39 days *(Figure 2)*. The correlation between altitude and days until fifty percent germination (DFPG) was very high (r = .66***) *(Table 5)*.

Percent plantable seedlings (PPS) at outplanting time was largely the function of percent germination in the nursery (PGN) (r = .90***). Therefore, populations that had low germination (Kapan and Hacibekar) also had the lowest number of seedlings available for outplantings.

The Hacibekar (H) population had the lowest number of cotyledons (NC) and were significantly different from all other populations *(Figure 2)*. With the expection of H, there was an increasing trend in NC with increasing elevation.

Hypocotyl length (HL) showed significant differences among populations. Seedling from the western transect (D, B, H) had longer hypocotyls *(Figure 2)*. There was a

Table 4. — Results of analyses of variance for seed and seed related characters in *Pinus brutia*.

Source of Variation	d.f.	Mean Squares of Plant Characters[1]) PSS	TFSW	PGL	PGN	DFPG	CN	HL	PS
Population, P	5	127.9^{NS}	633.6*	199.8^{NS}	3926.0***	13.29***	.368**	3.2***	2774.0***
Families, F(P)	54	114.3***	244.6***	184.9***	207.0***	0.77***	.084***	0.62***	171.0***
Within Cells	120	12.4	3.8	31.9	39.0	0.32	.022	0.13	31.0

[1]) PSS: % sound seed, TFSW: 1000 full seed wt., PGL: % germination in lab., PGN = % germ. in nursery, DFPG: Days until 50% germination, CN: Cotyledon number, HL = Hypocotyl length, PS: Percent seedlings.

NS, *, **, ***: Nonsignificant and significant at the 5, 1 and 0.1 percent levels respectively.

