

PREDICTION MODELS FOR JUVENILE-MATURE CORRELATIONS FOR LOBLOLLY PINE GROWTH TRAITS WITHIN, BETWEEN AND ACROSS TEST SITES

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ABSTRACT

Measurements up to 20 years of age from 15 progeny tests of loblolly pine (*Pinus taeda* L.) in North Carolina were used to test models to predict genetic, juvenile-mature (age-age) correlations for height and stem volume. Results were compared to a phenotypic, juvenile-mature correlation prediction model developed by Lambeth (1980) using LAR (natural log of the younger measurement age over the older measurement age) as the independent variable in a linear regression.

Estimated genetic, juvenile-mature correlations for height were considerably higher and slopes of the regression lines using LAR as the independent variable were considerably lower (for 13 of the 15 trials) than Lambeth's phenotypic model would have predicted. LAR^2 was a consistently better predictive independent variable than LAR . Analyses across series of trials (series having the same set of families planted across test sites) gave better-fitting models than single-site analyses. Regression slopes varied considerably from site to site or from series to series. Optimum selection age using the LAR^2 model for height was calculated to be four to six years.

Genetic, juvenile-mature correlations between sites (for height) were generally high for most series but the fit to LAR and LAR^2 were poor. The utility of this type of correlation is discussed.

Key words: genetic correlation, juvenile-mature correlation, gain efficiency, early selection, growth rate, *Pinus taeda* L.

INTRODUCTION

Optimum age for genetic evaluation and predictions of rotation-age genetic gain depend on the degree of change in family ranks and heritability as the trees age. Genetic gain (CG) at rotation age (referred to as the mature age) from early selection (referred to as the juvenile age) is determined with the correlated gain equation (FALCONER 1960):

$$CG_m = i_j h_j h_m r_{g_{j,m}} \sigma_{P_m} \quad [1]$$

where: subscripts signify m – mature trait age, j – juvenile trait age, g – genetic, p – phenotypic. i – selection intensity, h – square root of the heritability, r – correlation between two traits, σ – standard deviation

Gain from selection at maturity is (G_m) expressed as (FALCONER 1960):

$$G_m = i_m h_m^2 \sigma_{P_m} \quad [2]$$

Efficiency of early selection (E), in terms of gain per generation, can be obtained by dividing equation [1]

by equation [2]. After appropriate cancellations and by assuming that selection intensity is the same at any age, the equation becomes:

$$E = \frac{h_j r_{g_{j,m}}}{h_m} \quad [3]$$

Therefore, in order to project gain from selection at any age in any new genetic test or to determine optimum selection age, it is clear that a model is needed to describe how heritability changes over time, if it is not constant, and a model to describe how age-age correlations change over time if they are less than one. These could be used to predict correlated gain at all possible ages. And by knowing the generation turnover time (evaluation age plus breeding time), gain per year can be calculated. Maximum gain per year is often an objective in the breeding and testing part of a tree improvement program. It is not usually considered feasible to wait until rotation age to make selections in a progeny test due to the resultant long generation interval. Nonetheless, the question of exactly what age to select has been debated for many years. The best age for selecting families or clones to be placed in production may be different from that for maximizing genetic

gain per year in a recurrent breeding and testing program and will not be addressed in this report.

The senior author (LAMBETH 1980) developed a model that seemed to give reasonably good predictions of juvenile-mature correlations for height across a number of coniferous species using data from several published articles. There was very little information on genetic juvenile-mature correlations at the time so phenotypic correlations were used, but information available at the time suggested that genetic correlations tended to be stronger than phenotypic correlations. Also, given that there was scant information on how heritability changes over time, he assumed that it would remain constant until evidence indicated otherwise. He also assumed that selection intensity would be the same for any selection age and estimated efficiency of early selection (before rotation age) as:

$$E = r_{p,j,m} \frac{t_m}{t_j} \quad [4]$$

where: E = efficiency of early selection relative to gain from selection at the mature age, i.e., $E = 1$ for selection at rotation t = time to turn a generation over for the selection age.

The model to predict juvenile-mature correlations was (LAMBETH 1980):

$$r_{p,j,m} = a + b(LAR) = 1.02 + .306(LAR) \quad [5]$$

where: a and b = slope and intercept, respectively, in a linear regression; LAR = natural log of the age ratio for

the two ages measured (younger age/older age).

