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Genetic Variation in *Pinus brutia* Ten. in Turkey

II. Branching and Crown Traits

By K. Isik[1]) and F. Isik[2])

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Abstract

The nature and extent of variation in certain crown (crown diameter, live crown ratio, crown shape index) and branching traits (branch angles, number of growth cycles, length of the longest branch) of *Pinus brutia* Ten. were investigated in this study. The data were collected destructively by thinning a provenance-progeny trial, first at age 13 and then at age 17 years. There were six natural populations each represented by 10 open-pollinated families, and each family by 10 half-sibs in the experiment. Populations were significantly different for all the branching and crown traits. Similarly, there were significant differences among families within populations for most traits. Populations from higher altitudes showed relatively wider branch angles, shorter branches and longer and narrower crowns. Crowns get narrower ($r = -0.59$, $p<0.0001$) and longer ($r=0.45$, $p<0.0001$) with the increase of altitude of origins. Families with straighter stems had narrower crowns ($r = -0.72$, $p<0.0001$). The percent of genetic variation due to populations in crown and branching traits was considerable, ranging from 2.4% (crown diameter) to 24.5% (crown shape index). Variance components due to families were in general below 10% for each trait, showing increasing tendency with age. Individual heritabilities for the branching traits were moderately high, ranging from 0.23 to 0.53. On the other hand, heritabilities for crown traits were weak at age 13, but for crown diameter and for crown shape index were comparatively high at age 17. The results indicated that combined population, family and within-family selection for branching and crown traits would result in considerable gain in *Pinus brutia*.

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[1]) Akdeniz University, Faculty of Arts and Sciences, Dept. of Biology, 07058 Antalya, Turkey
E-mail: kani@pascal.sci.akdeniz.edu.tr

[2]) S/W Anatolia Forest Research Institute (SAFRI), Orman Araştırma Müd., PK: 264, Antalya 07002, Turkey
E-mail: fikret-isik@rocketmail.com

Key words: Pinus brutia, branching and crown traits, genetic variation, tree breeding, provenance trail, heritability.

Introduction

Most tree breeding programs have focused on growth traits such as height, diameter or stem straightness mainly due to their apparent economic importance. As the breeding programs progressed, wood quality traits, branching or crown traits have also been taken into consideration in tree improvement activities (Frampton and Rockwood, 1983; Libby, 1987; Ladrach and Lambeth, 1991; St. Clair, 1994b). These traits have major impact on stem and wood quality characteristics (St. Clair, 1994a and b). Furthermore, consideration of crown and branching traits as selection criteria in tree improvement programs could potentially increase unit-area wood production and timber value beyond that possible from genetic improvement of only growth traits (Dickmann, 1985; St. Clair, 1994a and b).

Studies on tree crown structure revealed that long narrow crowns, large number of branches per whorl, and high crown shape ratios (crown length/crown width) have increasing effects on wood production (Kuuluvainen, 1988; Cannell, 1989; McCrady and Jokela, 1996). Trees with narrow and long crowns are preferred in order to have higher stock numbers in plantations, because narrower crowns require smaller horizontal space (Kuuluvainen, 1988). Thus, crown shape is an important factor of high quantity of stem wood production in a given area. In Scots pine and Norway spruce significant relationships were detected between crown characteristics, branching and growth traits (Kuuluvainen *et al.,* 1988; Cannell, 1989; Pulkkinen and Pöykkö, 1990; McCrady and Jokela, 1996).

Branching traits too, may have major impact on stem wood quality (Vellin and Tigertstedt, 1984), particularly with respect to size and number of knots (St. Clair, 1994b). Thickness and angle of a branch might have considerable influence on the knot size. Genotypes with acute angles to the stem in general leave bigger and unregular knots, which is undesirable in terms of board quality (Raymond and Cotterill, 1990). Attention has been given to branch thickness, branch angles and uninodal traits in tree improvement programs; and breeders have exerted considerable selection for these traits (Dean *et al.,* 1986; Carson, 1987; Burdon *et al.,* 1992). For example, up to two meters long internode-knot-free genotypes are being preferred by some industry in New Zealand (Carson, 1987). In Australia, selection favoured long clear internode of *Cunninghamii,* resulting in special genotypes (Dieters *et al.,* 1990).

Crown shape and branching characteristics may also have important consequences on self-pruning, and withstanding snow and wind damage.

Previous observations in natural stands of *Pinus brutia* (Turkish red pine) showed that populations growing at lower elevations tend to have coarse branches with acute angles, wide crowns, generally crooked or twisted stems and multiple forks. Populations growing at middle and higher altitudes, however, seem to have wide-angled, thin branches, narrow-long crowns and straight stems (Arbez, 1974; Isik, 1986). To exploit the economic potential of the species, genetic parameters relevant to mature traits need to be investigated especially in common garden experiments. If the observed phenotypic differences between and within populations in natural stands are proved to be partially controlled by additive genetic effects, these traits could be used when constructing selection indices in the improvement programs of the species. In addition, it could be possible to increase per unit area volume production through „ideotype breeding" (Dickmann, 1985).

The overall goal of this study was to investigate the degree and extent of genetic variation on crown and branching traits between and within six natural populations of *P. brutia* planted in a common garden experiment. The specific objectives were (i) to estimate proportions of variation contributed by populations and families within populations, (ii) to estimate narrow sense heritabilities and (iii) to investigate degree of relationships among the traits studied, and relationships between the traits and altitude of the family origins.

Material and Methods

Genetic Material

Six populations were sampled from two altitudinal transects extending from the Mediterranean coast to the Taurus Mountains in Antalya region, in southern Turkey (*Table 1*). Two of these populations were from low, two from middle and two from high altitudes origins (*Table 1*).

