AGE TRENDS IN GENETIC CONTROL OF *JUGLANS NIGRA* L. HEIGHT GROWTH

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Abstract: Age-related trends in narrow-sense and family heritabilities for black walnut height and dbh from a southern Illinois open-pollinated progeny test are evaluated through age 20 years. Narrow-sense heritability for height tends to be relatively stable between ages 10 and 20 at 0.55 - 0.65 with similar patterns and values for family heritabilities for both height and dbh. Individual phenotypic age-age correlation coefficients increased from approximately 0.1 at age 1 to 0.8 at age 8 and remained above this level through age 20.

INTRODUCTION

Genetic gain, the quantitative estimate of the amount of improvement per generation resulting from selection, is the product of heritability and selection intensity. Thus, precise estimates of heritability are needed for calculating gain. Although such estimates are available for juvenile black walnut (Rink 1984, Rink and Clausen 1989), precise estimates of heritability for growth traits from mature trees are not available. Since it is known that heritabilities differ with tree age, changes in these genetic parameters need to be evaluated over the course of a generational rotation. Also, relationships between early and later estimates of heritabilities need to be explored along with phenotypic age-age correlations. The objective of this study is to evaluate heritabilities for black walnut tree height and dbh and age-related growth trends.

METHODS

Open-pollinated seeds collected in 1971 from 54 trees were used to produce 1-0 seedlings for the Pleasant Valley progeny test in southern Illinois. Parent trees were selected from within a 250-mile radius south of the plantation location (Fig. 1), the area most frequently cited as the optimum provenance for obtaining a growth stimulus from geographic seed source selection for artificial regeneration in southern Illinois (Bresnan et al., in press). This included an area bounded by southern Illinois, western Kentucky, western Tennessee, and southeast Kansas. However, most of the seed collections were from west Kentucky and west Tennessee. In most cases seed was collected from one tree per stand. Although trees of better than average form were sought at the time of collection, no rigid minimum selection criteria were applied. Open-pollinated progeny of these trees were planted in 5-tree row plots at a spacing of 1.8 m within rows and 3.7 m between rows, in a randomized complete block design with 10 blocks.

The test was established in early spring 1973 on a Haymond silt loam on the floodplain of Sexton Creek, Alexander County, Illinois. The Haymond loam is characterized as a coarse-silty, mixed, nonacid, mesic Typic Udifluvent classified as suitable for walnut culture (site index 50 at age 70) (Losche et al. 1980). The site was an abandoned fescue pasture on which 1.2 m strips were machine sprayed with a simazine, dalapon, 2,4-D mix before planting, spot sprayed in spring 1974 and 1975, and mowed annually. In addition, the test was rogued (thinned) after the 10th growing season to remove 3 of the smallest trees per 5-tree plot and again after the 14th growing season to retain the most vigorous, best formed tree per family-row plot. The trees were measured for total height 14 times and dbh

