GENETIC ANALYSES FOR HEIGHT AND DIAMETER GROWTH OF 9-YEAR-OLD RED MAPLE PROGENIES IN FIVE PLANTATIONS

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Abstract.--Several growth measurements were made on nine-year-old red maple progenies growing in Ohio, Indiana, Michigan, Minnesota, and Wisconsin. Significant differences occurred among stands and among families within stands for caliper (measured 6 in above base of tree), height, and diameter at breast height (DBH) in most plantations. Seedlings froth north central seed sources (the southern twothirds of the Lake States and of New England) generally were above average in height and caliper in all plantations, whereas those from southern sources were below average. East central sources were average in height but above average in caliper and DBH. Heritabilities (h²) for height on a within stand single tree basis varied from .02 in Indiana and Minnesota to .42 in Michigan. The highest heritability values for DBH and caliper were .23 and .25, respectively. Heritabilities calculated on a basis in which stands were disregarded were much higher. Growth performance of the same progenies growing in most plantations was significantly correlated. However, the presence of some degree of genotype-plantation interaction did occur and was mostly a result of unique progeny response in growth in Wisconsin and Minnesota. This interaction will complicate but will not preclude the development of effective breeding and selection strategies for growth improvement of red maple.

Additional keywords: Acer rubrum, selection, tree breeding.

A range-wide provenance test of red maple [Acer rubrum L.) has revealed a wide degree of genetic variation in numerous traits examined in laboratory and field studies. Variation among progenies grown from seed collected from different stands and identified according to different parent trees within stands was first examined in nursery bed studies near Delaware, Ohio (Townsend 1977). Seedlings transplanted from the nursery bed to five NC-99 regional test sites showed wide variation at the age of five years in heights, fall color, and stem form (Townsend et al. 1979). Other studies have indicated that sufficient genetic variation exists to select for such traits as cold hardiness, early or late

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bud break, and precocity and frequency of flowering (Townsend et al. 1982).

This paper reports on geographic patterns, analyses of variance and heritabilities for height and diameter measurements of nine-year-old red maple progenies growing in Ohio, Michigan, Indiana, Wisconsin, and Minnesota.

MATERIALS AND METHODS

Seed collected from 51 stands located throughout the species' range was brought to Delaware, Ohio, where replicated nursery bed tests were established in 1972. Details of latitude, longitude, and elevation can be found in previous papers (e.g. Townsend et <u>al.</u> 1982). Nursery-grown seedlings were used to establish, either in 1974 or 1975, progeny tests in Ohio (51 stands represented), Michigan (39 stands represented), Indiana (21 stands), Wisconsin (24 stands), and Minnesota (16 stands).

In all plantations seedling identity was maintained not only by stand of origin but also by parent tree within stands. All plantations followed a randomized block design. In Ohio and Michigan, open-pollinated families served as the experimental unit randomized in each block. In Indiana and Minnesota, seedlings from each stand were planted together as a "major" plot in each block, with open-pollinated families within stands forming cohesive "minor" plots. The Wisconsin planting was similar except that seedlings from all families within a given stand were completely randomized throughout the plot for a given stand.

All growth measurements were made and recorded on individual trees in the fall of 1980 or before growth began in 1981. Height was measured in all plantations and caliper, which is the diameter of the main stem 6 in above the root collar, was measured in all sites except Indiana. Diameter at breast height (DBH) was recorded on those trees taller than breast height in Ohio, Indiana, and Minnesota. Genetic analyses were carried out using both LSML76, the "mixed model least squares" program developed by the junior author (Harvey 1982) and SAS GLM (SAS Institute 1979).

RESULTS AND DISCUSSION

Differences among plantations in average growth after nine years were quite marked (Table 1). The Minnesota planting showed the highest average growth, Wisconsin the lowest, and Michigan and Ohio were appreciably taller than Indiana. In contrast, these same trees when only 5 years old were largest in Ohio and Michigan, and smallest in Wisconsin and Minnesota (Townsend et al. 1979). The Minnesota trees therefore have gone from the shortest to the tallest average height between five and nine years old, increasing their height nearly five-fold during that time. However, less variation among progenies in growth traits was found in Minnesota than in other states (Table 1).

