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Site and Age Effects on Genotypic Control of Juvenile Juglans Nigra L. Tree Height

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Summary

Trends in heritabilities for tree height and coefficients of genetic prediction from three black walnut progeny tests were compared from establishment through age 13. Although the trend in genetic variance components was relatively uniform from location to location, the patterns of variation for heritabilities and other variance components differed, underscoring the site sensitivity of the species. It is concluded that black walnut progeny tests should employ single-tree plots or noncontiguous family plots for more precise estimation of genetic and environmental parameters.

Key words: Coefficients of genetic prediction, genotype × environment interactions, genotype × block interactions, heritability.

Annotation

Compares genetic variance components for height in three black walnut progeny tests. Concludes that differences in heritability patterns resulted from site sensitivity of black walnut.

Although the amount of genetic improvement that can be achieved in black walnut from selection has already been estimated, most estimates are either based on data from very young trees (Kucera *et al.*, 1974) or on data from only one outplanting location (Rink, 1984). Because estimates of genetic variation in other tree species change with age and are also affected by outplanting site conditions (Franklin, 1979; Namkoong and Conkle, 1976; Namkoong *et al.*, 1972), estimates of genetic variance and gain for black walnut are needed from different sites and from trees of different ages. Such estimates are of particular value due to the extreme site sensitivity of black walnut. The objective of this paper is to compare age-related changes in black walnut variance components, heritabilities and coefficients of genetic prediction from progeny tests at three outplanting locations.

Methods

Height measurements from three open-pollinated progeny tests of stand-grown trees in southern Illinois were used in this study. For two of the progeny tests seed was collected in 1969, cleaned, stratified overwinter, germinated, and outplanted in the spring of 1970 as germinating nuts at a depth of 5 cm. These two progeny tests were established on an upland sideslope (the University Farm plantation) and a narrow floodplain site (the Union County plantation). The University Farm plantation is located at 89.2° W., 37.7° N, elevation 152 m, in Jackson County on a Hosmer silt loam previously used as agricultural cropland. The Union County progeny test is located at 89.4° W, 37.5° N, elevation 134 m, on Haymond and Elsah silt loams that had been in fescue sod since 1965. The third progeny test (Pleasant Valley plantation) was established with 1-0 seedlings in spring 1973 on a Haymond silt loam in a wide floodplain of Sexton Creek, Alexander County, Illinois (89.3° W, 37.3° N, elevation 146 m) on an abandoned pasture. Weed control at all three progeny tests consisted of strip-spraying a simazine, dalapon, 2,4-D mix prior to outplanting and spot-spraying for 3 years thereafter. At age 13 the trees averaged 5.0, 4.9, and 5.2 m at Union County, University Farm, and Pleasant Valley, respectively.

All three progeny tests were designed to be converted to seedling seed orchards at a subsequent age; seedlings of open-pollinated families (a family is defined as a group of seedlings of a single mother tree) were randomly assigned to row plots in blocks in a randomized complete block design. Only trees that were „above average" in form quality were included in the progeny tests, although no rigid criteria were applied during selection of mother trees. Most mother trees were from within a 250-mile radius of the plantation locations, which included southwestern Missouri, western Kentucky and Tennessee, northwestern Arkansas, and southern Illinois, although some seed from southeastern Kansas was also included at Pleasant Valley. At the University Farm and Union County tests, germinants from 87 mother trees were outplanted in 5 blocks, while at Pleasant Valley seedlings of 54 families were planted in 10 blocks. Although the same families were represented at the Union County and University Farm tests, the Pleasant Valley plantation contained seedlings of different families. Spacing in the University Farm and Union County tests was 1.2 m between trees within rows and 3.0 m between rows, while at the Pleasant Valley test spacing was 1.8 m within and 3.7 m between rows. As a result, blocks were approximately 0.18 hectares in area at each of the three tests.

Due to the closer spacing in the Union County and University Farm tests, earlier roguing was needed; they were thinned after the fifth growing season, removing the smallest two trees from each five-tree family plot. At Pleasant Valley the roguing was applied after the twelfth growing season, removing the three smallest trees in each five-tree family row plot.