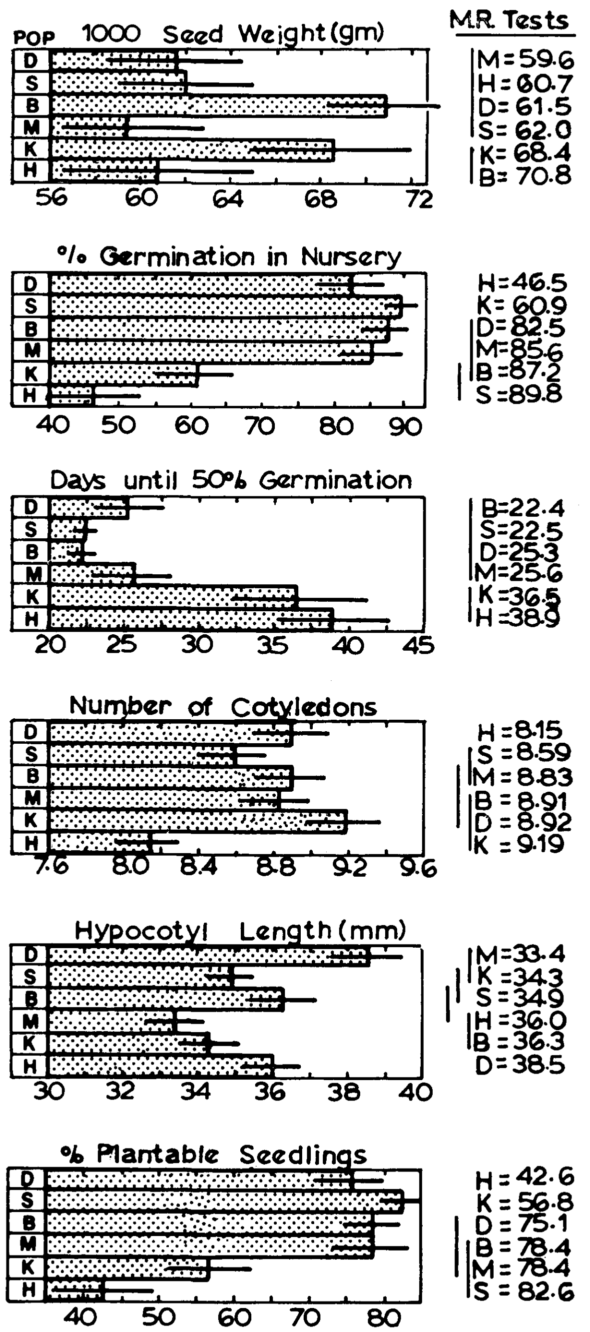

Figure 2. — Means, 95% confidence intervals (horizontal lines) and Duncan's Multiple Range Tests of differences between means of seed and seedling characters in six population samples in *Pinus brutia* (Populations covered by a vertical line on the right side of the figure are not different from each other at the 5% level. Population means are based on 100 seedlings for NC and HL, and on 30 seedlots for the other characters. D:Doyran, S:Sarilar, B: Buk, M:Murtbeli, K:Kapan, H:Hacibekar).

significant negative correlation between HL and longitude (*Table 5*).

All of the seed and seed related characters studied showed highly significant differences among families within populations (*Table 4*).

Growth Characters: Terminal growth, root collar diameter and seedlings fresh weight showed significant differences among populations (*Table 6, Figure 3*). Seedlings from coastal populations (S, D) were taller and thicker at the root collar and consequently heavier than both middle (M, B) and higher elevation (K, H) populations. Among the growth characters, terminal growth showed the highest differences among the population. All but B and M (both middle elevation populations) were different from each other (*Figure 3*). Highly significant negative relationships existed between seedling growth characters and the altitudes of origin (*Table 5*), an example of which is illustrated for terminal growth of seedlings in *Figure 4*.

Altitudes and latitudes of origin of seedlots were positively correlated (r = .93***) which results from the particular physiography of the sampling region. Consequently, plant characters that showed strong relationships with altitude also showed it with latitude (*Table 5*).

Even though differences among the populations were not significant at the 5% level, a statistically significant negative relationship existed between root length and altitude with coastal seedlots having longer roots (*Table 5*).

As for seed and seed-related characters, all growth characters showed highly significant differences among families within populations (*Table 6*). In other words, *P. brutia* exhibits great variation within stands as well as among populations.

Phenological characters: Percent seedlings with terminal buds, percent seedlings with secondary needles, percent seedlings with occasional three needle fascicles (PSTN) and number of lateral branchlets did not show significant differences among populations. However, all but PSTN were significantly different among families within populations. There were also no differences among populations in water content (PW). None of these characters were correlated with the geographic variables (Işık 1980).

3. *Variation Patterns*

Coefficients of variation (CV) for the characters that showed significant differences among populations are presented in *Figure 5*. It is apparent that all of the populations do not have similar levels of variation for a given character. For example, of the 10 characters, three (TFSW, PGN, PPS) were the most variable and two (NC, TG) were the second-most variable in population H. Similarly, two characters (DFPG, HL) were the most variable and three characters (TFSW, PGN, PPS) were the second-most variable in population K. Therefore, populations K and H from upper-middle and high elevations were the most variable populations whereas population B from middle elevation was the least variable phenotypically.

It is also evident from *Figure 5* that all characters are not equally variable within a population. For example, among the ten characters, number of cotyledons was the least, and fresh weight was the most variable characters.

The degree of similarity or dissimilarity of CV among the populations for a given character is also depicted in *Figure 5*. For instance, there is only a nine percent difference between the lowest and the highest CV for hypocotyl length whereas the difference is 76 percent for number of days until germination (DFPG). The conclusion is that the variability in hypocotyl length is the most homogeneous and the variability in DFPG is the most heterogeneous among the populations.

Estimates of variance components and relevant ratios are presented in *Table 7*. As observed, distribution of total variation among sampling levels is not the same for all characters. Greater differentiation among populations (V^2_p/V^2_g > .46) was shown for PGN, DFPG, PPS and TG than for other characters. From 46 to 57 percent of the total variation in *P. brutia* for these characters was due to differences among populations. That these four characters

Table 5. — Correlations between three geographic variables and family mean values of 15 seed and seedling characters in *Pinus brutia*.

