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Predicting age-age genetic correlations in tree-breeding programs: a case study of *Pinus taeda* L.

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Abstract A meta-analysis of 520 parents and 5 1,439 individuals was used to develop two equations for predicting age-age genetic correlations in *Pinus taeda* L. Genetic and phenotypic family mean correlations and heritabilities were estimated for ages ranging from 2 to 25 years on 31 sites in the southern U.S. and Zimbabwe. Equations for predicting age-age correlations based on *P. taeda* populations from west and east of the Mississippi River proved statistically different. Both predictive equations proved conservative for validation datasets consisting of younger tests in the U.S. and Zimbabwe. Age-dependent log-linear predictive equations were favored over growth-dependent equations. All *P. taeda* predictive equations based on genetic correlations favored earlier selection when compared to a generalized conifer predictive equation based on phenotypic correlations. The age-age correlations structure showed stability independent of planting density and across a wide range of family sizes.

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Introduction

Predicting age-age genetic correlations is essential for optimizing selection age in conifer improvement programs. Generalized equations for predicting age-age genetic correlations, derived from older tests with measurements spanning juvenility to harvest age, are used to estimate optimal selection age in younger tests to determine the earliest age for selection. The abundant genetic test data for *Pinus raeda* in Zimbabwe and in the southern U.S provide a test of a combined or meta-analysis approach (*sensu* Femandez-Duque and Valeggia 1994). A meta-analysis based on many large genetic tests planted throughout the natural range of the species should yield a robust method for predicting age-age correlations for *P. taeda.*

There are three constraints: (1) there is a tradeoff between restricting genetic parameter estimates to local populations and combining estimates across populations in order to obtain robust predictive equations for genetic age-age correlations, (2) phenotypic correlations should not be substituted for genetic correlations in robust predictive equations because they result in conservative selection age decisions, and (3) predictive equations based on old test data tend to be too conservative due to archaic silvicultural practices.

The best predictive equation for *P. raeda* selection age decisions must be shaped by all three constraints. The first constraint is inherent to the estimation of genetic correlations. Estimating genetic correlations requires hundreds of families in order to reduce sampling errors (see review in Visscher 1998) yet genetic parameters apply only to a reference population (Falconer and MacKay 1996, pp. 127-128). At one extreme, combining species for prediction will not be stable. The other extreme, restricting predictive equations to a local population, is rare for long-lived woody perennials because of the sheer requirements for space. For example, a predictive equation was derived using *P. taeda* test data from an exotic Zimbabwe population (Gwaze et al. 1996) but this predictive equation would be robust only if it could be generalized to the indigenous U.S. populations of *P.* east and west of the Mississippi River.

The second constraint is that genetic correlations cannot always be estimated and yet phenotypic correlations are poor substitutes. Phenotypic correlations are often similar in sign and magnitude to genetic correlations but phenotypic family mean correlations are downwardly biased estimates of genetic correlations (Searle 1961; Hegman and deFries 1970; Cheverud 1988). Error variances and error covariances inherent to phenotypic family mean correlations can also cause wide fluctuations in age-age correlation structure unless family sizes are quite large (n>100) (Gwaze et al. 1997). Family sizes decrease with age due to density dependent mortality and systematic thinning. It is this steady reduction in family size over time that undermines the efficiency of predictive equations based on phenotypic correlations. Since phenotypic correlations' tend to underestimate genetic correlations, their use biases selection toward older ages. Using phenotypic correlations to substitute for genetic correlations in predictive equations is overly conservative for determining optimum selection age.

The third constraint is the use of old test data to construct generalized predictive equations. Old tests, planted 40 or even more than 80 years previously, are often based on unreplicated testing designs or archaic silvicultural methods no longer used in present-day testing. Similarly, Kremer (1992) asserts that improving juvenile growth by silvicultural means may increase age-age genetic correlations. The first predictive equation reported for conifers is a good example. It was based upon phenotypic correlations in several boreal and temperate conifer tests (Lambeth 1980), some of which were poorly established tests with low survival. Some of these poor-quali‘ty tests dated back to the turn of the 20th century (Namkoong et al. 1972). Phenotypic correlations between the same trait measured at different ages could be predicted based on the natural logarithm of the ratio of the measurement ages (log age atio or LAR).

