GENETIC VARIATION IN *PINUS BRUTIA* TEN. IN TURKEY: I. GROWTH, BIOMASS AND STEM QUALITY TRAITS

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ABSTRACT

A provenance-progeny trial of *Pinus brutia* Ten. containing six populations each with ten families was thinned at ages 13 and 17 years. Certain biomass (fresh stem weight, live branch weight), growth (height, diameter) and stem quality (forking, taper, bole straightness) characters were assessed. Populations originating from mid altitudes showed better growth, exhibited more desirable bole straightness and allocated a higher proportion of biomass to the stem. The proportion of variation in most traits accounted for by genetic differences between populations and that between families were in general less than 10% each. For bole straightness, however, more than 25% of the total variation originated from the differences between populations. Narrow sense heritabilities for height (0.12) and bole straightness (0.21) varied little between ages at 13 and 17 years. Family heritability values were highly correlated with the individual heritabilities. Genetic correlations between fresh stem weight and growth traits were positive and high (0.92 with height, 0.83 with dbh) at age 13, but relatively smaller at age 17. Fresh stem weight can linearly be predicted on a single tree basis by using diameter square as an independent variable.

Keywords: *Pinus brutia*, provenance test, heritability, genetic correlation, biomass traits

INTRODUCTION

Turkish red pine (*Pinus brutia* Ten. or *Pinus brutia* subsp. *brutia* as called by some authors) is naturally distributed mainly in the Mediterranean and Aegean region of Turkey, along with east Aegean Islands, Crete in Greece, Cyprus, Syria, and northern Iraq. In recent years the species has been introduced to several other countries with Mediterranean climate, such as France, northern Africa, Israel, Australia, California, and Mexico (SELIK 1958, CHRITCHFIELD & LITTLE 1966, ARBEZ 1974, PANETSOS 1981, KARA *et al.* 1997).

The species can form closed stands from sea level up to 1200 meters above sea level, and exhibits a considerable phenotypic variation in bole straightness, branching, crown and growth traits (ARBEZ 1974, ISIK 1986). Populations growing naturally at low altitudes seem to have relatively larger and thicker branches and poorer bole straightness compared to populations growing naturally at higher altitudes. There is also significant variation in stem taper among trees growing in the natural populations of the species. If these traits are genetically controlled, then significant genetic gain could be realised using tree improvement techniques of selection and breeding.

Growth traits such as height and diameter have a great impact on wood production. If a genotype allocates a greater quantity of biomass production to branches or to foliage, rather than to stem, then, the expected harvestable return from plantations may be reduced. Furthermore, if the allocation of wood between lower and upper parts of the stem is not in balance, the percent and quality of sawlogs could be low because of taper. Biomass distribution may also affect stem wood quality. Branches with large diameter will reduce lumber grade by creating larger knots. Biomass partitioning among the elements of a tree is considered to be one of the most important components of stand productivity (CANNELL 1989); and biomass partitioning between branches, foliage and stem is amenable to change by genetic improvement and by stand management (CANNELL 1985). Wood production of trees can be increased by selection of fast growing populations and individual genotypes.

To assess the capability of genotypes in the production of the harvestable portion of the stem, the term 'Harvest Index' has been proposed. It is defined as the proportion of stem wood weight to the above

ground weight (KÄRKI & TIGERSTEDT 1985, CANNELL 1989, ST. CLAIR 1994). It was found that for *Pinus sylvestris* L., heritability of the harvest index was higher than heritability of diameter at breast height; and that the two traits were highly genetically correlated (KÄRKI & TIGERSTEDT 1985). Such information is needed for Turkish red pine as a basis for planning effective tree breeding programs.

New plant breeding concepts such as 'ideotype' and 'crop ideotypes' have been proposed in forestry in relation to yield increase per unit area (CANNELL 1978, KUULUVAINEN 1991, ST. CLAIR 1994). Such ideotypes are expected to use resources more efficiently. For example, tall, narrower crowns (with less biomass allocation to branches and foliage and greater partitioning to stem) are desirable characteristics associated with a good crop ideotype for Douglas-fir, Scots pine and Norway spruce (ST. CLAIR 1994, KÄRKI & TIGERSTEDT 1985, KUULUVAINEN *et al.* 1988, KUULUVAINEN 1988).

Provenance-progeny trials of Turkish red pine were set up in southern Turkey in 1979 (ISIK 1986, ISIK *et al.* 1987) in order to investigate the magnitude and distribution of variation within the species for various traits and to evaluate the relative performances of different populations on different sites. This particular paper is based on one of those early test sites referred to as Duzlercami, located in southern Turkey. Although a large number of traits were originally measured, only those traits associated with biomass partitioning and stem quality are presented here. Detailed results on growth, branching quality and crown traits are given elsewhere (ISIK 1998). The objectives of this particular study are (i) to estimate genetic parameters of the traits studied (ii) to investigate genetic differences between and within populations in biomass and stem quality traits, (iii) to examine biomass partitioning between different parts of the tree, (iv) to derive linear models which can predict stem biomass indirectly through employing more easily measurable traits.