Each population was represented by ten randomly-selected open pollinated families (Isik, 1986). Seedlings were raised in 1978 in Zeytinköy state nursery, near Antalya, and were transplanted to five experimental sites as 1+0 bare root seedlings in the winter of 1979 (Isik *et al.,* 1987). There were three replications at each test site, each population being represented by 10 open-pollinated families, and each family by 10 half-sib trees within each replications. This paper is based on the data destructively collected from one of the test sites located at Düzlerçami forest (altitude 350 m), 20 km north of Antalya city. The field experimental design applied on the test site was a completely randomized non-contiguous plots design with three interlocked replications (Libby and Cockerham, 1980). Excluding the border trees, the initial stocking in the experiment was 1800 trees, with 2 meters x 2 meters spacing in a hexagonal

Table 1. – Geographic information on six *P. brutia* populations included in this study[1]).

Populations	Nearest settlement (all in Turkey)	Alt. (m)	Latitude (N)	Long. (E)	No. of families
D (Doyran)	Doyran Village	61	36° 52'	30° 32'	10
S (Sarilar)	Sarilar village	92	36° 48'	31° 26'	10
B (Bük)	Bük forest Houses	481	36° 58'	30° 36'	10
M (Murtbeli)	Beydigin Village	486	37° 01'	31° 24'	10
K (Kapan)	Beydigin Village	932	37° 06'	31° 24'	10
H (H.bekar)	Hacibekar Village	1033	37° 19'	30° 11'	10

[1]) Isik (1986)

arrangement. The first thinning was performed at age 13, from November 1990 to March 1991. In the first thinning, one of the interlocked replications (initially 600 trees) was removed and 60 open pollinated families (normally 10 trees per family) were assessed. The second thinning, which removed another replication (originally composed of 600 trees), was done when the trees were at age 17 years in 1995. The statistical analysis of any single thinning was performed as a completely randomized design (i.e., no blocks), since the field layout would inherently permit such statistical handling (LIBBY and COCKERHAM, 1980).

Measurement of the Traits

Diameter at breast height (dbh, mm) and total height (HT, cm) of each tree were measured on the thinned trees. For age 13, branch angles of the largest two branches on the sixth main whorl from the tip of the tree were measured with a protractor to the nearest five degrees. For age 17, similar measurements were made on the fifth whorl from the tip. The average of measurements on two branches was taken as the mean branch angle (BA) of a given tree at a given age (*Figure 1*). It was observed during these measurements that branches originating from the younger (top) whorls had narrower angles than those originating from the older (lower) stem whorls.

P. brutia has multiple growth cycles (flushes) in a growing season. It is quite easy to distinguish each year's growth by simply observing the main whorls that form at the end of each growing season (ISIK, 1990). Numbers of flushes between any two main whorls were counted to determine the number of yearly growth cycles. The number of growth cycles of the last five or six years was averaged to find the mean number of annual growth cycles (NGC) of a tree.

Crown length (CRL, cm) was the distance from the terminal tip of a tree to the lowest live branch. Live Crown Ratio (LCR) was estimated by dividing crown length by tree height. Naturally pruned stem (NPS) part does not have any live branches. Crown diameter (CRD, cm) was taken as the diameter of the projection on the ground of the longest branch and the opposite branch of a tree (*Figure 1*). Crown Shape Index (CSI) was determined by dividing the crown diameter by crown length.

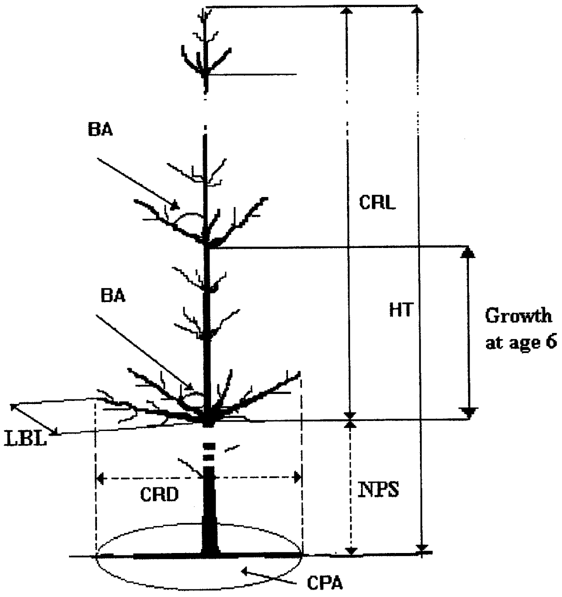

Figure 1. – Illustrations of some branching and crown traits studied (BA = Branch angle, CPA = Crown projection area, CRD = Crown diameter, CRL = Crown length, HT = Total height, LBL = Longest branch length, NPS = Naturally pruned stem length).

Statistical Analyses

The following model was used for the analyses of variance: Where :

$$Y_{ijk} = \mu + P_i + F(P)_{j(i)} + e_{ijk} \qquad \text{(EQ. 1)}$$

Y_{ijk} = Observation on the k'th tree in the j'th family, in the i'th population.

μ = Overall mean,

Table 2. – Two level nested ANOVA model and EMS equations used in the study.