A comparison of the predictive equation with post-1980 tests show that the Lambeth (1980) predictive equation based on phenotypic correlations is overly conservative for *P. raeda* as well as for slow-growing boreal conifers (Lambeth et al. 1983; Newman and Williams 1991; Gwaze et al. 1996). Use of these data results in overly conservative selection-age decisions because present-day tests tend to grow faster and are more uniform. It is important to validate a predictive equation against present-day test data.

Our case study is based on *P. taeda* L., an aggressive colonizing conifer indigenous to the southern United States. The species has a nearly continuous range throughout the southern U.S. The eastern range of the species extends from southern Delaware (39021' N) through Maryland, Virginia, North Carolina, South Carolina, Georgia into central Florida then westward through Alabama, southern Tennessee, eastern Mississippi. The Mississippi River Valley forms a natural gap of 50–200 km, delineating the western range of Louisiana, southwestern Arkansas, southeastern tip of Oklahoma and eastern Texas. Population divergence follows the east-west division of the Mississippi River. Breeding programs, started after 1954, were designed for population-level improvement. Most, *P. taeda* programs are completing two breeding cycles.

P. taeda is used as an exotic timber species in countries which have no indigenous pine species. *P. taeda* has been planted in Zimbabwe since 1927. The original seed source is closely related to *P. taeda* east of the Mississippi River, possibly Georgia Piedmont (Mullin et al. 1978, p 190). The *P. taeda* breeding program was established in 1958. The parents were selected in Zimbabwean plantations planted with seed collected in plantations from South Africa (Mullin et al. 1978, p 190).

Our objectives were: (1) to use a meta-analysis approach to develop a generalized prediction equation for *P. taeda* L., (2) to validate the generalized predictive equation with younger tests and Zimbabwe populations, and (3) to determine if a growth-dependent predictive equation is superior to an age-dependent predictive equation.

Materials and Methods

Materials

This study is based on a total of 51,439 *P. raeda* trees from 520 parents located in 3 1 randomized complete block tests (Table 1). Two generalized predictive equations were developed using 233 parents originating from east of the Mississippi River (EAST) and 190 parents originating from west of the Mississippi River (WEST). Tests were coded according to landowner identity (Table 1). All tests selected for the analyses met three criteria: (1) periodic measurements at ages up to 15 years or older, (2) represented a randomized complete block design with single-, block- or row-plots, and (3) composed of ten or more parents in the mating. design. Validation with a third dataset was based on 22,033 trees: 23 Zimbabwe parents tested across four sites and 74 U.S. parents valuated on five sites east and west of the Mississippi River (Table 1).

The Crown Zellerbach (CZ) test was composed of offspring from parents selected in natural stands in southeastern Louisiana and southwestern Mississippi, east of the Mississippi River. The test was composed of 11 open-pollinated, first-generation seed orchard parents. Systematic thinning was completed at age 8 (Table 1). Height was measured from 1 to 8. IO and 15 years. Data at 3, 5, 8. IO and 15 years were selected for analyses. The CZ test was planted in southeastern Louisiana (Foster 1986).

The lntemarional Paper Co. (IP) data were measurements from offspring of parents randomly selected in natural stands in Georgia. Two genetic tests were established in southern Georgia with offspring from a nested mating design. Each test was comprised of three replicates and 12-tree row plots. Systematic thinning was completed at age 10 years (Table I). The tests were measured at ages 1–17, and at 25 years. Data at 3, 5, 10. 15, 17 and 25 were selected for analyses. The IP data were described by Balocchi et al. (1993).