MATERIAL AND METHODS

Genetic Material

The original trials were set up at different altitudes in the Mediterranean region of Turkey in 1979 (ISIK *et al.* 1987). For the trials, six natural populations were sampled from two altitudinal transects extending from the Mediterranean coast through the Taurus Mountains (Figure 1, Table 1). Two populations from low (S, D), two from middle (B, M) and two from high altitudes (K and H) were sampled (ISIK 1986). Populations S, M, and K are from eastern transects, whereas populations D, B, H are from the western transect near Antalya city.

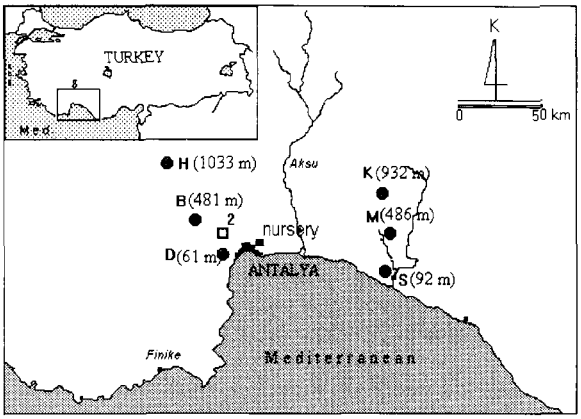

Figure 1. The location of populations (S, D, B, M, K, H) sampled, and Duzlercami test site (2) in southern Turkey.

Seedlings were raised in a state-owned forest nursery in 1978 (altitude 40 m) and were transferred to four test sites, each at different altitudes, as 1+0 bare-root seedlings in winter of 1979. The field experimental design applied on the test sites was single-tree-plot, randomised complete block design with three interlocked replications (LIBBY & COCKERHAM 1980). At each test site, each population was represented by 10 open pollinated families (parent trees), and each family

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

Populations	Nearest settlement	Altitude (m)	Latitutde (N)	Longitude (E)	No. of parent trees
S (Sarilar)	Sarilar village	92	36° 48'	31° 26'	10
D (Doyran)	Doyran village	61	36° 52'	30° 32'	10
M (Murtbeli)	Beydigin village	486	37° 01'	31° 24'	10
B (Buk)	Buk forest houses	481	36° 58'	30° 36'	10
K (Kapan)	Beydigin village	932	37° 06'	31° 24'	10
H (Hacibekar)	Hacibekar village	1033	37° 19'	30° 11'	10

[1] ISIK (1986)

by 10 trees within each replication (block). Excluding the border trees, the initial stocking was 1800 trees with 2 m. spacing between any two trees in a hexagonal arrangement. The design enabled systematic thinnings whenever competition began among the trees at later stages of development.

Data for this study came from the Duzlercami site (Site 2 on Figure 1), which is 20 km away from the coast, at an altitude of 350 m above the sea level. This site was the most fertile among the four sites, with faster growth rates and earlier canopy closure relative to the other sites. The trial at Duzlercami was first thinned at age 13 by removing one of the interlocked replications, originally consisting of 600 trees. The second thinning was carried out at age 17 years removing another replication of similar number of trees. Assessments of the traits in this study were carried out on the thinned trees.

Assessment of the traits

The following growth, biomass and stem quality traits were measured or derived:

Height (HT): Height of felled tree to the nearest cm.

Diameters over bark (DGL, dbh) and under bark (DGLu, dbhu): Diameters over and under bark were measured to the nearest mm on disks taken at 5 cm above ground level (DGL, 0.05 m) and at breast height (dbh). Two measurements at right angles to each other were done and then averaged to obtain a single value.

Bark thickness (BKGL, BK13): Half of the difference between diameter over bark and diameter under bark represented bark thickness (mm) at the relevant heights (ground level = BKGL, and breast height level = BK13).

Dead Branch Weight (DBW): Before trees were felled, dead branches were removed and weighed fresh to the nearest gram. This trait was used as a component of total biomass above the ground.

Live Branch Weight (LBW): After trees were felled, live branches on each tree were cut, and weighed to the nearest gram. This trait was also used as a component of total biomass above the ground.

Fresh weight of stem wood (FSW): Following branch removal, the stem was cross cut at breast height (1.3 m). Each section was weighed to find stem weight below 1.3 m (SW1) and stem weight above 1.3 m (SW2) to the nearest gram. The sum of the weights of these sections gave the total fresh stem weight (FSW).

