

Age–Age Correlations and Early Selection for Height in a Clonal Genetic Test of Norway Spruce

Kani Isik, Jochen Kleinschmit, and Wilfried Steiner

Abstract: Heights of rooted cuttings from 40 clones of Norway spruce (*Picea abies* [L.] Karst) were measured at ages 3, 5, 8, 10, 13, and 17 from rooting at seven test environments in northern Germany. To determine the optimal age for juvenile selection for height, age-related changes in variance components, clone-mean heritability, and age–age correlations were estimated. Partitions of variance components were essentially constant after age 8. Clone-mean heritabilities were highest at age 3 (0.94) and were essentially stable after age 5. Age–age correlations were generally high between similar ages but declined as the difference between pairs of measurement ages increased. Genetic correlations were greater than corresponding phenotypic correlations but were similar in value. Trait–trait correlations between height and diameter ($r_G = 0.83$) and height and volume ($r_G = 0.90$) at age 17 were also high. Simple linear regressions of genetic and phenotypic age–age correlations on LAR (natural log of the ratio of younger age to older age) were significant ($R^2 \geq 0.76$). Predicted efficiencies of selection suggested that for a rotation age of 60 years, the optimum selection age would be as early as 13 years. Furthermore, gains per year would be increased by about 1½ times if selections were made at about age 15 rather than age 60. FOR. SCI. 56(2):212–221.

Keywords: juvenile–mature correlations, genetic correlation, efficiency of selection, indirect selection, *Picea abies*

THE ULTIMATE PURPOSE of plant breeding is to change the genetic properties of a population so that it will increase crop yield and value at final harvest. One way to accomplish this is to select individuals with desirable traits at harvest age and then use them as parents in subsequent generations in a breeding program. In most animal and agricultural crop species, the harvest age is relatively short, and individuals with desirable traits can easily be identified and selected directly (direct selection) (Allard 1960, Falconer and Mackay 1996). In forest trees, however, the target crop is usually “wood” and harvest age (or rotation length) generally ranges from 20 to 100+ years, depending on species and site quality (Libby 1973). Therefore, instead of waiting until rotation age, forest tree breeders ought to develop theoretical grounds for early (indirect) selection to minimize the generation interval and to maximize the gain per year (Franklin 1979, Lambeth 1980, Kang 1985, Burdon 1989, Gwaze et al. 2000, Lambeth and Dill 2001). The primary question now becomes: What is the optimal age for early selection?

Determination of optimum selection age requires examination of age trends in genetic parameters involving variances, heritabilities, and age–age correlations of the traits of interest (Lambeth 1980, Foster 1986, Huehn and Kleinschmit 1993, Mullin and Park 1994, Chen et al. 2003). There have been numerous studies on different forest tree

species to address age–age correlation and/or early selection (e.g., Cotterill and Dean 1988, McKeand 1988, Xie and Ying 1996, Gwaze et al. 2002, Kumar and Lee 2002, Lee et al. 2002, Jansson et al. 2003, Osorio et al. 2003). Estimates of the optimum selection age from such studies differ, depending on the species, site quality, rotation age, traits, choice of model, and underlying assumptions. Lambeth (1980), for example, evaluated data on various species of Pinaceae and then estimated that optimum selection ages were 6 and 8 years for 30- and 40-year rotations, respectively. McKeand (1988) reported that expected gain per year was greatest for loblolly pine (*Pinus taeda*) when early selection is made between 6 and 8 years. Riemenschneider (1988) suggested that selection as early as age 1 would be an efficient strategy for improving rotation-age growth in jack pine (*Pinus banksiana*). Xiang et al. (2003) indicated that volume would be more effective than height in determining early selection age in loblolly pine. Jansson et al. (2003) concluded that the optimal age for selection for height in Scots pine (*Pinus sylvestris*) ranged between 10 and 15 years, suggesting that the optimal age for selection occurs earlier for fast-growing than for slow-growing tests.

In contrast to these studies, our study is based on clonal trials on a long-rotation species, Norway spruce (*Picea abies* [L.] Karst.). To our knowledge, there are only four studies on age–age correlations and early selection for

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height growth in *P. abies*. Huehn and Kleinschmit (1993) estimated phenotypic age–age correlations for five clones planted at five test sites. Danusevicius et al. (1999), Soneson et al. (2002), and Karlsson et al. (2002) raised seedlings in growth chambers under various treatments and then compared them with 10+-year-old progenies in field tests derived from the same seed orchard in Sweden. In these studies, age–age correlations between the growth chamber and field materials were generally weak and inconsistent, and the authors recommended further research for more efficient early selection methods for the species.

We used data from *P. abies* clonal tests, including 40 clones established on seven test sites. The growth performance and survival of these clones were analyzed in two earlier studies (StClair and Kleinschmit 1986, Isik et al. 1995). The present study is based on data from trees surviving for 17 years after rooting and examines age–age correlations and early selection for height growth. The specific objectives of the study were to describe age trends in variance components and heritabilities for height growth, estimate age–age genetic and phenotypic correlations, and estimate gain efficiencies and the optimal age for early selection in breeding programs of the clonally propagated *P. abies* population started in Germany (Kleinschmit 1974, Kleinschmit and Schmidt 1977).

Materials and Methods

Experimental Materials

The selection, breeding, and large-scale propagation programs of *Picea abies* (L) Karst in Germany have been described in detail by Kleinschmit et al. (1973), Kleinschmit (1974), and Kleinschmit and Schmidt (1977). The plant materials were ramets (rooted cuttings) of 40 selected clones (ortets) in the program. The clones originated from 13 provenances that represented selected and registered seed stands used in Germany (Kleinschmit 1974). The cuttings were derived from the third cycle of vegetative propagation. The best clones from each provenance were selected at each propagation cycle based on nursery and field performance for height growth at age 4 (StClair and Kleinschmit 1986). When the program started in 1968, there were about 20,000 clones in the breeding population. By following repeated selection and repropagation, the numbers of remaining clones decreased, whereas the numbers of ramets per clone increased (Kleinschmit 1974, Kleinschmit and Schmidt 1977). Because the 13 provenances were sufficiently separated from each other and because the initial number of clones in the program was so high, the probability of coancestry between ortets is rather low. Initially, height growth was the primary focus, with a selection intensity of 1 plant in 1,000. At later stages of the program, traits such as flushing time, disease resistance, and cold hardiness were also considered (Kleinschmit 1974). The 40 clones used in this study are the result of this truncation selection (Kleinschmit 1974, StClair and Kleinschmit 1986).

