VARIATION AMONG PROGENY OF MASS-SELECTED BALSAM FIR[1]

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ABSTRACT.--Open-pollinated progeny of mass-selected and average balsam fir (*Abies balsamea* (L.) Mill.), growing in half-sib progeny test plantations in Vermont and Maine, were evaluated for genetic variation in growth rate and branching characterisitcs. Family variation in height, terminal shoot length, number of branches per whorl and number of internodal buds per unit of terminal shoot is substantial and considerable improvement in the growth and quality of balsam fir Christmas trees can be expected through family selection. Although the family x plantation component was significant for height, most of the fast-growing families in the Vermont plantation also grew fast in the Maine plantation. Family rankings for the number of internodal buds was remarkably consistent over the two plantations. Progeny height and terminal shoot length, whether considered at individual plantations or by combined family averages over both plantations, were unrelated to parental growth rate. In fact, correlations between parental and progeny growth rate were either negative or approached zero. Furthermore, the mean height of progeny from average trees was equal to or exceeded the mean height progeny from trees that were phenotypically-selected for rapid growth. As practiced in this study, mass selection for growth rate was ineffective.

INTRODUCTION

Balsam fir (*Abies balsamea* (L.) Mill.) is a major component of northern forest regions of North America. It is frequently harvested for pulpwood and is the most commonly used Christmas tree species in New England and eastern Canada. Genetics research in balsam fir has focused primarily on its taxonomic affiliation with related species and the nature and extent of intraspecific geographic variation. Rangewide provenance tests of balsam fir in the Lake States and New England have revealed considerable genetic variation in growth rate, leafing-out phenology (Lester *et al*., 1976a; Lowe *et al*., 1977), insect susceptibility (DeHayes, 1981), wood properties (Dery and DeHayes, 1981) and the concentrations of foliar monoterpenes (Lester, 1974). Few studies have quantified the extent or

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distribution of localized genetic variation. In one such study, Lester et al. (1976b) reported significant variation among and within six Lake States provenances in growth rate, leafing-out phenology and branching characteristics. Provenance variation exceeded that attributable to family within provenance indicating the importance of provenance selection in balsam fir even at the local level.

In New England there has been great demand for genetically improved balsam fir seed for the production of Christmas trees, yet little is known about the most effective approach toward improving the growth rate and quality of balsam fir. Many private organizations and state agencies in New England have invested in mass selection programs designed to improve balsam fir and provide an accessible source of quality seed. Information contrasting selection strategies is urgently needed so that tree improvement programs can follow an efficient route and progress in a judicious manner. This study documents genetic variation in growth rate and branching characteristics among open-pollinated progeny of mass-selected balsam fir from New England and assesses the effectiveness of mass-selection as a means of improving growth rate in balsam fir.

MATERIALS AND METHODS

In 1965, the Spruce-fir Committee of the U.S. Forest Service initiated a plus-tree selection program designed to improve the growth rate of balsam fir. Between 1966 and 1968, with the cooperation of state, industrial and academic agencies in New England, individual trees were selected based on growth superiority in natural stands in Maine, New Hampshire and Vermont. Using the comparison-tree method of selection, candidate trees were either rejected or accepted based on their height and radial growth rate relative to three adjacent trees of comparable age. All selected trees surpassed each of their comparison trees in growth rate and exceeded the average of comparison trees by at least 25-30% in height and radial growth rate. Additional selections were made on an informal basis in natural balsam fir stands in Nova Scotia. Individual trees from Nova Scotia were selected for desirable Christmas tree characteristics (form, color, etc.) rather than for growth rate. In fact, trees selected in Nova Scotia are assumed to be random selections with respect to growth rate.

In 1970, seed was collected from several of the selected trees and from some comparison trees in New England and sown in the Maine State Nursery in Greenbush. That same fall, seed was collected from eleven selected trees from Nova Scotia and sown in the University of Vermont Nursery in Wolcott. After two years in seedbeds, seedlings were lined out in transplant beds at both nurseries. The Vermont nursery contained a mixed planting of seedlings representing families from the New England and Nova Scotia selections, while the Maine nursery contained only seedlings representing the New England families.