Taper Index (TPR): The ratio of dbh to the diameter at ground level (DGL) was taken as a measure of stem taper at age 13 years (TPR = dbh/DGL). At age 17 years TPR was calculated as the ratio of diameter at height 3.30 m (D33) to dbh (TPR = D33/dbh). The closer the taper is to 1.0, the more cylindrical is the stem. No buttresses had been formed distinctly at ground level at either 13 or 17 years in *P. brutia*.

Forking (FRK): Forking was assessed visually. If a tree had any fork it was assessed as 1, if not 0.

Bole straightness (BST): Bole straightness was assessed visually using a 5 point score at age 13 and a 6 point score at age 17. The former scoring method requires the assessor to decide whether a tree is below or above average, and as 5 point scoring has a median number (which is 3), assessors might tend to give that number as "average" score too frequently (COTTERILL & DEAN 1990, DIETERS 1996).

Total Biomass (TB): This was estimated as the total above ground fresh weight

TB = FSW + DBW + LBW (gram).

Harvest Index (HI): Harvest index was calculated as the proportion of fresh stem weight (FSW) to the total above ground fresh weight, $HI = FSW / TB$ (ST. CLAIR 1994).

Statistical Analyses

Analysis of variance (ANOVA) was used to detect if there were any differences between populations and between families within populations. If the differences between populations were found to be significant for the traits studied at the 0.05 level on the basis of F test, then, Duncan's Multiple Range Test was used to rank the populations (SOKAL & ROHLF 1995).

The following linear model was used for the ANOVA:

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

where: Y_{ijk} = observation in the k^{th} tree in the j^{th} family in the i^{th} population; μ = overall mean; 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.

The variance components were estimated using REML (Restricted Maximum Likelihood) option in the GLM procedure of SAS (SAS/Stat, 1989) according to the equations given in Table 2. Estimation of the cross products was carried out using the MANOVA option. Then, cross products between any two traits were partitioned according to the equations given in Table 2.

The relationships between altitude of family origin and the characters studied were detected by applying standard regression analyses techniques. Regression models were derived to predict biomass traits, particularly fresh stem weight based on more easily measured characters. Maximum coefficients of determination

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

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

*) P = populations (p = 6), $F(p)$ = families within populations (f = 10), n = number of individuals observed within each family (depending on the character and the family, n ranged from 6 to 10). d.f. = degree of freedom, σ_e^2 = error variance, $\sigma_{f(p)}^2$ = variance due to families, σ_p^2 = variance due to populations. k_1, k_2, k_3, variance components' coefficients.

(R^2), and minimum error mean square were used to help in choosing the best independent variable/variables (SOKAL & ROHLF 1995).

Individual (narrow sense) heritability was estimated according to NAMKOONG *et al.* (1966):

$$h_i^2 = \frac{\sigma_A^2}{\sigma_u^2} \qquad [2]$$

where: $\sigma^2_A = 3\sigma^2_{f(p)}$ is the within population additive genetic variance and $\sigma_u^2 = \sigma^2_{f(p)} + \sigma^2_e$ is the corresponding phenotypic variance. In the absence of epistacy, theoretically additive genetic variance is considered to be four times the family genetic variance for open pollinated families (FALCONER 1989). In this study, σ^2_A is taken as three times of $\sigma^2_{f(p)}$ as a precautionary consideration, due to probability of close breeding and inbreeding within natural populations (SQUILLACE 1974, SORENSEN & WHITE 1988). Standard errors of individual heritabilities were estimated using the equation given by BECKER (1984, page 48). Heritability estimates reported in this study could be biased upwardly, because the data is based on only one site, and because the genotype-environment interaction effect that was not separated from the family component in the ANOVA model applied.

In applied tree breeding programs family mean heritability is often of great interest and was estimated according to the following formula (SHELBOURNE 1992):

$$h_{fm} = \frac{\sigma_{f(p)}^2}{\sigma_{f(p)}^2 + \sigma_e^2/n} \qquad [3]$$

where: n is the number of individuals per family. Standard errors of family mean heritabilities are estimated by applying the general formula given BECKER (1984, pages 38–39).

Variances are not independent of the scale and the mean of the respective traits (SOKAL & ROHLF 1995). Therefore, to relatively compare the genetic and phenotypic variances of the different traits, coefficients of genetic and phenotypic variation were calculated as below:

$$CV_g = \frac{\sqrt{\sigma_A^2}}{\bar{x}}100 \qquad [4]$$

$$CV_p = \frac{\sqrt{\sigma_u^2}}{\bar{x}}100 \qquad [5]$$

where: CV_g = coefficient of additive genetic variation, CV_p = coefficient of phenotypic variation of individual values, $\bar{x}$ = test mean of a character. The higher the values of CV_p and CV_g, the higher is their relative variation.