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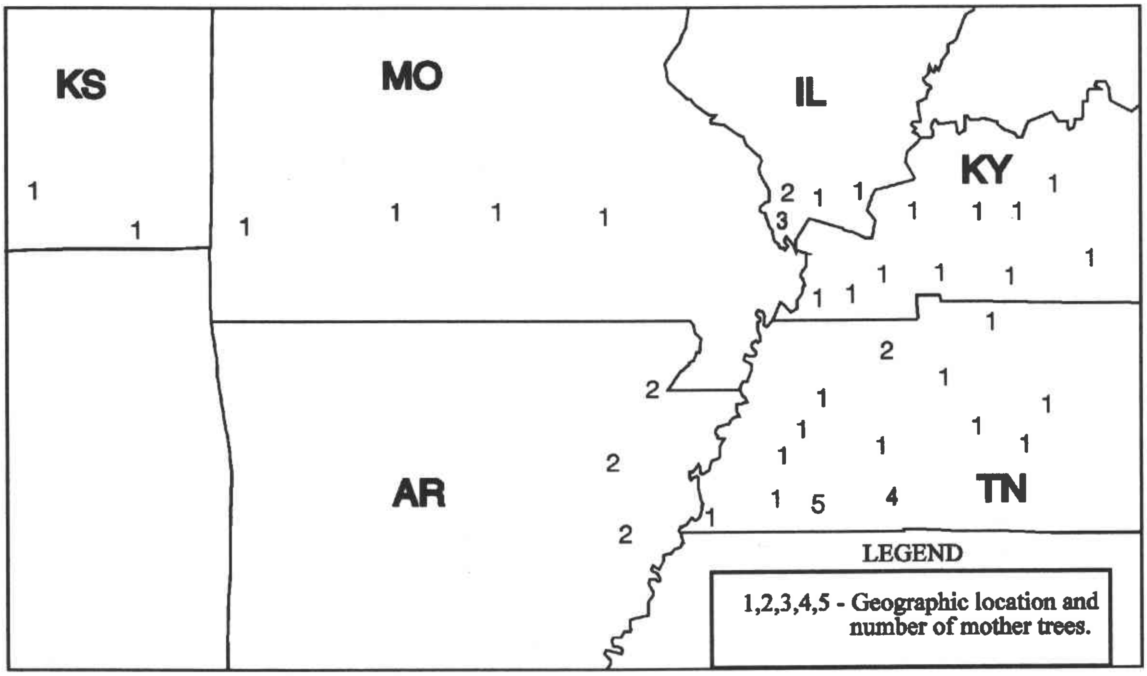

Figure 1. Location of mother trees from which seed were collected for Pleasant Valley open-pollinated progeny test.

11 times during the 20-year period through the 1992 growing season. Statistical analyses were applied to data sets which included only the trees present at age 20 (i.e., the earlier data sets were censored to include only one tree per family-row-plot retained after the last thinning).

Annual measurements were subjected to univariate analysis of variance on an individual tree basis using the following model:

Source of Variation	Mean Square	Expected Mean Square
Blocks (b)	MS_b	$\sigma_e^2 + 0.099\,\sigma_f^2 + 47.277\,\sigma_b^2$
Family (f)	MS_f	$\sigma_e^2 + 9.076\,\sigma_f^2$
Error (e)	MS_e	σ_e^2

Variance components were generated from the Type I sums of squares in the General Linear Model of the Statistical Analysis System (SAS Institute 1982). The Type I method was used in order to obtain an unbiased estimate of the family variance component; by this method all ambiguous variance is assigned to the first variance component entered into the estimation procedure (in this case the block term). Resulting variance components were used to generate narrow-sense and family heritabilities. Pearson correlation analysis was also used to develop phenotypic age-age correlations on an individual tree basis, but only correlations of height at age 20 with height at earlier ages are presented.

RESULTS AND DISCUSSION

Mean cumulative height of black walnut trees in the Pleasant Valley progeny test was contrasted for the ten tallest and ten shortest families (Fig. 2). The group of 10 families which were tallest and shortest at outplanting remained tallest and shortest, respectively, at age 20; the cumulative growth curves never cross. Analyses of variance of the three family groups (10 tallest families, average families, and 10 shortest families) indicated significant differences in height every year beyond the first year, and Duncan's Multiple Range tests consistently separated the three groups of mean heights after age 8. Growth of the 10 tallest families exceeded the plantation average by 8 percent every year beyond age 2. The average height at age 20 was 9 meters.

