HEIGHT AND DIAMETER VARIATION IN TWELVE WHITE ASH PROVENANCE/PROGENY TESTS IN EASTERN UNITED STATES

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Abstract: Results from 12- and 13-year-old rangewide provenance/progeny tests of white ash (*Fraxinus americana* L.) planted at 12 locations throughout the eastern United States are reported. Although heritability of white ash tree height and dbh is high at both the provenance and family levels, the trend in variance components is for increasing provenance and declining family components. Tree height is negatively correlated with latitude in southern outplantings and positively correlated with latitude in the north. Plantations with the tallest trees were those that had been clean cultivated for several years after establishment.

INTRODUCTION

Rangewide provenance/progeny tests of white ash (*Fraxinus americana* L.) were established in 1976 and 1977 with plantings at more than 20 locations throughout the eastern United States and Canada. The study was initiated because of the increased importance and value of the white ash. Several papers have reported early growth and survival results from that study, including preliminary white ash seed source recommendations for planting in different parts of the geographic species range (Bey et al. 1977, Clausen 1982, Clausen 1984, Clausen et al. 1981). Summarizing those early recommendations, at age 5 northward movement of seed or seedlings not exceeding 322 km (200 miles) generally resulted in some growth increases over local plant material, except in the northernmost parts of the species range where only local seed sources should be used. This paper reports growth results through age 13.

MATERIALS AND METHODS

Open-pollinated seeds were collected from up to 10 native parent trees at each of 59 locations throughout the natural range of white ash in 1973 and 1974 and then sown in a southern Illinois nursery (Bey et al. 1977, Clausen et al. 1981). Resulting 1-0 seedlings were used to establish 22 plantations throughout the eastern United States and Canada in 1976. By the 1988-1989 dormant season, when these data were collected, many personnel changes, budget

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constraints, and shifts in program emphasis among cooperating agencies had resulted in abandonment of test sites in northern Alabama, Tennessee, New York, and Ontario, Canada. In other cases, high tree mortality and poor growth precipitated abandonment of plantings in Minnesota, northern Wisconsin, and Missouri, as well as plantings in Ontario and New Brunswick, Canada. As a result, 13-year measurements were only available from 10 plantations; this paper is based on height and dbh data from trees 13 years after outplanting in those 10 plantations in addition to two plantings that were established 1 year later (Nebraska and Michigan) and from which measurements reflected growth 12 years after outplanting. The latter two provenance outplantings were established in 1977 with surplus stock after seedling distribution to the 1976 planting sites. Unfortunately, there were not enough seedlings of different open-pollinated families for a progeny test, and family identity of seedlings at the Michigan and Nebraska sites was not retained.

The number of provenances in each plantation ranged from 16 in Alabama to 35 in the Michigan plantation, and the number of families per plantation ranged from 39 to 52 (table 1). The geographic origins of the families also varied from plantation to plantation. Most plantations contained families from portions of the range near their particular geographic location in order to minimize mortality of more distant, nonadapted trees. Three plantations (OH, AL, and IL) were designed to have 45 families from 19 widely separated provenances in common so provenance x environment interactions could be evaluated. All plantations were established in a randomized complete block design with five-tree row plots and five replications at a spacing of 3.7 m except in OH where a completely random design (no blocks) was used.

Table 1.--Location of plantations and number of white ash provenances and families in each[1]

Plantation (state)	County	Latitude °N	Longitude °W	Number of provenances	Number of families
Ohio (OH)	Muskingum	40.0	82.0	21	49
Alabama (AL)	Macon	32.4	85.6	16	42
Illinois (IL)	Union	37.5	89.3	26	52
Kentucky (KY)	Rowan	38.2	83.4	23	43
West Virginia (WV)	Tucker	39.0	79.7	22	45
Kansas (KS)	Jefferson	39.0	95.2	27	44
Louisiana (LA)	St. Landry	30.4	92.0	19	45
Indiana (IN)	Crawford	38.2	86.3	22	39
Arkansas (AR)	Montgomery	34.6	93.6	18	42
Wisconsin (WI)	Iowa	43.0	90.1	24	40
Michigan (MI)	Kalamazoo	42.3	85.3	35	--
Nebraska (NE)	Adams	40.5	98.3	27	--

[1]Family identity of seedlings was not retained at the Michigan and Nebraska outplantings.

Differences in performance among provenances and families in each plantation were tested by the General Linear Model analysis of variance technique based on plot means to accommodate missing data. Variance components were calculated for between- and within-provenance comparisons. When appropriate, correlation and regression analyses were used to estimate the relationship between tree height and provenance latitude, longitude, and elevation. Data were analyzed using programs of the Statistical Analysis System (SAS Institute 1982).