| Seed source No. and | e | | | | | | | - | | | | | | | | |
|------------------------|------|-----|--------|------|------|-----|---------|-----|-----------------------|-------|-----|------|------|-------|-------|------|
| State or | 141 | 1 | leight | N.Y. | 101 | ar | Calip | er | 1.007 | | DBH | 1.01 | - | Heigh | t/Cai | iper |
| novince | OH | ML | IN | WI | MN | (1) | MI of s | MI | MN ation A | (ean) | IN | MN | OH | MI | WI | MN |
| Northern seed lots: | | | | | | | | | , and a second second | (cut) | | | | | | |
| 105 NF | 95 | 82 | 69 | 71 | 102 | 89 | 84 | 64 | 102 | 82 | 79 | 109 | 101 | 94 | 108 | 95 |
| 167 NB | 92 | 104 | 87 | 95 | 98 | 86 | 100 | 97 | 96 | 76 | 64 | 100 | 103 | 103 | 97 | 103 |
| 166 QU | 103 | 96 | 80 | 90 | 103 | 96 | 100 | 82 | 100 | 94 | 86 | 104 | 103 | 93 | 103 | 101 |
| 150 UN | 91 | 80 | | 100 | 101 | 91 | 89 | | | 82 | | | 100 | 91 | | |
| 155 08 | 106 | 100 | 95 | 100 | 101 | .95 | 93 | 109 | 92 | 100 | 86 | 87 | 105 | 109 | 85 | 108 |
| 157 40 | 100 | 105 | 11.1 | 117 | 99 | 110 | 107 | 121 | 108 | 127 | 107 | 96 | 94 | 101 | 95 | 92 |
| 161 VT | 110 | 96 | | 20 | | 113 | 91 | 100 | | 91 | 107 | | 107 | 104 | 90 | |
| 157 MN | 105 | 80 | 72 | 93 | 100 | 25 | 73 | 85 | 94 | 97 | 57 | 96 | 107 | 109 | 110 | 106 |
| 159 MN | 95 | 87 | | 116 | | 71 | 69 | 115 | | 73 | - | | 122 | 125 | 93 | 100 |
| 162 51 | 106 | -94 | 104 | 95 | 100 | 110 | 100 | 100 | 104 | 115 | 107 | 100 | 93 | 93 | 90 | 92 |
| K. | 102 | 94 | 89 | 97 | 0.01 | 26 | 92 | 98 | 99 | 96 | 87 | 99 | 103 | 102 | 92- | 100 |
| Vorthern | | | | | | | | | | | | | | | | |
| Central | | | | | | | | | | | | | | | | |
| seed lots: | | | | | | | | | | | | | | | | |
| 144 RI | 96 | 98 | | | | 96 | 100 | 100 | | 97 | | | 94 | 97 | 100 | |
| 146 CT | 113 | 113 | 110 | 124 | | 127 | 118 | 148 | 100 | 142 | | | 85 | 97 | 83 | |
| 160 SY | 107 | 105 | 100 | 114 | 107 | 120 | 111 | 124 | 100 | 136 | 129 | 100 | 93 | 94 | 86 | 101 |
| 149 01 | 107 | 110 | 100 | 91 | 00 | 100 | 98 | 85 | 96 | 109 | 107 | 96 | 103 | 112 | 113 | 109 |
| 164 ON | 126 | 113 | 112 | 100 | 39 | 116 | 104 | 101 | 30 | 12/ | 107 | 30 | 105 | 112 | 115 | 103 |
| 137 MI | 117 | 127 | 116 | 105 | | 116 | 122 | 106 | | 124 | 100 | | 001 | 103 | 103 | |
| 141 MI | 121 | 124 | 127 | 99 | | 118 | 124 | 91 | | 136 | 121 | | 98 | 98 | 105 | |
| 145 WI . | 120 | 99 | 93 | 132 | 1.00 | 105 | 93 | 136 | 100 | 127 | 79 | 104 | 109 | 109 | 93 | 98 |
| 155 WI | 119 | 104 | 106 | 122 | 109 | 107 | 98 | 130 | 112 | 124 | 100 | 117 | 107 | 106 | 90 | 97 |
| 139 MN | 122 | 97 | 104 | 120 | 105 | 111 | 87 | 124 | 108 | 133 | 100 | 109 | 105 | 112 | 90 | 95 |
| λ. | 116 | 110 | 111 | 112 | 103 | 112 | 105 | 114 | 102 | 126 | 105 | 104 | 99 | 104 | 97 | 100 |