This model had a very close fit and was applicable to several studies used by LAMBETH (1980) and has since been found to be useful in other situations covered in the Results and Discussion of this paper. However, for the model to have broad applicability, not only must there be a good fit with LAR but the values of the a and b coefficients (1.02 and .306, respectively) in the equation must be repeatable or repeatable coefficients must be developed by species and/or region. A number of authors have tested the model with mixed results that will be reviewed in the Results and Discussion section. BURDON (1989) suggested that the model be used if no better model is available.

The model needs verification using genetic correlations rather than phenotypic correlations. Furthermore, the assumption that heritability remains constant over time also needs further examination. The assumption that selection intensity is the same at any selection age will not be challenged although selection intensity should be higher with smaller trees given that more trees can be tested in a given land area, thus favoring younger evaluation ages (LAMBETH 1983).

OBJECTIVES

1. To test the juvenile-mature correlation prediction model developed by LAMBETH (1980), and other predictive models, using genetic correlations rather than phenotypic correlations.
2. To use any appropriate models from objective one to compare correlations within and across test sites of a series and across series tests.

Table 1. North Carolina progeny tests used in the analyses and ages of height measurement. Numbers in bold italics are measurement ages for stem volume determinations.

Test (site)	Series	Measurement ages (years)	Number of parents	Total number of trees
1	A	3, 4, 5, 6, 7, 8, 15	12	1210
2	A	4, 5, 6, 7, 8, 15	12	1210
3	A	3, 4, 5, 6, 7, 8	12	1368
4	A	3, 4, 5, 6, 7, 8, 14	12	1368
5	B	2, 3, 4, 5, 6, 7, 10	12	1428
6	B	2, 3, 4, 5, 6, 7, 10	12	1422
7	B	2, 3, 4, 5, 6, 10	12	1419
8	B	2, 3, 4, 5, 6, 10	12	1422
9	C	4, 7, 10	36	1470
10	C	4, 7, 10	36	1462
11	C	3, 6, 10	36	1480
12	C	3, 10	36	1480
13	D	4, 8, 12, 16	26	1653
14	E	4, 8, 13, 20	15	3775
15	E	4, 8, 11, 20	15	1857

3. To examine whether or not heritability changes over time in a predictable manner.
4. To use any models developed to estimate E(ffi-ciency) of selection at various ages with the objec-tive of finding an optimum selection age(s).

MATERIAL AND METHODS

Fifteen Weyerhaeuser Company progeny tests of loblolly pine (*Pinus taeda* L.) in North Carolina had multiple measurements for height and diameter between the ages of two and 20 years (Table 1). For each measurement age and trait, breeding values of the parents were estimated using the BLUP method (best linear unbiased prediction) (WHITE & HODGE 1989). Genetic correlations between breeding values at different ages were estimated within each test, within each series across tests (a series is a group of tests or test sites that have the same set of families at each test site) and between tests within a series. In the case of the within-series analyses (across test sites with test sites as main effects), when necessary, the average age was used in the *LAR* (log of age ratio) equations when there was only one year difference in age. For example, in series C tests 9 and 10 measurement was at age seven while test 11 was measured at age 6 so, for the within-series analyses across the three tests, the measurement age was set at 6.67 years. Overall mean, individual-tree heritability and coefficient of variation were also estimated at each age for all traits analyzed.

Genetic correlations between traits at various ages and across sites were calculated using a procedure outlined by LU (1999) and values greater than one were set to one. This genetic correlation estimation method is based on correlation of estimated parental GCA's (general combining ability) with adjustment for GCA prediction accuracy instead of the commonly used analysis of covariance of genetic effects (BURDON 1977, YAMADA 1962). It was used because it was computationally convenient (an important factor when thousands of genetic correlations are generated) and because it compares very favorably with previously used methods in terms of low bias and precision (LU 1999).

Genetic correlations were used to develop the prediction model:

$$r_{g_{age-age}} = a + b(LAR) \quad [6]$$

where: the age-age sub-subscript indicates a correlation between any two ages.

As suggested by MATHESON *et al.* (1994), *LAR*² and *LAR*³ were also tested in simple and polynomial regres-sion models along with *LAR*. The Degree of Nondetermination (DON) model suggested by FAN

KUNG (1993) was also tested.

