



Age-age correlations and prediction of early selection age for diameter growth in a 35-years old *Pinus brutia* Ten. genetic experiment

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Abstract

Aim of study: Forest geneticists developed various methods to predict an early selection age for forest tree species in order to shorten the breeding cycles. This study aims to estimate age-age correlations among diameter growth of trees at different ages and predict early selection age for *Pinus brutia* Ten.

Area of study: *P. brutia* populations in the study were sampled from the most productive distribution range of the species, which is an important forest tree in the eastern Mediterranean Basin. To understand genetic variation and determine early selection age for the species, a common garden experiment was established in two test sites near Antalya city, Turkey, in 1979.

Materials and methods: Wood increment cores at breast height were collected at age 30 years, and diameters (dbh) were measured for the ages 13, 15, 19, 21, 23, 25, and 27 years on the cores. Diameters at ground level (dgl) and dbh were also measured on live trees at age 35. Variance components, age-age correlations, heritability and selection efficiency were estimated for the diameters.

Main results: Age-age genetic correlations for diameters were high (mostly > 0.90). Genetic correlations between dgl (at age 35) and dbh (at all measurement ages) ranged from 0.84 to 0.99. Regressions of genetic correlation on natural log of age ratio (LAR) of juvenile age to older age were significant ($P < 0.0001$). Selection efficiencies estimated by employing the prediction equation indicated that for rotation age 40, the optimum selection age would be between 3 to 5 years, and for rotation age 100 it would be between 5 to 9 years.

Research highlights: The results of this study provide information that can be used to find early selection ages in *P. brutia*. On relatively poor test sites most trees may not attain enough height growth to have measurable dbh trait. In such cases, dgl and/or tree height traits (both of which are highly correlated with dbh traits of all ages) can be measured and used instead of dbh trait for evaluations.

Keywords: Correlated response; selection efficiency; trait-trait correlations; brutian pine.

Authors' contributions: Experimental design: KI. Data collection: YK. Statistical analysis: KI. Drafting of the manuscript: YK and KI.

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Supplementary material: Tables S1 and S2 accompany the paper on FS website.

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Introduction

Selection and breeding of plant species require genetically screening the best individuals for a “desired character”, traditionally at harvest time (direct selection). This process is relatively easy in short-rotation agricultural crop species (Lin *et al.*, 2014). However, forest tree species are long-lived, and many years are needed to detect and evaluate the desired character, which is usually “wood volume” in most tree improvement programs (Libby, 1973; White *et al.*, 2007).

Consequently, in tree breeding programs theoretical models have been developed and implemented to detect and select best genotypes at early ages (indirect selection) (Lambeth & Dill, 2001; Osorio *et al.*, 2003). To maximize genetic gain, genetic and / or phenotypic correlations among different ages need to be estimated (Xiang *et al.*, 2003; Rweyongeza, 2016). This process is typically known as “age-age correlations” in addition to “juvenile age (young) - mature age (older, harvest) correlations” in the literature (Gwaze *et al.*, 2000; White *et al.*, 2007; Isik *et al.*, 2010).

Tree height, dbh (diameter at breast height), and wood volume are typically the analyzed traits for age-age correlations in timber-oriented breeding programs. Tree height and tree diameter are the major components of wood volume and so are the ones mostly used in early selection estimates. In estimating early / optimum selection age, age-age genetic and phenotypic correlations have been reported for the above traits for various forest tree species. For example, McKeand (1988), in a study on 18 tests on *Pinus taeda*, found that optimum selection age for selecting the top families ranged from 3 to 10 years, the greatest expected gain per year being between ages 6 and 8 years. Cotterill & Dean (1988), based on observations by age 16 years on *Pinus radiata*, a relatively fast growing pine species, suggested that optimum ages for early selection on height growth could range from 2.5 years to 6.5 years. However, they also cautioned that, regardless of the test site conditions, trees should reach around 10 m height before deciding on early selection age. Xie & Ying (1996), measuring height of trees from 42 open-pollinated families of *Pinus contorta* ssp *latifolia* in Canada, found that annual genetic gain was maximized at selection age seven years. Jansson *et al.* (2003) reported on *Pinus sylvestris* progeny test sites in Sweden in which optimal age for parental selection for height on this relatively slow growing pine was about 11 years. The estimated optimal ages in the southern test sites in Sweden were several years earlier than that in the northern ones.

Turkish red pine (*Pinus brutia* Ten.) is a native and important forest tree species both economically and ecologically in the eastern Mediterranean Basin, mostly in southern and western parts of Turkey. It is a relatively fast growing tree species (annual increment in plantations over 10 m³ / ha) compared with other Mediterranean conifers. The harvest age of the species could range from 30 to 100 years depending on the desired wood quality, seed origins and plantation site conditions (Boydak, 2004). *P. brutia* covers about 5.6 million ha of forest land, which constitutes 25.1% of the total forest areas in Turkey. The altitudinal distribution range of the species begins at sea level and goes to 1500 m, thriving under diverse ecological conditions on the Taurus Mountains (Boydak, 2004; TOD, 2019).