Source*	d.f.	Expected Mean Squares (EMS)	F value
P_i	p-1	$\sigma_e^2 + k_2\sigma_{f(p)}^2 + k_3\sigma_p^2$	$EMS_p/EMS_{f(p)}$
$F(P)_{j(i)}$	p(f-1)	$\sigma_e^2 + k_1\sigma_{f(p)}^2$	$EMS_{f(p)}/EMS_e$
$e_{k(ij)}$	pf(n-1)	σ_e^2	

*) Populations (P) were fixed, families F (p) within populations were random in the model. σ^2_e = Error variance, $\sigma^2_{f(p)}$ = Variance due to families, σ^2_p = Variance due to populations. k_1, k_2, k_3 variance components coefficients. In this study, p = 6, f = 10, and n = Depending on the available number of sample trees ranged from 6 to 10 (harmonic mean numbers k_1 and k_2 at age 13 and at age 17 range from 7.6 to 9.3).

P_i = Effects due to the i'th population, i=1 to 6,
$F(P)_{j(i)}$ = Effects due to the j'th family, in the i'th population, j=1 to 10,
e_{ijk} = Normally and independently distributed random deviation of k'th tree, of family j, in population i, k=1 to 10.

Prior to analyses, branch angles (BA) were transformed into log values, and number of growth cycles (NGC) into square root values according to BOX *et al.* (1978). Values that lie more than three standard deviations from the experimental mean were excluded from the original data as outliers, to avoid their undue effects on the variance components (MAGNUSSEN and SORENSEN, 1991). The analyses of variance were performed using SAS programs (SAS/STAT, 1989). The variance components were estimated using SAS VARCOMP /REML procedure applying the model in *table* 2. DUNCAN's Multiple Range Tests were applied to compare populations for a given character.

Individual (narrow sense) heritability (h_i^2) was estimated after NAMKOONG *et al.* (1966):

$$h_i^2 = \frac{\sigma_A^2}{\sigma_u^2} \qquad \text{(EQ. 2)}$$

Where, $\sigma_A^2 = 4\ \sigma_{f(p)}^2$ = Total additive genetic variance, and $\sigma_u^2 = \sigma_{f(p)}^2 + \sigma_e^2$ = Phenotypic variance of the related trait. Theoretically, for open pollinated families, additive genetic variance is four times of family genetic variance component (FALCONER, 1989). Standard errors of individual heritabilities were determined according to BECKER (1984, page 46):

$$\text{SE}\ (h_i^2) = 4\sqrt{\frac{2(1-t)^2\left[1+(k-1)t\right]^2}{k(k-1)(s-1)}} \qquad \text{(EQ. 3)}$$

Where, t is the interclass correlation ($t = \sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_e^2$), k= is harmonic mean number of individuals per family, s= number of families (f=60).

Family mean heritability (h_f^2) and genetic gain (ΔG) were estimated after SHELBOURNE (1992):

$$h_f^2 = \frac{\sigma_{f(p)}^2}{\sigma_{fm}^2} \qquad \text{(EQ. 4)}$$

$$\Delta G = i_1 \frac{\sigma_{f(p)}^2}{\sigma_{fm}} + i_2 \frac{\frac{3}{4}\sigma_A^2}{\sigma_w} \qquad \text{(EQ. 5)}$$

Where,

$\sigma_{fm} = \sqrt{\sigma^2_{f(p)} + \frac{\sigma_w^2}{n}}$ = Phenotypic standard deviation of the related trait for the family means, $\sigma_w = \left(\frac{n-1}{n}\right)\ \frac{3}{4}\sigma_A^2 + \sigma_e^2$ = Within family phenotypic standard deviation.

n= The number of individuals per family.

i_1 = Selection intensity for the between family component,

i_2 = Selection intensity for the within family component.

Standard errors of family means heritabilities were estimated after ANDERSON and BANCROFT (1952):

$$\text{S.E.}\ (h_{fm}^2) = \frac{S.E.\left(\sigma_{f(p)}^2\right)}{\sigma_{fm}^2} \text{ where, S.E.}\left(\sigma_{f(p)}^2\right) = \sqrt{\frac{2}{k^2}\sum_f \frac{MS_{f(p)}^2}{df_{f(p)}+2}} \qquad \text{(EQ. 6)}$$

Where; k=Harmonic mean number of individuals per family, $df_{f(p)}$=Degrees of freedom of families within populations, $MS_{f(p)}^2$ = Mean squares of family. Simple correlation coefficients among the traits and regression analyses between altitudes of origins and certain crown and branching traits were also carried out (SOKAL and ROHLF, 1995).

Results and Discussion

Comparison of Populations and Families

Growth, biomass and bole straightness traits of populations and families are not discussed here, since these traits were examined in detail elsewhere (ISIK, F., 1998; ISIK *et al.,* 1999). Briefly, populations M and K were the best performers in their height growth and biomass formation, while population D, S (both originating from low altitudes) and H (from the highest altitude) were smaller than the test site mean. Higher altitude population K had straighter boles, whereas low altitude populations D and S had poor bole forms.

Branching Traits

Populations were significantly different for the longest branch length (LBL), number of growth cycles (NGC), and branch angles (BA) both at ages 13 and 17 years (*Table 3a*). Population D had the longest branches, whereas H had the shortest (*Table 3a*). Population M, too, had long branches. This was expected due to the larger crown and faster growth performance of this population (ISIK *et al.,* 1999). BROWN and DORAN (1985) also observed high and positive phenotypic correlations between branch length and tree size (stem diameter, height) for *Pinus attenuata.* At age 13, *P. brutia* families with longer branches tended to show better height and diameter growth performance ($r=0.62$, $p<0.001$, $r=0.74$, $p<0.001$), narrower branch angles ($r=-0.40$, $p<0.001$) and higher number of growth cycles ($r=0.48$, $p<0.001$) (*Table 4*). These relationships were also statistically significant at age 17, yet they were not as strong as at age 13 years.