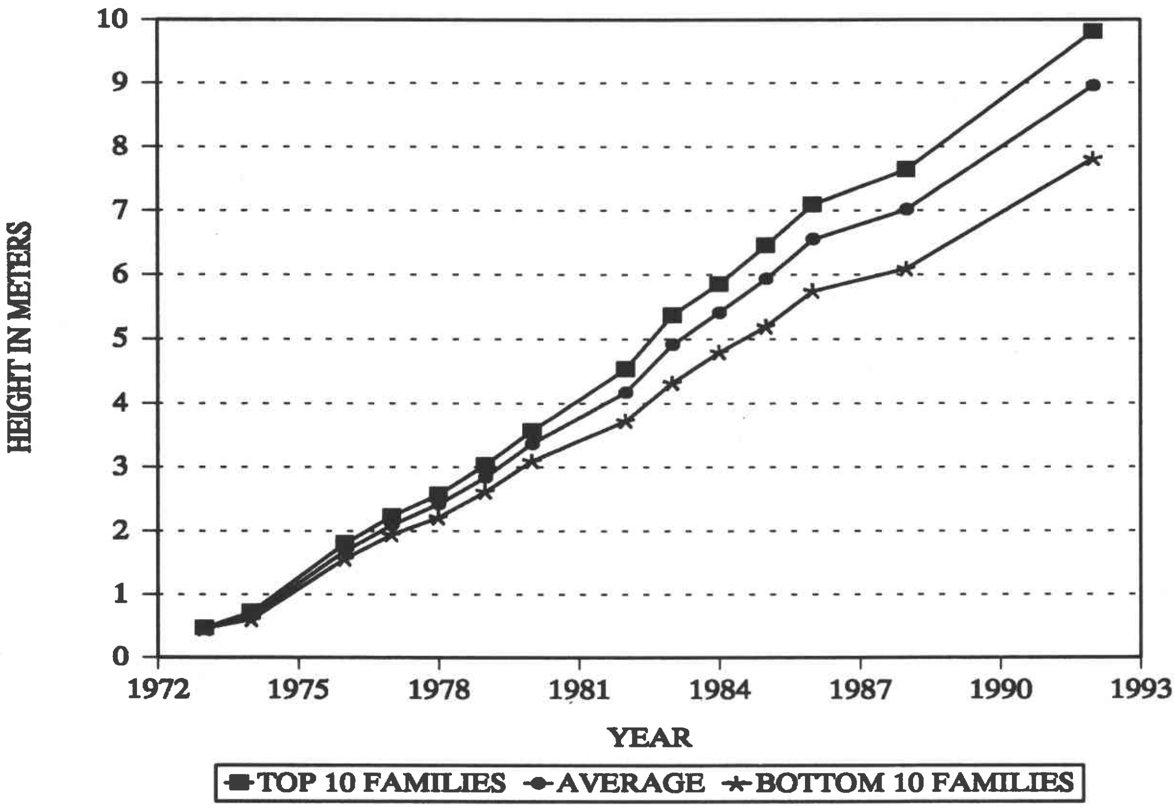

Figure 2. Average cumulative black walnut tree height in Pleasant Valley progeny test, from establishment in in the winter of 1973 through the 20th growing season, including averages of the ten fastest and ten slowest growing families.

The distribution of mean annual height increment was less uniform during this period (Fig. 3). The low height increment during the 1986-1988 period corresponded to a 3-year drought in which growing season precipitation was below average. Similarly, the 1982-1983 high mean annual height growth corresponded to above average precipitation during the 1983 growing season. Differences between the family groups (10 tallest, average and 10 shortest families) were significant during these dry and very wet periods, although significant height increment differences were inconsistent in other years. Patterns of cumulative dbh and mean annual dbh increment were very similar to the patterns displayed for tree height.