Genetic correlations were estimated according to FALCONER (1989) as follows:

$$r_g = \frac{cov_{f(x,y)}}{\sqrt{\sigma_{f(x)}^2}\sqrt{\sigma_{f(y)}^2}} \qquad [6]$$

where: r_g = genetic correlation between any two traits, $cov_{f(xy)}$ = genetic covariance of variables x and y, $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are family component genetic variances of traits x and y respectively. Standard errors of genetic correlations were estimated by the equation given by FALCONER (1989, page 317).

RESULTS AND DISCUSSION

Comparison of Populations

Growth

There were significant differences between populations and families for height (HT) and diameters (dbh, dbhu) at age both 13 and 17 years (Table 3). Mid-altitude population M (Murtbeli, 486 m) was the best performing, followed by lower-high elevation population K (Kapan, 932 m). Population M was also the best performer for HT at age six (ISIK *et al.* 1987, ISIK & KARA 1997, ISIK 1998). All mid and high altitude populations allocated a higher proportion of biomass to the stem rather than to branches than the two low-altitude populations (Table 5). The better growth performance of mid and upper mid altitude populations was explained by adaptive shoot growth patterns and 'liberal growth strategy' (LANNER 1976, ISIK *et al.* 1987, YILDIRIM 1992).

Table 3. Comparison of populations for height and diameter.

Population	Height (m)		dbh# (cm)		dbhu# (cm)	
	13 years $p^* < 0.0012$	17 years $p^* < 0.0001$	13 years $p^* < 0.02$	17 years $p^* < 0.0003$	13 years $p^* < 0.02$	17 years $p^* < 0.0002$
S	5.51 b	7.69 c	6.4 bc	9.6 b	5.5 bc	8.3 bc
D	5.30 b	7.14 d	6.3 bc	9.0 b	5.5 bc	7.7 c
B	5.52 b	8.20 b	6.1 bc	9.7 b	5.4 bc	8.6 b
M	6.25 a	8.98 a	7.5 a	11.3 a	6.6 a	9.9 a
K	5.99 a	8.45 b	6.8 ab	10.0 b	6.0 a	8.9 b
H	5.20 b	7.59 cd	5.6 c	9.0 b	5.1 c	8.1 bc
Mean	5.64	8.01	6.5	9.8	5.7	8.6

dbh = Diameter over bark at breast height, *dbhu* = Diameter under bark at breast height (1.3 m).
* Probability levels, by ANOVA tests. Population means having the same letter in a given column are not significantly different at the 5% level from each other.

Table 4. Comparison of populations for stem quality traits

Population	Taper index		Forking	BST#
	13 years; $p^* < 0.0094$	17 years; $p^* < 0.0001$	17 years; $p^* < 0.0001$	17 years; $p^* < 0.0001$
S	0.50 dc	0.67 c	0.18 a	3.0 d
D	0.51 bdc	0.68 c	0.22 a	2.8 d
B	0.52 abc	0.72 ab	0.05 b	4.6 b
M	0.55 a	0.74 a	0.03 b	4.8 b
K	0.54 ab	0.72 ab	0.03 b	5.2 a
H	0.48 d	0.71 b	0.08 b	3.9 c
Mean	0.52	0.71	0.10	4.1

BST: Bole straightness. Grading: 6 straight, 1 crooked.
* Probability levels by ANOVA tests. Population means having the same letter in a given column are not significantly different at the 5% level from each other.

Quality traits

Taper Index (TPR) is a good indicator of how well a stem deviates from a cylinder. The higher the TPR, the more cylindrical is the stem. There were significant differences between populations at age 13 years. By age 17, the magnitude of differences between the low and high altitude populations had increased (Table 4). M, K and B from mid elevations showed the most desirable TPR, whilst S and D from lower elevations had more conical stems which are less desirable for sawlogs. Families were significantly different for taper both at age 13 and 17.

There were significant differences among populations for forking behaviour (FRK) at age 17 (Table 4). *P. brutia* seems to grow with only one dominant apical shoot when it is young, i.e. until about age 10 years. As the trees get older, the upper crown grows wider, and tends to develop more than one terminal shoot, especially in the populations from lower elevations. Populations from lower altitudes (S and D) had higher FRK frequency at age 17 (Table 4), whilst the remaining four populations from mid and higher altitudes had low FRK frequency, and were very similar. The mean FRK value of S and D was six or seven times greater than K and M. This implies an important stem defect for the lower altitude populations.