Table 2.--Plantation averages for height, dbh[1], survival, standard deviations, and ratios of tallest to shortest trees[2]

Plantation	Height (m)	Standard deviation (m)	Ratio of tallest: shortest	Dbh (cm)	Standard deviation (cm)	Survival (%)	Number of surviving trees
OH	7.7	1.7	2.6	9.4	3.0	62	710
AL	7.0	0.9	1.5	7.9	1.1	97	1025
IL	6.8	1.1	1.7	7.7	2.7	92	1192
KY	4.0	0.7	2.0	4.9	1.2	63	676
WV	3.5	0.7	1.9	3.8	1.2	52	581
KS	3.2	0.6	2.0	3.2	0.9	93	1031
LA	3.0	1.3	5.0	2.7	1.5	74	829
IN	3.0	1.0	7.2	---	---	69	670
AR	2.9	0.8	3.2	3.3	1.4	50	525
WI	2.5	0.5	2.0	2.5	0.7	57	570
MI	5.7	0.6	2.0	5.8	0.9	83	726
NE	3.3	0.5	1.9	4.5	0.8	56	375

[1] Dbh data for the Indiana outplanting were not available.
[2] Michigan and Nebraska data reflect age 12 measurements. Data for all other plantations reflect age 13 measurements.

RESULTS AND DISCUSSION

After 13 years in the field, survival ranged between 97% and 50% (table 2). Average height of white ash trees ranged from 2.5 m at the southern Wisconsin site to 7.7 m in Ohio (table 2), a threefold difference in height growth between outplantings with the slowest and fastest growth, respectively. As observed earlier by Clausen (1984), the three plantations with the fastest growth (OH, AL, and IL) were all clean cultivated during the first 2 to 3 years after outplanting. The implication is that white ash is extremely sensitive to competition from weeds and brush during the early establishment phase and that the effects of plantation maintenance persist for a long time thereafter.

The trend in diameters at breast height (dbh) closely mirrors the pattern in tree height; as expected, on the average the tallest trees tend to have the greatest diameters (table 2). The overall correlation of height with dbh was 0.78. The height-to-height ratios for the of tallest to shortest provenances ranged from 1.5 at the Alabama plantation to 7.2 at the Indiana plantation (table 2).

Analysis of variance for height and dbh indicates a predominance of statistical significance, as indicated by probabilities of greater F-values (table 3). The provenance effect was statistically significant at all outplanting sites for both height and dbh at age 13 (table 3). In an earlier report on this study, the provenance effect for height was nonsignificant at the Indiana, Kansas, and Wisconsin locations at age 5 (Clausen 1984). By age 13 this effect had become significant at all sites, including the latter three. However, statistical significance for the family effect was less common than for the provenance effect.

Table 3.--Probabilities of greater F-values in analyses of variance of white ash height and dbh.

	Block		Provenance		Family/provenance	
Plantation	Height	Dbh	Height	Dbh	Height	Dbh
OH	----	----	0.0001	0.0001	0.0003	0.0001
AL	0.0015	0.0015	0.0001	0.0001	0.0001	0.0001
IL	0.0001	0.0001	0.0001	0.0001	0.0016	0.0001
KY	0.0341	0.0154	0.0001	0.0001	0.0472	0.0069
WV	0.0675	0.2821	0.0001	0.0001	0.1143	0.0664
KS	0.0160	0.0581	0.0001	0.0001	0.0001	0.0001
LA	0.6123	0.9030	0.0001	0.0001	0.0066	0.0007
IN	0.3288	----	0.0002	----	0.3273	----
AR	0.0001	0.0001	0.0001	0.0008	0.9708	0.4687
WI	0.0002	0.0002	0.0001	0.0001	0.8768	0.9363
MI	0.0001	0.0001	0.0001	0.0001	----	----
NE	0.0001	0.0002	0.0001	0.0057	----	----

Provenance variance components for height (table 4) appear to be increasing; the overall mean provenance component averaged over all locations increased from 28.6% at age 3 to 38.5% at age 13, although this trend was not consistent at all sites. For example, at the Kentucky site the provenance component decreased from 30% at age 3 to 14% at ages 5 and 13. In Kansas, this component increased from 4% at age 3 to 18% at age 5 and dropped to 10% by age 13.

At the latest measurement the provenance component was greater than the family component at all but two locations for height and at all but one location for dbh. For both height and dbh the mean provenance component was more than three times greater than the family component at age 13. In contrast to the trend for increasing provenance components, family variance components for height appear to be declining in magnitude; the mean family component decreased from 11.9% of total variance at age 3 to 7.5% at age 13 (table 4).