Earlier studies reported large variabilities in various growth characteristics among and within natural populations of *P. brutia*. For example, Isik (1986) working on seedling traits of *P. brutia* in nursery found significant differences on growth characters among different populations. Even at the nursery stage, close relationships of seedling growth characters with the altitudes of seed sources suggested that the species shows a clinal variation, with locally adapted races. Isik & Kaya (1997) reported that, when the trees were six years old, middle elevation populations had better height growth and better uniformity than both the lower- and higher-elevation populations

on provenance test sites. Furthermore, isozyme analyses in the same study indicated that populations originating from middle-elevations have a higher heterozygosity level and higher numbers of alleles per locus, which means higher genetic variability within the middle-elevation populations. Isik & Isik (1999) collected and analyzed data from individual trees cut during the thinning process, first at age 13 and then at age 17 years at the same test sites as the present study. Their study on genetic variation of certain crown and branching traits of *P. brutia* showed that populations from higher altitudes exhibited relatively shorter branches, wider branch angles, and longer and narrower crowns. Isik *et al.* (1999) also assessed certain growth, stem quality and biomass characters on the same material cut during the thinning process. Populations originating from middle altitudes showed better growth, exhibited more desirable bole straightness and allocated a higher proportion of biomass to the stem. When the trees in the same experimental sites were 30-year-old, Guller *et al.* (2011, 2012) studied wood density traits of *P. brutia*.

Kurt *et al.* (2012) provided new information on genetic diversity of *P. brutia*, using both cpSSR markers and quantitative traits. They suggested that genetic diversity in the species, particularly in quantitative traits, is more associated with altitude of seed sources than with geographical proximity among populations in the Antalya region. Their overall analyses suggested that *P. brutia* has higher levels of quantitative differentiation than of molecular genetic differentiation.

This study on *P. brutia* is the first of its kind on age-age correlation and on estimation of optimum selection age related to a native forest tree species in the eastern Mediterranean basin. We expect that this study will also set the example for similar studies on provenance + progeny studies on other forest tree species in the region. Our objective is to estimate relevant genetic parameters and age-age correlations in order to predict optimum age for early selection. For this purpose, we measured diameters of the same trees at eight different ages growing on two 35-years old provenance + progeny test sites.

Materials and Methods

Plant materials, test sites and data collection

The plant material included six natural populations of *Pinus brutia* from two altitudinal transects extending from the Mediterranean coast up to 1100 m on the Taurus Mountains (Fig. 1). The cones (seeds intact) were collected from 10 mother trees within each population and kept separate by mother trees. There were at least 100-meter distance between any two mother trees in a given stand. Therefore, trees derived from the seeds of a given mother tree were considered half-sibs. The seeds were first sown by mother

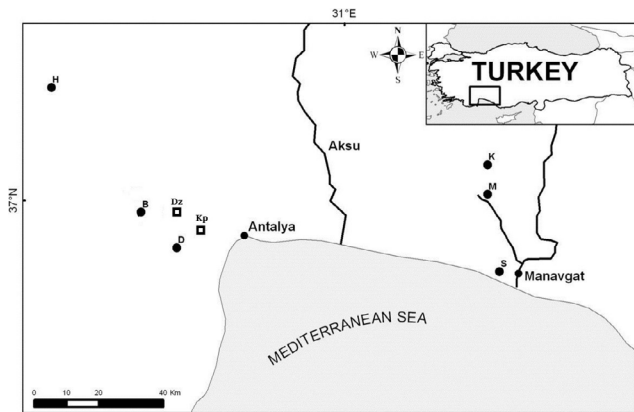


Figure 1. Location of Turkish red pine populations (S, M, K, D, B, and H, dark circles) and common garden test sites (Kp and Dz, squares) in the study (see also Table 1) (Modified from Kurt *et al.*, 2011, 2012).

tree at Zeytinköy forest nursery near Antalya, and then were transferred as 1 + 0 seedlings to common garden test sites in 1979 in southwestern Turkey (Fig. 1, Table 1). The sampled population names and the test site codes in the rest of the text are abbreviated as they appear in Table 1.

The experimental design at the test sites was non-contiguous single-tree plots in a randomized complete block with three interlocked replications (Libby & Cockerham, 1980; Isik, 1988). At each replication, there were six provenances (populations), 10 families (mother trees) within each provenance, and 10 trees (half sibs) within each family. Therefore, initially there were 600 trees on each of the three replications. This design allows systematic thinning by sequentially removing one replication at a time when trees reach a competing stage. Trees in the third replication (initially 600 trees) may be left until harvest age for additional studies on mature tree traits. By the time of data collection for this study, two of the replications wi-

thin each test site had been thinned, and the cut trees were used to evaluate growth, biomass, stem quality (Isik *et al.*, 1999), branching and crown traits (Isik & Isik, 1999).

For diameter (dbh) data we collected wood increment cores (12 mm thick) at breast height (1.3 m) from bark to pith of all live trees, by taking one core per individual tree. When mortality and the cut trees were not counted, there were 1010 live trees at the two test sites. Trees at the test sites were 29 years old at the time of increment core sampling. The core samples were processed and made ready for diameter measurements as described in Guller *et al.* (2011, 2012). Diameter values (in mm) of trees at seven different ages (13, 15, 19, 21, 23, 25, and 27 years) were obtained, and 852 trees belonging to 60 families were included in statistical evaluations. We also measured two other diameter characters on the same trees at age 35 years [i-the diameter at ground level (dgl) (taken 30 cm above the ground, above bark), ii-dbh (both under- and above bark)].

Statistical analyses

ANOVA (Analysis of Variance) tests are crucial to estimate genetic parameters in quantitative genetic studies (Becker, 1992; Falconer & MacKay, 1996; Lynch & Walsh, 1998). Depending on the design of the experiment in question, models and types of ANOVA tests can differ considerably. Any error in determining a proper ANOVA model for a given experimental design would lead to misestimating of variance components and relevant genetic parameters. Therefore, we first determined an appropriate ANOVA model to fit to the study's experimental design (Hicks, 1964; SAS, 2011; Sokal & Rohlf, 2012). Considering the experimental design in our study [*i.e.*, 2 test Sites, 6 Populations within each test site, 10 Families (mother trees within each

Table 1. Information about the locations of (A) *Pinus brutia* seed origins and (B) common garden test sites included in the study (see also Fig. 1).