Table I Details of loblolly pine genetic tests used in the analyses

Data Sets		Provenance	No. of sites	No. of parents	Reps per site	‘No. of trees	Measurement ages (Years)
Crown Zellerbach	(CZ)	Eastern USA	2	2::	4	1475	3, 5, 8*, IO, 15
International Paper	(IP)	Eastern USA				425 I	3.5, 10*, 15, 17, 25
Georgia Pacific	(GP)	Western USA	5	61	i-9	14033	10. 15”. 20, 25
Texas Forest Service.0	(WEY1)	Western USA	14	137	3-16	9641	5, 10, 15.20
Weyerhaeuser	(WEY2)	Eastern USA	2	37	8	4122	2, 3, 4, 7, IO
Weyerhaeuser		Eastern USA	3		8	4407	3, 5, 7, 10
Zimbabwe	(ZIM)		4	23	4	13504	2. 10*, 14*, 23

* Indicates measurement age(s) after which tests were thinned

Table 2 Mean heights (m). narrow-sense heritabilities and their standard errors for seven tests representing different regions

Age	East of the MS River				West of the MS River				Validation					
	CZ		IP		GP		TFS		WEY1		WEY2		ZIM	
	Ht	h² (SE)	Ht	h² (SE)	Ht	h² (SE)	Ht	h² (SE)	Ht	h² (SE)	Ht	h² (SE)	Ht	h² (SE)
2	-	-	-	-	-	-			1.5	0.11 0.05			1.0	0.24 0.08
3	3.1	0.20 0.10	2.0	0.10 0.02	-	-			2.9	0.15 0.06	1.9	0.11 0.03	-	-
4	-	-	-	-	-	-			4.2	0.19 0.08			-	-
5	6.5	0.20 0.10	4.0	0.14 0.03	-	-	3.7	0.11 0.02			4.1	0.13 0.04	-	-
7	-	-	-	-	-	-			8.2	0.14 0.06	6.5	0.12 0.03	-	-
8	11.2	0.20 0.10	-	-	-	-							-	-
10	13.3	0.42 0.18	10.2	0.25 0.04	9.0	0.23 0.04	9.2	0.21 0.03	11.2	0.21 0.08	10.4	0.15 0.04	13.7	0.50 0.14
14	-	-											18.9	0.24 0.07
15	18.2	0.49 0.20	15.7	0.28 0.04	13.6	0.27 0.05	13.2	0.21 0.03					-	-
17	-	-	17.6	0.25 0.04									-	-
20	-	-			17.5	0.37 0.06	16.2	0.30 0.04					-	-
23	-												24.1	0.23 0.06
25	-	-	23.5	0.18 0.03	21.6	0.30 0.06							-	-

The Texas Forest Service (TFS) and Georgia Pacific (GP) tests were composed of offspring from parents selected in natural stands located in Arkansas, Louisiana, and Texas. Data from TFS and GP were grouped into subsets with each subset having tests measured at the same ages. The TFS data were height measurements from six tests of full-sib, and eight tests of half-sib, offspring with height measurements at 5, IO. 15 and 20 years. No TFS tests were thinned (Table I).

The GP data were pooled, full-sib height measurements from five tests with a total of 61 first-generation parents selected for good growth with height measurements at IO, 15, 20 and 25 years. Data were pooled across sites rather than analyzed separately in order to improve the precision of the genetic correlation estimates. Some of the tests were thinned at age IO or 15 years (Table I).

The Weyerhaeuser data sets were open-pollinated offspring from first-generation parents selected in coastal North and South Carolina. One test was planted locally (WEY I) in eastern North Carolina and the other (WEY2) was planted in southeastern Oklahoma; neither test was thinned prior to measurement.

The Zimbabwe (ZIM) equation was previously developed from pooled data from four genetic tests planted in 1972 (Gwaze et al. 1997). The mating design was a factorial among 23 parents producing 140 full-sib families. The tests were systematically thinned at ages IO and 14 years (Table 1).