Table 4.--Provenance and family-within-provenance variance components as a percent of total variation and heritabilities for age 13 height and dbh[1]

	Height						Dbh		Heritability			
	Provenance			Family			Prov.	Fam.	Height		DBH	
	Age (yrs)			Age (yrs)			Age (yrs)					
Plantation	3	5	13	3	5	13	13	13	Prov.	Fam.	Prov.	Fam.
	---- % ----			---- % ----			--- % ---					
OH	24	43	17	5	1	5	22	4	0.82	0.56	0.85	0.60
AL	51	65	68	12	9	0	46	9	0.96	0.75	0.91	0.77
IL	64	60	46	6	12	4	68	3	0.91	0.54	0.96	0.61
KY	30	14	14	6	2	16	15	20	0.77	0.38	0.80	0.51
WV	17	28	47	17	4	0	40	5	0.90	0.29	0.88	0.34
KS	4	18	10	17	26	31	10	37	0.79	0.74	0.80	0.81
LA	57	67	75	8	7	3	64	8	0.97	0.48	0.96	0.57
IN	0	0	28	30	10	16	--	--	0.87	0.12	--	--
AR	30	21	25	18	20	0	27	0	0.73	0	0.63	0
WI	9	6	57	0	13	0	47	0	0.87	0	0.80	0
mean	28.6	32.2	38.7	11.9	10.4	7.5	37.6	10.8	0.86	0.39	0.84	0.47

[1] Variance components for ages 3 and 5 previously published by Clausen (1984).

Heritabilities for height and dbh (table 4) indicate that a great deal of variation in these plantations is heritable. The mean provenance heritability of 0.81 to 0.85 is the same order of magnitude observed for loblolly pine (Pinus taeda) of this age and indicates that most of the variation among provenances can be utilized for growth improvement (Kung 1989). Similarly, the mean family-within-provenance heritability of 0.39 to 0.47 is consistent with heritability values for height in black walnut (Rink 1984, Rink and Clausen 1989).

Combined location analyses of variance across all planting sites indicated significant provenance x plantation location interactions for both height and diameter. These interactions imply that provenance selection for optimum growth at different geographic localities and perhaps for specific sites within localities may be important for artificial regeneration of white ash. Because these combined location ANOVA's were so highly imbalanced, variance component extraction from them would produce variance components less precise than would be possible from a completely balanced design. To aid in interpreting the interaction, we used an individual location response surface model with linear and quadratic provenance latitude and longitude and their crossproducts as independent variables; response surface regressions are commonly used to model genotypic response to environment. Results of these analyses indicated that latitude contribution to the model was statistically significant at 10 of 12 outplanting locations, while longitude had a significant contribution at only 4 sites (table 5). Although the patterns were not clearcut, the most frequent response surface solutions indicated that seed sources south of planting sites resulted in maximizing growth. Similarly, in a more recent analysis of 5-year white ash tree height using growth response functions, Roberds et al. (in press) found that trees from southern provenances tended to be broadly adapted and grew well considerably north of their origin. The only definite exception to this pattern was at the West Virginia site where a seed source from northern New York or southern Ontario was projected to maximize growth; this may be the result of a combination of northerly latitude and high elevation (330 m) of this planting location.

Table 5.--F-values and coefficients of determination response surface model for white ash tree height[1]

	F-value[2]		Model
Plantation	Latitude	Longitude	R-square
OH	19.94**	3.70*	0.88
AL	10.98**	0.09	0.82
IL	6.77**	1.67	0.67
KY	2.04	1.93	0.64
WV	2.43	2.17	0.42
KS	7.46**	3.07*	0.59
LA	19.33**	1.66	0.90
IN	9.34**	9.50	0.84
AR	10.81**	0.97	0.79
WI	6.10**	5.22**	0.66
MI	6.82**	1.25	0.47
NE	4.17*	1.83	0.45

[1] Equation for model: $y = a + b_1 \text{(prov. lat.)} + b_2 \text{(prov. lat.)}^2 + b_3 \text{(prov. long)} +$

$$b_4 \text{(prov. long.)}^2 + b_5 \text{(prov. lat. x prov. long.)}$$

where: a = y intercept and
b_1 through b_5 = coefficients

[2] Statistical significance of F-values: ** significant at $P < 0.01$
* significant at $P < 0.05$

Pearson correlation coefficients between mean tree height at age 13 and provenance latitude, longitude, and elevation are listed in table 6. The most apparent result of this analysis is the trend for statistically significant negative correlations between tree height and provenance latitude in the southernmost outplantings. Correlations between height and provenance latitude are positive for the northernmost sites. Similarly, there are negative correlations between tree height and provenance elevation at the southernmost sites, but several of these correlations are not statistically significant. There was no readily apparent trend between provenance longitude and tree height. Similarly, at age 5 latitude of seed origin also had a greater effect on height than either longitude or elevation, especially at the northern and southern fringes of the species range (Clausen 1984).