| West Central | | | | | | | | | | | | | | | | |
| Seed lots: | - | | | | | | | | | | | | | | | |
| 142 PA | 101 | 98 | | 83 | | 98 | 98 | 76 | | 94 | | | 100 | 101 | 106 | |
| 143 PA | 106 | 99 | | | | 100 | 104 | | | 100 | | | 101 | 93 | 1000 | |
| 154 PA | 109 | | | | | 109 | | | | 115 | | | 96 | 125 | | |
| 133 WV | 99 | 90 | 100 | 101 | 12 | 95 | 87 | | | 91 | | | 101 | 103 | | |
| 128 04 | 101 | 101 | 108 | 101 | 34 | 112 | 102 | 115 | 96 | 118 | 86 | 96 | 94 | 96 | 80 | 98 |
| 133 IN | 108 | 85 | 33 | 33 | 41 | 118 | 93 | 58 | 30 | 121 | 95 | 87 | 96 | 94 | 113 | 94 |
| X | 105 | 94 | 103 | 100 | 92 | 105 | 96 | 93 | 96 | 105 | 90 | 91 | 96 | 96 | 100 | 96 |
| Fast | | | | | | | | | | | | | 17.7 | | | |
| Central | | | | | | | | | | | | | | | | |
| seed lots: | | | | | | | | | | | | | | | | |
| 138 NJ | 112 | | | | | 134 | | | | 142 | | | 80 | | | |
| 127 DE | 116 | 1.1 | | 1. | | 120 | | | | 130 | | | 91 | | | |
| 122 VA | 105 | 112 | 109 | 67 | 95 | 123 | 124 | 42 | 102 | 127 | 157 | 91 | 83 | 88 | 144 | 104 |
| 119 VA | 95 | 110 | | | | 109 | 107 | | | 109 | | | 93 | 101 | | |
| 140 WV | 125 | ac | | | | 100 | | | | 106 | | | 119 | | | |
| 117 KY | 101 | 65 | | | | 96 | 91 | | | 100 | | | 105 | 94 | | |
| 123 TN | 84 | 86 | | | | 22 | 130 | | | 145 | | | 87 | 94 | | |
| 36 TN | 89 | 99 | | | | 102 | 0.8 | | | 04 | | | 95 | 101 | | |
| 118 TN | 101 | 123 | | | | 109 | 120 | | | 106 | | | 91 | RO | | |
| | 104 | 102 | 109 | 67 | 95 | 111 | 110 | 42 | 102 | 113 | 157 | 91 | 93 | 95 | 144 | 104 |
| Southern | | | | | | | | | | | | | | | | |
| seed lots: | | | | | | | | | | | | | | | | |
| 113 NC | 69 | | | | | 89 | | | | 61 | | | 93 | | | |
| 116 NC | 93 | 85 | | | | 88 | 84 | | | 70 | | | 103 | 97 | | |
| 124 NC | 82 | 80 | 83 | 57 | | 82 | 87 | 54 | | 70 | 79 | | 96 | 93 | 103 | |
| 121 NC | 73 | | | | | 75 | | | | 58 | | | 98 | | | |
| 132 GA | 64 | | | | | 71 | | | | 61 | | | 100 | | | |
| LLI GA | 69 | | | | | 64 | | | | 36 | | | 107 | | | |
| LIO AL | 48 | | | | | 59 | | | | 30 | | | 111 | | | |
| 170 10 | 00 | 20 | 97 | | | 00 | 0.4 | | | 51 | 24 | | 109 | 107 | | |
| 112 \R | 84 | 63 | 40 | | | 70 | 04 | | | 64 | 90 | | 101 | 102 | | |
| 115 \8 | 20 | 91 | | | | 114 | 100 | | | 91 | | | 79 | | | |
| 103 LA | 100 | | | | | 86 | | | | 88 | | | 111 | 40 | | |
| 7 | *6 | 86 | 83 | 57 | | 81 | 89 | 54 | | 65 | 82 | | 101 | 95 | 103 | |
| Actual | 278 | 298 | 215 | 174 | 518 | 56 | 45 | 33 | 50 | 33 | 14 | 23 | 54 | 68 | 59 | 66 |
| plantation | cm | сm | cm | cm | cm | 111 | mm | mm | 1000 | mm | mm | 1020 | | | | |
| stand | | | | | | | | | | | | | | | | |
| Significan | ce** | | ** | | NS. | | | | NS | ** | | NS | | | | NE |