Annual height measurements were analyzed with univariate analysis of variance techniques using a random effects two-way model on an individual tree basis; sources of variation in the model included blocks, families, and their interaction. To minimize bias during variance component estimation, however, data from each progeny test had to be selectively balanced by deleting measurements from families not equally represented in all blocks. In addition, one complete block was deleted from the data set at each location due to low survival in these blocks. Determination of which trees and families to retain in the data set was made on the most recent set of measurements at each location, and only these data were retained for variance component estimation for all prior measurement years. However, variances and heritabilities based on this data set were not greatly different from those based on an unthinned data set with less selective balancing. The final data set used for variance component estimation included 49 families at University Farm, 44 families at Union County, and 24 families at Pleasant Valley. Resulting variance components were used to generate annual narrow-sense individual tree heritabilities. In addition, a combined location analysis of variance was used for data from Union County and University Farm. Variance components were estimated by the Maximum Likelihood Procedure of the Statistical Analysis System (SAS Institute, 1979). For this procedure the data set had to be further balanced to include only 29 families. Variance components were also used to generate BARADAT's (1976) coefficients of genetic prediction (CGPs). Trends in variance components, heritabilities, and CGPs for all measurement years were compared among all three progeny tests.

Results and Discussion

Statistical significance ($p < 0.001$) in analyses of variance was indicated for all effects at all outplanting sites in all measurement years except for the block effect at the Pleasant Valley site in the first year after establishment. After the second growing season, however, this effect was also highly significant.

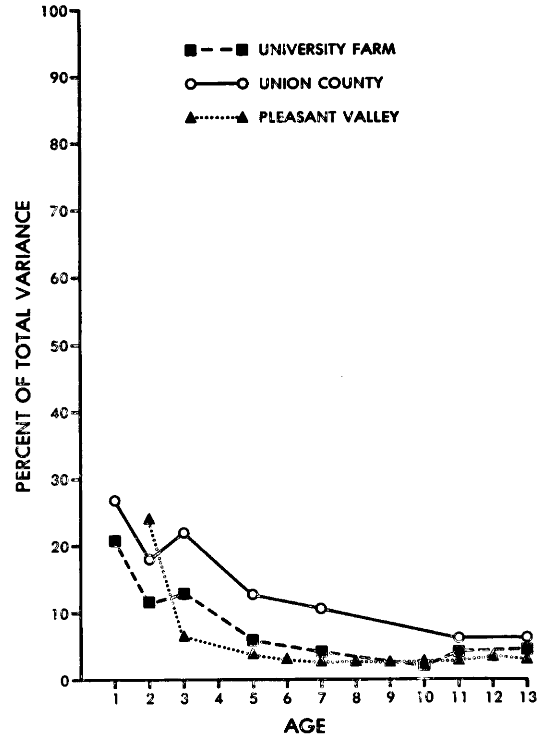

Figure 1. — Trends in variance components for tree height among half-sib families (σ^2_f, expressed as a percent) for three black walnut progeny tests over 13 growing seasons.

Genetic control over black walnut height growth as reflected in family variance components (expressed as a percent of total variance) appears to follow a similar trend at all three plantations (*fig. 1*). Four years after plantation establishment the trend in family variance components appears relatively stable, with the lines gradually converging by the last measurement; at age 5, the family variance component accounts for 3.9, 6.2, and 12.8 percent of total variation (*tab. 1*). However, the plot of heritability (*fig. 2*) shows distinctly different trends in the different progeny tests. In all three cases heritability is at a maximum in the year of establishment and decreases rapidly with age. Following the initial decline, however, there does not seem to be any common trend in heritability, as three different patterns corresponding to the three progeny tests emerge. The trend at Pleasant Valley is for increasing heritability from age 7 until age 12 while at the Union County progeny test heritability declines to age 11 and then stabilizes. At University Farm, heritability continues to decrease until age 10 and then increases again. By age 13 heritability is relatively stable in all three plantations.