Table 3 Parameter estimates for regression equations and fit statistics

Data Set	βb_0	SE	βb_1	SE	RMS	*df*	R^2
Genetic correlations-Log age ratio							
1. **CZ**	0.97	0.047	0.253’ [1/]	0.053	0.0047	**8**	0.74
2. IP	1.03	0.015	0.294 [a]	0.013	0.0009	**13**	0.97
3. GP	**1.04**	0.022	**0.218** [b]	0.039	0.0005	**4**	0.89
4. TFS	**1.02**	0.043	**0.202** [b]	0.051	0.0022	**4**	0.80
5. **WEY1**	**1.02**	0.024	**0.134** [c]	0.026	0.0011	8	0.77
6. WEY2	1.01	0.030	0.155 [c]	0.040	**0.0009**	4	0.78
7. **ZIM**	0.98	0.044	0.076 [c]	0.029	0.0030	4	0.64
Combined:							
CZ&IP (Eastern)	1.01	0.019	0.279 [a]	0.018	0.0023	23	0.91
GP&TFS (Western)	1.03	0.021	**0.215** [b]	0.029	0.0012	11	0.85
WEY **1,2&ZIM** (Validation)	0.99	0.016	**0.090** [c]	0.016	0.0017	20	0.63
Genetic correlations-Log Height Ratio							
1. **CZ**	0.92	0.058	0.175	0.059	0.0086	8	0.52
2. **IP**	**1.00**	0.015	0.230	0.011	0.0010	13	0.97
3. GP	**1.04**	0.018	0.229	0.034	**0.0004**	4	0.92
4. TFS	**1.01**	0.022	0.179	0.023	**0.0007**	4	0.94
5. WEY 1	1.01	0.030	0.097	0.026	**0.0018**	8	0.63
6. WEY2	1.00	0.032	0.104	0.031	0.0011	4	0.74
7. **ZIM**	0.95	0.045	0.038	0.022	0.0047	4	0.43
Combined:							
CZ&IP (Eastern)	0.97	0.023	0.212	0.019	0.0040	23	0.84
GP&TFS (Western)	1.02	0.012	0.192	0.016	0.0005	10	0.93
WEY **1,2&ZIM** (Validation)	0.97	0.018	0.053	0.012	0.002s	20	0.47
Family mean correlations-Log Age Ratio							
1. cz	0.91	0.046	0.284	0.052	0.0045	**8**	0.79
2. IP	0.86	0.085	0.310	0.07s	0.0275	**13**	0.57
3. GP	**1.00**	0.264	0.811	0.471	0.0768	**4**	0.42
4. TFS	**0.97**	0.025	0.210	0.030	0.0008	**4**	0.91
5. WEY 1	0.98	0.300	0.144	0.033	0.0018	**8**	0.71
6. **WEY2**	0.98	0.017	0.100	0.024	0.0003	**4**	0.82
7. ZIM	0.92	0.118	0.457	0.079	0.0227	4	0.89
Combined:							
CZ&IP (Eastern)	0.93	0.058	0.325	0.056	0.0216	23	0.59
GP&TFS (Western)	0.83	0.155	0.208	0.216	0.0652	**10**	0.08
WEY **1,2&ZIM** (Validation)	1.03	0.077	0.447	0.072	0.0372	**20**	0.66

[1/] Slopes followed by the same letter are not statistically different at the 95% confidence level

Methods

Genetic-parameter estimates were based on residual **maximum-likelihood** methods (see Tables 2-6). Individual-tree heritabilities and their standard errors were estimated using a univariate model. Genetic correlations and their standard errors were estimated using a **bivariate** individual wee model, ASREML (**Gilmour** et al. 1997). The general linear model was:

$$Y_{ijk}=\mu m+S_i+R_j+A_k+\varepsilon e_{ijk} \qquad (1)$$

where:

Y_{ijk} is the observation on the lth tree in the ith site in the jtb block and in the kth family,
μm overall test mean,
S_i fixed effect of the ith site,
R_j **fixed** effect of the jth **block,**
A_k additive genetic effect of the kth tree, and
εe_{ijk} residual term.