Geogr. Variables	Plant Characters[1)] PSS	TFSW	PGL	PGN	DFPG	CN	HL	PSBD	PSBF	PPS	TG	RL	RCD	FW	NLB
Altitude	.26	.11	-.17	-.66	.66	-.09	-.22	-.00	.23	-.66	-.83	-.34	-.54	-.56	-.07
Latitude (N)	.24	-.02	-.20	-.72	.68	-.22	-.10	-.06	.16	-.71	-.79	-.36	-.58	-.58	-.17
Longitude (E)	-.08	-.16	-.06	.28	-.16	.13	-.42	.09	-.01	.29	.10	-.05	.17	.18	.14

[1)] PSS: % sound seed, TFSW: 1000 full seed wt., PGL: % germination in lab., PGN = % germ. in nursery, DFPG: Days until 50% germination, CN: Cotyledon number, HL = Hypocotyl length, PSBD and PSBD: Percent seedlings with terminal buds in Dec. and Feb. respectively. PPS: Percent plantable seedlings, TG: Terminal growth, RL: Root length, RCD: Root collar diameter, FW: Fresh weight, NLB: Number of lateral branchlets. Critical r values: $r_{.05} = \pm .25$, $r_{.01} = \pm .33$, $r_{.001} = \pm .41$ with d.f. = 58.

may have a greater adaptive value on different elevational zones can also be inferred from (between population)/(between family) ratios. Here the characters can be grouped into three rather distinct classes: Those with the largest $V^2_p/V^2_{f(p)}$ ratios (> 1.8), listed above, those with intermediate ratios (between 0.45 and 1.23) which include the growth related characters of cotyledon number, hypocotyl length, root length, root collar diameter and fresh weight, and those with least ratios (< 0.17) which represent all other characters (*Table 7*).

Three seed (PSS, TFSW, PGL) and two phenological characters (PSBD, PSBF) showed greater variation among families within populations than among other levels ($V^2_{f(p)}/V^2_g$ ratio > 0.60). Except for TFSW, these characters did not show significant differences among populations. The among family variation accounted for less than 12 percent of the total variation for the growth characters of TG, RL, RCD and FW (*Table 7*).

The highest level of within family variation was observed in root length (V^2_w/V^2_g ratio = 0.97). Other growth related characters (CN, HL, NLB, RCD and FW) also showed a high degree of within-family variation.

Heritabilities

The narrow sense heritabilities were estimated on a single tree basis on three growth characters: Terminal growth ($h^2 = 0.72 \mp 0.205$), root collar diameter ($h^2 = 0.30 \mp 0.085$) and root length ($h^2 = 0.05 \mp 0.084$).

IV. Discussion

Pinus brutia populations in southern Turkey vary genetically for nine germination and seedling characters. Elevations of the parent-trees origin accounted for the 69% of variation in terminal growth, and 44% of variation in percent germination.

Table 6. — Results of analyses of variance for growth characters in *Pinus brutia*.

Source of Variation	d.f.	Mean Squares of Characters[1)] TG	RCD	RL	FW
Replication, R	2	525.4***	13.44***	35.68NS	621.1***
Populations, P	5	3158.9***	13.82***	44.63NS	425.9***
R x P	10	73.2*	0.77NS	15.71NS	32.9NS
Families, F(P)	54	113.6***	2.00**	21.91*	67.3*
R x F(P)	108	35.8***	0.95***	18.85***	37.7***
Within Cells	1620	9.0	0.37	6.32	12.0

[1)] TG: Terminal growth, RCD: Root collar diameter, RL: Root length, FW: Fresh weight.
NS, *, **, ***: Nonsignificant and significant at the 5,1 and 0.1 percent levels respectively.

Seeds from high elevation sources germinated more slowly and had lower germination --less than 50 percent for some families--than those from other elevations. Slow germination of high elevation origins was also reported by Iktueren (1977). Low germination apparently was not due to unsound seeds, since significant positive correlations existed between altitude and percent sound seeds. In addition, there were no differences among the populations when seed germination was done under laboratory conditions. The stratification process before the laboratory tests apparently eliminated any dormancy mechanisms existing in seeds of high elevation families (Fowler and Dwight, 1964). High elevation seedlots kept germinating even after 10 months following sowing in nursery beds which further indicates that low germination was not due to unsound seeds.