Population D from the lower elevation had the narrowest branch angles, and it differed significantly from the remaining five populations at age 13 (*Table 3*). Population H from higher elevation had 3.7% and 14% greater BA than the test site mean and population D, respectively, at age 13.

Population M from the central part of the elevational distribution range of the species had the highest number of growth cycles (NGC) per year, followed by population K, both at 13 and 17 ages. M had about 9% more growth cycles than that of the test site mean, and 20% more than that of population H. On the other hand, populations D and H from perimeter of the distribution range had relatively lower number of growth cycles. YILDIRIM (1992) reported that, in both population K and M, the major portion of total height originated from the summer shoots. The differences in height growth among the populations were arose mainly due to differential number and differential cumulative height of summer shoots (YILDIRIM, 1992). Populations M and K also showed higher number of growth cycles at the age of six (ISIK *et al.,* 1987). In a separate study at the seedling stage of *Pinus brutia,* KAYA and ISIK (1997) reported that families originated from mid-elevation had more terminal shoot flushes (growth cycles) than those from both higher and lower elevation.

P. brutia exhibits "free shoot growth pattern" as described by LANNER (1976). In the free growth pattern, stem elongation occurs as a result of simultaneous initiation and elongation of new flushes. BRIDGWATER *et al.* (1985) found significant differences among six *Pinus taeda* families for number of summer shoots and their contribution to the annual height growth.

Total tree height and dbh were strongly correlated with number of growth cycles (NGC) (*Table 4*). Correlation coefficients between dbh and NGC were $r=0.77$, $p<0.001$ and $r=0.62$, $p<0.001$ at ages 13 and 17, respectively. NGC was negatively correlated with crown shape index ($r=-0.38$, $p<0.01$ to $r=-0.44$, $p<0.001$), and showed favourable phenotypic correlations with bole straightness (BST) ($r=0.43$, $p<0.001$ to $r=0.53$, $p<0.001$). Furthermore, genetic correlations between height and NGC (0.76 ± 0.10, 1.12 ± 0.00) and between diameter and NGC (0.78 ± 0.09, 0.64 ± 0.45) were relatively high both at ages 13 and 17 respectively. All these indicate that NGC trait may be considered when defining an „ideotype“ for *Pinus brutia*.

Population D from the lower altitude had longer branches and narrower branch angles, which are undesirable branching characteristics. In contrast, populations K and H from the higher altitudes showed the most desirable branching characteristics. The results at the test site showed in general that, populations originating from lower altitudes inherently have coarse and acute branches, whereas those from high altitudes have fine and wide-angled branches.

Although both populations H and K are originated from higher altitudes, they exhibited different branching and shoot growth patterns from each other. This may be attributed to the differences in geographical origins of the two populations: Population K from the eastern transect, is located on the southern slopes of the Taurus Mountains where Mediterranean climate dominates. On the other hand, population H from the western transect is somewhat isolated from the main natural distribution range of the species, and is located on a transition region between Mediterranean and continental climates where average annual rainfall is much lower (ISIK *et al.*, 1987).

In the lower distribution range of *P. brutia*, the climate is characterised by long, dry summers and relatively high temperatures (mean temperature in July 28.1°C). Middle and higher elevations above approximately 500 m from the sea level are relatively cool and receive relatively more rain during the growing season. Therefore, the slower height growth

Table 3. – Comparison of populations for certain branching and crown traits at age 13 and 17 years.

a) Branching traits

Pop	LBL#		NGC#		BA#	
	13 years $p^+<0.0013$	17 years $p^+<0.035$	13 years $p^+<0.0009$	17 years $p^+<0.0001$	13 years $p^+<0.0008$	17 years $p^+<0.0246$
D	210 a	234 a	2.87 bc	2.62 d	48.7 b	52.5 b
S	190 bc	215 b	2.92 b	2.80 c	54.8 a	55.3 a
B	183 cd	225 ab	2.93 b	2.89 bc	55.6 a	55.7 a
M	200 ab	236 a	3.20 a	3.14 a	55.8 a	55.2 a
K	179 cd	211 b	3.16 a	3.07 ab	53.8 a	52.5 b
H	174 c	208 b	2.72 c	2.60 d	56.4 a	57.1 a
overall mean	**190**	**221**	**2.99**	**2.86**	**53.9**	**54.7**

b) Crown traits

Pop	LCR#		CRD#		CSI#	
	13 years $p^+<0.0006$	17 years $p^+<0.0004$	13 years $p^+<0.0028$	17 years $p^+<0.0045$	13 years $p^+<0.0001$	17 years $p^+<0.0001$
D	0.78 bc	0.74 c	231 ab	450 a	0.57 a	0.85 a
S	0.77 c	0.76 bc	231 ab	414 b	0.56 a	0.72 b
B	0.79 ab	0.75 bc	213 bc	434 ab	0.50 b	0.70 b
M	0.80 ab	0.78 a	244 a	453 a	0.49 b	0.65 c
K	0.81 a	0.78 a	207 c	407 b	0.44 c	0.62 c
H	0.80 ab	0.78 ab	207 c	402 b	0.52 b	0.69 b
overall mean	**0.789**	**0.765**	**223**	**426**	**0.509**	**0.703**

#) LBL = Longest Branch Length (cm), NGC = Number of Growth Cycles, BA = Branch Angle, LCR = Live crown ratio (Crown length/Tree height), CRD = Crown Diameter (cm), CSI = Crown Shape Index (crown diameter/Crown length).