A. Populations sampled					
Sampled populations (Provenances = Seed origins), Name (Code)	Transect	Mean Altitude (m., asl.)	Latitude (N)	Longitude (E)	Nearest settled locality
Sarilar (S)	East	92	36° 48'	31° 26'	Sarilar
Murtbeli (M)	East	490	37° 01'	31° 24'	Beydigin
Kapan (K)	East	933	37° 06'	31° 24'	Beydigin
Doyran (D)	West	61	36° 52'	30° 32'	Doyran
Buk (B)	West	480	36° 58'	30° 26'	Buk
Hacibekar (H)	West	1033	37° 19'	30° 11'	Hacibekar
B. Test sites included in this study					
Test sites Name (Code)	Transect	Altitude (Elevation) (m., asl.)	Latitude (N)	Longitude (E)	Soil type
Kepez (Kp)	West	90	36° 55'	30° 36'	Sandy loam
Duzlercami (Dz)	West	350	36° 58'	30° 32'	Sandy loam

population) and initially 10 individual trees (observed trees, *i.e.*, half sibs) within each family], we applied the ANOVA Model as in Equation 1 (Falconer & MacKay, 1996; Lynch & Walsh, 1998; White *et al.*, 2007; SAS, 2011):

$$Y_{ijkl} = \mu + S_i + P_j + SP_{ij} + F(P)_{k(ij)} + SF(P)_{ik(j)} + e_{l(ijk)} \quad (\text{Eq. 1})$$

Where:

Y_{ijkl} = Observation on the l 'th tree in the k 'th family in the j 'th population in the i 'th Site;

μ = Overall mean; S_i = Effects due to i 'th site; P_j = Effects due to the j 'th population; SP_{ij} = Effects due to interaction between site and population; $F(P)_{k(ij)}$ = Effects due to the k 'th family in the j 'th population in the i 'th site; $SF(P)_{ik(j)}$ = Effects due to interaction between site and family; $e_{l(ijk)}$ = Normally and independently distributed random deviation of l 'th tree, of family k , in population j , in site i .

Populations (P_j) were analyzed as fixed effects, whereas sites (S_i) and mother trees (families) within populations [$F(P)_{k(ij)}$] were considered as random effects in the model. Variance components of random effects were estimated based upon the expected mean squares derived from this model and are presented in Table S1 [suppl.] (Becker, 1992; Sokal & Rohlf, 2012).

Broad sense (family means, H^2_F) heritabilities were estimated as defined by Becker (1992) and Falconer & Mackay (1996) by:

$$H^2_F = \sigma^2_{F(P)} / \sigma^2_{TF} \quad (\text{Eq. 2})$$

Where: H^2_F = Family means (broad sense) heritability; $\sigma^2_{F(P)}$ = Variance caused by family differences within populations;

$$= \sigma^2_{F(P)} + \sigma^2_{SF(P)} / s + \sigma^2_e / (s \times n_x)$$

Details of these and other abbreviations derived from the ANOVA test are shown in Table S1 [suppl.]. Standard errors of broad sense heritabilities were estimated according to Anderson & Bancroft (1952), as cited and detailed in Isik & Isik (1999).

Genetic correlation coefficients (r_{GJM}) between any two observed J-M character pairs were estimated as in Falconer & Mackay (1996), by applying:

$$r_{GJM-O} = COV_{GJM} / (\sqrt{\sigma^2_{GJ}} \times \sqrt{\sigma^2_{GM}}) \quad (\text{Eq. 3})$$

Where:

r_{GJM-O} : Genetic correlation coefficient calculated (observed) for any two dbh characters based on measured data at early (J) and later (M) ages.

COV_{GJM} : Genetic covariance for ages J and M,

σ^2_{GJ} : Genetic variance for diameter for an early age, J,

σ^2_{GM} : Genetic variance for diameter for a later age, M.

Genetic variances (σ^2_{GJ} and / or σ^2_{GM}) of each diameter character for a given age, and genetic covariances

(COV_{GJM}) of each character pairs for any early (J) and any later (M) age were estimated by applying PROC GLM, MANOVA option (TYPE III SS and TYPE III SSCP Matrix tables) in SAS (2011).

Developing a prediction equation for *Pinus brutia*

Lambeth (1980) developed a linear regression model to predict the genetic correlation coefficient (r_{GJM-P}) between any two different ages (J and M), by applying available data from certain species of *Pinaceae* family. Following Lambeth's approach, we developed a prediction equation specific to *P. brutia* for the diameter character. At the first step, we calculated observed genetic correlation coefficients (r_{GJM-O}) for 28 pairwise dbh combinations by employing Eqn. 3. Secondly, we applied regression analyses by using LAR values as independent variable (on X axis) and r_{GJM-O} values (on Y axis) [PROC REG, SAS (2011)]. We then estimated "a" and "b" coefficients, and from there developed a prediction equation applicable to diameter characters for any J and M age pairs of *P. brutia*. The regression equation thus obtained (Eq. 7 in the "Results" section) could be employed to predict r_{GJM-P} values between ages beyond measurement ages.

Estimating genetic gains

Genetic gain based on direct selection at mature (M) age is expressed from the following equation (Lambeth, 1980; Jansson *et al.*, 2003):

$$G_M = i_M \times H^2_{FM} \times (\sqrt{\sigma^2_{TF}}) \quad (\text{Eq. 4})$$

Where:

G_M = Genetic gain based on direct selection at mature age,

i_M = Selection intensity at age M,

H^2_{FM} = Family means (broad sense) heritability at age M,

σ^2_{TF} = Total Phenotypic variance (as defined under Eqn. 2).