For sets with full-sib families, the family was fitted as an extra random effect to estimate dominance variance. The adjusted **least-square** family means were estimated using SAS (PROC GLM) and the family mean correlations were estimated as product-moment correlations using SAS (**PROC** CORR) (SAS 1988):

$$r_g=\beta b_0+\beta b_1 \log, \text{(younger age/older age)}. \qquad (2)$$

An equation of the same form as (Eqn 2) was fitted using age-age genetic correlations from each individual subset of genetic tests from the U.S. and to the combined genetic correlations (see Table 3). Two other regression equations were developed: (1) a predictive equation was based on family mean age-age **correlations** (r_{pf}) regressed on the natural logarithms of younger ages to older ages, and (2) a log-linear model of height ratios of younger vs. older ages (LHR) was used to predict genetic age-age correlations in place of the log-age ratio (LAR).

Results

There was no single best-generalized prediction equation for age-age genetic correlations for ***P. taeda*** tests. Two separate equations were developed for ***P. taeda*** populations east and west of the Mississippi River. Age-age genetic correlations for total height were positive and **lin-**

Table 4 Comparison of age-age genetic and family mean correlations for the Eastern tests

Test	Age-Age	r_g 1/	SE	r_{pf} 1/	r_g - r_{pf}
	3,5				
CZ	3.8	0.96	0.03	0.94	+0.02
	3,10	0.80 0.65	0.13 0.20	0.71 0.58	+0.07
	3.15	0.53	0.25	0.50	+0.03
	5,8	0.92	0.06	0.90	+0.02
	5.10	0.80	0.12	0.11	+0.03
	5.15	0.84	0.19	0.66	+0.02
	8,10	0.76	0.11	0.82	+0.02
	8,15		0.15	0.79	-0.03
	10,15	0.80	0.12	0.80	0.00
	3,5		0.04		
IP	3.10	0.90 0.62	0.09	0.56 0.68	+0.34
	3,15	0.56	0.10	0.27	+0.29
	3.17	0.53	0.10	0.37	+0.16
	3,25	0.39	0.13	0.02	+0.37
	5,10	0.77	0.06	0.42	+0.35
	5,15	0.72	0.07	0.62	+0.10
	5.17	0.70	0.07	0.57	+0.13
	5.25	0.56	0.10	0.63	-0.07
	10,15	0.90	0.03	0.70	+0.20
	10,17	0.90	0.03	0.77	+0.13
	10.25	0.79	0.06	0.30	+0.49
	15.17	0.97	0.01	0.94	+0.03
		0.88	0.04	0.82	+0.06
	15.25	0.94	0.03	0.72	+0.22

1/ r_g and r_{pf} are the genetic and family mean phenotypic correlations, respectively

ear, equal to or exceeding phenotypic family mean correlations in 51 out of 59 pairs. Validation indicated that both generalized prediction equations for eastern and western *P. taeda* populations were conservative. Age-age genetic correlations for WEY 1, WEY2 and ZIM tests had higher age-age genetic correlations at earlier ages than predicted. Predictive equations constructed on height as the dependent variable were similar to the age-dependent predictive equations.

Genetic parameter estimates

Heritability estimates for the IP test increased with age from 0.1 and peaked at 15 years of age at 0.28 (Table 2). The trend for heritabilities in the Zimbabwe trials was similar to the IP test although the peak occurred at different ages. In contrast, heritability estimates for all other tests continued to increase with age. Heritability estimates at young ages for the tests in Zimbabwe were higher than those for the USA tests. It was interesting to note that although heritability for the Zimbabwe tests and those for IP peaked at different ages, they peaked at the same mean height. Ten years, after planting, genetic tests in Zimbabwe had higher growth rates than those in USA.