Estimates of genetic, juvenile-mature correlations from two simple correlation-prediction regressions, with *LAR* and *LAR*² as independent variables, were eventually used to solve the efficiency equation:

$$E = r_{g_{j,m}} \frac{t_m}{t_j} \quad [7]$$

for all possible selection ages assuming a 32-year rotation age (mature age and approximate clearcut age for solid wood product rotations in loblolly pine) and assuming that four years are needed for breeding and progeny growing from the time of selection to establish the next-generation trial for any potential selection age in loblolly pine. The four years assumes top-grafting for flower induction to speed breeding for selections as young as two years of age (BRAMLETT & BURRIS 1995).

RESULTS AND DISCUSSION

Juvenile-Mature Correlation Prediction Models:

The model developed by LAMBETH (1980) for predict-ing phenotypic correlations for height using *LAR* as the prediction variable has been tested by several research-ers with mixed results. Several authors have found *LAR* to provide a close fitting model (JOHNSON *et al.* 1997) but sometimes with different slope or intercept than that found by Lambeth. RIEMENSCHNEIDER (1988) found that phenotypic correlations in jack pine (*Pinus bank-siana* Lamb.) followed very closely to the Lambeth slope and intercept but genetic correlations were higher than the model would have predicted. Others have also found that genetic correlations may fit the model but, more often, they tend to be larger than the Lambeth model would have predicted, usually meaning slopes were flatter (DIETERS *et al.* 1995, GWAZE *et al.* 1997, HODGE & WHITE 1992, HUHN & KLEINSCHMIDT 1993, JENSEN *et al.* 1996, KING & BURDON 1991, KREMER 1992, LAMBETH *et al.* 1983, MCKEAND 1988, XIE & YING 1996). Results from this study also indicate generally higher genetic, juvenile-mature correlations than the Lambeth model would have predicted (Table 2) for within-site, within-series and between-sites correlations for height. For the most part, correlations were high with only a few exceptions at some sites. Correlations for individual-tree volume tended to be lower than those for height as has been found by other authors (HODGE AND WHITE 1992, MAGNUSSEN 1989a).

MATHESON *et al.* (1994) did not find a good fit with the Lambeth model for diameter in *Pinus radiata* D. Don because the relationship was not linear. They did find that a cubic equation using *LAR*, *LAR*², and *LAR*³

Table 2. Intercept (a), slope (b), R^2 and sample size (n) for linear regression equations (for both height and volume) to predict juvenile-mature correlations in loblolly pine progeny tests in North Carolina: Juvenile-mature genetic correlation = $a + b(LAR)$; Juvenile-mature genetic correlation = $a + b(LAR^2)$; where $LAR = \log_e$ (younger age / older age), where younger and older age are measurement ages used in the juvenile-mature correlation.