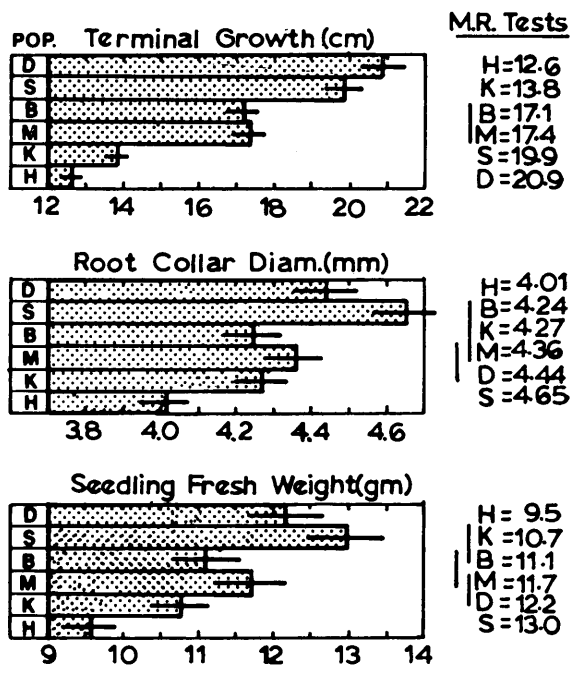

Figure 3. — Means, 95% confidence intervals (horizontal lines) and Duncan's M. R. Tests of differences between means of seedling growth characters in six population samples in *P. brutia* (Comparisons and abreviations are the same as in *Fig. 2.* Population means are based on 300 seedlings for each character).

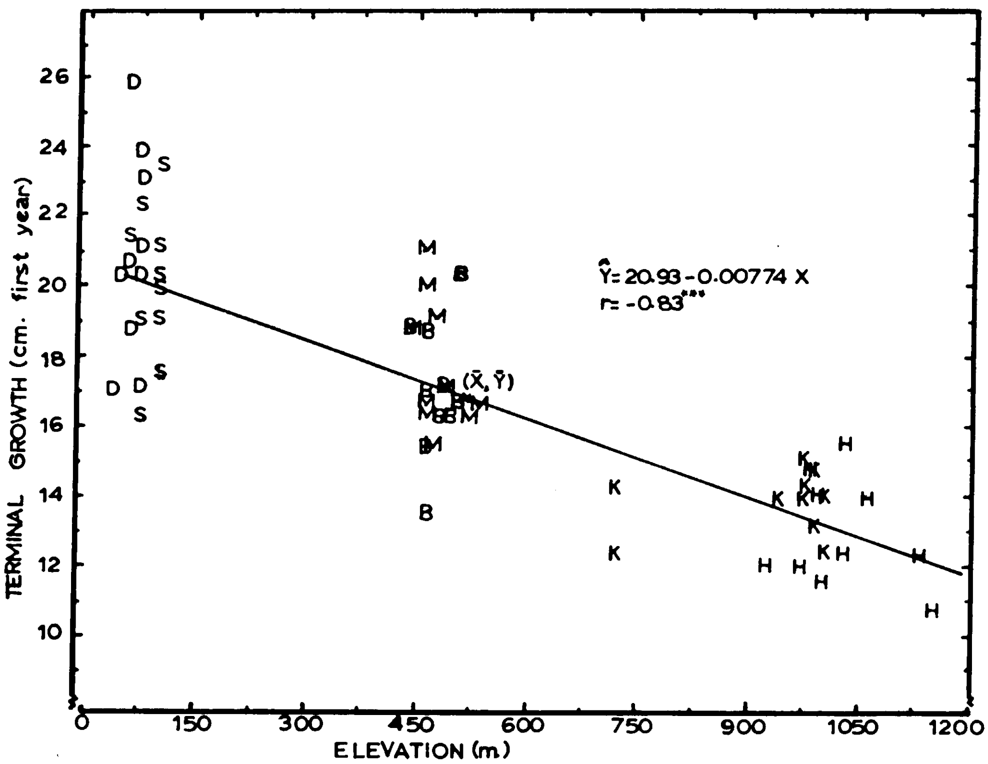

Figure 4. — Relationships between the altitudes of parent trees and terminal growth of progenies of *Pinus brutia* in first year at nursery (Letters indicate population codes; d.f. = 58).