Cuttings were rooted in the spring of 1974 in the nursery, and the rooting percentage was >90% (Kleinschmit 1974). The ramets were transplanted to the nursery until they were

outplanted in the spring of 1977 at seven test sites. The test sites were located in different forest districts in northern Germany (P, Paderborn [Paderborn]; H, Holzminden [Neuhaus]; L, Lautenthal [Seesen]; S, Syke [Hasbruch]; B, Binnen [Nienburg]; M, Medingen [Goehrde]; and K, Kattenbuehl [Kattenbuehl]). The test sites were chosen to represent the range of environments where *P. abies* might be planted in the future. Three of the test sites (S, M, and B) are located in the low coastal plains between 39 and 50 m elevation, whereas the other four (P, K, H, and L) are located farther south at elevations between 340 and 575 m. A location map and description of the test sites are presented in StClair and Kleinschmit (1986), Isik et al. (1995), and Isik and Kleinschmit (2005). The initial spacing between trees was 2×2 m at all the test sites. The experimental design at each test site was a single-tree plot randomized complete block design with 20 blocks.

Total heights (HT) of all trees at the test sites were measured at ages 3, 5, 8, 10, 13, and 17 years from rooting. The measurement just after planting in spring 1977 was considered as HT3 (cm) (i.e., height at age 3). HT5 (age 5) refers to the height on the test sites at the end of the 1978 growing season. Diameters at breast height were measured at age 17 (dbh17, mm). Volume index (VI17, dm³) values for the same age were calculated according to $VI = (dbh/2)^2 \times HT \times 3.1416$ (Isik et al. 1995). Only trees surviving to age 17 were included in the analyses so that the numbers of observations at different measurement ages are equal. The overall average survival rate at the latest measurement age was 84% (Isik et al. 1995). These data were checked for errors, and outliers, if any, were excluded from the analyses. No transformations were applied to the data.

Statistical Analysis

Variance and Covariance Estimates

The following model was fitted to the data to estimate variance and covariances:

$$Y_{ijk} = \mu + S_i + C_j + CS_{ij} + e_{ijk}, \quad (1)$$

where Y_{ijk} is the k th tree (ramet) of the j th clone at the i th site, μ is the overall mean, S_i is the random effect of the i th site $\sim \text{NID}(0, \sigma_s^2)$ ($i = 1, \dots, s$; $s = 7$, site), C_j is the random effect of the j th clone $\sim \text{NID}(0, \sigma_c^2)$ ($j = 1, \dots, c$; $c = 40$), CS_{ij} is the random effect of the interaction between the i th site and j th clone $\sim \text{NID}(0, \sigma_{cs}^2)$, e_{ijk} is the random (within clone) error term $\sim \text{NID}(0, \sigma_e^2)$ ($k = 1, \dots, n$; where initial $n = 20$). The block effect is not included in the model because initial analyses showed that there were no significant differences among blocks.

The model above can also be given in a matrix format,

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}, \quad (2)$$

where \mathbf{y} is the column vector of individual phenotypic values for a response variable, \mathbf{X} is the incidence matrix of fixed effects (overall mean or the intercept) and $\boldsymbol{\beta}$ is the column vector of fixed effects, \mathbf{Z} is the incidence matrix of random effects, \mathbf{u} is the column vector of random site, clone, and clone \times site interaction effects with expected

zero mean $\mathbf{E}(\mathbf{u}) = 0$, and \mathbf{e} is the column vector of residuals assumed to be randomly and independently distributed with expected zero mean $\mathbf{E}(\mathbf{e}) = 0$. The covariance matrix \mathbf{V} for the vector of observations \mathbf{y} is $\mathbf{V} = \mathbf{ZGZ}^T + \mathbf{R}$ (Little et al. 1996), where \mathbf{G} is the genetic covariance matrix of random genetic effects, \mathbf{R} is the diagonal matrix of residual errors, and \mathbf{Z}^T is the transpose of the design matrix (Lynch and Walsh 1998).

The univariate model (in Equation 2) can be expanded to define a bivariate mixed model to estimate genetic covariances or genetic correlations between traits. Similar to the univariate mixed model, the variance of the bivariate model (two response variables) would be $\text{Var}(\mathbf{y}_i) = \mathbf{ZGZ}^T + \mathbf{R}_i + \mathbf{\Sigma}$. The covariance matrix of residuals includes the variances of random residual errors associated with two traits ($\sigma_{e1}^2, \sigma_{e2}^2$) but the off diagonal elements would be zero. When two traits are perfectly correlated, then $\mathbf{e}_i \sim N(0, \mathbf{\Sigma})$ (Verbeke and Molenberghs 2000). The covariance matrix of random effects includes genetic variances ($\sigma_{G1}^2, \sigma_{G2}^2$) in the diagonal for two traits. The off diagonal elements would be genetic covariances (σ_{G12}) or genetic correlations between two traits (Verbeke and Molenberghs 2000, Thiebaut et al. 2002). The RANDOM statement in the SAS Mixed procedure (SAS Institute, Inc. 1996) was used to define the \mathbf{G} matrix, and the REPEATED statement was used to build the residual covariance matrix $\mathbf{\Sigma}$ (Fikret Isik, pers. comm. North Carolina State University, Raleigh, NC, Jan. 27, 2007).