Site-series or series	LAR						LAR ²					
	Height			Volume			Height			Volume		
	a	b	R^2, n	a	b	R^2, n	a	b	R^2, n	a	b	R^2, n
Within site:												
1-A	1.16	.421	.77, 21	1.10	.294	.78, 10	1.05	-.285	.89, 21	1.03	-.219	.90, 10
2-A	1.06	.189	.76, 15	1.09	.249	.65, 10	1.02	-.144	.86, 15	1.04	-.201	.86, 10
3-A	1.01	.032	.53, 15	1.04	.162	.70, 6	1.00	-.034	.71, 15	1.01	-.160	.80, 6
4-A	1.06	.149	.57, 21	1.04	.090	.51, 10	1.03	-.113	.80, 21	1.03	-.069	.79, 10
5-B	1.00	.000	-, 21	1.01	.035	.49, 10	1.00	.000	-, 21	1.01	-.039	.68, 10
6-B	1.01	.037	.30, 21	1.00	.000	-, 10	1.00	-.023	.31, 21	1.00	.000	-, 10
7-B	1.04	.071	.56, 15	1.01	.039	.55, 6	1.02	-.048	.77, 15	1.01	-.040	.72, 6
8-B	1.05	.098	.59, 15	1.09	.286	.81, 6	1.02	-.064	.75, 15	1.03	-.278	.93, 6
9-C	1.00	.000	-, 3	-	-	-, 1	1.00	.000	-, 3	-	-	-, 1
10-C	1.11	.268	.93, 3	-	-	-, 1	1.04	-.210	.98, 3	-	-	-, 1
11-C	1.00	.000	-, 3	-	-	-, 1	1.00	.000	-, 3	-	-	-, 1
12-C	-	-	-, 1	-	-	-, 0	-	-	-, 1	-	-	-, 0
13-D	1.03	.058	.54, 6	1.00	.000	-, 3	1.01	-.038	.69, 6	1.00	.000	-, 3
14-E	1.33	.575	.83, 6	1.00	.000	-, 3	1.09	-.288	.86, 6	1.00	.000	-, 3
15-E	1.00	.000	-, 6	-	-	-, 1	1.00	.000	-, 6	-	-	-, 1
Sites pooled	1.06	.145	.28,172	1.05	.154	.44, 78	1.02	-.097	.35,172	1.02	-.127	.56, 78
Within series: (i.e., across sites)												
A	1.08	.244	.66, 21	1.10	.312	.67, 10	1.02	-.161	.75, 21	1.01	-.215	.75, 10
B	1.01	.020	.55, 15	1.03	.104	.55, 6	1.00	-.014	.76, 15	1.02	-.108	.72, 6
C	1.09	.184	.87, 3	-	-	-	1.03	-.128	.94, 3	-	-	-, 1
E	1.15	.245	.67, 6	1.00	.000	-, 3	1.07	-.132	.82, 6	1.00	.000	-, 3
Series pooled	1.06	.154	.40, 45	1.09	.257	.53, 20	1.02	-.098	.47, 45	1.03	-.198	.66, 20
Between sites by series:												
A	.93	.238	.18,219	.83	.402	.17,114	1.01	-.188	.45,156	.96	-.274	.34, 76
B	1.02	.067	.18,216	1.04	.289	.21, 96	1.01	-.025	.27,132	1.01	-.201	.36, 56
C	.76	.183	.09, 36	.53	-.297	.07, 11	.97	-.192	.25, 22	.86	.586	.11, 7
E	1.24	.470	.67, 13	1.00	.000	-, 5	1.07	-.172	.52, 13	1.00	.000	-, 5
Series pooled	.94	.135	.07,484	.96	.429	.18,226	.91	-.085	.07,484	.86	-.314	.20,226

in a multiple regression equation provided good fit but concluded that the relationship was too unwieldy to be useful. We too found the cubic equation to give consistently better fit than the simple LAR regression and we also agree that it is unwieldy. However, using LAR^2 alone in a simple regression also yielded a somewhat more linear relationship and consistently better fit than LAR (Table 2) and the equation is not unwieldy though the improvement over LAR may be of marginal value to

some tree breeders. The Degree of Nondetermination model suggested by KUNG (1993) gave better fit than LAR for some sites but gave poorer results overall.

Slope varied considerably from site to site and series to series though less so with the latter (Table 2) which resulted in better fit to the models for a given site or series than when results were pooled. This result means that a general model will not accurately predict the juvenile-mature correlation at any given site or for

any given series. MAGNUSSEN and YANCHUK (1993) noted similar and other problems with models that use only age as a predictive variable and MAGNUSSEN (1989b) has suggested that a model that incorporates variance changes over time would yield better results. In the tests studied here, some sites and series had genetic correlations near one for all ages while others did not. The reasons for this phenomenon are not readily apparent but may be related to test condition or the particular set of families being tested.

Correlations for different ages between pairs of sites were generally good, indicating little genotype-environment interaction and good correlations between different ages of measurement. However, predictive models had very poor fit using this type of correlation as evidenced by low R^2 (Table 2) for models with LAR and LAR^2 .

Between-site correlations are interesting to study because they are partly independent of the auto-correlation that is caused by the fact that the later measurement is made up partly of previous measurement plus an increment of growth. The auto-correlation can be significant (KANG 1991), especially when the two height measurements being correlated are close in age. The auto-correlation is very small for ages far apart, especially for volume (LAMBETH *et al.* 1983). Also, the estimated correlation between the same trait (e.g., height) at the same age is not forced to 1.0 as is the case within a test site. The disadvantage of between-site correlations is that they confound genotype-environment interactions with the effect of aging on juvenile-mature correlations. Furthermore, between site correlations are more variable due to a small number of trees per family as is also true for correlations within a single site.