Correlated (predicted) Genetic gain at age M based on indirect selection at an early age (J) was estimated according to equation (Lambeth, 1980; Jansson *et al.*, 2003; Xiang *et al.*, 2003; Isik *et al.*, 2010):

$$CG_{M-J} = i_J \times H_{FJ} \times H_{FM} \times r_{GJM-P} \times (\sqrt{\sigma^2_{TFJ}}) \quad (\text{Eq. 5})$$

Where:

CG_{M-J} = Correlated (predicted) Genetic gain at age M based on indirect selection at age j,

i_J = Selection intensity at age J,

H_{FJ} = Square root of Family means (broad sense) heritability at age J,

H_{FM} = Square root of Family means (broad sense) heritability at age M,

σ_{TF}^2 = Total Phenotypic variance.

In our study, we assumed that $i_j = i_M = 1.365$ (Falconer & Mackay, 1996). This value corresponds to backward family selection of top 20% of 60 families included in the study (*i.e.*, 12 out of 60 in the study).

Genetic gain per year was estimated for both direct (G_{MPY}) and indirect (CG_{M-JPY}) selection as the ratio between the relevant estimated genetic gain and the corresponding assessment age, T (McKeand, 1988; Xiang *et al.*, 2003). Before completing the calculations of genetic gain per year values, an additional time “t”, which is the time required to complete the breeding cycle, needs to be added to T. We assumed “t” to be 3 years for *P. brutia* [*i.e.*, time needed to establish the next generation in the field (collecting seeds + growing seeds in nursery for one year + transferring to the field), following completion of juvenile selection in the previous generation] (McKeand, 1988).

selection (Lambeth, 1980; Xie & Ying, 1996; Falconer & Mackay, 1996; Jansson *et al.*, 2003; Xiang *et al.*, 2003). In short, it is shown as:

$$SE_{GPY} = CG_{M-JPY} / G_{MPY}$$

When the values on the right side of the equation are replaced by their equivalents (and assuming $i_j = i_M$), then the full equation becomes:

$$SE_{GPY} = CG_{M-JPY} / G_{MPY} = [(H_{FJ} \times r_{GJM-P}) / (H_{FM})] \times [T_M / T_J] \quad (\text{Eq. 6})$$

As H_{FJ} value in Eq. 6, we used the corresponding heritability values estimated for each diameter as presented in Table 2B. For early ages before the first measurement at age 13, we used the same value as that of age 13 (*i.e.*, $H_{FJ}^2 = 0.217$). For later (older) ages beyond age 35, we used the value as that of dbh age 35 (*i.e.*, $H_{FM}^2 = 0.282$) for the related calculations. SE_{GPY} can be predicted for any harvest age such as 40, 45, 50, ..., 100 years, using r_{GJM-P} values.

Results

Estimating per year selection efficiency

Selection efficiency per year (SE_{GPY}) is simply the ratio of gain per year between indirect selection and direct

Growth trends of dbh characters at the test sites

There were statistically significant differences between the two test sites at all ages. Differences among the

Table 2. Variance components (A) and heritability values (B) for tree diameters (dbh and dgl) at different measurement ages in *Pinus brutia* (“dbh” = diameter at breast height; “dgl” = diameter at ground level).

A-Variance components in absolute and percent values (% value for each characteristic in a column is shown in parenthesis)									
Source of variation (and Variance)*	Diameter characteristics (Traits)**								
	dbh13	dbh15	dbh19	dbh21	dbh23	dbh25	dbh27	dbh35	dgl35**
S, (σ_s^2)	262 (23.5)	432 (32.2)	822 (42.8)	1098 (47.0)	1454 (51.1)	1903 (54.2)	2302 (56.0)	1715 (48.7)	3293 (50.7)
P, (σ_p^2)	46 (4.2)	50 (3.3)	59 (3.1)	70 (3.0)	82 (2.9)	103 (2.9)	118 (2.9)	77 (2.2)	273 (4.2)
S×P, (σ_{SP}^2)	38 (3.4)	38 (2.8)	41 (2.1)	43 (1.8)	48 (1.7)	57 (1.6)	66 (1.6)	67 (1.9)	112 (1.7)
F(P), ($\sigma_{F(P)}^2$)	21 (1.8)	22 (1.6)	30 (1.5)	37 (1.6)	41 (1.4)	50 (1.4)	54 (1.3)	62 (1.8)	130 (2.0)
S×F(P)($\sigma_{SF(P)}^2$)	51 (4.5)	63 (4.7)	70 (3.7)	72 (3.1)	84 (3.0)	98 (2.8)	116 (2.8)	104 (2.9)	170 (2.6)
Within (Error) (σ_e^2)	699 (62.6)	737 (54.9)	899 (46.8)	1016 (43.5)	1134 (39.9)	1300 (37.1)	1456 (35.4)	1500 (42.5)	2523 (38.8)
Total	1117 (100)	1342 (100)	1921 (100)	2336 (100)	2844 (100)	3511 (100)	4112 (100)	3525 (100)	6501 (100)
B- Family means heritability values [H^2_F , and their Standard Errors (in italics)]									
	dbh13	dbh15	dbh19	dbh21	dbh23	dbh25	dbh27	dbh35	dgl35**
H^2_F	0.217 <i>0.481</i>	0.205 <i>0.483</i>	0.235 <i>0.480</i>	0.257 <i>0.475</i>	0.253 <i>0.476</i>	0.261 <i>0.472</i>	0.250 <i>0.474</i>	0.282 <i>0.467</i>	0.332 <i>0.456</i>

*S: Sites; P: Populations, F: Families. The remaining abbreviations are the same as in Table S1 [suppl.].