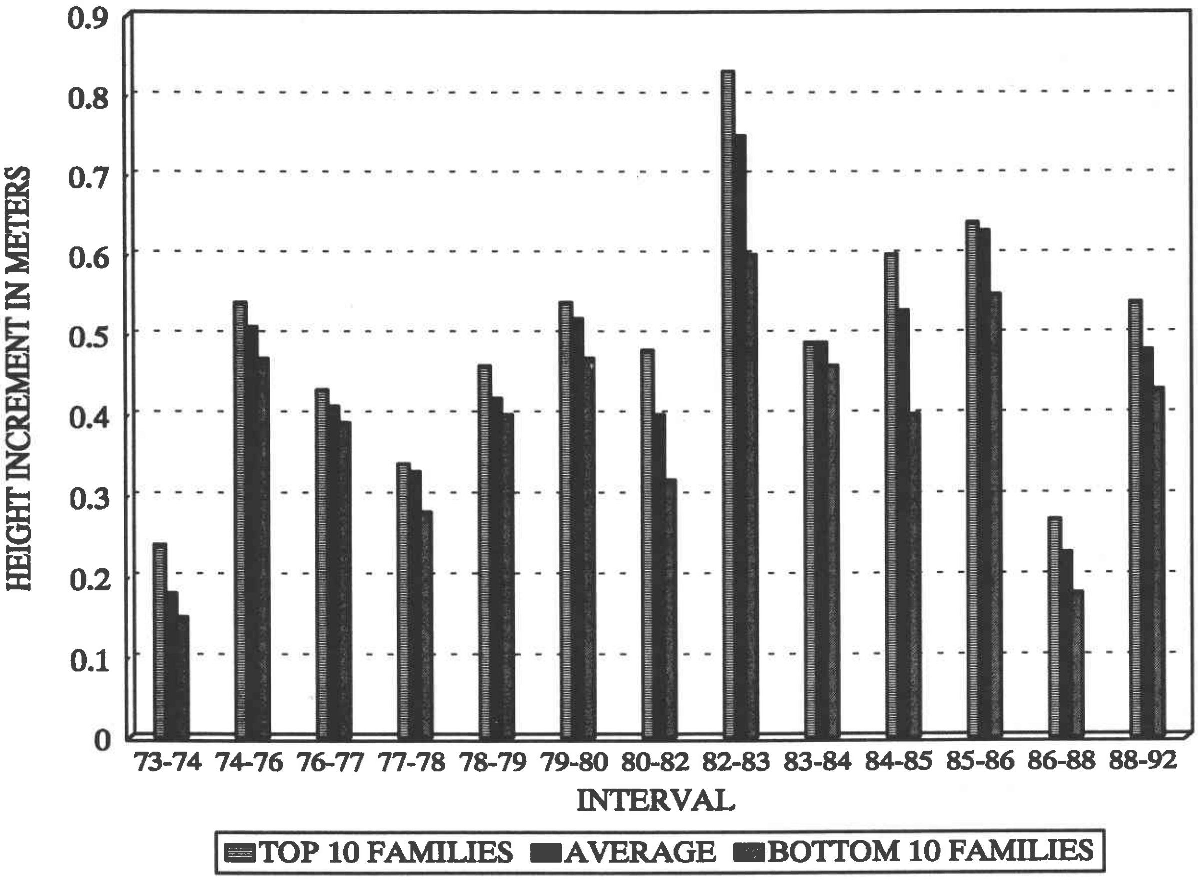

Figure 3. Mean annual height increment in Pleasant Valley black walnut progeny test, including averages of the ten fastest and ten slowest families.

Results from analyses of variance of height and diameter data indicated significance for both block and family effects in all 14 measurement years. Such results are common in experiments with large numbers of families and blocks and reflect an efficient experimental design. Due to missing plots a trivial coefficient (0.099) for the family variance component in the block effect was indicated; this reflected only minor confounding of the block effect.

The absolute magnitude of the family variance components consistently increased throughout the 20-year period of this progeny test (Table 1). However, on a percentage basis, in relation to total variance, the family variance component was at a maximum the year after establishment and decreased consistently during this 20-year period (Table 1). By the end of the 20th growing season, the family component accounted for 2.7 percent of total variance. The trend for family variance components was consistent with that reported by Rink and Clausen (1989) for this experiment through age 13 years and prior to thinning. Block variances, both absolute and as a percentage of total, increased over time, accounting for approximately 80 percent of total variance by the end of the 20th growing season (Table 1). Such a trend of rising block variance components may reflect intensified site occupancy over time by growing root systems of a site-sensitive tree species such as black walnut.

Table 1. Mean height (m) and dbh (cm), variance components, narrow-sense and family heritabilities[1], and respective standard errors for black walnut trees in Pleasant Valley progeny test.