Correlations based on analyses across tests within a series are more desirable than single-site correlations due to better estimates of family means and due to the fact that both backwards and, to a lesser extent, forward selections are commonly made on the basis of across-sites analyses. In our search for an improved juvenile-mature correlation, prediction model we were most interested in analyses of complete series. It is obvious that selection short of rotation age is necessary in tree improvement programs for any long-rotation crops such as many tree species. Therefore, it is sometimes necessary to make decisions regarding selection age even if highly accurate and generally applicable juvenile-mature correlation prediction models are not available. The model developed by LAMBETH in 1980 tends to underestimate genetic, juvenile-mature correlations so an alternative is needed. In the absence of a better model, we chose to use the model [8] based on pooling correlations ran by series and using LAR^2 as the independent variable to study selection age efficiency

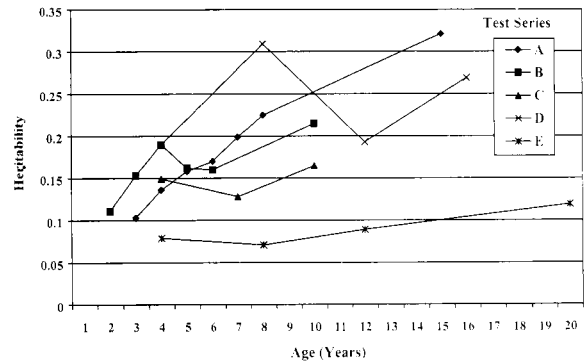


Figure 1. Height heritability estimates by age in five series of N.C. progeny tests.

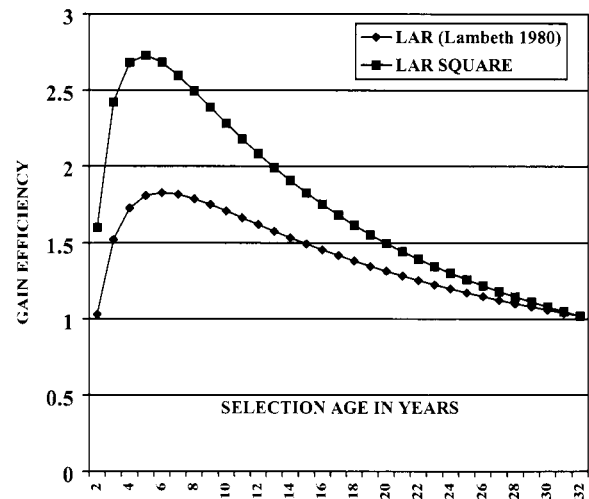


Figure 2. Calculated genetic gain efficiency (gain per year relative to rotation-age, 32 years, selection) at various selection ages using LAR (log of the age ratio) from LAMBETH's (1980) model and LAR^2 to predict juvenile-mature correlations. The calculations assumed that four years are needed after selection for breeding and progeny growing for planting the next generation progeny test, i.e., generation turnover is selection age plus four years.

(section below):

$$r_{g,m} = 1.02 - .098 (LAR^2) \quad [8]$$

While the R^2 is not very strong, it is not weak and it does predict poorer correlation between ages far apart versus ages close together as many studies indicate (KREMER 1992). The observed slope can be thought of as a weighted average across the four multi-site series studied in these North Carolina tests. We recommend that further work be done to understand how and why juvenile-mature correlations change with age, from site to site and from one set of families to another as was observed in this study. Nonetheless, given all the uncertainties of early genetic evaluation models, it is

wise to use them with caution (KANG 1985).

Age Trends in Heritability

There was no clear age-related trend for heritability for the four series and a single site (called series D in Figure 1) although there was an upward trend with age for series A and B. Others have found heritability in conifers to be mostly flat over time (COSTA & DUREL 1996, KING & BURDON 1991, KREMER 1992, LAMBETH *et al.* 1983, RIEMENSCHNEIDER 1988, XIE & YING 1996) while some have noted an increase, or increase followed by a plateau, with age (BALOCCHI *et al.* 1993, COTTERILL & DEAN 1988, FOSTER 1986, MCKEAND 1988, DIETERS *et al.* 1995). JOHNSON *et al.* (1997) found that height heritability was mostly stable over time for Douglas-fir while diameter showed an increase with age.

It seems to be more common that heritability increases with age rather than decreases with age. However, the effect of the onset of intense competition is poorly studied in most reports. FOSTER (1989) reviewed the forestry literature and concluded that competition affects variances, heritability and genetic gain (inflating the latter two). It is likely that competition can result in the better families getting bigger at the expense of smaller ones in tests where family members are planted in rows or at random, especially for diameter or stem volume (FOSTER 1989). This could tend to inflate heritability and the result may not be indicative of what would happen in pure family blocks. Pure family-block planting in commercial plantations of loblolly pine is commonplace in the forest products industry. GWAZE *et al.* (1997) found that, when juvenile-mature correlations are high as they were in this study, changes in heritability with age would not affect optimum selection age significantly.