+) Probability levels for ANOVA tests. Population means having the same letter in a given column are not significantly different at the 5% level from each other.

performance of populations D and S could be due to adaptation to drought and less growth during the summer months (ISIK *et al.,* 1999). On the other hand, relatively slow growth of H from the higher elevation zone can be explained by avoidance from early and late frosts. This could be an adaptive shoot growth pattern that has advantages for population H in its natural habitat, where early and late frosts are common. The faster growth of M and K may be partly due to the optimal growth conditions in their natural habitats and wider genetic base. Suitable factors in the middle elevation zones might have favoured individuals who have developed a "liberal growth strategy" (ISIK *et al.,* 1987). In other words, families from the mid-altitudes were more opportunistic for utilising favourable conditions (KAYA and ISIK, 1997). Snow and wind pressure in high elevations might have acted as selective forces and favoured genotypes with thin, short and wider angled branches. In connection with this study, we observed striking differences in crown defect between seed origins after a heavy snowfall at the highest plantation site. Trees with wider crowns and coarse branches most of which originated from lower altitudes were severely damaged by the snow, whereas trees with narrower crowns were not affected. These results strongly suggest that the differences among the populations in branching traits have adaptive significance. Therefore, before suggesting any movement of population out of its natural origin, it is necessary to do investigations on genotype-environment interactions with the inclusion of these populations on wide range of sites.

Families within populations were also significantly different both at age 13 and 17 years for LBL ($P_{13}=0.0027$, $P_{17}=0.001$), NGC ($P_{13}=0.001$, $P_{17}=0.05$), and BA ($P_{13}=0.001$, $P_{17}=0.001$).

Crown Traits

Populations showed significant differences for live crown ratio (LCR), crown diameter (CRD) and crown shape index (CSI) both at 13 and 17 years (*Table 3*). Families within populations were different for CRD and CSI at age 17.

For LCR, the differences between populations were not discrete but overlapping (*Table 3*). Populations K, M and H, generally from higher altitudes, had relatively longer crowns. Lower altitude populations (D and S) showed relatively shorter crowns at age 13 years. Similar ranking of populations for live crown ratio was observed at age 17; yet the proportion of crown to total height decreased as the trees get older as a result of natural pruning of lower branches.

Population M had the largest CRD, followed by D and S (*Table 3*). Higher altitude populations H and K showed the narrowest crowns. Crown width decreased as the altitude of family origins increased (at age 13 $r=-0.40$ $p<0.001$, at age 17 $r=-0.30$ $p<0.05$).

Wider crown pattern of M is expected because of the fast growth rate of this population. Thus, comparing populations on the direct measurement of crown width might not reflect the actual crown patterns of a tree and/or a population. Therefore, we employed so-called crown shape index (CSI) value to compare populations and families (*Table 3*). Smaller CSI indicates a narrow and conical crown shape, since it is calculated by dividing crown width by crown length. Populations originating from high altitudes showed relatively narrower crowns compared to those from lower elevations (*Table 3*). The smaller the CSI the narrower the crown becomes. The crown shape index difference between the narrowest-crowned population K and widest-crowned D was much higher, and increased from 29% to 37% as the trees aged. Although M had a larger crown diameter, it had the second narrowest crown shape index when expressed in relative values. Ranking of the populations for CSI were stable by age, K and M consistently having narrowest, D and S consistently having widest crown shapes (*Table 3*). In terms of crown shape index and live crown ratio, K and M are the most, S and D are the least desirable populations.

Families with wider crowns (CRD) had relatively larger stem diameters at age 13 ($r=0.74$, $p<0.001$) and at age 17 ($r=0.62$ $p<0.001$) (*Table 4*). Families with longer crowns (LCR) tended to have straighter boles (BST) both at age 13 ($r=0.41$ $p<0.001$) and at age 17 ($r= 0.39$ $p<0.01$). At the phenotypic level, crown width was highly correlated with height and diameter ($r=0.49$ to 0.74 $p<0.001$). Strong phenotypic correlation between height

Table 4. – Estimated simple (phenotypic) correlation coefficients between the traits at age 13 (above diagonals) and 17 years (below diagonals) based on family means[1]).

Traits*	HT	dbh	BST	LBL	NGC	BA	LCR	CRD	CSI
HT	–	0.92	0.59	0.62	0.79	–0.04	0.05	0.67	–0.48
dbh	0.88	–	0.44	0.74	0.77	–0.14	–0.02	0.74	–0.31
BST	0.56	0.39	–	0.01	0.53	0.07	0.41	0.05	–0.77
LBL	0.49	0.62	–0.10	–	0.48	–0.40	–0.09	0.85	0.15
NGC	0.71	0.62	0.43	0.21	–	0.02	0.06	0.52	–0.38
BA	0.08	0.05	0.02	–0.16	0.04	–	0.11	–0.10	0.00
LCR	0.38	0.43	0.39	0.23	0.21	–0.13	–	–0.07	–0.42
CRD	0.49	0.62	–0.10	0.99	0.20	–0.18	0.22	–	0.27
CSI	–0.49	–0.27	–0.67	0.45	–0.44	–0.21	–0.41	0.46	–

[1]) Correlation coefficients are significant: $r \geq 0.25$ at 0.05, $r \geq 0.32$ at 0.01 and $r \geq 0.39$ at 0.001 levels (n = 60)

*) HT = Tree height, dbh = diameter at breast height, BST = Bole straightness (See ISIK *et al.,* 1999, for further information on these traits). See footnote in *table 3* for the full names of the other traits.

and crown diameter at age 13 ($r=0.72$ $p<0.001$) was also reported by YILDIRIM (1992).