				Variance Components				Heritability[1]			
Yr	Age	Mean	Std	Block	Family	Error	Total	Ind.	SE	Family	SE
						HEIGHT					
73	1	0.48	0.13	0.0002	0.0041	0.0127	0.0170	0.97	0.251	0.74	0.063
74	2	0.66	0.20	0.0032	0.0044	0.0344	0.0420	0.46	0.154	0.54	0.039
76	4	1.69	0.39	0.0280	0.0142	0.1100	0.1523	0.46	0.136	0.54	0.034
77	5	2.10	0.50	0.0812	0.0146	0.1608	0.2566	0.33	0.100	0.45	0.025
78	6	2.43	0.65	0.1696	0.0320	0.2318	0.4333	0.48	0.104	0.56	0.026
79	7	2.86	0.79	0.3057	0.0394	0.3074	0.6525	0.45	0.089	0.54	0.022
80	8	3.38	0.94	0.5353	0.0499	0.3561	0.9413	0.49	0.075	0.56	0.019
82	10	4.19	1.35	1.2477	0.0981	0.6147	1.9605	0.55	0.066	0.59	0.017
83	11	4.93	1.60	1.8299	0.1475	0.7600	2.7374	0.65	0.066	0.64	0.017
84	12	5.41	1.66	2.0336	0.1429	0.7715	2.9481	0.63	0.061	0.63	0.015
85	13	5.94	1.96	3.0129	0.1772	0.9337	4.1238	0.64	0.053	0.63	0.013
86	14	6.57	2.14	3.7270	0.1899	1.0293	4.9463	0.62	0.048	0.63	0.012
88	16	7.03	2.34	4.3719	0.2118	1.3177	5.9014	0.55	0.047	0.59	0.012
92	20	8.98	3.19	8.8437	0.2981	1.9031	11.0449	0.54	0.036	0.59	0.009
						DBH					
77	5	1.73	0.84	0.1431	0.0588	0.5168	0.7187	0.41	0.127	0.51	0.032
78	6	2.33	1.14	0.4594	0.1077	0.7895	1.3566	0.48	0.113	0.55	0.028
79	7	3.14	1.53	1.0079	0.1490	1.2835	2.4405	0.42	0.094	0.51	0.023
80	8	4.17	1.90	1.8367	0.2508	1.6958	3.7833	0.52	0.091	0.57	0.023
82	10	5.65	2.38	3.2980	0.3481	2.3499	5.9960	0.52	0.080	0.57	0.020
83	11	6.69	2.68	4.3814	0.4602	2.7617	7.6034	0.57	0.079	0.60	0.020
84	12	7.67	2.87	5.1486	0.4903	3.1269	8.7658	0.54	0.075	0.59	0.019
85	13	8.51	3.17	6.6255	0.5264	3.5360	10.6880	0.52	0.067	0.57	0.017
86	14	9.34	3.38	7.9461	0.5681	3.7849	12.2992	0.52	0.063	0.58	0.016
88	16	10.53	3.81	9.7916	0.6471	5.0398	15.4785	0.46	0.061	0.54	0.015
92	20	13.46	4.89	17.3099	1.0297	7.2604	25.6001	0.50	0.056	0.56	0.014

[1] Narrow-sense individual tree heritability = $\frac{4\sigma_f^2}{\sigma_e^2+\sigma_f^2}$

Family heritability = $\frac{\sigma_f^2}{\frac{\sigma_e^2}{9.076}+\sigma_f^2}$

Between ages 1 and 5 years, narrow-sense individual tree heritabilities for height declined from 0.97 to 0.33. This was followed by steady increases to a maximum of 0.65 at age 11, remaining relatively stable until age 20 (Table 1, Fig. 4). Family heritabilities for height were slightly higher than for individual tree heritabilities, but the overall trend over time was nearly identical. Heritabilities for diameter at breast height were also similar in magnitude and had similar age trends (Table 1, Fig. 5).