Because the ramets of a given clone are identical genotypes, variance due to clones (σ_C^2) is assumed equal to the total genetic variance (σ_G^2). Using variance components from the mixed model, individual-tree phenotypic variance (σ_P^2), phenotypic variance of clone means (σ_{Pc}^2) and repeatability of clone means (or clone-mean heritability, σ_e^2) for all traits were estimated according to

$$\sigma_P^2 = \sigma_c^2 + \sigma_{sc}^2 + \sigma_e^2, \quad (3)$$

$$\sigma_{Pc}^2 = \sigma_c^2 + \sigma_{sc}^2/s + \sigma_e^2/sk_1, \quad (4)$$

$$H_{\bar{c}}^2 = \sigma_c^2/\sigma_{Pc}^2, \quad (5)$$

where σ_{sc}^2 is the clone \times site interaction variance, σ_e^2 is the error variance, and $k_1 = 16.8$ is the mean number of trees (ramets) per clone per site. Standard errors of the repeatabilities of clone means were estimated using the Delta method (Lynch and Walsh 1998) and implemented with a SAS IML code (Fikret Isik, pers. comm., North Carolina State University, Raleigh, NC, Jan. 27, 2007).

Juvenile–Mature Correlations

When a given trait of the same genotype is measured at two different ages (juvenile [J] and mature [M]), correlations between the ages concerned are called “age–age” correlations. Depending on the relative status of the “later” age, the terms “juvenile–mature,” “younger age–older age,” “early age–target age,” or “early age–rotation age” have also been used in the literature. The age–age total genetic

correlation coefficients between different ages for height were estimated using

$$r_{GJM} = \sigma_{GJM} / \sqrt{\sigma_{GJ}^2 \sigma_{GM}^2}, \quad (6)$$

where σ_{GJM} is genetic covariance between the same trait measured at juvenile and mature ages and σ_{GJ}^2 and σ_{GM}^2 refer to genetic variances at the juvenile and mature ages, respectively. The respective variance-covariance values for each pair of different ages were estimated by the MIXED procedure of SAS (SAS Institute, Inc. 1996), according to the bivariate model explained above. The equation used to calculate phenotypic age–age correlations is similar to that given in Equation 6, except that the subscript G is replaced by the subscript P. We used the CORR procedure of SAS to calculate Pearson product-moment estimates of phenotypic correlations. Regression slopes were compared according to Sokal and Rohlf (1995, p. 495–498).

Because a juvenile height (for example, HT3) contributes to variation in the mature height (e.g., HT5, ..., HT17), a juvenile height–mature height (HT_J–HT_M) correlation may exist purely due to autocorrelation (Lambeth et al. 1983), because of the similarity of the two variables and their being adjacent in space and time. Therefore, we also calculated the correlation between a younger-age height (HT_J) and subsequent height increments (I_M) to older ages. For example, the 2-year increment from HT3 to HT5 (i.e., I5 = HT5 – HT3) or the 5-year increment from HT3 to HT8 (i.e., I8 = HT8 – HT3) (Table 1).

Genetic Gains and Selection Efficiencies

Gain due to direct selection on the mature trait (G_M) was expressed as

$$G_M = i_M H_{cM}^2 \sqrt{\sigma_{PcM}^2}. \quad (7)$$

Correlated (predicted) gain in the M trait based on indirect selection on the J trait (CG_{M-J}) is

$$CG_{M-J} = i_J H_{cJ} H_{cM} r_{GJM} \sqrt{\sigma_{PcM}^2}, \quad (8)$$

where i_J and i_M are the selection intensities, and H_{cJ} and H_{cM} are the square roots of the repeatabilities of clone means at J and M ages, respectively. We assumed that $i_J = i_M = 1.365$, which corresponds to 20% selection intensity. Gain per year from direct selection at the mature age is $G_{MPY} = G_M/T_M$, and the correlated gain per year from indirect selection is $CG_{M-JPY} = CG_{M-J}/T_J$, where $T_J = J + t$ is the generation interval for juvenile selection (where J = 3, 5, ..., and 17 years), $T_M = M + t$ = the generation interval for mature selection (where any older age M > any younger age J; maximum M in this study = 17), and t = additional years to complete the breeding cycle. We assumed that the next generation could be established 7 years after juvenile selection. Therefore, $t = 7$ years was included in the generation intervals T_J and T_M to account for the phase to complete the breeding cycle.

Selection efficiency (SE_{GPy}) is simply the ratio of gain per year between indirect selection and direct selection (Lambeth 1980, Xie and Ying 1996, Falconer and Mackay

Table 1. Estimates of genetic and phenotypic parameters in *P. abies*

Character ^a	HT3	HT5	HT8	HT10	HT13	HT17	dbh17	VI17
A. age-age genetic (r_{GJM} , below diagonals) and phenotypic (r_{PJM} , above diagonals) correlations, and repeatabilities (H_c^2 , on the diagonals)								
HT3	0.94 (0.015)	0.82 ^b	0.38	0.30	0.31	0.31	0.22	0.31
HT5	0.85 (0.052)	0.91 (0.023)	0.74	0.65	0.59	0.56	0.54	0.60
HT8	0.40 (0.147)	0.75 (0.078)	0.91 (0.023)	0.87	0.79	0.77	0.78	0.81
HT10	0.31 (0.156)	0.67 (0.096)	0.88 (0.040)	0.91 (0.023)	0.96	0.91	0.84	0.89
HT13	0.32 (0.156)	0.61 (0.111)	0.81 (0.061)	0.97 (0.011)	0.92 (0.021)	0.98	0.86	0.91
HT17	0.33 (0.154)	0.59 (0.115)	0.79 (0.066)	0.93 (0.026)	0.98 (0.007)	0.93 (0.019)	0.84	0.89
dbh17	0.22 (0.160)	0.55 (0.119)	0.80 (0.067)	0.85 (0.049)	0.86 (0.048)	0.83 (0.055)	0.92 (0.020)	0.97
VI17	0.32 (0.152)	0.62 (0.106)	0.83 (0.056)	0.91 (0.032)	0.92 (0.029)	0.90 (0.034)	0.98 (0.009)	0.92 (0.020)
B. genetic correlations between the HT _J at the younger age and height increment, I _M (I5–I17), between the younger age and the older age measurements								
I5	0.06							
I8	0.13	0.53						
I10	0.15	0.54	0.48					
I13	0.20	0.51	0.59	0.86				
I17	0.23	0.51	0.67	0.83	0.90			

The repeatability value for a given character is given in bold italics on the diagonal. Values in parentheses are SE for the corresponding parameters.