Populations and families within populations differed significantly in bole straightness (BST) at age 17 (Table 4). The mid-altitude population K showed the straightest stems, followed by two other mid-elevation populations M and B (Table 4). Lower altitude populations D and S had particularly poor bole straightness with scores that were about 2 points lower than those of

Table 5. Performance of populations for bark thickness, fresh stem weight and harvest index

Population	Bark at age 17		HI		FSW (kg)	
	BKGL# (mm) $p^* < 0.0023$	RBA# (%) $p^* < 0.0001$	13 years $p^* < 0.1887$	17 years $p^* < 0.0009$	13 years $p^* < 0.011$	17 years $p^* < 0.0001$
S	24.2 a	0.52 a	.607 a	.844 bc	21.7 bc	34.4 bc
D	20.8 b	0.50 ab	.604 a	.836 c	19.7 bc	27.9 c
B	20.7 b	0.47 cd	.616 a	.866 a	19.9 bc	34.6 bc
M	23.6 a	0.47 cd	.615 a	.864 a	28.0 a	48.3 a
K	20.2 b	0.46 d	.628 a	.869 a	24.1 ab	37.3 b
H	21.1 b	0.49 bc	.609 a	.860 ab	16.7 c	29.6 bc
Mean	21.8	0.48	.610	.860	21.8	35.5

BKGL = bark thickness at ground level (mm), RBA = relative bark basal area at ground level (Bark area / Total basal area), HI = harvest index, FSW = fresh stem weight.

* Probability levels by ANOVA tests. Population means having the same letter in a given column are not significantly different from each other.

the better populations' score.

The forking and crooked-stem-form tendency of lower altitude populations was explained as an adaptation mechanism to compete with the dense maqui (woody) shrubs within the immediate surroundings of *P. brutia* at younger stages of their development (ISIK *et al.* 1987). At lower altitudes, intense competition between trees at their younger stages and neighbouring maqui (woody) shrubs for light and moisture could have favoured trees with wider crowns. Disgenic selection might have also contributed to higher frequency of forking and crookedness at lower elevation populations of the species (ISIK *et al.* 1998). Selection of straight trees for harvest in lower altitudes, which have been easily accessible by man for millennia (WISSMANN 1972, RUNNELS 1995), might have altered the genetic composition of lower altitude populations toward genotypes with higher frequency of forking. Similar case has been also observed on *Pinus massoniana* in China (C.J.A. Shelbourne pers. comm.).

Bark Thickness

Bark thickness at ground level (BKGL) differed among and within populations at age 17 (Table 5). Populations S and M had the thickest bark, while the four remaining populations with relatively thinner barks did not differ from each other. Bark thickness at breast height also showed similar trends as bark thickness at ground level.

In general, trees with faster growth rate also had relatively thick barks (Table 8-A). Therefore, comparing populations by bark thickness alone, may not be an acceptable criteria for certain purposes. In that case, one must consider the relative bark basal area (RBA) within the cross section of the stem. For example, although population M had the second thickest bark, it had a relatively low bark percentage (Table 5). When populations were ranked for RBA at ground level at age 17, population S and D from low elevations ranked first and second. Bark thickness at ground level decreased as the altitude of family origin increased ($r = -0.36$, $p < 0.01$ at 13 years, $r = -0.29$, $p < 0.05$ at 17 years). Relatively thicker barks in low-elevation populations might have an adaptive advantage to avoid frequent forest fires, especially ground fires, during the long dry summers in this part of the Mediterranean region.

Biomass traits

Harvest Index (HI), which is the proportion of fresh stem weight to the total above ground biomass is of major importance among the biomass traits. The higher it is, the larger the allocation of photosynthetic products to the stem. Populations did not differ for HI at age 13, but by age 17 years, mid-altitude populations K, M and B had significantly better HI than lower-altitude populations S and D. HI ranged from 84 % (D) to 87 % (K) at age 17 (Table 5). On the average, the proportion of biomass accumulated in the stem (HI) was 61 % at age 13, and 86 % at age 17 which indicates progressive decline of the formation of new branches as the tree gets older in *P. brutia*. According to these results, mid elevation populations K, M and B are more efficient in allocating biomass to the stem than the others. Harvest Index of low-altitude populations D and S were below the test site mean, allocating relatively higher biomass to branches and needles.

Table 6. Derived models to predict fresh stem weight (FSW) and harvest index (HI) using height and diameter as independent variables.

Age	Models+	R^2	Probability	N*
13	$FSW = 0.6483 + 0.004257\ dbh^2$	0.96	<0.0001	547
	$HI = 0.5089 - 0.001614\ dbh + 0.000042\ HT$	0.18	<0.0001	547
17	$FSW = -17.77 + 0.27274\ dbh^2 + 0.03052\ HT$	0.88	<0.0001	523
	$HI = 0.76 + 0.00991\ dbh$	0.30	<0.0001	523
	$HI = 0.83429 + (8.7859E{-}5)\ Alt - (5.597E{-}8)\ Alt^2$	0.31	<0.0001	60
	$HI = 0.784307 + (2.726E{-}5)\ Alt$	0.23	<0.0001	60

+ HT = height, dbh = diameter over bark at breast height, Alt = altitude, HI = harvest index,
* N = number of observations used in regression analysis.

When the absolute value of Fresh Stem Weight (FSW) was considered, the differences between popu lations were more obvious. M exhibited the largest FSW (48 kg), while D had the lowest (28 kg) at age 17. On the average, M accumulated 60 % more biomass on stem than D.