Table 1. Height, caliper, DBH, and ratio of height to caliper of nine-year-old red maple progenics growing in five locations.

 $\gamma, Significant of the [0.05 level;**, significant at the 0.01 level; and NS, not significant$

Seedlings from the north central seed lots (southern Lake States and southern two-thirds of New England) generally showed above average height, caliper and DBH in all plantations whereas trees from southern seedlots were below average in these same measurements (Table I). Progenies from the northern, west central and east central seed sources were generally about average in height in all plantations, but specific exceptions did occur. For example, seedlings representing stands from Bethel, Maine (163 ME) and Alfred, Maine (152 ME) were above average not only in height but also DBH and caliper in most plantations, and perhaps are more closely associated in growth potential with north central rather than northern stands (Table 1). Most of the fastest growing progenies in all plantations were from north central sources, sue' as Stayner, Ontario (164 ON); Storrs, Connecticut (146 East Lansing, Michigan (137 MI); and Bradford, Pennsyl-CN): vania (149 PA).

Trees in Ohio were larger in caliper than those trees in Minnesota and Michigan, even though these two plantations showed the greatest average height (Table 1). The shorter, stockier nature of trees in Ohio is also reflected in their lower average height to caliper ratio. Ohio has more southern progenies than Minnesota and Michigan, but the winter injury to the tops of the southern seedlings (Townsend et al. 1982) does not explain the relatively low height to caliper ratio found in Ohio because southern progenies have about the same ratio as northern progenies (Table 1). When five years old, the red maple progenies from east central sources were far above average in height in all five plantations (Townsend et al. 1979). The decrease in height growth performance of these east central sources, relative to other regions between five years and nine years old, can partly be explained by the greater winter injury sustained by these trees compared to trees from other seed lots during these four years (Townsend et al. 1982).

Tables 2, 3, and 4 present the format used for the analyses of variance and give the expected mean squares for the various plantations. Trees with missing DBH or caliper measurements were omitted for these analyses. Note that a component labeled "common environment" is included in the expected mean squares fob all plantations. Because trees from the same openpollinated family represent the randomized experimental unit in each block in Ohio and Michigan, the "common environment" component is used to take into account that part of the plot variance not due to family x block interaction but instead is a result of common environmental effects on trees of the same family growing in the same plot (Table 2). The family x block interaction contributes to the plot variance but because it cannot be separated from the common environmental effect, is enclosed in the same parentheses in the expected mean squares.

For Indiana and Minnesota data, two "common environment" components were developed: one $(\sigma c1)$ for the environment common to trees of the same family in the same sub-sub plot, the other (σc_2) for the environment shared by trees of the same stand in a given sub-plot (Table 3). Because each tree from all families