** dbh13, ... dbh35: Diameters (under bark) at breast height at ages 13 ... 35 years. And, dgl35: diameter above bark at ground level at age 35 years.

populations within the test sites and among families within populations were also significant. Population by Site interactions were significant for all the diameter characters studied. Since our primary aim in this article is to focus on prediction of early selection age, details of the ANOVA tests on diameter characters are not presented here.

Mean dbh at age 13 years was 50.3 mm at Kp, and 74.1 mm at Dz test sites. By age 35, they reached to 129.7 mm at Kp, and 189.9 mm at Dz (Fig. 2). At the Kp test site (located at low elevation), low elevation populations (S and D) showed the fastest dbh growth, and high elevation populations (H and K) showed the slowest dbh growth (Fig. 2A). At the Dz test site (located in mid-elevation), population M (from a mid-elevation) exhibited distinctly the fastest dbh growth through all observed ages. Population M was also racing for the second rank at the Kp test site (Fig. 2A, 2B). Population H, is also the slowest growing origin at the Dz test site, as it is at the Kp test site (Fig. 2B).

Trends in variance components and heritabilities

As expected, the error (within sites) variance showed a high proportion (*i.e.*, 63%) at age 13, declining steadily until age 27 years, after which it remained around 40% (Fig. 3). The site effect arising because of environmental differences between the test sites was also high. Its proportion was 23% at age 13 years, it doubled (56%) by age 27, and smoothed down to 49% by age 35. Each of the other variance components (population, site × population, site × family, family within population) were less than 5%, up to the latest observation age of 35 years (Table 2A, Fig. 3).

Family means (broad sense) heritability values for dbh trait steadily increased from 0.21 to 0.28, remaining within a relatively narrow band through the measurement ages (Table 2B). Heritability of dgl was slightly higher than the others (*i.e.*, 0.332). Standard errors for heritabilities were quite high compared to heritability values (Table 2B).

The age-age correlations

The results based on dbh data of *P. brutia* showed that the genetic age-age correlations were positive and rather high (mostly > 0,90) (Table 3). As the age interval between any two dbh character pairs increased, age-age correlation between them gradually decreased. For example, genetic correlation between dbh13 and dbh15 was very strong ($r_{GJM} = 0,99$), whereas this value became smaller between dbh13 and dbh35 ($r_{GJM} = 0.72$ yet; statistically still significant). There were also strong genetic correlations between ground level diameter at age 35 (dgl35) and dbh characters of trees at all ages, ranging from 0.84 to 0.99 (Table 3).

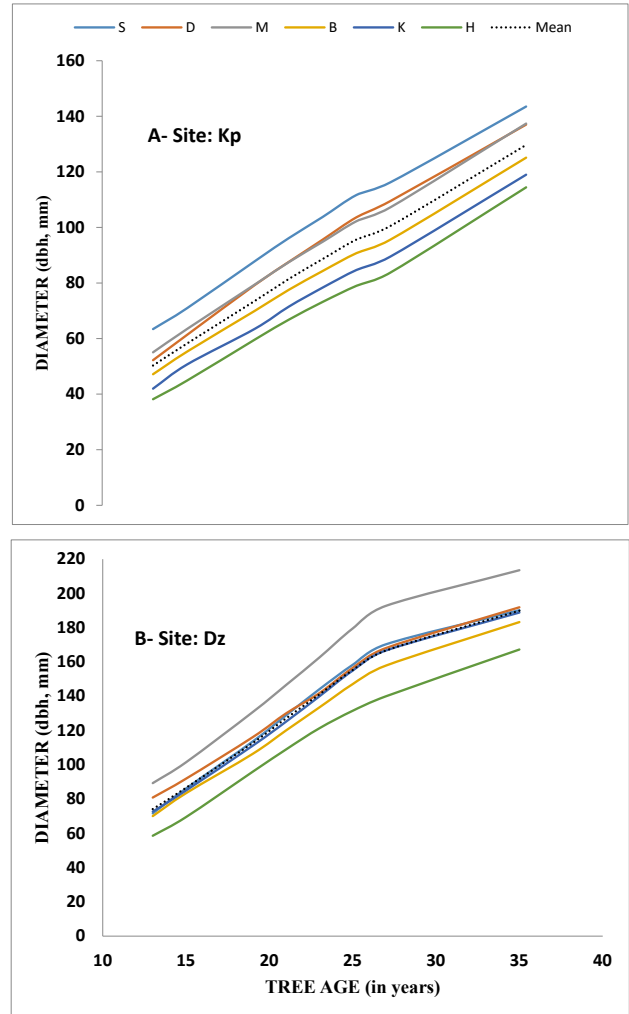


Figure 2. Age trends in diameter growth (mm) of six different populations (S, D, M, B, K, H) from age 13 to age 35 years at two Common Garden Experimental Sites in *Pinus brutia* (broken line indicates the overall test site mean. Test Sites: A- Kepez, B- Duzlercami).

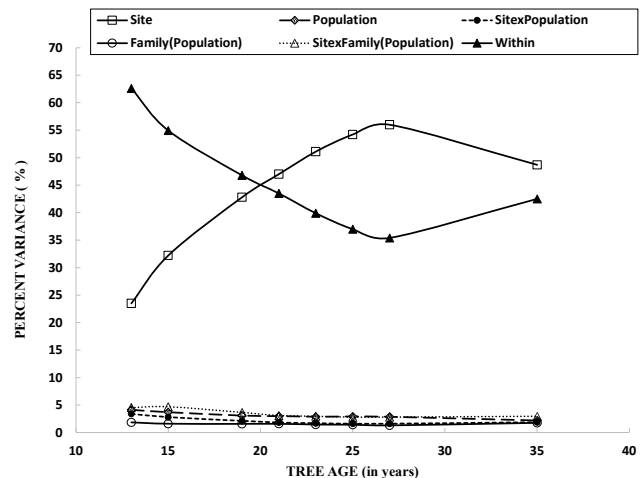


Figure 3. Age trends in variance components (%) for dbh (diameter at breast height) in *Pinus brutia*. (Variances due to: S = Sites; P = Populations; S×P = Interaction; F(P) = Families within P; S×F(P) = Sites×Family interaction; Within = within families).