In spring 1976, 2-3 seedlings from both nurseries were used to establish half-sib progeny test plantations in Maine and Vermont. All plantations follow a randomized complete block design with 4-tree row plots and were established with a power auger. The Lake Willoughby, VT (LW,VT) plantation, established with seedlings from the Wolcott, VT nursery, includes 41 families from New England and Nova Scotia and 10 replications. The Dover-Foxcroft, ME (D-F,ME) plantation, established with seedlings from the Greenbush, ME nursery, includes 17 families from New England and 10 replications. The Veazie, ME (V,ME) plantation contains only eight families and 4 replications. Most families included in the Maine plantations were also represented in the Vermont plantation.

Height and terminal shoot length were measured in the Lake Willoughby, VT plantation at age 11 years from seed and in the two Maine plantations at age 9 years. In addition, the number of internodal buds per centimeter of terminal shoot was computed at LW,VT and V,ME. The number of branches in the upper-most whorl was also recorded in the LW,VT plantation. At time of measurement, all plantations appeared vigorous and survival in each exceeded 98%.

Plot means for each trait and plantation were subjected to analysis of variance to determine the significance of differences among half-sib families. Family, plantation and family x plantation variance components were also computed for multi-plantation data. Correlation and/or linear regression analyses, using family means as observations, were used to ascertain the relationship between parental and progeny growth rates and the consistency of family performance in different plantations.

RESULTS

Family Variation

Growth rate. Family variation in height and terminal shoot length was large and highly significant at Lake Willoughby, VT and Dover-Foxcroft, ME plantations, but relatively unimportant at the small planting in Veazie, ME. At LW,VT and D-F,ME plantations, there was a 30 to 40% difference in height between extreme families and about one-third of the total variance was attributed to differences among half-sib families (Table 1). Family mean height was strongly correlated with mean terminal shoot length ($r = 0.772$ and $r = 0.800$, $P < .01$) at LW,VT and D-F,ME suggesting that tall families are continuing to grow at a rapid rate. Terminal shoot length also varied significantly among families at the V,ME plantation, but was uncorrelated with family mean height and indicative of a change in relative growth rate with age. Although selected parents were derived from a broad geographic area, there was no apparent relationship between family growth rate and geographic location of parent tree.

When variation in height was examined through combined analysis over the LW,VT and D-F,ME plantations, the family component of variance remained significant but was surpassed in importance by family x plantation interaction (Table 2). This interaction, however, is slightly inflated because it also includes a component attributable to family x age. The interaction is further exemplified by the relatively low and non-significant correlation ($r= 0.389$) among family means from the two plantations.

Table 1. Family variation in height, number of internodal buds per unit of terminal shoot and number of branches per whorl in balsam fir half-sib progeny test plantations located in Lake Willoughby, Vermont (LW,VT), Dover-Foxcroft, Maine (D-F,ME), and Veazie, Maine (V,ME).

Trait	Plantation	No. of families	Age	Mean	Family Range	Family Variance
					% of mean	% of total
Height	LW,VT	41	11	226 cm	78-115	31**
	D-F,ME	17	9	157 cm	84-113	29**
	VE,ME	8	9	134 cm	86-107	ONS
No. branches/whorl	LW,VT	41	11	4.86	89-117	8**
No. buds/cm	LW,VT	41	11	.38	67-136	37**
	VE,ME	8	9	.60	80-129	39**

Note: **, significant at 1% level
NS, non-significant

Despite the significance of the interaction and the relatively low family mean correlation between plantations, most of the fast-growing families in the LW,VT plantation also grew fast in D-F,ME (Table 3). In fact, if only those families in common to both plantations are considered, selection of the four fastest-growing families at LW,VT resulted in trees 9.3% taller than average at both plantations. The significant interaction appears to have resulted largely from the inconsistent performance of families 189 and 148, which were relatively fast-growing at D-F,ME and slow-growing at LW,VT, and families 187 and 182, which showed the reverse pattern (Table 3).

<u>Branching characteristics</u>. Family variation in the number of branches in the uppermost whorl and the number of internodal buds per cm of terminal shoot was significant in all measured plantations. Trees at LW,VT, averaged 4.86 branches per whorl and family means ranged from 4.3 to 5.7 branches per whorl. Although family variation in this trait was highly significant, it accounted for a relatively low proportion of the total variance (Table 1). Family mean number of branches per whorl showed a weak, but significant positive correlation ($r = 0.334$, $p < .05$) with family mean height. Thus, it seems possible that family selection for rapid growth rate may be accompanied by a slight increase in number of branches.