Harvest Index was highly correlated with height (r_p = 0.60, $p < 0.001$) and diameter at breast height (r_p = 0.55, $p < 0.001$) at age 17 (Table 8-B). Trees with high stem quality (better straightness) were associated with higher *HI* and higher *FSW*. For example, *HI* was correlated with bole straightness (*BST*) (r_p = 0.41, $p <$ 0.001) at age 17. Correlation coefficients between *FSW* and growth traits (*dbh* and *HT*) were high and positive, ranging from r_p = 0.80 to r_p = 0.94 at both ages. Due to the practical difficulties in weighing oven-dry biomass, the relationships between fresh weights and dry weights were not investigated. However, it may be interesting to note that for a 16 year old progeny trial of Scots pine, strong correlation was detected between stem fresh weight and air dry weight in family ranking (VELLING & TIGERSTEDT 1984).

Since biomass traits (*FSW, HI,* Live Branch Weight) are time consuming and quite expensive to measure, we attempted to derive some models to predict certain biomass traits using easily measurable growth traits such as height and diameter (Table 6). The predictive power of models were evaluated by the size of the coefficients of determination (R^2) (SOKAL & ROHLF 1995).

The relationship between *FSW* and dbh^2 at age 13 years was significantly linear (Figure 2), and the proposed equation best explained the variation in FSW (R^2 = 0.96) (Table 6). The other prediction models on *FSW* and *HI* are presented in Table 6 at ages 13 and 17 years.

A positive relationship r = 0.48, p<0.001) was found between *HI* and the altitudes of family origin at age 17. Families from higher altitudes tend to allocate more biomass to stem than to the other parts of a tree. The linear model constructed for *HI* and altitude of family origin explained 23% of variation. A curvilinear model seems to fit better than the linear model, R^2 being 0.31 (Table 6).

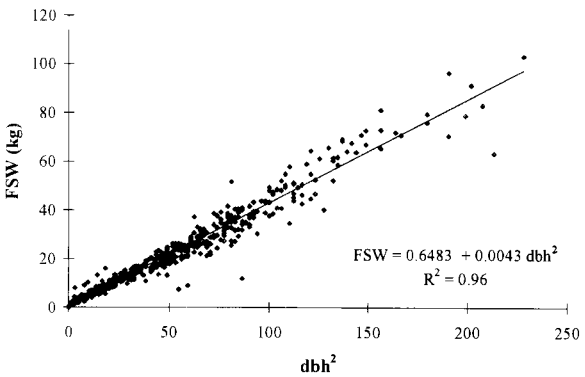

Figure 2. The relationship between diameter square (independent variable) and Fresh Stem Weight (FSW, response variable) at age 13 (N = 547).

Distribution of variation and heritabilities

For each entry in the ANOVA model the variance components as a proportion of the total variation, heritabilities, coefficients of phenotypic and genetic variation are shown in Table 7-A and 7-B for each trait.

The proportion of variation due to populations and families was less than 10% for all the traits studied, with the only exception of bole straightness (BST). Variances within families were in general over 86% of the total variance, again except for BST. Among-population-variance components generally increased with age, while among family variance components decreased substantially (Table 7). Similar age dependency trends were also reported by ISIK *et al.* (1995) on *Picea abies*. Reduced between-family-variances were

Table 7. Genetic parameters for some traits in *Pinus brutia*.

Traits*	Genetic parameters*						
	σ^2_P (%)	$\sigma^2_{f(p)}$ (%)	σ^2_e (%)	$h^2_i \pm$ s.e.	$h^2_f \pm$ s.e.	CV_g	CV_p
13 years							
HT	5.2	3.8	91.0	0.12 ±.081	0.28 ±.20	9.6	27.5
dbh	3.2	6.8	90.0	0.21 ±.093	0.41 ±.19	20.2	43.8
dbhu	3.0	5.3	91.7	0.16 ±.087	0.35 ±.19	17.4	43.1
BK13	3.3	5.4	91.3	0.17 ±.087	0.35 ±.19	28.9	70.9
BKGL	6.7	6.6	86.7	0.21 ±.093	0.41 ±.19	15.0	32.6
FRK	0.0	4.8	95.2	0.14 ±.084	0.31 ±.20	103.3	273.6
BST	24.2	5.4	70.4	0.21 ±.093	0.41 ±.19	16.0	34.7
TPR	4.1	8.0	87.9	0.25 ±.098	0.45 ±.19	9.8	19.5
FSW	3.3	4.9	91.8	0.15 ±.086	0.33 ±.19	31.3	80.1
17 years							
HT	12.0	3.2	84.8	0.11 ±.084	0.25 ±.19	7.1	21.5
dbh	5.4	1.8	92.8	0.06 ±.077	0.15 ±.19	7.9	32.7
dbhu	6.1	2.7	91.2	0.09 ±.081	0.20 ±.19	9.2	31.7
BK13	3.4	1.4	95.2	0.04 ±.074	0.11 ±.20	12.5	60.5
BKGL	5.7	7.8	86.5	0.25 ±.104	0.44 ±.19	14.1	28.4
FRK	6.2	1.9	91.9	0.06 ±.077	0.16 ±.19	73.7	295.9
BST	39.5	4.3	56.2	0.21 ±.099	0.40 ±.19	14.0	30.2
*TPR***	8.8	0.0	91.2	–	–	–	11.7
FSW	7.2	2.1	90.7	0.07 ±.078	0.17 ±.19	17.5	67.7