Selection Age Efficiency

Given that heritability trends with age are not clear nor consistent, we have chosen to assume that it remains constant with age. In addition it was felt that there may be competition effects which bias heritability upward in those reports that show heritability increasing with age. When this assumption is made the simplified genetic gain efficiency equation [7] can be used.

For purposes of illustration, the juvenile-mature correlation prediction model mentioned above [8] was used for calculations and plots of E (Figure 2) and similarly for the original LAR model [5] developed by LAMBETH (1980). The LAR^2 model had much higher efficiency and peak selection efficiency at ages four to six years, which was only slightly younger than the original LAMBETH (1980) model which gave a peak at

five to seven years of age.

Results point to earlier evaluation ages for selection for the next generation of breeding than may have been thought possible in the past. While selection age modelling should be viewed with caution, these results are not likely to lead to too early evaluations because of some factors not considered that, when considered, could point to even earlier evaluations. These factors include:

1. A thorough evaluation of the efficiency of early selection should include an analysis of the net present value impact of delivery of genetic gain to a production program for each selection age. An economic analysis will not be included in this report but it should be noted that such an analysis suggests younger selection age than does an analysis without NPV consideration (BALOCCHI 1990, NEWMAN & WILLIAMS 1991).
2. Selection intensity is likely to be higher at early evaluation ages than would be possible with older evaluation owing to the prohibitive space needed to grow trees to older ages and the difficulty of measuring and the cost of maintaining them. Additionally, the large numbers of individuals that can be tested per family at young ages can strengthen the estimates of juvenile-mature correlations (LAMBETH 1983).

NEWMAN and WILLIAMS (1991) found that 6-year evaluations gave slightly higher gain per generation and entailed lower risk than four-year selection but the NPV was higher for the latter and was robust to the greater risk. They recommended four-year selection over two- or six-year selection.

Nonetheless, the reader is reminded (see above section on Age Trends in Heritability) of the potentially countervailing aspect of the assumption made about the behaviour of heritability over time.

It should be noted that these results apply to selection for height growth. Several other traits may be of importance in applied tree improvement programs such as stem form, wood quality, disease resistance and adaptation to environmental extremes. If the other traits of interest can be evaluated as early as height then the selection ages suggested herein should apply. It would be desirable to study juvenile-mature correlations for multi-trait selection indices of interest but the necessary data to do so are very limited.

CONCLUSIONS

1. The regression equations using LAR as a predictor of genetic, juvenile-mature correlations for height do not match those of the equation developed by LAMBETH (1980) using phenotypic, juvenile-mature correlations. The slopes for within-site and within-

series analyses were much lower than those in the Lambeth model indicating that genetic correlations are much higher than their phenotypic counterparts. The *LAR* model fit was very good for a given site but the fit was not so good when results across sites were pooled ($R^2 = .28$). This was due to the fact that the regression slopes were different by site and by series. The same conclusion held for series but the fit across series was somewhat better and perhaps even acceptable for future application of the model ($R^2 = .40$).

2. The fit for models using LAR^2 were consistently better than those for *LAR* though slopes still varied by site and by series. The model for within-site correlations (pooled across locations) and within series (pooled across series) R^2 values were .35 and .47, respectively.
3. The efficiency curve for early selection using the LAR^2 model peaked at age four to six years. The LAMBETH (1980) model using *LAR* to predict phenotypic correlations peaked at five to seven years. In general, age-age, genetic correlations were very strong, with the exception of a couple of sites; and they point to the probable success of earlier genetic evaluations than those used in the past.
4. Even the age-age correlations between sites were, for the most part, strong. These correlations have the advantage of not being affected by the autocorrelation (caused by the fact that later measurements are a function of earlier measurements) found within sites or series. However, they have the disadvantage of downward bias from possible genotype-environment interaction. These factors are the likely explanation for lower intercepts in prediction models using either *LAR* or LAR^2 for between sites versus within sites while the corresponding slopes were only slightly lower.
5. There was no clear age related trend in heritability though there was an upward trend with age in two of the five series analyzed and no downward trend in any of the series. This upward tendency agrees with results from some other studies.

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