^a See the text (Material and Methods) for abbreviations of the characters.

^b Significance levels for r_{PJM} values above diagonals: $r_{0.05,38} = 0.312$; $r_{0.05,38} = 0.403$.

1996, Jansson et al. 2003, Xiang et al. 2003). If we assume that $i_j = i_M$,

$$SE_{GPY} = CG_{M-JPY}/G_{MPY} = [(H_{cJ} r_{GJM})/(H_{cM})] \cdot [T_M/T_J]. \quad (9)$$

Lambeth Model to Predict Juvenile–Mature Correlations

Genetic correlations between earlier ages J and older ages M until age 17 were predicted using the methods of Lambeth (1980). We analyzed our data using the regression model $r_{GJM} = a + b$ (log of age ratio [LAR]) and used the estimated intercept (a) and slope (b) to predict age–age genetic correlations (r_{GJM}) for all pairs of ages from age 3 to rotation age. The rotation age for unimproved *P. abies* is approximately 80 years, and it is expected to be approximately 60 years for genetically improved planting stock. SE_{GPY} was estimated for all pairs of predicted correlations using Equation 9. Observed H_{cJ}^2 values were used in calculations until age 15. Thereafter we assumed that $H_{cM}^2 = 0.92$, because it was essentially stable after age 3 (Table 1).

Selection Efficiency Assessment

Estimation of correlated gain (CG_{M-J}) and SE_{GPY} become more precise when the maximum measurement age becomes closer to the rotation age (see Equations 8 and 9). In the current study, the maximum measurement age (l) was 17 years, about one-fourth of the rotation age. To assess the precision of using an earlier age instead of using rotation

age, we used (Xiang et al. 2003, Jansson et al. 2003),

$$\frac{r_{GJM}}{r_{GJl}} = 1 - b \ln\left(\frac{M}{l}\right) / r_{GJl}, \quad (10)$$

where r_{GJM} is the genetic correlation between the juvenile age and the rotation age and r_{GJl} is the genetic correlation between the juvenile and maximum measurement (testing) ages. When applied to this study (i.e., $l = 17$ years and $M = 60$ years), the equation becomes

$$\frac{r_{GJM}}{r_{GJl}} = \frac{r_{GJ60}}{r_{GJ17}} = 1 - b \ln\left(\frac{60}{17}\right) / r_{GJ17} = 1 - 1.2611b/r_{GJ17}. \quad (11)$$

If the ratio from Equation 11 remains approximately constant over age J, then selection efficiency criteria, i.e., SE_{GPY} , should provide reasonable comparisons among early selections (Jansson et al. 2003).

Results and Discussion

Estimates of Genetic Parameters

There were significant differences among the clones and among the test sites for height, dbh, and volume index (StClair and Kleinschmit 1986, Isik et al. 1995). The range in average clone height at age 17 was 530 to 749 cm. The overall mean at all test sites was 648 cm.

For total height, the proportion of variance due to sites (σ_s^2) increased steadily from the 3rd to the 8th year (Figure 1). All the other variance components decreased steadily,

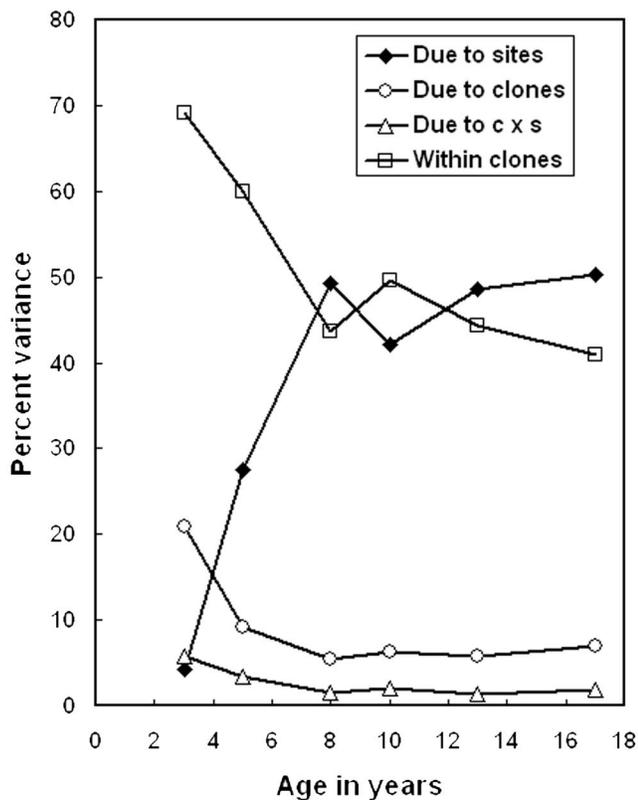


Figure 1. Age trends in variance components for total height in *P. abies*.

each becoming more or less stable after age 8 (the contribution to total variance was approximately 7% for clones and approximately 50% for sites). Genotype \times environment (clone \times site) interaction (σ_{CS}^2) was quite small (i.e., 1.92% of total variance) (Figure 1). These trends are similar to those reported by Huehn et al. (1987) and Isik et al. (1995). Consequently, clone-mean heritability decreased from 0.94 at age 3 to 0.91 at age 5, after which it remained within a narrow range of 0.91 to 0.93 (Table 1, bold italics on diagonal). These results indicate that substantial genetic gain can be obtained through selection of desirable clones.