Table 3. Observed genetic correlation coefficients (r_{GJM}) among diameter pairs measured at different ages on *Pinus brutia*

Diam.*	dbh13	dbh15	dbh19	dbh21	dbh23	dbh25	dbh27	dbh35	dbh35b¶
dbh15	0.99	-							
dbh19	0.99	0.98	-						
dbh21	0.99	0.99	0.98	-					
dbh23	0.98	0.97	0.96	0.99	-				
dbh25	0.96	0.95	0.94	0.98	0.99	-			
dbh27	0.95	0.93	0.93	0.98	0.99	0.99	-		
dbh35	0.72	0.72	0.78	0.86	0.91	0.94	0.95	-	
dbh35b¶	0.76	0.75	0.81	0.89	0.93	0.96	0.97	0.98	-
dgl35b#	0.84	0.86	0.85	0.91	0.96	0.98	0.99	0.96	0.99

* : dbh13. ... dbh35: Diameter (under bark) at breast height at ages 13 ... 35 years.

¶ : dbh35b: Diameter above bark at breast height at age 35 years.

dgl35b: Diameter above bark at ground level at age 35 years.

Prediction equation for *Pinus brutia*

We developed an equation to predict genetic correlation coefficients for any two dbh characters for any J and M ages in *P. brutia* (Fig. 4). Prediction equation for the dbh traits of *P. brutia* can be expressed as:

$$r_{GJM-P} = 1.034 + 0.241 \times \text{LAR.} \quad (\text{Eq. 7})$$

We used r_{GJM-P} values to estimate selection efficiencies and optimum early selection year.

Selection Efficiency per Year

Estimated selection efficiency per year (SE_{GPY}) values for different selection ages (J) and harvest (rotation, M)

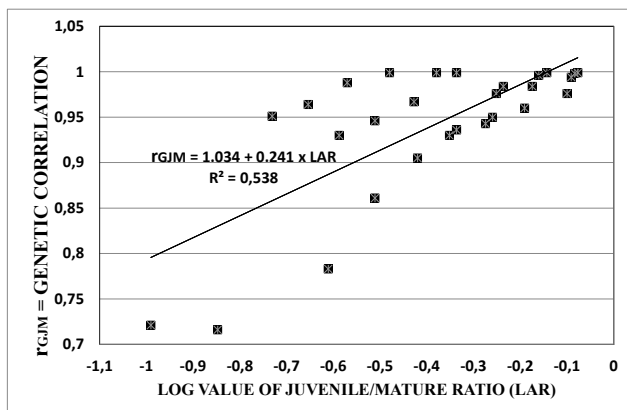


Figure 4. Prediction of genetic correlation coefficients (r_{GJM}) on Y axis, using LAR values on X axis for *Pinus brutia* dbh (diameter at breast height) (Each square dot on the graph represents observed r_{GJM} values on Y axis for each character pair as seen in Table S2 [suppl.].

ages are presented in Table S2 [suppl.]. Rotation age for *P. brutia* may differ depending on various management decisions and plantation site conditions. In Table S2 [suppl.], we presented five different rotation ages ranging from 30 to 100 years. Selection age, J, which corresponds to the highest SE_{GPY} value in a given harvest age, is determined as the optimum selection age for the relevant harvest age. For example, if the harvest age has been decided as 60 years for future plantations, then the highest SE_{GPY} value is 3.020, which corresponds to optimum selection age 4 years in the first column (Table S2 [suppl.]). The highest SE_{GPY} value under each harvest age is written in bold and underlined. Values with plus (+) sign (and the values between two + signs) in a given column are within the range of 95% of the related optimum SE_{GPY} value in the same column. Depending on harvest age of future plantations and considering the 95% values of optimum SE_{GPY} values, we found in *P. brutia* that early selection ages for selecting families ranged from 3 to 9 years, whereas **optimum** selection ages were between ages 4 to 6 years (Fig. 5).

Discussion

Test sites differences: Larger diameter growth at the Dz test site than the Kp test site at all ages could be attributed to environmental differences between test sites. Dz has a first quality site class conditions (index 19,8), whereas Kp is second class (index 13,7) (Usta, 1991). In addition, the Dz site is located on a relatively higher elevation (Table 1) and likely to receive more rainfall than the Kp site (Kantarci, 1991).

Population variation: The differential growth performances of the populations at the test sites can be explained mainly by two interrelated factors: One is the widely accepted theory that “local populations (or local races) are