| Source of | 011 | df | Encoded Mana Samana C |
|---|--|---|---|
| variation | OH | MI | Expected Mean Squares |
| Stands (S) | 50 | 38 | $\sigma_{w}^{2} + k_{5}(\sigma_{c}^{2} + \sigma_{fB:s}^{2}) + k_{8}\sigma_{sB} + k_{11}\sigma_{f:s}^{2} + k_{12}\sigma_{s}^{2}$ |
| Families:Stands(FS) | 81 | 54 | $\sigma_{W}^{2} + k_{4}(\sigma_{c}^{2} + \sigma_{fB:s}^{2}) + K_{10}\sigma_{f:s}^{2}$ |
| Blocks (B) ^a | 5 | 9 | $\sigma_{W}^{2} + k_{3}(\sigma_{c}^{2} + \sigma_{fB:s}^{2}) + k_{7}\sigma_{sB}^{2} + k_{0}k_{p}^{2}$ |
| Stands x Blocks(SX | B) 242 | 254 | $\sigma_{W}^{2} + k_{2}(\sigma_{c}^{2} + \sigma_{f}^{2}; Bs) + k_{6}\sigma_{sB}^{2}$ |
| FB:S ^b | 370 | 141 | $\sigma_{\rm w}^2$ + k ₁ ($\sigma_{\rm c}^2 + \sigma_{\rm fB;s}^2$) |
| Trees:SFB | 2127 | 440 | σ _W ² |
| 721-12-12-12-12-12-12-12-12-12-12-12-12-1 | | | |
| $b\sigma_c^2$ is the variance same family as gro ^c Coefficients of V | due to wn in th ariance | common en ne same bl component | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro ^C Coefficients of V $k_1 = 3.8787$ | due to wn in th ariance kg | common en ne same bl component 9.5662 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro c Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ | due to wn in th ariance k_8 $k_{10} = 2$ | common en ne same bl component 9.5662 21.5296 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ $k_4 = 3.8123$ | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ | common en ne same bl component 9.5662 21.5296 21.4947 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro C Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ $k_4 = 3.8123$ $k_5 = 3.7996$ | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 5$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ $k_4 = 3.8123$ $k_5 = 3.7996$ $k_6 = 9.5177$ | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 5$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ $k_4 = 3.8123$ $k_5 = 3.7996$ $k_6 = 9.5177$ Coefficient for M | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 5$ ichigan: | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_c^2$ is the variance same family as gro C Coefficients of V $k_1 = 3.8787$ $k_2 = 3.7681$ $k_4 = 3.8123$ $k_5 = 3.7996$ $k_6 = 9.5177$ Coefficient for M $k_1 = 1.8393$ | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 5$ ichigan: $k_8 = 1$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_{c}^{2}$ is the variance same family as gro C Coefficients of V $k_{1} = 3.8787$ $k_{2} = 3.7681$ $k_{4} = 3.8123$ $k_{5} = 3.7996$ $k_{6} = 9.5177$ Coefficient for M $k_{1} = 1.8393$ $k_{2} = k.8940$ | due to wn in th ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 9$ ichigan: $k_8 =$ $k_8 =$ $k_{10} =$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 3.6563 6.6663 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_{c}^{2}$ is the variance same family as gro Coefficients of V $k_{1} = 3.8787$ $k_{2} = 3.7681$ $k_{4} = 3.8123$ $k_{5} = 3.7996$ $k_{6} = 9.5177$ Coefficient for M $k_{1} = 1.8393$ $k_{2} = k.8940$ $k_{4} = 1.8638$ | due to wn in the ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 5$ ichigan: $k_8 =$ $k_{10} =$ $k_{10} =$ $k_{11} = 1$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 3.6563 6.6663 | nvironmental effects for trees of the lock (plot). ts for Ohio: |
| $b\sigma_{c}^{2}$ is the variance same family as gro Coefficients of V $k_{1} = 3.8787$ $k_{2} = 3.7681$ $k_{4} = 3.8123$ $k_{5} = 3.7996$ $k_{6} = 9.5177$ Coefficient for M $k_{1} = 1.8393$ $k_{2} = k.8940$ $k_{4} = 1.8638$ $k_{5} = 1.9386$ | due to wn in the ariance k_8 $k_{10} = 2$ $k_{11} = 2$ $k_{12} = 3$ ichigan: $k_8 =$ $k_{10} =$ $k_{10} =$ $k_{11} = 1$ $k_{12} = 2$ | common en ne same bl component 9.5662 21.5296 21.4947 55.9582 3.6563 6.6663 12.5217 23.7654 | nvironmental effects for trees of the lock (plot). ts for Ohio: |

Table 2. Form of the analyses of variance and expected mean squares for the

Table 3. Form of the analyses of variance and expected mean square for

| Source of | (| lf | |
|------------------------------|-----|-----|--|
| variation | IN | MN | Expected Mean Squares ^C |
| Whole Plots Stands (S) | 20 | 13 | $\sigma_{w}^{2} + k_{5}(\sigma_{c_{1}}^{2} + \sigma_{Bf:s}^{2}) + k_{8}(\sigma_{c_{2}}^{2} + \sigma_{sB}^{2}) + k_{11}\sigma_{f:s}^{2} + k_{12}\sigma_{s}^{2}$ |
| Blocks(B) ^a | 4 | 5 | $\sigma_{w}^{2} + k_{3}(\sigma_{c_{1}}^{2} + \sigma_{Bf:s}^{2}) + k_{7}(\sigma_{c_{2}}^{2} + \sigma_{SB}^{2}) + k_{9}K_{B}^{2}$ |
| S X B | 77 | 26 | $\sigma_{W}^{2} + k_{2}(\sigma_{c_{1}}^{2} + \sigma_{f:s}^{2}) + k_{6}(\sigma_{c_{2}}^{2} + \sigma_{sB}^{2})$ |
| Sub-Plots Families | 42 | 28 | $\sigma_{\hat{w}}^2 + k_4 (\sigma_{c_1}^2 + \sigma_{Bf:s}^2) + k_{10} \sigma_{ff:s}^2$ |
| B.F:S ^b | 131 | 122 | $\sigma_{W}^{2} + K_{1}(\sigma_{c_{1}}^{2} + \sigma_{Bf:s}^{2})$ |
| Sub-Sub Plots Trees :SF B | 274 | 93 | σ_{W}^{2} |

the Indiana and Minnesota plantations

^aBlock effects are assumed to be fixed.