Variance among clones (σ_C^2) is primarily due to genetic differences among them, and it can be regarded as an estimate of genetic variance (σ_G^2). Genetic variance can be further partitioned into additive (σ_A^2), and nonadditive genetic (σ_D^2 = dominance; σ_I^2 = interaction) components (Falconer and Mackay 1996). Among the components of σ_G^2 , σ_A^2 , being the variance of the breeding value and the primary cause of resemblances between relatives, is typically used in the estimation of genetic parameters. However, estimation of σ_A^2 in clonal tests requires specific experimental designs such as those using a family structure with clonally replicated families, usually involving a combination of clonal tests and progeny tests (Foster and Shaw 1988, Mullin et al. 1992). For example, Isik et al. (2003) estimated the additive, dominance, and epistatic (interaction) portions of genetic variances from a clonally replicated test of loblolly pine families. They found that the major source of σ_G^2 for growth traits was σ_A^2 , whereas σ_I^2 and σ_D^2 effects seemed to have no significant role. Similarly, Costa e Silva et al. (2004) estimated that the σ_A^2 was the only

significant genetic component affecting diameter growth in *Eucalyptus globulus*. The experimental design in this study did not allow separate estimates of σ_A^2 , because the clonal tests did not include any seedling progeny tests. As a result, we assumed that $\sigma_G^2 = \sigma_C^2$ and used σ_G^2 instead of σ_A^2 in this study. Theoretically, this strategy may lead to overestimates of genetic parameters. However, the relatively small contribution of nonadditive genetic variance to σ_G^2 , as reported by Isik et al. (2003) and Costa e Silva et al. (2004), suggests that the upward bias that arises by using σ_G^2 instead of σ_A^2 is unlikely to be significant.

C Effects

Our assumption that $\sigma_G^2 = \sigma_C^2$ could also be questioned in the context of C effects, because ramets derived from the same genotype may perform differently when grown in field conditions. Such nongenetic factors (arising due to cyclophysis, topophysis, and periphysis) are common to members of a clone and are referred to as C effects (Frampton and Foster 1993). C effects may also cause inflated values for variance components and other genetic parameter estimates (Burdon and Shebourne 1974, Foster et al. 1984, Cannell et al. 1988, Frampton and Foster 1993). Fortunately, problems associated with C effects can be reduced over time through procedures such as hedging, cytokinin application, and serial propagation (via rooted cuttings and in vitro micropropagation) (Libby and Hood 1976, StClair et al. 1985, Cannell et al. 1988, Frampton and Foster 1993). Cannell et al. (1988) reported that C effects may be important only in short-term clonal tests, and in second-cycle tests it accounted for less than 1% of the total variation in 5th year height of both *Picea sitchensis* and *Pinus contorta*. StClair et al. (1985), working on *P. abies*, concluded that serial vegetative propagation considerably slowed and perhaps arrested maturation processes and associating C effects. The clones used in our study were serially propagated (third cycle) and had undergone intense selection. In addition, clonal variance accounted for only about 7% of the total variance (Figure 1), which suggests that C effects among clones were unlikely to be important. We therefore assumed that C effects among and within clones in this study are absent or negligible, and the consequent bias of genetic parameters is not significant.

Age-age Genetic and Phenotypic Correlations

Genetic and phenotypic correlations were about equal (Table 1). Age-age correlations were always positive, and genetic correlations were almost always higher than the corresponding phenotypic correlations, which is consistent with results from other species (e.g., Cotterill and Dean 1988, Pswarayi et al. 1996, Gwaze et al. 2001). Genetic and phenotypic age-age correlations showed steady declines as pairs of measurement ages became more separate in time. For example, HT3 was significantly correlated with HT5 ($r_{GJM} = 0.85$), but poorly correlated with HT17 ($r_{GJM} = 0.33$) (Table 1). It appears that this steady decline originates from the relatively larger rate of increase in the variance of

the mature trait (i.e., σ_{GM}^2) compared with the rate of increase in the covariance of the same trait measured at juvenile and mature ages (i.e., σ_{GJM}) as the trees become older and larger (see Equation 6).

Genetic correlations between height at the younger age (HT_J) and height increment to the older age (I5, I8, ..., I17) (Table 1) were lower than the corresponding genetic HT_J - HT_M correlations (Table 1). The gaps (differences) between these two types of genetic correlations were particularly large whenever HT3 was involved. For example, the genetic correlation between HT3 and HT5 is 0.85 (Table 1), whereas the genetic correlation between HT3 and I5 (i.e., the height increment from HT3 to HT5) (Table 1) is only 0.06. The trend of having considerably smaller values of the genetic correlations between HT_J - I_M compared with those corresponding age-age correlations suggests that the variance associated with HT_J has a significant contribution to the HT_J - HT_M (juvenile age-older age) correlations. This occurs because the genetic correlation between HT_J - HT_M can be partitioned into two contributing parts: the variance of juvenile height (σ_{GJ}^2) and the covariance (σ_{GJM}) between the juvenile height and increment to older age (Langbeth et al. 1983, p. 211). Another reason for the relatively lower values of HT_J - I_M correlations (in Table 1) may be the relatively smaller values of genetic covariance between HT_J - I_M compared with that of HT_J - HT_M (see Equation 6).

For traits other than HT3, genetic correlations involving height and height increment were not greatly different from the corresponding HT_J - HT_M correlations. For example, HT5-HT10 genetic correlation is 0.67 (Table 1), whereas HT5-I10 genetic correlation is 0.54 (Table 1). The relative differences in HT_J - HT_M correlations and the corresponding HT_J - I_M correlation gradually diminish as the age J approaches age M. These results suggest that the gains achieved by making a selection based on HT_J - HT_M correlations at an early age are slightly overestimated. The results also showed that the relationships between HT3 and increments in later years are weak compared with those of other years. Therefore, a juvenile height immediately after planting is a relatively unpredictable indicator of subsequent

height increments, probably due to nursery effects and transplant shock.

Height at age 13 showed greater genetic correlations with diameter (0.86) and volume (0.92) than with HT at other ages (Table 1). Gwaze et al. (2001) reported similar trends between height and diameter in *P. taeda*. This finding indicates that early selection for height will also be efficient for improving diameter and volume traits.