Because the family variance components are relatively homogeneous in all progeny tests, and heritability is a ratio of additive variance (i.e., 4 × family variance) divided by phenotypic variance, the explanation for the discordant heritability trends must be with the phenotypic variance. In this experiment phenotypic variance is the sum of family, block × family, and error variance components. At both the Union County and University Farm progeny tests the sum of the error and block × family interaction components accounts for more than 60 percent of total variance in every measurement. By contrast, at Pleas-

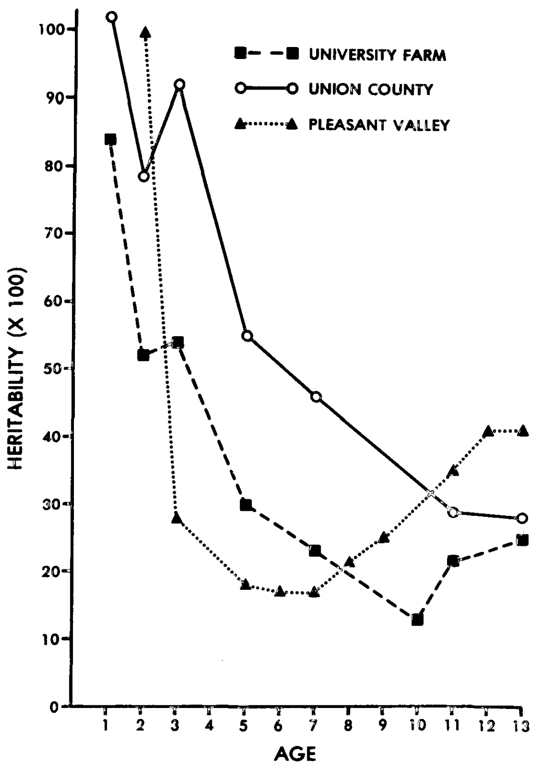

Figure 2. — Trends in heritability (h^2) of tree height based on growth data from three half-sib progeny tests over 13 years after establishment.

ant Valley this sum is only high through age 7 but below 35 percent after age 11 (*tab. 1*).

Differences in heritability trends between Pleasant Valley and the other progeny tests apparently lie in how efficiently the tests were blocked. The Pleasant Valley progeny test is located on a wide, relatively level floodplain. Site gradients and microsite variation on such a wide floodplain tend to be relatively gradual, enabling efficient partitioning of the area into blocks. By contrast, the Union County test is located on a much narrower, more sloping floodplain surrounded on two sides by a steep bluff. Blocks on this site were located on a slope that included more abrupt microsite variation. The University Farm test is situated on a highly eroded upland hillside which was even more difficult to subdivide into site-uniform blocks.

The variance components reflect site conditions at the respective locations. In all three cases the block variance component is low during the plantation establishment phase and increases gradually (*fig. 3*). At Union County and University Farm the block component tends to level off after the initial increase (ages 7 to 10) but a Pleasant Valley the block component continues to increase. Furthermore, the Pleasant Valley test consistently has the lowest block × family interaction component (*fig. 4*), which indicates that this site has the least within-block site heterogeneity and substantiates the high blocking efficiency at this site. Similarly, the greater site heterogeneity at the Union County and University Farm progeny test is reflected in the larger block × family interaction and within-plot variance components (*figs. 4* and *5*, resepectively) which, when used in the denominator of the heritability ratio, also result in lower heritability estimates at those sites.

Variance components from combined-location analyses of Union County and University Farm progeny tests (tab. 1) disclosed abrupt differences in components between ages 3 and 5. The differences were most pronounced

Table 1. — Variance components for tree height as a percent of total variance.