The results suggest that populations from high elevation sources exhibit a genetic polymorphism in their germination behavior. A very low percentage of seeds germinate within 20—25 days, some seeds germinate later, while others remain dormant at least until the next growing season. This may be an opportunistic adaptative strategy in high elevation populations to take advantage of intermittent summer rains at high elevations. The seeds of *P. brutia* mature in March—May of the second year following pollination. The cones open in June—August by solar heat and seeds are disseminated, usually ready for germination under favorable conditions. In the coastal zones where severe summer droughts prevail, favorable conditions for seed germination are often lacking, but summer rains encourage seed germination at high elevations. However, because of inconsistencies in moisture availability, many seedlings die during the critical period following germination in summer. Thus, natural selection operates against early germinators at high elevation populations. Yet, not all early germinators are eliminated since there can be occasional microsites and years permitting survival of young seedlings through summer. Such a process, acting like a disruptive selection, results in germination polymorphism in high elevation populations. Koller (1964) indicates that such an adaptation mechanism is common among plant species. Studies on some forest tree species show that germination rate and germination period may change from provenance to provenance, and even from family to family within a provenance (Fowler and Dwight 1964, McLemore and Barnett 1966, Wilcox 1968, Webb and Farmer 1968, Bramlett *et al.* 1983).

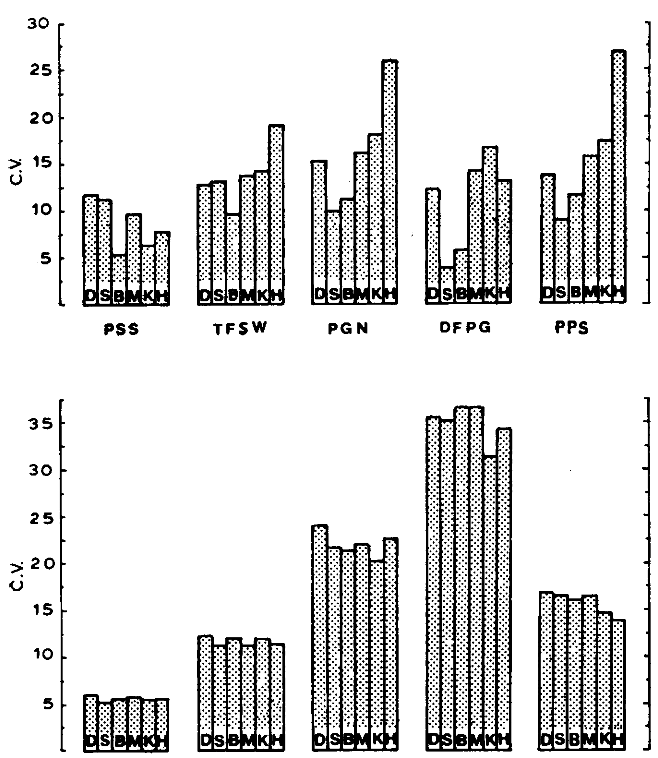

Figure 5. — Coefficients of Variation (CV) of some seed and seedling characters by populations in *Pinus brutia* (PSS: percent sound seed, TFSW: 1000 full seed wt, PGN: Percent germination in nursery, DFPG: Days until 50% germination, PPS: Percent plantable seedlings, NC:Number of cotyledons, HL:Hypocotyl length, TG: Terminal growth, FW:Fresh weight, RCD:Root collar diameter, D:Doyran, S:Sarilar, B:Buk, M:Murtbeli, K:Kapan, H:Hacibekar).

Pinus brutia seedlings exhibited decreasing growth, fresh weight and root collar diameter with an increase in the elevation of seed sources which is a common phenomenon in most forest tree species (Herman and Lavender 1968, Conkle 1973, Hamrick 1976, Madsen and Blake 1977, Campbell 1979, Harry *et al.* 1983). This strong elevational differentiation of growth characters corresponds to the cli-

Table 7. — Estimate of variances and ratios of selected variances to the total within-species variance and the between family variance[1]).