Prediction Model, Selection Efficiencies, and Optimal Age for Early Selection

Lambeth (1980) suggested that correlations involving very young ages (usually 1–3 years in the field) with all subsequent ages should be excluded from the regression equation, because such correlations were usually lower than the expected trend of correlations between later ages. The prediction equation he developed is $r_{PJM} = 1.02 + 0.308 \times \text{LAR}$ (Lambeth 1980).

In our study we applied the regression models, both including and excluding the age 3 data (Table 2, Figure 2). Both phenotypic and genetic age-age correlations were linearly related to LAR (Table 2; Figure 2). Both regression equations were very similar to the prediction equation of Lambeth (1980). The equations using phenotypic and genetic correlations in our study were also quite similar for the data sets that included or excluded age 3 data (Table 2). The linear relationships were highly significant for both data sets with $R^2 \geq 0.756$.

The Lambeth model is useful in many situations (e.g., McKeand 1988, Riemenschneider 1988, Vargas-Hernandez and Adams 1992, Gwaze et al. 2001). Several researchers have used both phenotypic (r_{PJM}) and genetic correlations (r_{GJM}) in the Lambeth prediction model (Cotterill and Dean 1988, Riemenschneider 1988, Burdon 1989, Xie and Ying 1996, Lambeth and Dill 2001). In this study, we used the prediction equation with genetic correlation value (r_{GJM}) as shown in Table 2 (i.e., $r_{GJM} = 1.0231 + 0.3837 \times \text{LAR}$). This equation was obtained by excluding age 3 data. We excluded the age 3 data, because four of the five correlation

Table 2. Regression models produced by different sets of data in *P. abies* to estimate genetic and phenotypic correlations between heights measured at a younger age (J) and at an older age (M)^a

Type of correlation	Regression equation: $r_{JM} = a + b(\text{LAR})$	<i>P</i>	<i>R</i> ²
A. Measurements of all ages are included, <i>N</i> = 15			
Genetic	$r_{GJM} = 1.0541 + 0.4779(\text{LAR})$ (0.053) (0.059)	0.0001	0.834
Phenotypic	$r_{PJM} = 1.0395 + 0.4817(\text{LAR})$ (0.052) (0.058)	0.0001	0.841
B. Measurements where age 3 are excluded, <i>N</i> = 10			
Genetic	$r_{GJM} = 1.0231 + 0.3837(\text{LAR})$ (0.051) (0.077)	0.0011	0.756
Phenotypic	$r_{PJM} = 1.0179 + 0.4039(\text{LAR})$ (0.050) (0.076)	0.0007	0.779
C. Only age 3 measurements are included, <i>N</i> = 5			
Genetic	$r_{GJM} = 0.9323 + 0.4157(\text{LAR})$ (0.191) (0.153)	0.0724	0.712
Phenotypic	$r_{PJM} = 0.8983 + 0.4029(\text{LAR})$ (0.216) (0.103)	0.0747	0.706

^a *a* and *b* in the regression models are coefficients estimated from actual data. Values in parentheses below each equation are SEs for the corresponding coefficients. The last two columns show the results of the test of significance for regression: *P*, significance level; *R*², coefficient of determination.

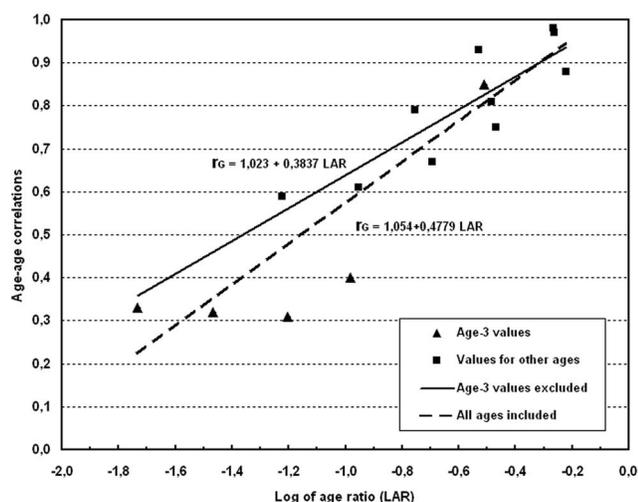


Figure 2. Relationships of LAR to age–age genetic correlations (r_{GJM}) for height in *P. abies*. LAR, natural logarithm of the ratio of younger age to older age.

coefficients involving age 3 were notably low (Table 1) and formed a separate cluster on the lower left part of the plot (Figure 2). In addition, the proportion of variance components involving age 3 deviated considerably from the general trend of other ages (Figure 1). However, it should be noted that the prediction equation including all ages was very similar to the equation excluding age 3 data (Table 2, Figure 2).

Based on actual data at the measurement ages, we estimated absolute gains, genetic correlations, and selection efficiencies (Table 3). The predicted r_{GJM} and SE_{GPY} values in Table 3 are slight overestimations, because the intercept (a) in the prediction equation is slightly larger than unity (i.e., $1.0231 > 1.0$). Kang (1985) noted that the intercept in the prediction equation should be 1.0; otherwise the model will be discontinuous when $J = M$ [i.e., when $\log(J/M) = 0.0$]. Yet, this value is only slightly different from 1.0 both in the Lambeth model ($a = 1.02$) and in other studies. For example, in this study a is equal to 1.023, whereas it is 1.07, 1.10, and 1.00 in Riemenschneider (1988), Xie and Ying (1996), and McKeand (1988), respectively.

Our results based on empirical values show that the highest selection efficiency per year (SE_{GPY}) was 1.30, which indicates that the optimum selection age to predict height at the target age of 17 years was age 10 (Table 3).

Similarly, application of the Lambeth prediction method to our data showed that the highest per year gain was 1.17 and the corresponding optimum selection age was age 8 (Table 3). These values show that the Lambeth equation predicts a slightly earlier optimum selection age than that indicated by our observed selection efficiency value. Observed r_{GJM} (i.e., 0.79) between age 8 and age 17 was relatively high, which indicates that age 8 could also be a good predictor of height at target age 17 (Table 3).