	Plantation age (years)							
Components	1	2	3	5	7	8	11	13
				Union County				
Block	9.35	10.22	5.00	6.77	6.45		14.01	13.44
Family	26.99	17.69	22.02	12.79	10.65		6.14	6.11
B x F	23.49	31.52	39.13	50.76	55.21		59.99	55.78
Error	40.01	40.57	33.85	29.69	27.69		19.85	24.67
h^2	1.19	0.79	0.92	0.55	0.46		0.29	0.28
SE (h^2)	0.34	0.28	0.31	0.26	0.26		0.24	0.23
				University Farm				
Block	2.24	9.47	7.80	18.58	28.27	27.20	22.84	29.87
Family	20.59	11.82	12.52	6.15	4.12	2.43	4.17	4.45
B x F	15.86	24.68	32.81	37.92	39.00	39.69	42.04	34.82
Error	61.31	54.03	46.87	37.35	28.61	30.69	30.96	30.87
h^2	0.84	0.52	0.54	0.30	0.23	0.13	0.22	0.25
SE (h^2)	0.17	0.21	0.22	0.20	0.20	0.18	0.20	0.20
				Union County, University Farm Combined				
Plantation	29.76	58.45	47.08	6.82	0		0	0
Blocks/Pl.	5.49	4.68	5.62	16.87	17.79		21.25	22.46
Family	7.36	4.02	10.02	7.46	6.63		6.71	4.36
Pl. x F	7.48	3.22	0.99	2.84	2.46		0	1.84
(BxF)/Pl.	16.74	11.55	17.92	39.28	45.35		45.89	43.23
Error	33.17	18.08	18.37	26.74	27.78		26.15	28.11
h^2	0.45	0.44	0.85	0.39	0.32		0.34	0.23
SE (h^2)	0.26	0.24	0.30	0.22	0.18		0.20	0.18

					Pleasant Valley					
	2	3	5	6	7	8	9	11	12	13
Block	0	3.73	14.34	27.80	33.56	46.25	55.40	64.26	66.27	68.73
Family	24.28	6.84	3.94	3.14	2.91	2.80	2.81	3.17	3.49	3.20
B X F	14.33	25.26	34.21	28.93	24.47	26.86	24.94	23.03	20.47	19.43
Error	61.40	64.18	47.50	40.13	39.07	24.10	16.85	9.54	9.78	8.64
h^2	0.97	0.28	0.18	0.17	0.17	0.21	0.25	0.35	0.41	0.41
SE (h^2)	0.33	0.15	0.14	0.14	0.13	0.15	0.16	0.20	0.21	0.21

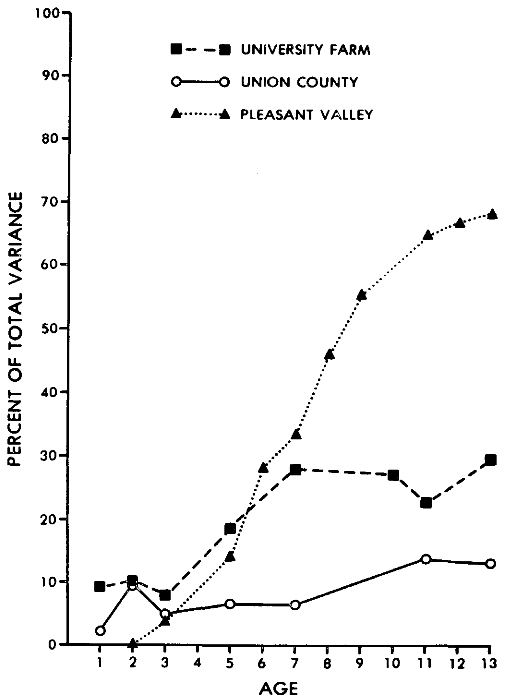

Figure 3. — Trends in among-block variance components for tree height (σ^2_b, expressed as a percent) for three black walnut progeny tests over 13 growing seasons.

for the plantation effect and presumably reflected seedling establishment through age 3. The single largest variance component beyond age 3 resulted from the interaction of blocks and families within plantations. Surprisingly, components for the interaction of plantations and families (estimates of genotype × environment interactions) were low in spite of statistical significance ($p < 0.01$). The implication of these results is that on these two sites microenvironmental variation is so great that it exceeds macroenvironmental differences between these upland and bottomland sites. It should also be emphasized, however, that these genotype × environmental variance components are based on only two sites in southern Illinois, not enough to get a good genotype × environment variance estimate.