Age to Age Correlations in Crown Traits

Age to age correlations were given in *table 5*. Families with narrower crowns at age 13, showed similar pattern at age 17 ($r= 0.56$ $p<0.001$). Similar age trends were observed for crown width ($r= 0.38$ $p<0.01$) and longest branch length (0.39 $p<0.01$). The traits BA and NGC were measured on different sets of annual shoots at different ages, with a difference of at least four subsequent years. Weak age to age correlations observed on these traits could be explained by differential growth and competition patterns among trees as they get older.

Elevational Trends in Crown Traits

Elevation of seed sources had a significant effect on tree crown form for *Pinus brutia* (*Figure 2*). It is found that, crowns get narrower ($r = -0.62$ $p<0.001$, $r= -0.56$ $p<0.001$) and longer ($r=0.47$ $p<0.001$, $r=0.43$ $p<0.001$) with the increasing altitude of origins at ages 13 and 17, respectively. Similar relationships were also observed by ISIK *et al.* (1987) at age six, and by YILDIRIM (1992) at age 13 at the same experimental site. Crown shape index was negatively correlated with bole straightness ($r= -0.67$ $p<0.001$, $r= -0.77$ $p<0.001$) at ages 13 and 17 years, respectively; meaning that narrow-crowned families tended to have straighter boles (*Figure 3*). ISIK (1998) reported positive relationships between bole straightness and altitude of family origins, implying that variation pattern in CSI and BST were similar, and changes gradually, although in opposite directions, in clinal pattern from the sea level to the higher altitudes. Narrow-crowned families, most of which originated from mid and high altitudes, also showed better stem diameter growth. Relationship between altitude and stem diameter were ($r= 0.31$ $p<0.05$) and ($r= -0.27$ $p<0.05$) ($n=60$) at ages 13 and 17 years, respectively.

Table 5. – Estimated age to age correlations for the traits ¹) (based on family means at age 13 and 17 years).

Traits*	LBL	NGC	BA	LCR	CRD	CSI
LBL	0.39					
NGC	-0.12	-0.11				
BA	-0.03	0.19	0.09			
LCR	-0.08	0.58	0.24	0.24		
CRD	0.39	0.26	-0.16	0.04	0.38	
CSI	0.36	-0.20	-0.40	-0.28	0.24	0.56

¹) Correlation coefficients are significant: $r \geq 0.25$ at 0.05, $r \geq 0.32$ at 0.01 and $r \geq 0.39$ at 0.001 levels ($n = 60$).

*) See footnote in *table 3* for the full names of the traits. BA and NGC were measured in different sets of annual shoots at different ages. See the text for the details.

When narrow-crowned families are selected for breeding, competition between neighbouring trees at plantation sites may be delayed; and plantations may be more productive per unit area of land (ST. CLAIR, 1994b). This, of course, is possible if only sufficient crown is present to ensure a large enough leaf area for photosynthesis. For example, crown projection area (CPA) of populations K and D were 3.66 m^2 and 4.81 m^2 respectively. If population K is selected for plantations, rather than D, it might be possible to have 31% more trees per hectare at age 17. In addition to that, genotypes like K were found to be allocating higher proportions of biomass to the stem rather than branches (ISIK *et al.,* 1999). These traits could also be important to increase gain per unit area, provided that population K is not maladapted to the plantation sites in question.

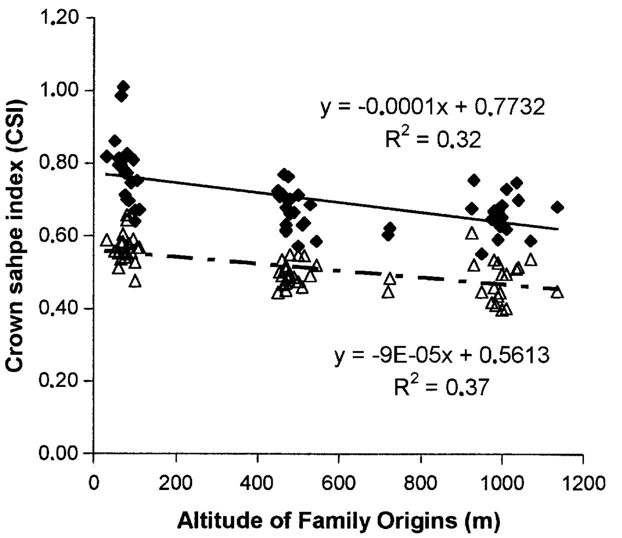

Figure 2. – Relationship between crown shape index and altitude of family origins at age 13 (dashed line) and at age 17 (solid line) based on family means ($n = 60$).

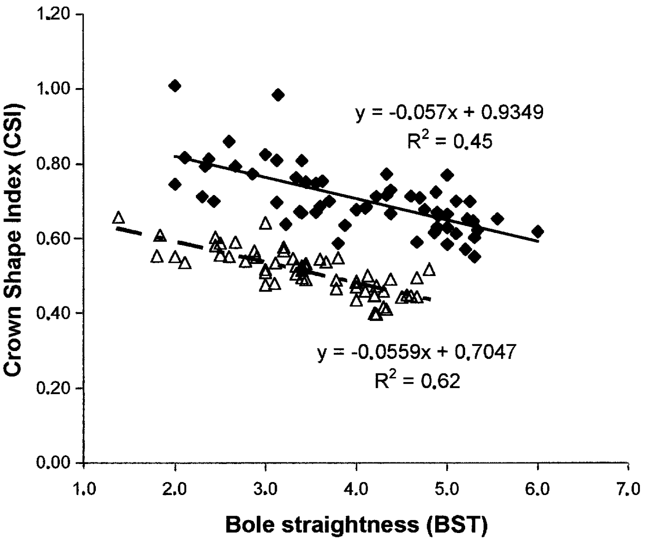

Figure 3. – Relationship between bole straightness and crown shape index at age 13 (dashed line and triangles) and at age 17 years (solid line) based on family means ($n = 60$).