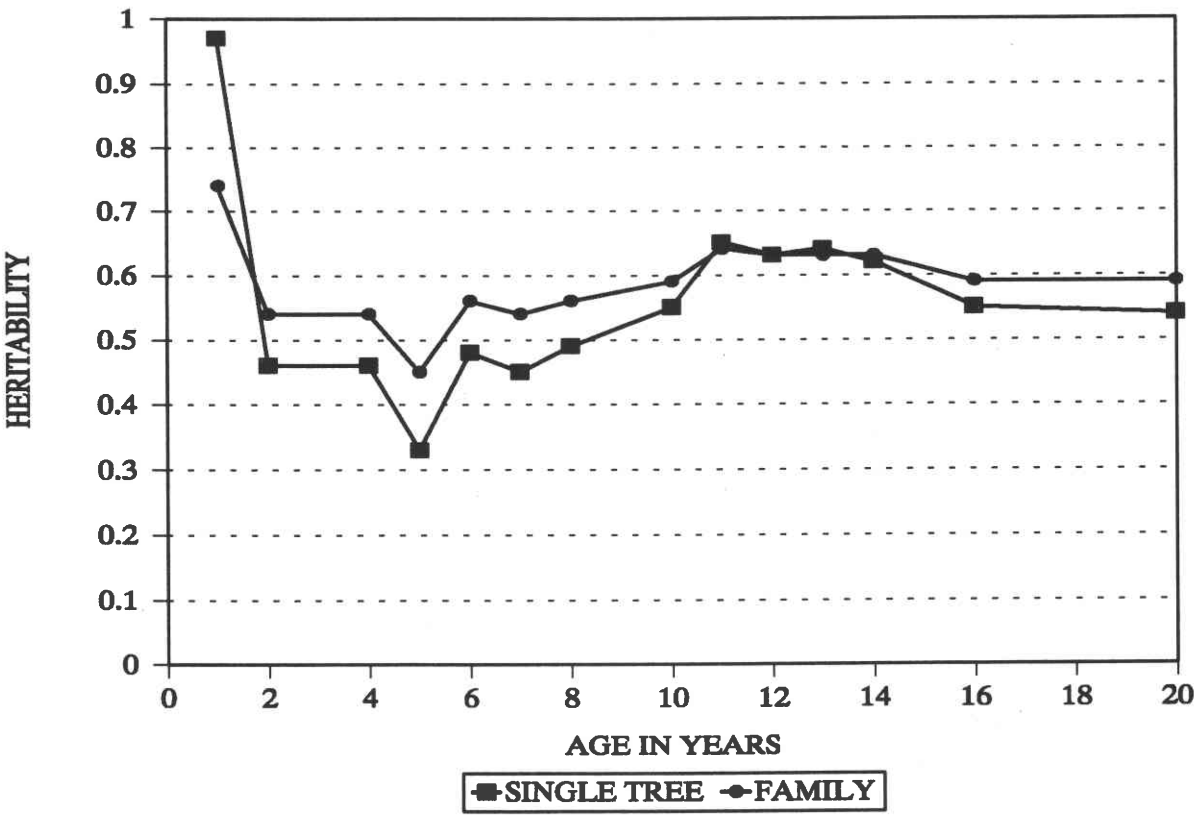

Figure 4. Narrow-sense (single-tree) and family heritability values for height at various ages of the Pleasant Valley black walnut progeny test.

The age-related pattern of heritability for black walnut tree height is similar to that described for North American conifers. Franklin (1979) proposed a hypothetical model with three genetic phases developed on the basis of heritability and additive genetic variance. The model consisted of a juvenile genotypic phase with a peak in heritability in the early to middle part of the phase, a mature genotypic phase with another peak in heritability occurring early in the phase, and a codominance-suppression phase characterized by rapidly declining heritability. The transition between juvenile and mature genotypic phases is characterized by a low in heritability (e.g., in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France) at age 16, $h^2 < 0.005$) and a mature genotypic phase which extends from age 15 to age 40 (Namkoong et al. 1972).

Although the absolute values for black walnut differ from values for coniferous species, the pattern of heritabilities is similar. Peak heritability was found at age 1 ($h^2 = 0.97$) with a low estimate at age 5 ($h^2 = 0.33$), corresponding to a juvenile phase. Heritabilities gradually increase to a high at age 11 ($h^2 = 0.65$) and diminish slightly to 0.54 by age 20. Although the black walnut heritabilities in this study tend to be substantially higher than those reported for North American conifers, there is a resemblance in the distribution of heritabilities with that of the conifers. Thus, the low