Characters[2])	V^2_p	$V^2_{f(p)}$	V^2_w	V^2_w/V^2_g	$V^2_{f(p)}/V^2_g$	V^2_p/V^2_g	$V^2_p/V^2_{f(p)}$	V^2_s/V^2_g
PSS	0.4549	33.955	12.455	.266	.724	.010	.013	.990
TFSW	12.964	80.282	3.769	.039	.827	.134	.161	.866
PGL	0.496	51.006	31.886	.382	.612	.006	.010	.994
PGN	123.97	55.974	39.057	.178	.256	.566	2.214	.434
DFPG	0.417	0.150	0.319	.360	.169	.471	2.781	.525
CN	0.0028	0.0062	0.0224	.713	.197	.090	.451	.910
HL	0.0259	0.0496	0.1333	.638	.238	.124	.523	.876
PSBD	-0.00	76.888	48.452	.384	.616	.000	.000	1.000
PSBF	12.098	101.224	55.079	.327	.601	.072	.010	.928
PPS	86.767	49.740	30.694	.187	.285	.528	1.856	.471
TG	10.027	2.592	9.037	.417	.120	.463	3.868	.537
RL	0.0862	0.102	6.3216	.917	.016	.013	.845	.987
RCD	0.0399	0.035	0.369	.831	.079	.090	1.140	.910
FW	1.211	0.987	12.057	.846	.069	.085	1.226	.915
NLB	0.0025	0.0697	0.2539	.779	.213	.008	.035	.992

[1]) V^2_w: An estimate of the variation between open-pollinated seedlings of a single tree. $V^2_{f(p)}$: an estimate of the genetic variation between open-pollinated families of the same population. V^2_p: an estimate of the genetic variation between the six populations studied.

V^2_g: Total within-species variance = $V^2_w + V^2_{f(p)} + V^2_p$.

V^2_s = within source variation = $V_w + V_{f(p)}$

[2]) PSS: % sound seed, TFSW: 1000 full seed wt., PGL: % germination in lab., PGN = % germ. in nursery, DFPG: Days until 50% germination. CN: Cotyledon number, HL = Hypocotyl length, PSBD and PSBD: Percent seedlings with terminal buds in Dec. und Feb. respectively. PPS: Percent plantable seedlings, TG: Terminal growth, RL: Root length, RCD: Root collar diameter. FW: Fresh weight, NLB: Number of lateral branchlets, PW: percent water.

matic variation pattern in the region. As elevation increases, temperature and length of growing season decrease in the study area. Such a topoclinal variation in growth characters probably results from natural selection which favors fast growing, relatively drought avoidant genotypes along the coast, and slow growing, relatively cold resistant types at higher elevations. Indeed, a significant negative correlation between altitude of seed source and root length *(Table 5)* may suggest the presence of drought avoidance in *P. brutia*. Similarly, the positive correlation (significant at the 7% level) between altitude and percentage of seedlings with a terminal bud in February (PSBF) *(Table 5)* indicates that a higher proportion of seedlings from high elevation families had terminal buds and were in dormancy, which may suggest presence of mechanisms against cold damage.

Rainfall and temperature gradients are postulated to have played an important role in the formation of clinal variation in germination and seedling growth characters in *P. brutia*. Similar adaptation strategies along altitudinal and latitudinal gradients have been suggested for several other forest tree species (Wright 1972, Rehfeldt 1983, Wells 1964, Hamrick and Libby 1972).

The west to east dimension has also been observed in one trait: eastern sources having shorter hypocotyls. Longer hypocotyls may have an adaptive significance to compete for light at the very early seedling stage. Conversely, seedlings with longer hypocotyls are more subject to such environmental hazards as predators and heat injury in summer at the soil-air interface. It is, therefore, difficult to attribute the east-west variation in hypocotyl length to any one selective environmental agent.

Variation in cotyledon number did not show any clear association with any of the geographic variables. Yet it appears that H, a somewhat interior population, has fewer cotyledons which may be the result of genetic drift or mutation in this marginal population.