Table 6.--Correlation coefficients of average provenance tree height with provenance latitude, longitude, and elevation[1,2]

Plantation	Latitude	Longitude	Elevation
OH	0.56	-0.24 ns	0.43
AL	-0.88	0.47 ns	-0.75
IL	-0.64	0.57	-0.17 ns
KY	-0.50	0.43	0.07 ns
WV	0.16 ns	-0.17 ns	0.41 ns
KS	-0.21 ns	0.39	-0.05 ns
LA	-0.91	0.58	-0.62
IN	-0.69	0.61	-0.23 ns
AR	-0.45	0.21 ns	-0.49
WI	0.39	0.37 ns	0.29
MI	0.43	-0.20 ns	0.27 ns
NE	0.00 ns	0.19 ns	0.32

[1] Based on family/provenance means at each location, except in Michigan and Nebraska where only provenance means were available.
[2] Unless noted with "ns" all correlations are statistically significant at least at the 95% level of probability.

Such variation patterns may be influenced by susceptibility to frost injury. In an analysis of the distribution of frost injury among white ash provenances in a related Ontario, Canada, seed source test, autumn frost injury was highly correlated with provenance latitude (Clausen 1982). Similarly, when white ash stem sections from ten geographic origins from a southern Michigan provenance test were exposed to controlled freezing, trees of northern origin were found to be more cold hardy than southern trees in early and midwinter (Alexander et al. 1984). Furthermore, a great deal of individual tree variation in cold hardiness within each provenance was observed.

CONCLUSIONS

Clausen (1984) pointed out the beneficial effects of plantation maintenance during the plantation establishment phase of this study. Present results confirm those observations. Perhaps fewer test plantings would have been abandoned if more plantation maintenance had been available.

Present 13-year data indicate that height growth improvements of 25 to 30% on sites with good growth and more than 50% on sites with poor growth may be obtained through proper provenance selection. Seed source recommendations made by Clausen (1984) are still applicable. This is further emphasized by significant provenance x site interactions.

The predominance of statistical significance for provenance effects for height and diameter and the magnitude of provenance variance components indicate the importance of proper provenance selection in artificial regeneration programs for white ash. High heritabilities, based on open-pollinated half-sib family variance components, indicate that individual tree selection is also effective in white ash. However, the latter variance components are relatively low and seem to be declining in magnitude with age. Because variance components follow fluctuating patterns that are probably species specific, we will have to track these patterns to determine how effective individual tree selection is at different ages.

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LITERATURE CITED

Alexander, Nancy L., Harrison L. Flint, and P. Allen Hammer. 1984. Variation in cold-hardiness of Fraxinus americana stem tissue according to geographic origin. Ecology 65:1087-1092.

Bey, C. F., F. H. Kung, and R. A. Daniels. 1977. Genotypic variation in white ash--nursery results. Cent. States For. Tree Improv. Conf. Proc., West Lafayette, IN 10:141-145.

Clausen, K. E. 1982. Variation in frost injury to white ash families in an Ontario plantation. Can. J. For. Res. 12:440-443.

Clausen, Knud E. 1984. Survival and early growth of white ash provenances and progenies in 19 plantations. Can. J. For. Res. 14:775-782.

Clausen, K. E., F. H. Kung, C. F. Bey, and R. A. Daniels. 1981. Variation in white ash. Silvae Genet. 30:93-97.

Kung, F. H. 1989. Optimal age for selecting loblolly pine seed sources. South. For. Tree Improv. Conf. Proc., Charleston, SC 29:302-308.

Rink, George. 1984. Trends in genetic control of juvenile black walnut height growth. Forest Sci. 30:821-827.

Rink, G. and K. E. Clausen. 1989. Site and age effects on genotypic control of juvenile Juglans nigra L. tree height. Silvae Genet. 38:17-21.

Roberds, J. H., J.O. Hyun, G. Namkoong, and G. Rink. In press. Analysis of height growth response functions for white ash provenances. Silvae Genet.

SAS Institute. 1982. Statistical analysis system user's guide: statistics. SAS Institute, Inc. Raleigh, NC.