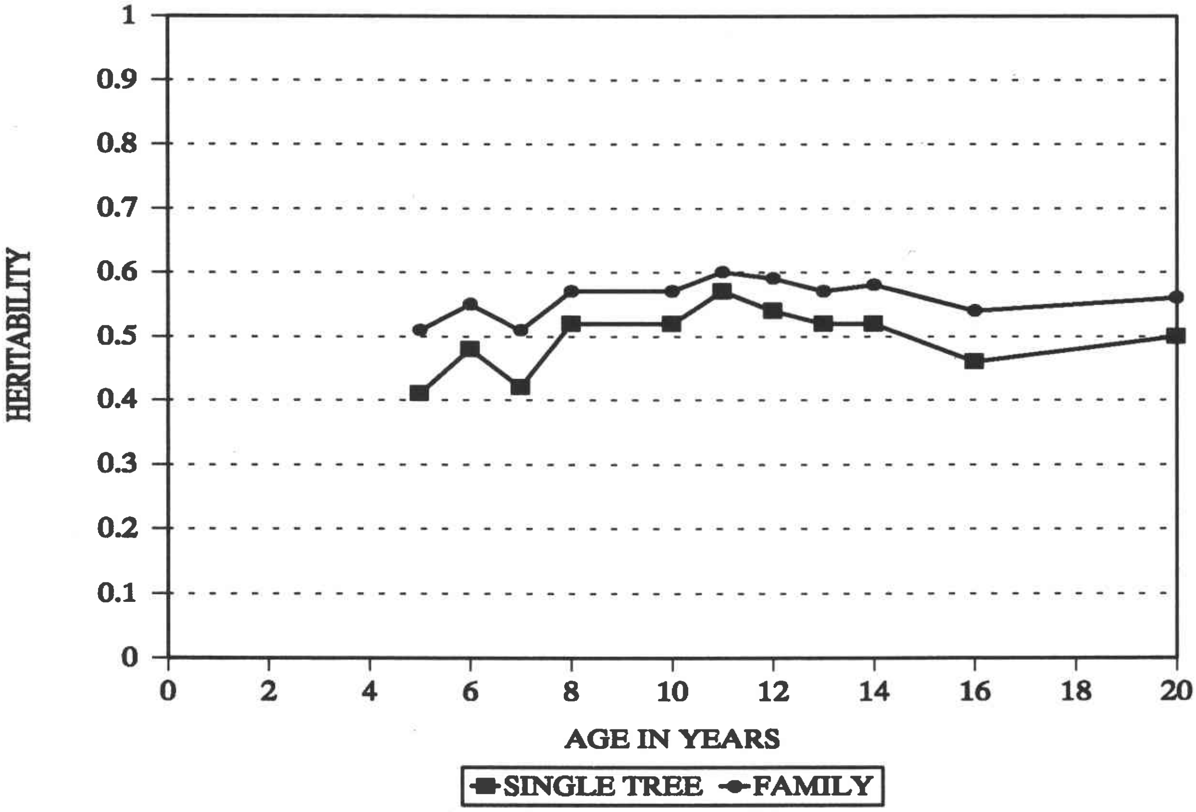

Figure 5. Narrow-sense (single-tree) and family heritability values for dbh at various ages of the black walnut progeny test.

heritability at age 5 may correspond to black walnut crown closure at this age and spacing and apparently occurs earlier than the age 15 in Douglas-fir (Franklin 1979).

It is possible that individual tree heritabilities presented here are overestimated due to potential confounding with a seed source effect (i.e., non-random mating within local seed sources) and a genotype x environment interaction, neither of which could be estimated from these data. Although age 13 genotype x environment interaction estimates presented elsewhere were very low (Rink and Clausen 1989) and would not have a great impact, the provenance effect potentially could have a substantial influence on these heritability estimates if trees represented in this study were in fact from more than one provenance. Thus, Squillace (1974) reported that overestimates of heritability result when data from unrelated families (e.g., such as from distant localities) are used for calculations. Strictly speaking, heritabilities should be estimated using data from open-pollinated families representative of a random-mating population in genetic equilibrium.