Presumably the greater heritabilities obtained at the Pleasant Valley test reflect more accurate estimates of inheritance of juvenile black walnut height growth. However, heritabilities and coefficients of genetic prediction (*tab. 2*) reported here are somewhat lower than those reported earlier for Pleasant Valley (RINK, 1984). Although there had been an effort to balance the earlier data set, the differences in heritabilities and CGPs are thought to result from the sensitivities of these parameters to data imbalance. Comparison of CGPs among the three progeny tests (*tab. 2*) reveals that CGPs from Pleasant Valley are higher than those from the other two tests for the most recent measurements. As with the heritabilities discussed earlier, reduced CGPs appear to result from a lack of within-block uniformity at University Farms and Union County.

Large block × family effects have also been reported in genetic analyses of tests in loblolly pine (*Pinus taeda* L.) and cottonwood (*Populus deltoides* BARTR.) (FOSTER, 1985; LAMBETH *et al.*, 1983). Such effects may be inherent with contiguous row plots in randomized complete block design plantings commonly associated with genetic experiments requiring large areas of land and embracing more site variability than once thought (MCCUTCHAN *et al.*, 1985). Single-tree plots or alternatively noncontiguous multi-tree plots randomized throughout blocks have been suggested for increasing the within-block uniformity required for more precise estimation of genetic parameters (LAMBETH *et al.*, 1983; LIBBY and COCKERHAM, 1980). Site uniformity within blocks is especially critical for black walnut because it is an extremely site sensitive species. However,

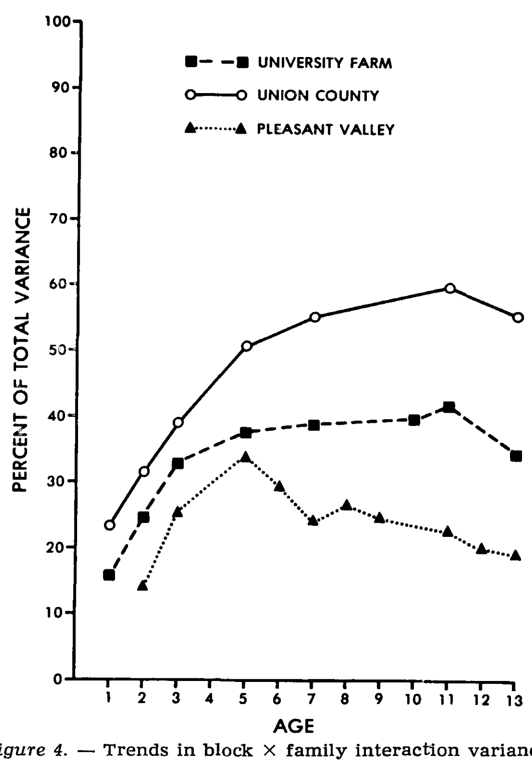

Figure 4. — Trends in block × family interaction variance components ($\sigma^2_{(bxf)}$, expressed as a percent) for three black walnut progeny tests over 12 growing seasons.

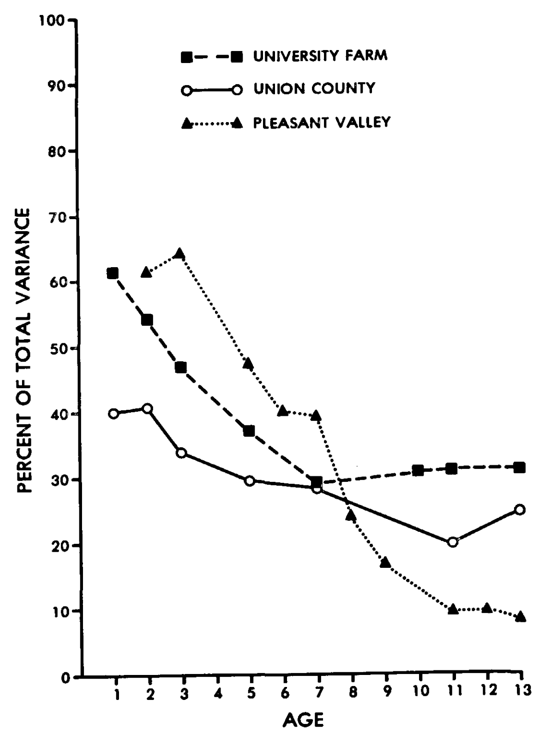

Figure 5. — Trends in within-plot (error) variance components for tree height (σ^2_e, expressed as a percent) for three black walnut progeny tests over 13 growing seasons.