Burdon (1989) suggested that, in the absence of empirical data, the best approach is to adopt the Lambeth model for extrapolating age–age correlations to rotation age to project gains from early selection. The efficiency of early selection in relation to direct selection at rotation age can be estimated using the extrapolated age–age genetic correlations based on the Lambeth model. Thus, we estimated genetic age–age correlations, per-year selection efficiencies of early selection, and optimum selection ages for various target ages (Table 4). When the rotation (or target) age is assumed to be 60 years, for example, the expected selection efficiency per year is maximized by selecting at age 17 ($SE_{GPY} = 1.51$). However, for a rotation age of 60 years, selection can also be made as early as age 13 ($SE_{GPY} = 1.46$) (Table 4). Results for three different target ages (age 60 [presented also in Table 4], age 30, and age 90 [both of which are not in Table 4]) are illustrated in Figure 3, which shows trends in selection efficiencies per year (from Equation 9).

Increasing the length of the breeding phase (t) slightly delays the optimum selection age. For example, in a rotation age of 60 years, the optimum selection age is 15 years when $t = 4$, and 19 years when $t = 10$. For the same rotation age, t values of 5 through 9 would all predict the same optimum selection age of 17 years. This trend is also apparent from the almost flat plateau around the highest point in Figure 3. These results concur with those of Jansson et al. (2003) on Scots pine who reported that prolongation of the breeding cycle by 4 years delayed the optimum selection age by 2 years.

Some general trends can be extrapolated from Figure 3 and Table 4. First, efficiency curves for each target age initially increase sharply, plateau at a maximum, and then gradually decline, finally approaching unity when the selection age (J) approaches to the target age (M). Second,

Table 3. Observed and predicted genetic correlations (r_{GJM}), predicted gains ($CG_{M,J}$), and selection efficiency (SE_{GPY}) values for the older age ($M = 17$), based on measurements at a younger age (J)

J ^a	M	r_{GJM}		$CG_{M,J}$ (cm)	SE_{GPY}	
		Observed	Predicted ^b		Observed	Predicted ^c
3	17	0.33	0.36	21.63	0.80	0.86
5	17	0.59	0.55	38.05	1.17	1.10
8	17	0.79	0.74	50.95	1.25	1.17
10	17	0.93	0.82	59.98	1.30	1.15
13	17	0.98	0.92	63.55	1.17	1.10
17	17	1.00	1.02	65.19	1.00	1.03

^a J = age from rooting (in years).

^b According to the regression model in Table 2, B, Genetic.

^c According to Equation 9, using predicted r_{GJM} .

Table 4. Predicted genetic correlation (r_{GJM}) and selection efficiency (SE_{GPY}) values for various selection (juvenile) and mature ages

Selection age, J (yr) ^a	Mature (or target) age, M									
	40 yr		50 yr		60 yr		70 yr		80 yr	
	r_{GJM}	SE_{GPY} ^b	r_{GJM}	SE_{GPY} ^b	r_{GJM}	SE_{GPY} ^b	r_{GJM}	SE_{GPY} ^b	r_{GJM}	SE_{GPY} ^b
8	0.41	1.26								
9	0.45	1.32	0.37	1.29						
10	0.49	1.35+	0.41	1.35						
11	0.53	1.37	0.44	1.39+	0.37	1.38				
12	0.56	1.38	0.47	1.42	0.41	1.42	0.35	1.40		
13	0.59	<u>1.39</u>	0.51	1.44	0.44	1.46+	0.38	1.45	0.33	1.42
14	0.62	1.38	0.53	1.45	0.46	1.48	0.41	1.49+	0.35	1.47
15	0.65	1.38	0.56	<u>1.46</u>	0.49	1.49	0.43	1.51	0.38	1.51+
16	0.67	1.37	0.59	1.45	0.52	1.50	0.46	1.53	0.40	1.53
17	0.69	1.37	0.61	1.45	0.54	<u>1.51</u>	0.48	1.54	0.43	1.56
18	0.72	1.35	0.63	1.44	0.56	1.50	0.50	1.54	0.45	1.57
19	0.74	1.33+	0.65	1.43	0.58	1.49	0.52	<u>1.55</u>	0.47	1.58
20	0.76	1.31	0.67	1.42	0.60	1.49	0.54	1.54	0.49	1.58
21	0.78	1.30	0.69	1.41	0.62	1.48	0.56	1.54	0.51	<u>1.59</u>
22			0.71	1.39+	0.64	1.47	0.58	1.53	0.53	1.58
23			0.73	1.38	0.66	1.46	0.60	1.53	0.54	1.58
24			0.74	1.36	0.67	1.45	0.61	1.52	0.56	1.57
25					0.69	1.44+	0.63	1.51	0.58	1.57
26					0.70	1.43	0.64	1.50	0.59	1.56
27					0.72	1.41	0.66	1.49	0.61	1.55
28							0.67	1.48+	0.62	1.54
29							0.68	1.46	0.63	1.53
30							0.70	1.45	0.65	1.52
31									0.66	1.51+
32									0.67	1.50
33									0.68	1.49

^a J = age from rooting, $t = 7$ (in years).

^b Optimum SE_{GPY} within each column is underlined. Values with a + sign (and the values between two + signs in a given column) are larger than 95% of the optimum SE_{GPY} in a given column.

maximum efficiencies and corresponding optimum selection ages increase as the target age increases. Third, to determine the optimum selection age for any target age, any point within 95% of the maximum value in the efficiency curve is nearly as efficient as the maximum. For example, for target age 60, selection age could be any age between age 13 and age 25 years (Table 4). Finally, the genetic correlation corresponding to the maximum efficiency decreases as the target age increases. These trends are consistent with those found by Lambeth (1980).