Age-age genetic correlations were estimated with high precision due to the large number of parents in the pooled analyses (Table 3). The exception was the CZ test, which had the smallest number of parents (11) (Table 3). Precision of the genetic correlations increased with the magnitude of the genetic correlations (Table 3). Age-age genetic correlations were higher than, or equal to, the corresponding family mean correlations in 51 out of 59 cases (see Tables 4-6). The greatest disparity occurred in the IP test at young ages where genetic correlations exceeded phenotypic family mean correlations (Table 4). Genetic correlations were as much as 95% higher than family mean correlations at young ages in the IP test (Table 4).

The generalized prediction equations for *P. taeda*

Positive linear relationships between age-age genetic correlations and log of age ratios were obtained in all cases (see Tables 3-6). The slopes of the western tests (GP and TFS) were similar to each other and this was also the case for the slopes of the eastern tests (IP and CZ). The sets differed significantly at the 5% level. Eastern and western *P. taeda* populations did not have the same age-age genetic correlation structure.

The two predictive equations also differed statistically from Lambeth's (1980) generalized predictive equation for conifers (Fig. 1). Student's "t" tests tested for significant differences between the mean slopes for Lambeth's five studies and the two predictive equations for *P. taeda* (original data from Lambeth's 1980 study were not available). The slope estimates in the *P. taeda* datasets used in this study were significantly lower than the five slopes based on phenotypic correlations reported in Lambeth (1980) at the 95% confidence level (Fig. 1).

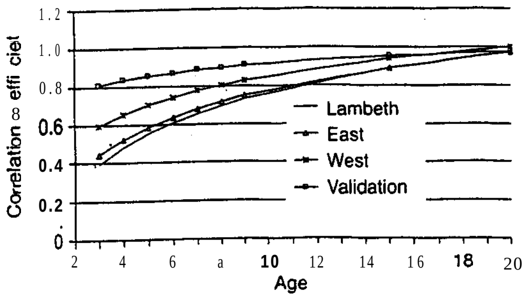

Fig. 1

Validation

Slopes for ZIM and the two WEY tests were not different at the 95% confidence level. The slopes of the equations for the CZ, GP, IP, and TFS tests were significantly steeper relative to the WEY1, WEY2 and ZIM tests (Fig. 1). The WEY and ZIM tests grew faster in well-designed, highly replicated tests. Validation results suggested that both the eastern (EAST) and western (WEST) predictive equations were conservative with respect to the younger tests (Fig. 1). It should be noted that the WEY tests sampled the northeastern range of the species and that, although the WEY parents were planted in both northeastern and western parts of the *P. taeda* range, the age-age correlations were the same (Table 5).

A Predictive Equation Using Growth As The Dependent Variable

Using the log of height ratio (LHR) as a predictor of genetic correlations was similar to predicting genetic correlations using the log of age ratio (LAR). There was one notable exception. Height was the superior choice for the

Table 5 Comparison of age-age genetic and family-mean correlations for the Western tests

Test	Age-Age	r_g 1/	SE	r_{pf} 1/	r_g-r_{pf}
GP	10,15	0.93	0.02	0.83	+0.10
	10,20	0.90	0.03	0.41	+0.49
	IO.25	0.83	0.05	0.13	+0.70
	15.20	0.98	0.01	0.39	+0.59
	15,25	0.96	0.02	0.92	+0.04
	20,25	0.98	0.01	0.86	+0.12
			0.06		0.00
TFS	5,15	0.88	0.05	0.80	+0.05
	5.20	0.77	[illegible]	0.7 I	+0.06
	10.15	0.95	0.01	0.88	+0.07
	IO.20	0.91	0.02	0.83	+0.08
	15.20	0.97	0.01	0.93	+0.04

1/ r_g and r_{pf} are the genetic and family mean phenotypic correlations. respectively

Table 6 Comparison of age-age genetic and family-mean correlations for the Weyerhaeuser and Zimbabwe tests