 ${}^{b}\sigma_{1}^{2}$ is the variance due to common environmental effects for trees of the same family as grown in the same sub-sub plot; $\sigma_{c_{1}}^{2}$ is the common environmental effect for trees of the same stand as grown in the same sub-plot. With standard conditions, $\sigma_{c_{1}}^{2} = \sigma_{c_{2}}^{2} = \sigma_{c_{2}}^{2}$ (see Table 2).

| COE | efficients | for Indiana: | Coefficients | for Minnesota: |
|----------------|------------|--------------------|------------------|--------------------|
| k_1 | = 1.8196 | $k_8 = 5.5942$ | $k_1 = 1.2809$ | $k_8 = 4.1730$ |
| k ₂ | = 2.2285 | $k_{10} = 7.5467$ | $k_2 = 1.5362$ | $k_{10} = 6.9457$ |
| k ₄ | = 1.8711 | $k_{11} = 10.2245$ | $k_4 = 1.3645$ | $k_{11} = 8.5758$ |
| k ₅ | = 2.3214 | $k_{12} = 25.9677$ | $k_{5} = 1.6755$ | $k_{12} = 22.9206$ |
| k ₆ | = 5.1500 | | $k_6 = 3.8562$ | |
| | | | | |

Table 4. Form of the analyses of variance and expected mean squares for the

| Sources of variation | df | Expected mean squares ^b | |
|----------------------------------|-------------------|---|--------------------|
| Whole Plots Stands(S) | 23 | $\sigma_{W}^{2} + \sigma_{c_{1}}^{2} + k_{5}\sigma_{Bf:s}^{2} + k_{8}(\sigma_{c_{2}}^{2} + \sigma_{sB}^{2}) + l_{11}\sigma_{f:s}^{2} +$ | $k_{12}\sigma_s^2$ |
| Blocks (B) ^a | 3 | $\sigma_{w}^{2} + \sigma_{c1}^{2} + k_{3}\sigma_{Bf:s}^{2} + k_{7}(\sigma_{c2}^{2} + \sigma_{sB}^{2}) + k_{9}K_{B}^{2}$ | |
| S X B | 67 | $\sigma_{w}^{2} + \sigma_{c1}^{2} + k_{2}\sigma_{Bf:s}^{2} + k_{6}(\sigma_{c2}^{2} + \sigma_{sB}^{2})$ | |
| Sub-Plots Family:Stands(F:S) | 42 | $\sigma_{W}^{2} + \sigma_{c_{1}}^{2} + k_{4}\sigma_{Bf:s}^{2} + k_{10}\sigma_{f:s}^{2}$ | |
| B:FS | 85 | $\sigma_{w}^{2} + \sigma_{c1}^{2} + k_{1}\sigma_{Bf:s}^{2}$ | |
| Trees:SFB | 239 | $\sigma_{\rm W}^2 + \sigma_{\rm c_1}^2$ | |
| aBlock effects are a | ssumed | to be fixed. See footnote on Table 3. | |
| ^b Coefficients of Var | iance Co | omponents for Wisconsin: | |
| $k_1 = 1.7743$ | k ₈ = | 5.3361 | |
| $k_2 = 2.2814$ | k ₁₀ = | 5.4991 | |
| $k_4 = 1.9084$ | k ₁₁ = | 8.3390 | |
| $k_5 = 2.5855$ | k ₁₂ = | 19.0880 | |
| $k_6 = 4.4318$ | | | |

Wisconsin plantation .

was completely randomized within each plot representing a stand, the $(\sigma^2 cl)$ component in Wisconsin has unity as it coefficient (Table 4).

Variance component estimates expressed as a percentage of the total variance are shown in Table 5. Significant stand effects were present for most traits in all plantations except in Minnesota, where the stand x block effect (which includes common environmental effects also) rather than the stand effect was significant. Significant differences among open-pollinated families within stands were shown for height in Ohio, Michigan, and Wisconsin (Table 5). Where significant, the percent of the total variance due to stands varied from 8 to 14%; the corresponding significant percentages for families within stands ranged from 5 to 9%. The family within stand component for height was also non-significant in Indiana and Minnesota at five years of age (Townsend et al. 1979). The common environmental effects for height, which includes family x block interaction, were significant and sizeable in three of the four plantations where these two sources of variation were confounded.