The degree of variability within each population was different for a given character. For instance, in seed and seed related characters population H showed the highest coefficient of variation while population B showed the lowest. It should be noted that population H is a marginal population, somewhat isolated from the others. Population B is a middle elevation population, located within the optimum range of the species' distribution. Theoretically, population B which is centrally located, should show a higher variability than population H since it receives genes through migration from all directions (Soulé 1973). Smaller variation in the centrally located B population can be explained on the basis of developmental homeostasis as defined by Lerner (1954) and Thoday (1955). According to this concept, a given genotype in a population is balanced so that moderately constant morphology and somewhat similar adaptive phenotypes result from a variety of genotypes in a range of environmental conditions. Therefore, even though there may be a high genetic variation within population B, most of this variation might have been buffered by developmental homeostasis in this optimum distribution range of the species. On the other hand, higher, variability in population H can be associated with the germination polymorphism observed in this group. Genes responsible for the quantitative characters studied might also be selected or favored along with genes that exert polymorphism on the germination behavior of the species.

The patterns of variation exhibited by various characters were substantially different at different levels. As observed from ratios of variance components, germination and seedling growth characters showed the greatest variation among the populations *(Table 7)*. The presence of such differences among populations has probably been produced by different intensities of natural selection acting upon these traits in their natural habitats.

The characters that showed higher values of $V^2_{f(p)}/V^2_g$ ratio are the traits that may be largely under maternal influences. Indeed, three of these (percent sound seed, 1000 full seed weight, and percent germination in lab) are strongly influenced by age, general health, macro and micro habitats of the parent trees (Sefik 1965).

Almost all the characters showed very high percentage of within source variation *(Table 7,* last column). This is expected in heterogeneous environments, since heterogeneity usually leads to a greater genetic variability in a population that is adapted to that environment (LEVINS 1963, BRADSHAW 1972). Because *P. brutia* grows under a wide array of physical and biotic factors in its range, young seedlings are selected by a multiplicity of factors, both in space and time, such as heat injury in summer drought, frost and predators. Further, because the species produce a large seed supply almost every year the opportunity exists for the fitting of different genotypic combinations with various microenvironments. All these and similar other factors leads to formation of spatial as well as temporal environmental heterogeneity within any given area in the species distribution. It follows that natural selection, acting differently on different microsites, may account for within source variation, resulting in high variability within populations and within families.

The intercorrelations found among some seed and seedling characters in *P. brutia* are consistent with those of the earlier studies (PALMBERG 1975, IKTUEREN 1977). Heavier seeds have a higher number of cotyledons, and seedlings with longer hypocotyls have a taller height in the first year. Significant correlations between seed weight and root characters (root length and root collar diameter) suggest that, following the completion of germination, seedlings allocate much of their energies for root development. This hypothesis is further supported by the significant correlations between the number of cotyledons and the root characters. Seedlings at the early critical stage of their establishment depend only on cotyledons for their photosynthetic assimilates. They first have to establish a dependable root system to avoid possible drought damage in summer. Thus, relationships between number of cotyledons and root characters suggest that young seedlings might actually be growing under the soil to a considerable degree before they show any substantial epicotyl growth following germination.

Heavier seeds in *P. brutia* also had heavier seedlings with longer roots, thicker diameters at the root collar, and higher number of lateral branchlets. Although not significant, seed weight and hypocotyl length, and seed weight and terminal growth were also positively correlated. ASLAN (1975) had a detailed study on the relations between seed dimensions and seedling quality in *P. brutia*. His results also indicated that larger and heavier seeds produced better quality of seedlings.

Conclusions

1) The significant differences in growth characters of seedlings from different stands, and their close relationship to the elevations of seed origin indicate that *P. brutia* has locally adapted races, with predominantly clinal variation patterns. The narrow sense heritability estimates of growth indicate that a considerable portion of variance is additive. High additive genetic variance and large variation within seed sources offer good chances for rapid genetic improvement of *P. brutia*. For selection and breeding, the best populations should be determined first with strong emphasis on family and parent tree selection.

2) So far, only 49 stands have been determined as seed production areas and about 800 plus trees have been selected within the entire range of the species in Turkey. Most of these stands and plus trees are located within middle elevational zones (Personal comm; M. TOPAK; Institute of Forest Tree Seeds and Improvement, Ankara). Since tree improvement programs will continue for several generations, first generation work must set the stage with a broad genetic base for future studies. For this reason, and in view of the great variation found between and within populations, higher numbers of stands (and plus trees) should systematically be selected covering entire altitudinal dimensions within the georgraphic range of the species.