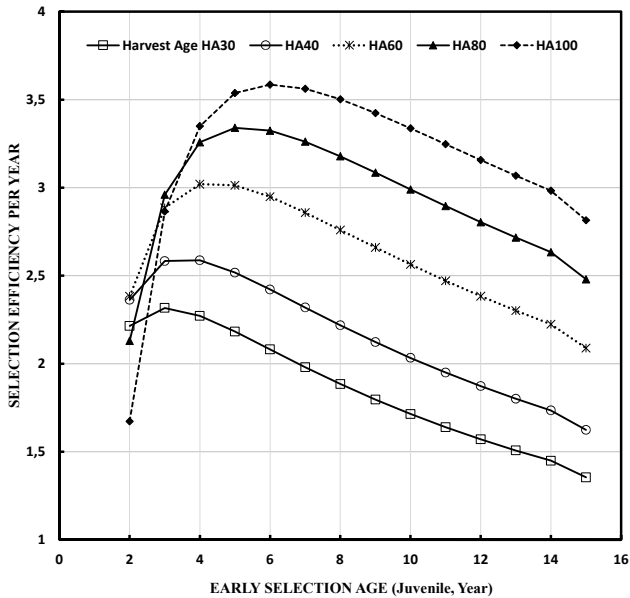


Figure 5. Trends in selection efficiency per year (SE_{GPY}) in relation to early selection ages for different rotation (harvest) ages (HA) of 30, 40, 60, 80 and 100 years. [The peak point on each curve for a given HA indicates the optimum selection age for the corresponding rotation age].

usually the best adapted populations in an area” (Zobel & Talbert, 2003; White *et al.*, 2007; Vander Mijnsbrugge *et al.*, 2010; Boshier *et al.*, 2015). Aside from the results at early ages, our dbh data at age 35 supports the theory of adaptive superiority of local races, such that low elevation populations (S, D) showed the fastest growth at the low elevation test site (Kp), while mid elevation population (M) performed the best at the mid elevation site (Dz).

The second factor might be the advantages of rich gene pool diversity, which bestows central populations with higher adaptability. Namely, the seed source of population M is located at the central part of both the vertical and horizontal distribution range of the species, and thus has higher gene pool diversity because of gene flow from both the lower and higher elevation populations. On the other hand, the seed source of population H is a peripheral population located at the upper margin of the vertical distribution range of the species, and thus has less gene pool variation and would be expected to be under a higher risk of selective pressures. Indeed, isozyme analyses (Isik & Kaya, 1997; Kaya *et al.*, 1997), RAPD (Kurt *et al.*, 2011) and SSR markers (Kurt *et al.*, 2012) also demonstrated that, when compared with the others, population H has a lower genetic variation.

Variance components: High proportion of Within (Error) variance at early ages is a common pattern in provenance + progeny trials of forest trees (White *et al.*, 2007; Diao *et al.*, 2016). The high Site effect in the study is attributed mainly to ecological differences associated with plantation sites (Li *et al.*, 2017).

Statistically significant interactions between sites \times populations indicate that genotypes of populations respond differently to different environmental conditions in expressing their quantitative traits. This differential response is not a surprising result for *P. brutia* which is a relatively complex species with relatively high variation and locally adapted populations in diverse altitudinal and associated climatic environments throughout its distribution range (Isik, 1986; Isik & Kaya, 1997; Kurt *et al.*, 2012). Such adaptations and genotype \times environment interactions are common phenomena in *P. brutia* (Kaya *et al.*, 1997; Isik *et al.*, 2000; Dangasuk & Panetsos, 2004) as well as in many other forest tree species (Li *et al.*, 2017).

Heritability values: Cornelius (1994), in his review on 67 published paper on various forest tree species, about 70% of which are pine species, reported that “heritabilities of height, diameter, volume, branching traits and straightness are generally below 0.4 and frequently in the range of 0.1 – 0.3”. Isik *et al.* (1999) found that on 17 years old *P. brutia* at the same test sites as the present study, family heritability for dbh (under bark) was 0.20, which is rather consistent with the results of the present study. The family heritability values in the present study are also in accord with different pine species such as *Pinus radiata* (0.38; Burdon & Banister, 1992), *Pinus sylvestris* (0.23; Haapanen, 2001), and *Pinus taeda* (0.13; Paul *et al.*, 1997). Standard errors of heritabilities for dbh were higher than the corresponding heritability estimates. This might arise primarily due to high variance among families within populations (which is closely related to small sample sizes), and partly due to high Site \times Family interactions.

Genetic correlations among characters: As expected, correlation is high and positive between the same traits at different ages. As the age interval between any two age pairs (*i.e.*, J and M) increases, both observed (r_{GJM-O}) and predicted (r_{GJM-P}) genetic correlation coefficients among them decreases, because predicted genetic correlations are found principally by employing observed genetic correlation values. All of these trends are consistent with those found by Lambeth (1980) and other studies on age-age correlations (*e.g.*, Xie & Ying, 1996; Lambeth & Dill, 2001; Jansson *et al.*, 2003; Isik *et al.*, 2010; Ye & Jayawickrama, 2012; Diao *et al.*, 2016).

Isik *et al.* (1999), when working on the same test sites as the present study when the trees were 13 years old, reported that genetic correlation between dbh and tree height was 0.89 ($P < 0.001$). In a subsequent study at age 17 years at the same test sites, Isik (1998) also reported high and positive genetic correlations between dbh and tree height (0.84), between dbh and volume (0.99), and between height and volume (0.91). When taking 265 sample plots throughout the natural distribution range in southern Turkey, Erkan (1996) found that *P. brutia* exhibits strong phenotypic correlations between diameter growth and height growth ($r = 0.838$; $P < 0.001$).

Presence of high genetic (and phenotypic) correlation coefficients between any two given characters offers plant breeders great opportunities for concurrent selection. Specifically, if one characteristic is selected for genetic improvement, the other characteristic could simultaneously be selected. For example, high positive genetic correlations between dgl (diameter at ground level) and dbh, and also between tree height and dbh characters at all ages suggest that if dgl and / or height is selected for genetic improvement at early ages dbh characteristics of later ages would also be selected indirectly (Falconer & Mackay, 1996; Lin *et al.*, 2014).