Genetic Variation and Heritabilities

The distribution of variation for each trait as a proportion of total variation, individual and family heritabilities, genetic and phenotypic coefficients of variation and genetic gain were given in *table 6.*

Considerable genetic variation was detected between and within populations for branching (BA, LBL, NGC) and some crown traits (CRD, CSI) at ages 13 and 17 years, implying that, selection on population, family and within family would result in significant improvement of these traits (*Table 6*).

Genetic variation for branching traits accounted for by populations ranged from 2.7% (LBL, at age 17) to 10.2% (NGC, at age 17). Family components were in general comparatively higher and ranged from 5.1% (NGC) to 12.6% (BA) at age 17. Family variance component for NGC decreased with age, whereas, family components for LBL and BA increased *(Table* 6).

Individual heritabilities for LBL were moderately high (0.26 and 0.33), being close in magnitude, whereas, individual heritabilities for NGC (0.42 and 0.23) and BA (0.36 and 0.53) were inconsistent between ages, yet relatively higher. Individual heritability for live crown ratio (LCR) was quite low (null) in *Pinus brutia.* In contrast, ST. CLAIR (1994b) reported in Douglas-fir low heritability value for branch angle (0.06), and a moderate heritability value for live crown ratio (0.17).

For live crown ratio (LCR) 3.7% to 5.3% of total variation came from the differences between populations. The contribution of families was negligible. The family and population components of genetic variation for crown diameter (CRD) were less then 5% each at age 13, but the family component increased to 8.1% by age 17.

Crown shape index (CSI) showed a very different pattern than the above traits in terms of the distribution of the variance components: The percentage of the variance attributed to populations was consistently high, and increased from 17% to 24.5% by age. This means that in order to improve crown shape quality in tree breeding programs of Turkish red pine, major emphasis should be given to provenances, particularly at the mass selection level, provided that maladaptation is not a problem. Variance due to families for this trait accounted for only 0.4% to 3.6%. Significant genetic variation among the seed sources for crown and branching traits was also reported for *Pinus attenuate* (BROWN and DORAN, 1985).

Contrary to the branching traits mentioned above, the individual heritabilities for crown traits were weak at age 13 (*Table 6*). Since the family variance of crown traits increased with age, individual and family heritabilities correspondingly increased at age 17, being 0.33 for CRD and 0.19 for CSI. These estimates at age 17 are encouraging for selective breeding programs. Genetic gain from selection on LCR was low based on the heritabilities estimated at age 17.

Family proportion of variance for crown diameter (CRD) and crown shape index (CSI) increased as the trees aged from 13 years to 17 years (*Table 6*). This may be the result of increasing competition among families as trees of large families suppress trees of small families in mixed family stands.

High genetic variation between and within *P. brutia* populations has been observed previously by ISIK (1986), and KAYA and ISIK (1997) on various seedling traits; and by ISIK *et al.* (1999) on height, bole quality traits, biomass traits; and by YILDIRIM (1992) on shoot growth patterns. It was reported that, genetic variation between populations is clinal for height, and under strong genetic control (ISIK *et al.,* 1987; ISIK and KARA, 1997; KARA *et al.,* 1997). Our findings related to genetic variation are in agreement with these previous studies.

To compare the genetic variation of different traits at the standard level, the coefficients of additive genetic and phenotypic variation were estimated for the traits studied (CORNELIUS, 1994). The coefficients of genetic variation (CV_g) varied from 0.0% (LCR) to 14.7% (CRD, LBL). Among the traits studied, live crown ratio was the least, whereas longest branch length was the most variable trait both genetically and phenotypically. Coefficients of phenotypic and genetic variation were parallel at both ages (*Table 6*). Individual heritabilities and coefficients of genetic variation were not always parallel in magnitude. For example, heritability for branch angle was high (0.53) but the coefficient of genetic variation was one of the lowest (9.8%) among the traits (*Table 6*). On the contrary, longest branch length and crown diameter had the highest level of genetic variation (both 14.7), yet the heritabilities (0.33) were lower compared to branch angle.

Crown shape index and live crown ratio had smaller coefficient of genetic variations (*Table 6*). This may be the result of relatively high environmental influences on these traits. Low genetic variation for CSI and LCR were also reported by ST. CLAIR (1994b), and CORNELIUS (1994). It was indicated that the additive genetic coefficient of variation for growth, morphostructural and branch traits was below 15%, and the heritabilities of these traits were not in parallel with the coefficients of genetic variation (CORNELIUS, 1994).

With the exception of LCR, family mean heritabilities for the traits ranged from moderate to high. These results indicate that a considerable portion of variation originated from the genetic differences between families, which contributes mainly to additive genetic variance. Thus, it seems possible to make rapid improvement of number of growth cycles (h^2_f= 0.52, 0.34 at ages 13 and 17 years respectively), branch angle (h^2_f=0.48, 0.57), longest branch length (h^2_f =0.39, 0.44) and crown diameter (h^2_f=0.44, at age 17) by performing recurrent selection on the family level. However, selection programs for crown shape index on family level alone will not be efficient. For CSI, combined population, family and within family selection schemes needs to be applied. Particularly for crown quality traits, selection at the population level would be quite effective in order to capture gain.