3) There has been a general tendency among foresters to disregard coastal populations as a seed source and as a base population for further breeding programs. This misconception arises mainly from the poor phenotypes of coastal natural stands which have been under dysgenic selection for centuries. Yet, coastal populations appear to be superior to others in their nursery performance, and still further, there are indications that they are more drought tolerant than middle and higher elevation sources. Genetic variability and possibly valuable genotypes in coastal stands have been eradicated by selective cutting, grazing, wildfires, and recently by massive conversion of forest lands for agricultural uses. Under these conditions, selection and conservation of low elevation populations appears to be especially urgent, because with each passing year the chances to select and utilize drought tolerant genotypes is rapidly diminishing. *P. brutia* appears to be one of the few pine species adapted to the summer drought of the Mediterranean basin which covers an extensive area and is potentially able to support trees. Loss of drought tolerant genotypes with desirable growth characters would thus be irreparable.

4) The study showed that *P. brutia* has strong genetic variation associated with seed source elevation. Reciprocal transplant experiments have been established on different elevations to determine further variations and possible genotype × environment interactions (ISIK *et al.* 1985). Until these studies provide information on the limits of elevational movement of planting stock, it will be necessary to restrict transfers to narrow elevational zones (ATALAY 1977).

5) High elevation populations exhibit a polymorphism in their germination behavior, possibly due to a dormancy mechanism that prevents rapid and uniform germination of seeds. However, pretreatment of seeds eliminates this dormancy. To obtain uniform germination and higher percentage of seedlings in the nursery, seeds of high elevation sources must be pretreated, preferably stratified in cold and wet sand for 45 days before sowing.

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Provenance Variation in Blue Spruce (Picea pungens) at Eight Locations in the Northern United States and Canada[1])

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Abstract

Blue spruce from 41 stands throughout the natural range were grown at eight locations in the northern United States and Canada. After eight years from seed, height and foliage color were measured at each test site, while data of bud-burst and winter injury were additionally measured at one test site in southern Michigan. The geographic variation patterns were analyzed by regression analysis. Geographic variables accounted for about 70% of the provenance variation in height, bud-burst and winter needle browning, but only about 50% for foliage color. In general, height growth decreased with increasing latitude and elevation, while winter injury declined with increasing latitude. For date of bud-burst, eastern trees were generally earlier than western trees, but the earliest trees were from southwestern Colorado, southern Arizona and New Mexico. The bluest trees originated in northern Arizona and the Colorado-New Mexico border area. Trees from north or south of this area were greener. For height, the degree of provenance differentiation appears to be less for blue spruce than for its Rocky Mountain associates.

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Key words: Geographic variation, ecotype, race, adaptation, provenance test.

Zusammenfassung

In den nördlichen USA und in Kanada wurden an 8 Standorten *Picea pungens*-Nachkommenschaften aus 41 Beständen im natürlichen Verbreitungsgebiet der Art angebaut. 8 Jahre nach der Aussaat wurden an jedem Teststandort die Höhe gemessen und die Nadelfarbe bonitiert, während die Daten für den Austrieb und die Frostschäden zusätzlich an einem Standort in Süd-Michigan aufgenommen wurden. Die geographischen Variationsmuster wurden mittels Regressionsanalyse bestimmt. Die geographischen Variablen trugen zu etwa 70% zur Herkunftsvariation bei der Höhe, dem Austrieb und dem Frostschaden und nur zu 50% bei der Nadelfarbe bei. Generell nahm das Höhenwachstum mit zunehmendem Breitengrad und mit zunehmender Höhenlage ab, während die Frostschäden mit der Zunahme des Breitengrades in Beziehung standen. Der Austriebstermin lag bei östlichen Herkünften früher als bei westlichen, aber die am frühesten austreibenden Bäume stammten aus dem südwestlichen Colorado, aus dem südlichen Arizona und aus Neumexiko. Die blauesten Bäume stammten aus dem nördlichen Arizona und aus dem Grenzgebiet zwischen Colorado und Neumexiko. Bäume nördlich oder südlich dieser Region waren grüner. Für die Höhe erschien der Grad der Herkunftsdifferenzierung für