Table 2. — Coefficients of genetic prediction (CGP) for black walnut tree height for University Farm (UF), Union County (UC), and Pleasant Valley (PV).

		Plantation age											
		1	2	3	5	6	7	8	9	10	11	12	13
1	UF	0.84	0.35	0.36	0.21	-	0.09	-	-	0.06	0.00	-	0.00
	UC	1.19	0.95	0.86	0.56	-	0.48	-	-	-	0.42	-	0.34
	PV	-	-	-	-	-	-	-	-	-	-	-	-
2	UF		0.52	0.50	0.39	-	0.21	-	-	0.18	0.14	-	0.15
	UC		0.79	0.75	0.53	-	0.46	-	-	-	0.41	-	0.33
	PV		0.97	0.45	0.26	0.22	0.12	0.17	0.13	-	0.13	0.19	0.14
3	UF			0.54	0.42	-	0.27	-	-	0.23	0.19	-	0.19
	UC			0.92	0.69	-	0.61	-	-	-	0.56	-	0.47
	PV			0.28	0.19	0.17	0.18	0.16	0.22	-	0.25	0.27	0.25
5	UF				0.30	-	0.19	-	-	0.15	0.14	-	0.15
	UC				0.55	-	0.49	-	-	-	0.44	-	0.35
	PV				0.18	0.18	0.17	0.19	0.20	-	0.25	0.28	0.27
6	UF					-	-	-	-	-	-	-	-
	UC					-	-	-	-	-	-	-	-
	PV					0.17	0.18	0.18	0.19	-	0.22	0.23	0.24
7	UF						0.23	-	-	0.18	0.21	-	0.22
	UC						0.46	-	-	-	0.41	-	0.35
	PV						0.17	0.18	0.20	-	0.22	0.23	0.24
8	UF							-	-	-	-	-	-
	UC							-	-	-	-	-	-
	PV							0.21	0.22	-	0.23	0.24	0.25
9	UF								-	-	-	-	-
	UC								-	-	-	-	-
	PV								0.25	-	0.29	0.29	0.29
10	UF									0.13	0.18	-	0.17
	UC									-	-	-	-
	PV									-	-	-	-
11	UF										0.22	-	0.23
	UC										0.29	-	0.27
	PV										0.35	0.38	0.38
12	UF											-	-
	UC											-	-
	PV											0.41	0.41
13	UF												0.25
	UC												0.28
	PV												0.41

although single-tree plots are efficient for estimating genetic parameters, they may not be practical for individual tree selection.

As expected when large block × family effects are present, family rankings among blocks within a location are inconsistent; the highest ranking family in one block may be below average in height in another block. The lack of consistency is so great that it is not surprising that there is also a lack of consistency among mean family performance from one outplanting location to another. However, some faster growing families tend to be faster growing at all locations, although they may be few in number. Perhaps the strategy for walnut improvement should be to select the consistently faster growing families even at a risk of sacrificing some growth gains, since such consistently high performers are not always the fastest growing families at all locations — i.e., selection for broad adaptability. The alternative to this strategy would be to select specific families for specific sites. Such a multiple selection approach is not a viable one in an improvement program limited by the low number of sites suited for walnut culture.

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Using Economic and Decision Making Concepts to Evaluate and Design a Corporate Tree Improvement Program

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Abstract

This paper describes how economic and decision making techniques were used, for a corporately owned timber tract to evaluate an existing Douglas-fir tree improvement program and to plan its future direction. We designed tree improvement alternatives to meet the projected seed requirements over time. The alternatives differ in the amount of gain they will provide, and in their cost. Considered are the collection of cones from designated parents in wild stands, first-generation seed orchards of two types, second-generation seed orchards of two types, and combinations of first and second generation orchards. After ensuring that each alternative is cost-effective, its net present value is calculated to determine the economically desirable alternative. For the specific case examined, interim seed collection should be from designated parents in wild stands,

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