We calculated the age correlation ratio (r_{GJ60}/r_{GJ17}) from Equation 11 and plotted the results against age (Figure 4). The correlation ratio remains fairly constant over age 10. In other words, the ratio difference between age 17 and age J is becoming progressively smaller as the earlier measurement age (J) approaches the maximum measurement age (I). This trend was true for three different values of b in our study, which means that the selection criteria appear to be appropriate for ages after 10 years. Jansson et al. (2003) applied the same equation and determined that the optimal ages for selection on *P. sylvestris* were between 10 and 15 years. At this age the heights of trees ranged from 3 to 5 m. The average size of the clones in our study was about 650 cm at the latest measurement age (age 17 from rooting).

Our data include a broad genetic base and seven test sites, both of which are representative of populations and probable planting sites of *P. abies* in northern Germany.

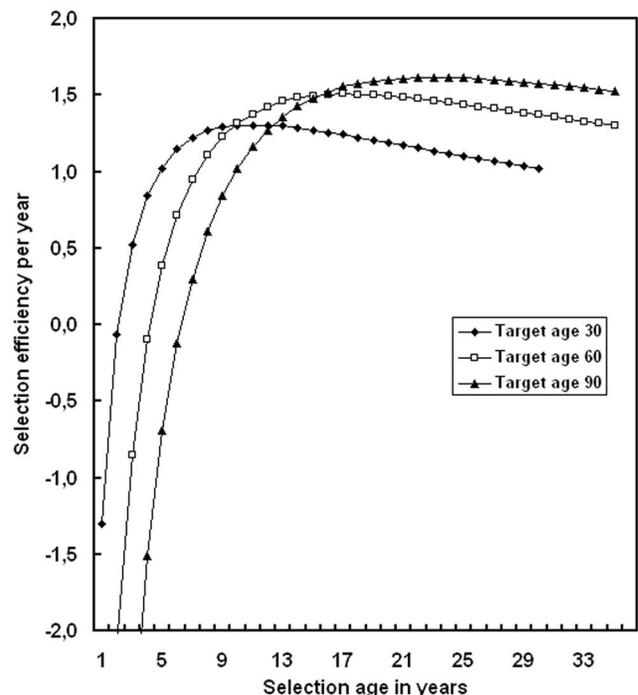


Figure 3. Trends in selection efficiency per year (SE_{GPY}) in relation to selection age for target ages of 30, 60, and 90 years.

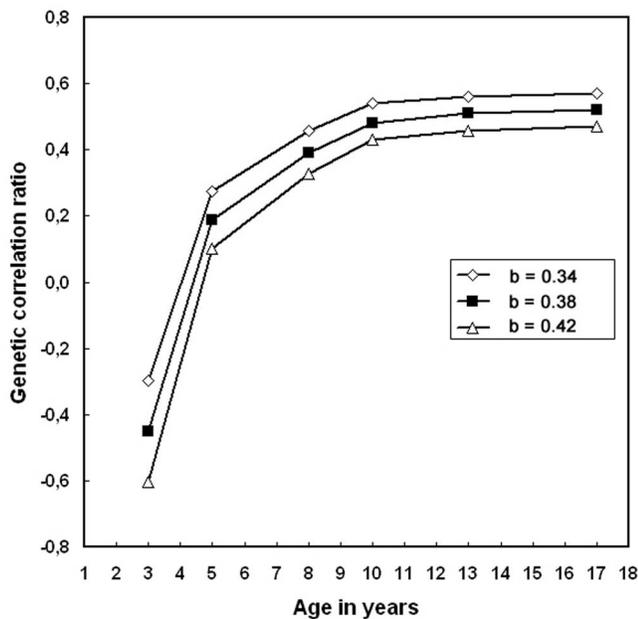


Figure 4. Genetic correlation ratio (r_{GJ60}/r_{GJ17}) estimated for height, with values of b ranging from 0.34 to 0.42.

Furthermore, a recent study on the same data by Isik and Kleinschmit (2005) indicated that clones (genotypes) screened and selected on the test site M could be planted efficiently on the other test sites without significant loss in genetic gains. Therefore, our results can be used in future selection and genetic improvement programs for this species. However, there are some limitations regarding the model and the underlying assumptions. First, we assumed that the clone-mean heritability remained more or less constant after the latest measurement age (i.e., age 17). Second, we assumed that the selection intensities at the juvenile and mature ages were equal ($i_J = i_M$). Because selection at juvenile ages may be more intense than that at mature ages ($i_J \geq i_M$), this assumption causes an underestimation of SE_{GPY} and an overestimation of the optimum selection age (Lambeth 1980). Third, we assumed that juvenile–mature correlations as predicted by the Lambeth model are also applicable to later measurement ages. Finally, we assumed that the nonadditive portion of the genetic variance among clones (and also C effects) is negligible or absent. These concerns are also shared by other researchers (e.g., Lambeth 1980, Kang 1985, Cotterill and Dean 1988, Riemenschneider 1988, Gwaze et al. 2000, Isik et al. 2003). Because early selection in tree breeding will save both time and money, there have been consistent efforts to develop new models to better predict the genetic parameters needed (e.g., Kang 1985, Burdon 1989, Huehn and Kleinschmit 1993, Frampton and Foster 1993, Woods et al. 1995, Lambeth and Dill 2001, Chen et al. 2003, Xiang et al. 2003).

Conclusions

Clone-mean heritability and variation in height growth were high among *P. abies* clones. Therefore, substantial genetic gain is expected through selection of desirable clones in this species. Observed age–age correlations were strong and always positive. Regression equations to predict

genetic correlations at ages beyond the measurement years were in close agreement with the Lambeth model (Lambeth 1980). Results from clonal data at age 17 years indicated that, under reasonable assumptions, early selection for height is effective in this species. For a rotation age of 60 years, selection efficiency per year was maximized by selecting at age 17, possibly even as early as age 13. The economic rotation age in *P. abies* is much longer than that in most species in the Pinaceae. As the target (rotation) age moves away from the last measurement age (i.e., in case of extreme extrapolations), the accuracy of prediction becomes less reliable because of the inherent nature of the regression model. It remains to be seen whether the Lambeth relationships will still be applicable, and the trends reported here still be evident, as data from later ages are also included in the analyses.

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