The curve of phenotypic age-age correlations between individual tree height in 1992 (at age 20) and individual tree height in earlier years is presented in Figure 6. By 1980 (age 8), the curve of age-age correlations appears to have attained a somewhat horizontal plateau; at this age, the correlation between 1992 height and 1980 height is 0.809, and the individual tree narrow-sense heritability is estimated at 0.49.

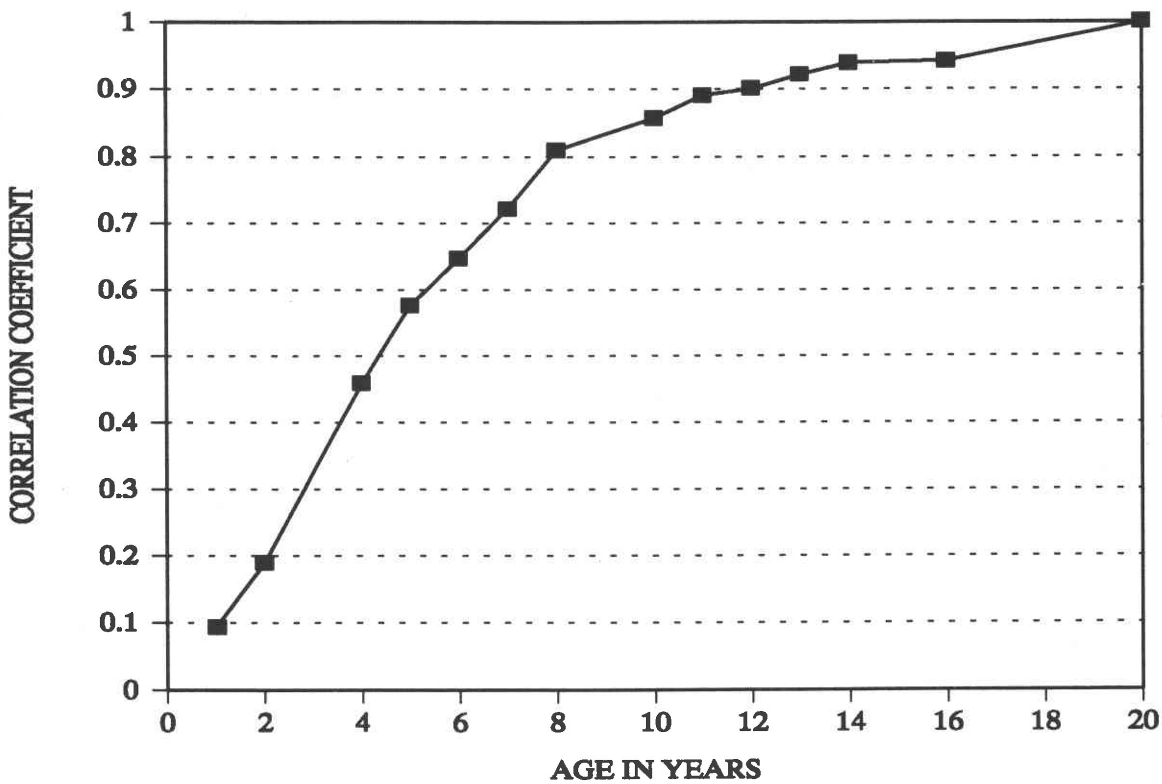

Figure 6. Age-age correlations of height of black walnut trees in 1992 (i.e., age 20) with height in other measurement years, on an individual tree basis.

Although the distribution of these heritability and phenotypic correlation values over time is based on a progeny test on only one site in southern Illinois, it would appear that selection of black walnut for improved height growth could be carried out with a high degree of confidence beyond age 8. Phenotypic correlations appear to have attained a plateau and seem to remain relatively stable. These results support the Indiana Division of Forestry (Coggeshall and Pennington 1982) effort in establishing close-spaced, short-term black walnut progeny tests for the purpose of juvenile testing and selection. Such approaches accelerate progeny testing and increase gain per unit time.

ACKNOWLEDGMENTS

The authors with to thank the Shawnee National Forest, USDA Forest Service, for providing the planting site for the Pleasant Valley black walnut progeny test.

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