Family variation in number of internodal buds per cm of terminal shoot was greater than any other trait measured at both the LW,VT and V,ME plantations. There was a difference of 50 to 70% between extreme families and nearly 40% of the total variance could be attributed to differences among half-sib families (Table 1). Furthermore, since there is no apparent relationship ($r = 0.027$) between family means for this trait and height, it appears possible to practice family selection for growth rate and number of internodal buds simultaneously.

Table 2. Multi-plantation analysis of variance and family mean correlation of height (Lake Willoughby and Dover-Foxcroft plantations) and number of internodal buds per unit of terminal shoot (Lake Willoughby and Veazie plantations) from a balsam fir half-sib progeny test.

Trait	No. of Families	Variance Component Family	 Family x Plantation	 Family x Block/Plantation	Family Mean Correlation
		- - - - - - - - - -	% of total variance	- - - - - - - - - - - - - - -	r - -
Height	15	10**	16**	74	0.389NS
Buds/cm	7	75**	4*	21	0.750*

Note: **, significant at 1% level
*, significant at 5% level
NS, non-significant

Table 3. Relative height of open-pollinnated progeny from mass-selected balsam fir in a half-sib progeny test planted in Vermont (age 11) and Maine (age 9).

UVM#	Origin	Relative Height of Families Planted at: Lake Willoughby, VT Age 11	Relative Height of Families Planted at: Dover-Foxcroft, ME Age 9
146	VT	115	113
166	NS	114	
160	ME	112	
172	NS	109	
162	ME	108	
178	ME	107	107
150	NH	107	108
169	NS	106	
154	VT	104	109
151	NH	103	102
163	ME	102	107
187	ME	104	91
182	NH	104	95
181	ME	101	95
188	ME	100	91
148	NH	96	106
189	ME	95	108
185	NH	92	100
Actual iE (cm)		226	157

Although only seven families were in common to both the LW,VT and V,ME plantations, the consistency of family rankings in number of internodal buds over the two plantations was remarkable (r = 0.75, P < .05). When variation in number of internodal buds was assessed on a multi-plantation basis, 75% of the total variance was attributed to differences among half-sib families and only 4% to family x plantation interaction (Table 2). Clearly, number of internodal buds is a highly heritable trait and, therefore, improvement in this trait would be expected to proceed rapidly with family selection.

Effectiveness of Mass Selection

Although progeny tests of mass-selected parents are frequently evaluated for magnitude of family variation, it is relatively uncommon that the actual effectiveness of phenotypic selection is assessed. In this study, parental height and age were recorded for most selected trees and some non-selected controls were included so the effectiveness of mass selection can be assessed.

Parent-progeny relationship. Parental growth rate, expressed as a height-to-age ratio, was unrelated to progeny height and terminal shoot length whether considered at LW,VT, D-F,ME or by combined family averages over both plantations. Simple correlations between parental and progeny growth rate, as tabulated below, were either negative or approached zero in each instance.

Balsam fir parent-progeny growth rate correlations at:

LW,VT	D-F,ME	LW,VT and D-F,ME
	r	
0.005	-0.212	-0.035

At LW,VT, two of the four tallest families were open-pollinated progeny of relatively slow-growing parents and parental selections which ranked second through sixth in growth rate produced progeny slower-growing than the plantation average (Figure 1). In fact, phenotypic selection of the four fastest-growing parents resulted in progeny of average height, whereas selection of the four tallest families resulted in progeny nearly 13% taller than average.

Progeny of selected vs. average parents. Although the low parent-progeny correlations indicate that mass selection for growth rate in balsam fir was ineffective, the results are not conclusive because growth rate differences among parents are confounded with site differences. A better assessment of the effectiveness of mass selection can be made by comparing the relative performance of progeny from average- vs. plus-tree selections.

Of the 41 families included in the LW,VT progeny test, 12 were either random selections with respect to growth rate or were comparison trees included as controls; 2 of the 17 families in the D-F,ME progeny test were comparison trees included as controls. In both plantations, the mean height of progeny from average selections was equal to or exceeded the mean height of progeny from parents that were phenotypically-selected for growth rate (Table 4). In fact, the tallest family at LW,VT was from a random selection and both control families at D-F,ME were taller than the plantation average. Even where progeny from phenotypically-selected trees and a comparison (average) tree from the same stand are compared (Table 5), progeny from the comparison tree performed as well or better than that from selected trees. Clearly, as practiced in this study, mass selection for growth rate in balsam fir was ineffective and would have resulted in no more improvement than randomly selecting individual seed trees.