Prediction equation for *P. brutia*: Estimated “a” (1.034) and “b” (0.241) values in prediction equation in *P. brutia* in this study are consistent with the corresponding values found by Lambeth (1980) and others [*i.e.*, in Lambeth (1980) a = 1.02 and b = 0.308; in Weng *et al.* (2007) a = 1.04, b = 0.13; in Isik *et al.* (2010) a = 1.023, b = 0.384].

Selection efficiency and optimum selection age: In predicting selection efficiencies in this study, we preferred to use genetic correlation coefficients. The preference is because genetic correlations among the characters are more stable and less influenced by environmental factors than that of phenotypic correlations, especially in long-lived organisms such as forest tree species (Libby, 1973; Falconer & Mackay, 1996; Li *et al.*, 2017). In some studies, instead of genetic correlations, phenotypic correlation coefficients have also been used in estimating selection efficiencies (*e.g.*, Burdon, 1989; Xie & Ying, 1996; Lambeth & Dill, 2001).

For any harvest age in *P. brutia*, as selection age (J) increases starting from early years, selection efficiency per year also increases until it reaches the highest (optimum) value. Then, it declines gradually and, when J becomes equal to M, it reaches the theoretical value 1.0. Selection efficiency curves in most studies also exhibit more or less similar trends as *P. brutia* (*e.g.*, Lambeth & Dill, 2001; Jansson *et al.*, 2003; Osorio *et al.*, 2003; Xiang *et al.*, 2003; Isik *et al.*, 2010). Obviously, if forest managers decide the harvest age to be a relatively young age, annual genetic gain is maximized at earlier years (*i.e.*, optimum early selection age is reached in earlier years on the test sites). However, there is no any correlation between harvest age and corresponding optimum selection age. For instance, for harvest ages 40 and 60 years, optimum early selection ages are the same.

Fast growing forest tree species, including *P. brutia*, reach optimum selection ages usually in earlier years compared with the slow growing tree species. For example, on *Pinus taeda*, which is a relatively fast growing species, Xiang *et al.* (2003) found that optimum selection age for height growth was 3 or 4 years. On the other hand, in *Pinus sylvestris*, which is a slow growing pine, optimum selection age (for height) was between 10 to 15

years (Jansson *et al.*, 2003). Isik *et al.* (2010), by working on a clonal experiment in *Picea abies*, a slow growing species, reported that for height growth early selection age could be as early as age 13.

Our data for predicting early selection age in *P. brutia* is based on the dbh characteristic. One can argue that most trees in the species cannot attain enough height to have measurable dbh at early ages. However, it should be emphasized that there are strong genetic correlations between ground level diameter (dgl) and dbh characters, as found in this study. In addition, Kurt *et al.* (2021) reported that there were very high correlations ($r = 0.99$) between the mean dgl and mean dbh on data obtained from seven different even-aged *P. brutia* plantations, ages of which ranged from 10 to 35 years. Isik (1998), based on measurements at age 17 years on the same test sites as the present study, reported high and positive genetic correlations between dbh and tree height (0.84), dbh and volume (0.99), and tree height and volume (0.91). Based on these strong relationships among diameter characters and height, dgl or tree height (or both) characters at early ages can also be measured instead of dbh character to predict optimum selection ages.

Conclusions and management implications

One of the challenges in breeding of forest trees, which are long-lived species, is the long-time interval between selection age and the harvest age. Determining the early selection age of forest trees instead of waiting until harvest age for direct selection is an effective tool to save both time and money. Development of new DNA sequencing technologies within the past 15 years in molecular biology offers great opportunities in various respects in plant and animal breeding. Genomic selection (GS), which uses large number of DNA markers to cover the whole genome, has been successfully applied in animal breeding, doubling genetic gain in milk yield per unit time (Goddard *et al.*, 2011). Forest geneticists / tree breeders also have embraced GS technology to select superior genotypes and to shorten the breeding cycles. However, Isik (2014) in his extensive review article cautioned that “Forest geneticists should avoid over-promising GS to the community, until all the necessary ingredients are in place”. In this respect, conventional field tests such as progeny trials are very important to characterize the base populations for molecular breeding approaches. Breeding programs for many forest trees, including *P. brutia* in Turkey, are still in their early stages. Therefore, we consider that both the present and relevant other studies of *P. brutia* are the pioneering efforts to provide “necessary ingredients” for genetic improvement, and subsequently genomic selection programs for this species.

There are some limitations regarding Lambeth's prediction model and the assumptions used in the present study. *First*, this study includes only six provenances (and 10 mother trees per provenance) planted on only at two test sites located on an elevational transect. However, it is worth noting that the provenances (and mother trees) covered in the present study represent the core and the most productive parts of the vertical and horizontal distribution range of *P. brutia* (Usta, 1991; Erkan, 1996). *Second*, this study is based on dbh characteristic, which cannot be directly measured before the trees attain certain height growth as in most forest tree species. Tree breeders thus need to observe other correlated traits, measurable at early ages. Diameter at ground level (dgl) and tree height, both of which are significantly correlated with dbh traits, can be measured at early ages to replace the dbh trait. *Third*, in estimating selection efficiency, we assumed that broad sense heritability (H^2_F) values for the dbh trait beyond the observation ages are the same as those of the nearest measurement ages. Our results also justify this assumption, since H^2_F values for dbh remain within a narrow band within the observation ages (*i.e.*, between 0.205 and 0.282). These concerns are also shared by several other researchers in their relevant studies (*e.g.*, Lambeth, 1980; Cotterill & Dean, 1988; Gwaze *et al.*, 2000; Isik *et al.*, 2010). It appears that additional studies are required to fine tune the optimum selection age reported in this study. It remains to be seen how genetic parameters reported here would change by studying larger numbers of populations (and mother trees) covering wider distribution ranges of *P. brutia*.

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