* *HT* = height, *dbh* = diameter with bark at breast height, *dbhu* = diameter under bark at breast height *BK13* = bark thickness at breast height, *BKGL* = bark thickness at ground level, *FRK* = forkness, *BST* = bole straightness, *TPR* = taper, *FSW* = fresh stem weight. % σ^2_p = percentage of variation due to populations, % $\sigma^2_{f(p)}$ = ercentage of variation due to families within populations, % σ^2_e = percentage of variation within families. h^2_i " SE = individual heritabilities and standard errors. h^2_f " SE = Family mean heritabilities and standard errors. CV_g = coefficient of genetic variation, CV_p = coefficient of phenotypic variation.

** heritabilities were not estimated for TPR at age 17, due to zero value of family variation.

reflected in lower heritability estimates at age 17 years. Within family variance components remained fairly constant from age 13 to 17 years. The distribution of variation in BST was clearly different, showing higher percentage attributed to the genetic differences among populations, i.e. 24.2% and 39.5% of the total variation at ages 13 and 17 years respectively. Hence, it will be quite effective to improve bole straightness by selecting the best populations alone.

Individual heritabilities for height (*HT*) (h^2_i = 0.12, h^2_i = 0.11) were moderate and remained constant from age 13 to 17 years (Table 7). These heritability values were consistent with that (*i.e.* h^2_i = 0.10) presented in ISIK *et al.* (1987), which was estimated using 6 year old data; and with that presented by PANETSOS (1981) on 7 year-old seedlings (*i.e.* h^2_i = 0.17). Heritabilities for diameter over bark (*dbh*) (h^2_i = 0.21) and diameter under bark (*dbhu*) (h^2_i = 0.16) were moderate at years 13. But, since the family variance decreased with age, heritability estimates for diameter at age 17 were correspondingly reduced (h^2_i = 0.06 and h^2_i = 0.09). Similar age trends were also observed for coefficients of genetic and phenotypic variation (Table 7).

Heritability for forking was low (h^2_i = 0.14 and h^2_i = 0.06 at ages 13 and 17), but for bole straightness (BST) and taper index (TPR) were moderate (h^2_i = 0.21 for BST, and h^2_i = 0.25 for TPR) at age of 13 years. Due to lack of significant among family variation, heritability for TPR was not estimated at age 17.

Bark thickness at breast height (BK13) and FSW showed moderate heritabilities (0.17 and 0.15) at age 13, but by age 17, these were reduced to 0.04 and 0.07 respectively (Table 7). Heritabilities were not estimated for derived traits due to various disadvantages (CARSON 1986 as cited in DIETERS 1996, COTTERILL & DEAN 1990).

Family mean heritabilities for all the traits were higher than individual heritabilities, and they usually

showed parallel changes.

Aside from forking, which was assessed on a present or absent basis, Fresh Stem Weight (FSW) was genetically (CV_g) and phenotypically (CV_p) the most variable trait studied (Table 7). Height and taper were the least variable traits at both ages, whilst diameters were more moderately variable. There was no significant relationship between CV_g and heritabilities (Table 7). CORNELIUS (1994) also reported that higher coefficients of additive genetic variation might not be reflected in higher heritabilities.

When these estimates are compared with published estimates for other pines, heritabilities reported in this study seem to be within the expected range of earlier estimates (ZOBEL & TALBERT 1984, COTTERILL & DEAN 1990, CORNELIUS 1994). Additive genetic variation and heritabilities decreased with age for the characters in *Pinus brutia*. This age trend for Turkish red pine is similar to the most of the heritabilities for conifers reported in the literature (BIROT & CHRISTOPHE 1983, DEAN *et al.* 1986, HODGE & WHITE 1992). The change in genetic parameters may be an outcome of sampling effect with different sets of trees used for estimating parameters at different ages. Furthermore such changes in genetic parameters are also expected because of different genes involvement at different developmental stages of the traits studied at different ages (NAMKOONG *et al.* 1988).