Caliper and DBH were usually affected significantly by stand of origin but only in Ohio did the family within stand component significantly influence these two traits. The ratio, height/DBH, was less often affected by genetic sources of variation (stands or families) than was the ratio of height to caliper. The "common environment" effect contributed heavily to caliper variation in most plantations.

Growth performance of seedlings (from the same stand or family within stands) growing in all plantations usually was significantly correlated (Table 6). Exceptions did occur, however. For example, neither stand nor family correlations in height between progenies in Michigan and Minnesota, Indiana and Wisconsin, and Indiana and Minnesota were significant. Some genotype-environment interaction therefore did occur and will complicate to some degree breeding of red maple for all environments.

Heritabilities on a within stand single tree basis varied greatly among plantations, with ranges of .02 to .42 for height and less extreme ranges for the other traits (Table 7). The ratio of height to DBH generally had lower heritabilities than height/caliper. Heritabilities without regard to stands are generally somewhat higher and reflect the greater potential gains one could make by selecting potential parents from many stands (Table 7). With loblolly pine (Pinus taeda L.), LaFarge (1974) has also found considerable variation among stands or provenances, in addition to that among parents within stands.

Growth parameters were highly correlated genetically and phenotypically (Table 8). The ratio height/DBH was negatively correlated with height in many locations. Genetic correlations are high enough between height, caliper, and DBH that selection for one of these traits will

| | | Height | | | | P | Caline | er | the star | t.r | DBH . | |
|--------------------|------|---------|------|----------|--------------|--------|--------|------|----------|------|-------|------|
| Components | OH | MI | IN | WI | MN | OH · | MI | WI | MN | OH | IN | MN |
| | | 1 | | (% 0 | of total var | iance) | | | | | | |
| Stands | 13** | 14** | 8** | 14** | | 12** | 18** | 15** | | 12** | 11** | |
| Families:Stands | 5** | 9** | | 5* | 1 | 5** | 3 | 5 | | 5** | | 6 |
| Stands x Blocks | _ª | | 7* | 4* | 16** | 1 | | / | 23** | 1 | 11** | 17** |
| Common Environment | 18** | 18** | 11** | | 3 | 11** | 14** | | 18** | 11** | 7 | |
| Trees: SFB | 64 | 59 | 74 | 77 | 80 | 71 | 65 | 80 | 59 | 71 | 70 | 77 |
| | Hei | ght/Cal | iper | | Heig | ht/DBH | | | | | | |
| | OH | MI | WI | MN | OH | IN | MN | | | | | |
| | | | (% | of total | variance) | | | | | | | |
| Stands | 12** | 6** | 7** | - | 11** | 4 | | | 1 | | | |
| Families:Stands | 3** | 9** | 6 | 6* | 3* | | 1 | | | | | |
| Stands x Blocks | 2* | | 8* | 13** | 1 | | | | | | | |
| Common Environment | 4 | 12* | | | 10** | 29** | | | | | | |
| Trees:SFB | 79 | 74 | 78 | 81 | 75 | 67 | 99 | 4 | ** | | | |

.

Table 5. Components of variance expressed as a percentage of the total variance.

*, ** Significant at the 0.05 and 0.01 levels, respectively.

^a A dash (--) indicates 0.5 per cent or less.

| 12 | | | | | |
|-------------------------|------------------|------------------|------------------|------------------|---------------|
| Plantations Compared | Height | Caliper | DBH | Height/Caliper | Height/DBH |
| OH and MI | .59** (.52**) | .80** (.55**) | | .74** (.45**) | |
| OH and IN | .50* (.46**) | | .64** (.53**) | 200 A | .57* (.22) |
| OH and WI | .70** (.59**) | .32 (.42**) | | 14 (.04) | |
| OH and MN | •32 (•38) | .45 (.40**) | .04 | .27 (.41**) | .20 (.19) |
| MI and IN | .74** (.60**) | | | | |
| MI and WI | •34 (•29*) | .05 (.15) | | 14 (04) | |
| MI and MN | .00 (.13) | .21 (04) | | .36 (.17) | |
| IN and WI | .15 (.05) | | | | |
| IN and MN | 23 (03) | | 15 | | •14 (•20) |
| WI and MN | .28 (.41**) | .28 (.42**) | | .31 | |

Table 6. Correlation coefficients between plantations of means of red maple progenies a.