Within family variation was high, generally over 80% for all the traits studied, indicating a considerable portion of variation originated from within family differences. As within family variation comprises the experimental error and the genetic differences among half sibs (NAMKOONG *et al.,* 1966), high within family variation implies a potential for within family selection, which is essential to keep the genetic base broad and maximise the genetic gain when sequential selections are applied on the breeding populations.

All the genetic parameters in this study were estimated from the data collected from only one experimental site. Therefore, the additive genetic variance contains family-environment interaction variance in the above results. For this reason, genetic parameters estimated in this study could be biased upward (NAMKOONG *et al.,* 1966; HODGE and WHITE, 1992).

Predicted Gain

Predicted genetic gains between families (Δ_1, absolute values), within families (Δ_2, absolute values) and total gain (Δ_T,%) as a percent of change in the mean for branching and crown traits were presented in *table 6.* If 10 families out of 60 and two best individuals out of 10 families were selected, the expected gain in NGC would be 8.8% of the test site mean. Predicted gain in CRD would be 14.3% at age 17 (*Table 6*, last column). Predicted gains for CSI at age 13 and for LCR at age 17 were lower, due to lower heritability values. It may be speculated that selection for crown and branching traits on combined population, family and within family levels at the initial stages of Turkish red pine breeding program would result in considerable improvement. It should also be noted that, families included in the experiment were randomly chosen trees from wild populations. If they were selected from among plus trees, gain from between family selection could have been much higher than those indicated in *table 6.*

Conclusions

There is considerable genetic variation between and within populations for branching (LBL, NGC, BA) and crown traits (CRD, LCR, CSI) in *Pinus brutia.* High genetic variation within populations for branching traits was also reflected in narrow sense heritabilities, which were moderately high, suggesting that high genetic gain could be obtained by practising selection on these traits. For crown traits, since the higher proportion of variation originated from the genetic differences among the populations, selection should be practised first at the population level and then at the family level. If selection is practised at the population level especially for crown shape index, genetic gain could be substantial. Yet, in such a selection program, higher priority should be given to height growth. The interpretations of heritabilities need to be evaluated further by analysing the data collected at later ages and from the other test sites under investigation. In conclusion, provided that better adaptation is ascertained for other tree characteristics, selection based on crown and branching traits would provide substantial genetic gains in *P. brutia* in southern Turkey. An ideotype *P. brutia* individual could be described as a fast growing tree with narrower and longer crown, smaller and wide-angled branches, straighter boles, and a tree that allocates higher proportion of biomass to its stem rather than to its branches.

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Table 6. – Certain genetic parameters for some traits in *Pinus brutia*[1]).

a) Age 13 years

Traits*	σ^2_p %	$\sigma^2_{f(p)}$ %	σ^2_e %	$h^2_i \pm$ SE	$h^2_f \pm$ SE	CV_g	CV_p	Δ_1	Δ_2	$\%\Delta_T$
LBL	5.6	6.2	88.2	0.26 ±.12	0.39 ±.20	13.5	26.5	11.7	11.1	12.1
NGC	7.4	9.7	82.9	0.42 ±.14	0.52 ±.19	12.6	19.4	0.2	0.2	13.5
BA	7.3	8.3	84.4	0.36 ±.13	0.48 ±.19	10.1	16.9	2.7	2.7	10.1
CRD	4.0	2.5	93.5	0.10 ±.10	0.19 ±.20	9.3	29.1	7.0	5.8	5.8
LCR	3.7	0.0	96.3	–[2]	–[2]	0.0	8.6	–	–	–
CSI	17.4	0.4	82.2	0.02 ±.09	0.05 ±.21	2.9	20.3	0.0025	0.002	0.9

b) Age 17 years

Traits*	σ^2_p %	$\sigma^2_{f(p)}$ %	σ^2_e %	$h^2_i \pm$ SE	$h^2_f \pm$ SE	CV_g	CV_p	Δ_1	Δ_2	$\%\Delta_T$
LBL	2.7	8.0	89.3	0.33 ±.14	0.44 ±.19	14.7	25.6	15.78	15.7	14.2
NGC	10.2	5.1	84.7	0.23 ±.12	0.34 ±.19	10.4	21.7	0.13	0.1	8.8
BA	4.0	12.6	83.4	0.53±.16	0.57 ±.19	9.8	13.5	2.87	3.1	10.7
CRD	2.4	8.1	89.5	0.33 ±.14	0.44 ±.19	14.7	25.5	30.5	30.3	14.3
LCR	5.3	0.6	94.1	0.02±.09	0.05±.19	1.4	9.2	0.002	0.0015	0.5
CSI	24.5	3.6	71.9	0.19 ±.12	0.30 ±.20	8.3	19.1	0.024	0.022	6.6

[1]) % σ^2_p = Percentage of variation due to populations, % $\sigma^2_{f(p)}$ = Percentage of variation due to families, % σ^2_e = Percentage of variation within families, $h^2_i \pm$ SE = Individual heritabilities and standard errors, $h^2_f \pm$ SE = Family means heritabilities and standard errors, CV_g = Coefficient of genetic variation, CV_p = Coefficient of phenotypic variation. Δ_1 = Predicted genetic gain between families (10 best families out of 60, $i_1 = 1.47$), Δ_2 = Predicted genetic gain within families (2 best individuals out of 10, $i_2 = 1.27$), % Δ_T = Combined between and within families genetic gain.

[2]) Heritability was not estimated for LCR at age 13, due to zero value of familiy variation in this trait.

*) See footnote in *table 3* for the full names of the traits.

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