Test	Age-Age	r_g 1/	SE	r_{pf} 1/	r_g-r_{pf}
WEY 1	2,3	0.96	0.03	0.91	+0.05
	2.4	0.93	0.04		+0.10
	2,7	0.91	0.06	0.83 0.72	+0.19
	2.10	0.80	0.12	0.77	+0.03
	3,4	0.99	0.01	0.98	+0.01
		0.96	0.03	0.87	+0.09
	3,7		0.03	0.86	-0.04
	3,10	0.82 0.95	0.04		+0.04
	4,10	0.86	0.08	0.91 0.87	-0.01
	7.10	0.97	0.02	0.90	+0.07
WEY2	3.5	0.93	0.03	0.94	-0.01
	3.1	0.91	0.05	0.91	0.00
	5,7	0.82	0.08	0.85	-0.03
	5.10	0.98 0.86	0.02 0.06	0.95 0.90	+0.03
	[illegible]				
	7,10	0.94	0.03	0.92	+0.02
ZIM	2.10	0.93	0.03	-0.02	-0.95
	2.14	0.85	0.07	-0.05	-0.90
	2.23	0.76	0.10	-0.02	-0.76
	10,14	0.96	0.01	0.75	-0.19
	IO.23	0.85	0.05	0.61	-0.24
	14.23	0.97	0.01	0.78	-0.19

1/ r_g and r_{pf} are the genetic and family mean phenotypic correlations, respectively

Table 7 Comparison of predicted age-age genetic correlations for Eastern and Western tests, Lambeth's equation and observed values for the validation tests

Age-Age	Validation Tests			Predicted genetic correlations (r_g) and deviation from validation tests					
	WEY1	WEY2	ZIM	East of the MS River		West of the MS River		Lambeth	
3.7	0.96			0.77	-0.19	0.85	-0.11	0.76	-0.20
3.10	0.82			0.67	-0.15	0.77	-0.05	0.65	-0.17
3,7		0.91		0.77	-0.14	0.85	-0.06	0.76	-0.15
3,10		0.82		0.67	-0.15	0.77	-0.05	0.65	-0.17
2,10			0.93	0.56	-0.37	0.68	-0.25	0.52	-0.41
2,14			0.85	0.47	-0.38	0.61	-0.24	0.42	-0.43
2,23			0.76	0.32	-0.43	0.50	-0.26	0.27	-0.49
10,14			0.96	0.92	-0.04	0.96	-0.00	0.92	-0.04
10.23			0.85	0.78	-0.07	0.85	+0.00	0.76	-0.09
14,23			0.97	0.87	-0.10	0.92	-0.05	0.87	-0.10

dependent variable in the CZ test (Table 3). The equation using the log of height ratio as the predictor of genetic correlations was as good, and at times better, than that using the log of age ratio (LAR). However, predicting genetic age-age correlations from height ratios assumes that the site index at harvest age is available. In general, predictions based on the log ages ratio (LAR) were considered the favored choice because site index cannot be reliably predicted from young tests.

Discussion

There was no one single generalized prediction equation for age-age genetic correlations. Separate predictive equations were developed for *P. taeda* populations east and west of the Mississippi River. The two predictive equations favored earlier selection compared to Lambeth's (1980) generalized conifer equation. Age-age genetic correlations for total height were positive and linear, equal to or exceeding the phenotypic family mean correlations in 51 out of 59 pairs. Validation indicated that the two generalized prediction equation were conservative. Age-age genetic correlations for the validation datasets had observed age-age genetic correlations which were higher than the predicted correlations. Phenotypic family mean correlations consistently under-estimated genetic correlations. Age-dependent (LAR) predictive equations were similar to the growth-dependent (LHR) predictive equations in all tests except one.

The prediction equations fell into two groups: the eastern (EAST) and western (WEST) range of *P. taeda* in the US. (Table 2). This difference could be attributed to: (1) genetic differences between east and western parts of the species range, (2) incomplete genetic sampling within the two respective; regions, and (3) imbalance across age-age correlation matrices. The latter two factors clearly contributed significantly.