Genetic and phenotypic correlations

Genetic correlations between growth characters (HT, dbh, dbhu) and stem biomass (FSW) were high and positive, being above 0.83 at age 13 years (Table 8), which implies that concurrent improvement of these traits will be relatively effective. Genetic correlations among growth traits, however, decreased at age 17, and associated with higher standard errors. High standard errors were mainly a consequence of low heritabilities and a limited number of families. On the other hand, phenotypic correlations between FSW and growth traits were high and positive at age both 13 and 17 years.

Genetic correlations between bole straightness (BST) and growth traits varied from moderately positive (0.48) to highly negative (–0.83), with large standard errors (Table 8-A, 8-B), making interpretation of these coefficients rather difficult. Yet, phenotypic correlations between BST and growth traits were moderately high and positive both at ages 13 and 17 years.

Table 8. Estimated genetic correlations (±their standard errors) (below diagonals) and phenotypic correlation coefficients (above diagonals) in *Pinus brutia*.

Trait*	*HT*	*dbh*	*dbhu*	*BKGL*	*FRK*	*BST*	*TPR*	*FSW*
A – Age 13 years								
HT	–	0.93	0.93	0.65	–0.16	0.51	0.81	0.87
dbh	0.89±0.12	–	0.99	0.73	–0.14	0.45	0.83	0.94
dbhu	0.91±0.10	0.87±0.12	–	0.71	–0.15	0.47	0.82	0.93
BKGL	0.35±0.47	0.58±0.29	0.53±0.34	–	–0.08	0.23	0.38	0.67
FRK	–0.51±0.46	–0.34±0.45	–0.41±0.46	–0.11±0.50	–	–0.23	–0.19	–0.10
BST	0.48±0.41	0.32±0.39	0.40±0.41	–0.20±0.42	–0.53±0.36	–	0.45	0.44
TPR	0.93±0.07	0.72±0.20	0.73±0.21	0.17±0.40	–0.28±0.44	0.58±0.28	–	0.69
FSW	0.92±0.09	0.83±0.15	0.85±0.16	0.52±0.36	–0.48±0.44	0.32±0.44	0.68±0.25	–
B – Age 17 years								
	HT	*dbh*	*dbhu*	*BK13*	*FRK*	*BST*	*FSW*	*HI*
HT	–	0.81	0.82	0.44	–0.16	0.42	0.80	0.60
dbh	0.47±0.79	–	0.98	0.70	0.01	0.29	0.92	0.55
dbhu	0.50±0.66	0.69±0.58	–	0.55	–0.03	0.33	0.93	0.56
BK13	–0.37±0.99	–0.62±0.93	–0.68±0.69	–	0.12	0.02	0.53	0.29
FRK	–1.29± –0.67	–1.08±–0.20	–0.60±0.70	–2.40± –6.99	–	–0.23	–0.03	–0.03
BST	–0.01±0.62	–0.83±0.26	–0.53±0.51	–1.47± –1.00	–0.56±0.52	–	0.32	0.41
FSW	0.15±0.92	0.25±1.20	0.36±0.92	–0.59±0.93	–0.68±0.65	–0.58±0.49	–	0.57

* See Table 7 for the full name of the traits.
Genetic correlation for Harvest Index and Taper Index at age 17 was not estimated due to the lack of additive genetic variance. Phenotypic correlations are significant if $r \geq 0.09$ at 0.05, $r \geq 0.12$ at 0.01 levels for $N = 550$ number of observations.

Forking showed negative genetic correlations with all the traits studied, exhibited moderate (r_g = –0.34) to strong values (r_g = –1.29), exceeding the theoretical lower limit (i.e., –1.0) (Table 8). Correlations >|1.0| are expected due to the errors in the estimation of genetic variances and covariances (FALCONER 1989, VAN BUIJTENEN 1992), and the scoring method (i.e., present or absent) of forking may also contribute to this. Forking was phenotypically adversely correlated with height (r_g = -0.16) at both ages. Fast-growing trees appear to have lower forking incidence which is desirable.

CONCLUSIONS

Populations from the mid and lower-high altitude origins among the six populations of Turkish red pine from Antalya Region performed best in height and diameter growth at the Duzlercami test site. These populations also showed desirable bole straightness, and allocated a higher proportion of biomass to stem rather than to the branches. Thus, major emphasis should be given mainly to mid altitude populations for further family selection and improvement in Antalya Region. Cautions are needed to apply these results to wider areas. Genetic variation in growth, quality and biomass traits between populations and between families within populations in *Pinus brutia* is quite high. Growth, stem quality and stem biomass traits are under moderate additive genetic control. The results suggest that considerable improvement could be realised by combined selection if selection is applied at population, family and within-family levels.

Forking was the only character which showed apparent adverse genetic correlations with growth and biomass traits, implying that forking and height are genetically controlled by the same set of genes, but at different directions. Growth characters and stem biomass were moderately to highly genetically correlated, suggesting that pulp and log quality improvement in the same breeding cycle is feasible. Fresh stem weight for single trees can be predicted linearly, using diameter square at breast height as an independent variable.

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