*,** Significant at the 0.05 and 0.01 level. A dash (---) indicates that no data were common to both plantations.

a Top value is correlation between stand means. Value underneath in parentheses is correlation between family means.

| anel - | | | Plan | itation | | |
|---|-----------------------------|---------|----------|---------|----------|-------------|
| Trait | | Ohio | Michigan | Indiana | Wisconsi | n Minnesota |
| Height | Within Stands | .25±.06 | .42±.13 | .02±.13 | .25±.17 | .02±.17 |
| and the second | Between Stands ^a | .34±.05 | .50±.13 | .10±.09 | .36±.15 | .02±.05 |
| Caliper | Within Stands | .24±.06 | .15±.09 | - | .25±.17 | neg. |
| The second se | Between Stands | .33±.05 | .30±.11 | - | .37±.15 | neg. |
| DBH | Within Stands | .22±.06 | - | .01±.13 | - | .23±.21 |
| | Between Stands | .32±.05 | - | .02±.09 | - | .23±.14 |
| Height/Caliper | Within Stands | .14±.05 | .37±.13 | - | .25±.17 | .23±.21 |
| te In | Between Stands | .24±.05 | .41±.12 | - | .30±.14 | .23±.14 |
| Height/DBH | Within Stands | .11±.05 | - | neg. | - | .03±.17 |
| | Between Stands | .20±.05 | - | .04±.05 | 121 | .03±.05 |

| Table 7. | Heritability (h ²) Estimates On A Within Stand Single Tree Basis and |
|----------|--|
| | On A Between Stand Basis For Nine-Year-Old Red Maples. |

^aCalculated from $(\sigma_s^2 + 4\sigma_{f:s}^2)/\sigma_p^2$, where σ_s^2 is the variance component for stands, $\sigma_{f:s}^2$ is the family within stand variance component and σ_p^2 is the total phenotypic variance.

| | | Cali | per | | DBH | | | Height/Caliper | | | | Height/DBH | | | |
|----------|--------|------|-------|--------------|-------|-----|-----|-----------------|------|------|-----|------------|----|-------|--|
| Traits | ОН | MI | WI | MN | ОН | IN | MN | OH | MI | WI | MN | OH | IN | MN | |
| Height | .88+ | .61± | 1.17- | ^b | .93± | | | 12 [±] | .54+ | 98 | ± | -1.00± | | | |
| | .06 | .22 | .20 | - cha | .04 | | | .30 | .23 | 1.03 | | .49 | | | |
| | .78 | .72 | .86 | .63 | .85 | .91 | .83 | 00 | .19 | 30 | 16 | 63 | 61 | 68 | |
| Caliper | | | | | 1.01± | | | 61± | .31+ | 86 | ± | 95+ | | | |
| | | | 1. | | .01 | | | . 37 | .42 | 1.02 | | .48 | | | |
| | | | | | .88 | | .66 | 59 | 48 | 64 | 73 | 64 | | 71 | |
| DBH | | | | | | | | 54+ | | | 40± | 94± | | 84+ | |
| | | | | | | | | .33 | | | .84 | .51 | | 1.12 | |
| | | | | | | | | 32 | | | 24 | 75 | 72 | 73 | |
| Height/C | aliper | | | | | | | | | | | .13± | | 1.34± | |
| | | | | | | | | | | | | .37 | | .51 | |
| | | | | | | | | | | | | .27 | | .58 | |

Table 8. Estimates of genetic and phenotypic correlations between growth traits of nine-year-old red maple progenies in several north central locations ^a

^a Calculated on a within stand basis. Stand x block interaction is assumed to equal zero. Listed vertically, the first value is the genetic correlation with standard error, and the second number is the phenotypic correlation.

^bNotestimable because of negative variance component estimates for families or because data were not available.

simultaneously affect another in the same direction.

CONCLUSION

Variation among stands and families in height and diameter of nine-year-old red maple progenies offers tremendous opportunity for genetic advances in growth potential of this species. Genotype-environment interaction was present, mostly because of the presence of differential growth response of the same progenies in the northern (Minnesota and Wisconsin) compared to some of the southern planting sites. However, heritabilities generally are sufficiently high to allow rapid progress in selection and breeding of this species. We are currently determining selection indices and breeding values that will enable us to plan and carry out an efficient advanced generational crossing system.

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