There was incomplete genetic sampling in the eastern dataset (Table 1). The EAST predictive equation was strongly influenced by the IP tests which had most of the parents (222 out of 232) and the widest range of ages (3-25 years; Table 2). Part of these data were also included in the sole *P. taeda* data set included in Lambeth's (1980) predictive equation. The use of IP tests caused EAST to be the more conservative of the two predictive equations (Table 3).

There was imbalance across ages between the eastern and western datasets; this can be seen most clearly in Table 2. Seven of the 11 measurements for the eastern dataset were taken at age 10 years or earlier. Only three of the eight measurements in the western dataset were taken at age 10 or earlier. It follows that the western predictive equation favored earlier selection; there were more data from younger measurements to support the predictive equation.

Genetic divergence was the least-likely explanation. True genetic differences in age-age correlations were confounded with. the imbalance in age-age distribution, in genetic sampling within each provenance and testing sites. The Zimbabwe parents are only two generations removed from putative southern Georgia sources yet they did not display a predictive equation similar to EAST when planted in the southern hemisphere (Table 2; Gwaze et al. 1997). Although eastern and western provenances are clearly divergent at both the phenotypic and the molecular level (e.g. Florence and Zink 1979), it would require a set of reciprocal plantings to demonstrate population divergence in age-age correlation structure. We hypothesize that the true age-age genetic correlation structure may actually contribute to the similarity between the two predictive equations.

The discrepancy between the validation datasets and the two predictive equations was likely to be due to a time lag in silvicultural practices. The older tests in the USA were established from 1954 to 1975 using less intensive site management and nursery grown seedlings. The WEY1 and WEY2 tests were planted in 1984 and 1985 and test management practices changed substantially over the decades. Post- 1980 genetic tests were grown in containers, then planted in highly replicated, multiple single-tree plots and intensively managed through age 6 years. Good test design, absence of root damage during nursery lifting, less herbaceous weed competition and less leader damage all improved early test establishment. Similarly, *P. raeda* grows vigorously in southern hemisphere countries and the well-designed Zimbabwe tests are very intensively managed during the early stages of establishment (Gwaze et al. 1997).

Faster growth rates alone did not account for the higher observed age-age correlations in the validation datasets. High genetic correlations were estimated from the younger, WEY 1 and WEY2 tests which were growing more slowly than the Zimbabwe tests (Table 2). Furthermore, the CZ test had lower genetic correlations even though it was growing faster than the Zimbabwe tests until age 10 years (Tables 4 and 6). Intensively managed seedlings may be better genetically correlated with older measurements because real genetic differences among families and individuals were not masked by micro-site environmental effects.

The difference between the genetic correlations and family mean correlations were smallest when family sites were large, and large when measurements were taken before and after thinning. Also, equations based on family mean correlations were less precisely estimated. This was partly attributed to the fact that family mean correlations were less predictable as age difference increased, probably as a result of thinning or competition. Hence predictive equations based on family mean correlations underestimate genetic correlations.

Trends for age-age genetic correlations were stable before and after thinning. Comparing genetic correlations (Tables 4-6) before and after thinning (Table 1) revealed no decline. For example, the GP tests which were thinned after age 15 (Table 5) and the TFS tests, which were not thinned (Table 5), had essentially the same genetic correlations at the same ages. The CZ and IP tests, which were thinned after age 8 and 10 measurements, respectively, also had essentially the same genetic correlations for the same pairs of measurement years (Tables 4–5). Changes in planting density or family size were not detected in age-age genetic correlations.

Age-dependent (LAR) predictive equations were similar to the growth-dependent (LHR) predictive equations. Although LAR and LHR were similar for predicting age-age correlations (LHR was even superior in the case of one test), LAR was favored for practical reasons. Estimating site index at harvest age is notoriously unstable in young tests.

Although there were at least two predictive equations for *P. taeda*, these equations have several worthwhile attributes: (I) the equations are species- and population-specific, (2) the equations can be applied widely within large geographic regions, (3) prediction of age-age correlations are conservative with newer tests, and (4) the prediction shows stability even with changes in planting density and a range of family sizes.

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