Since form and branching characteristics are generally more heritable than growth rate, as indicated for number of internodal buds, one would expect mass selection for such quality characteristics to be effective. In this study, progeny of parents selected for superior Christmas tree form did not differ from progeny of parents selected for growth rate in either number of branches per whorl or internodal buds per unit of terminal shoot. However, the exact form criteria considered in the selection of these parents is not known so the effectiveness of mass selection can not be adequately assessed.

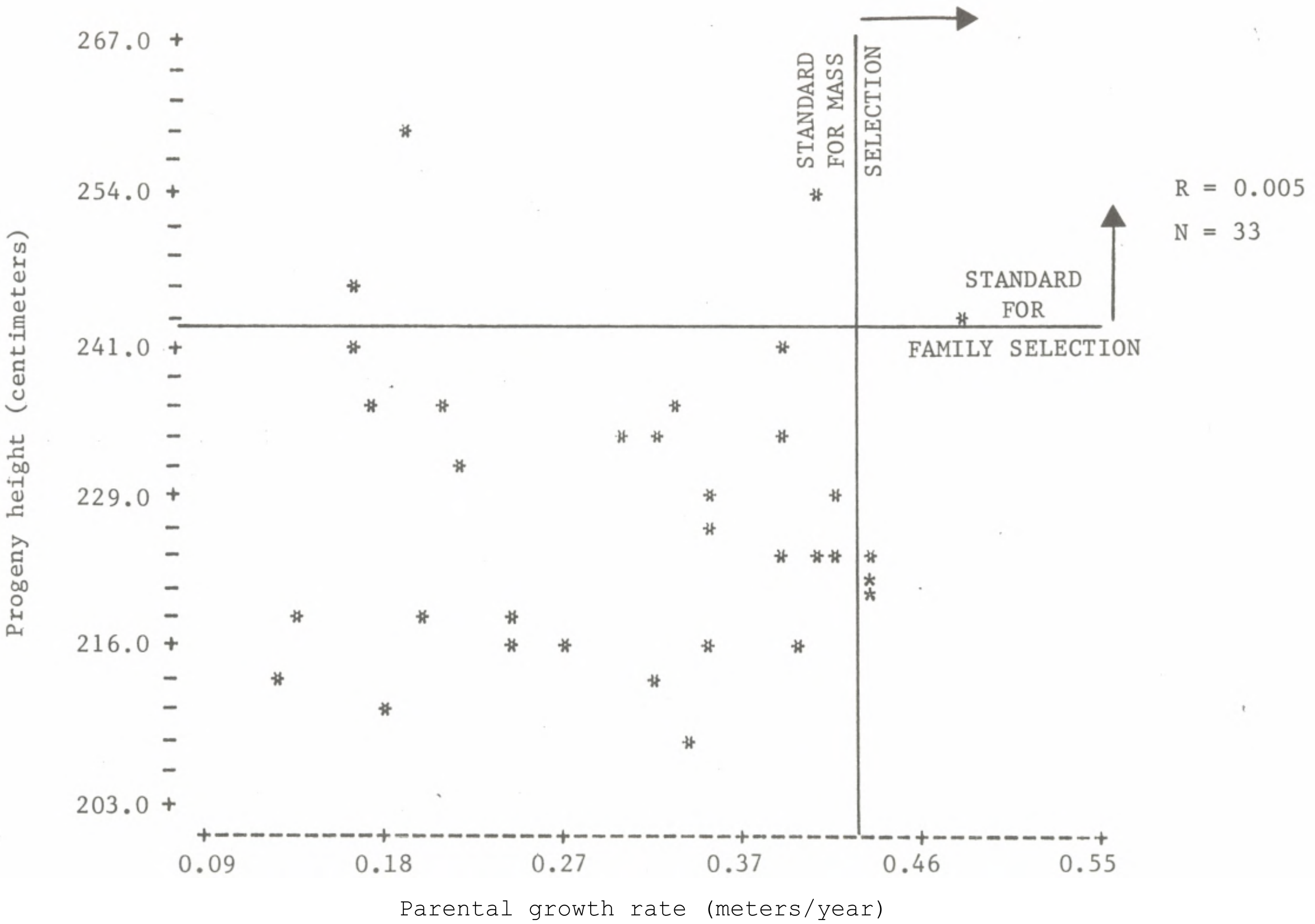

Figure 1. Relationship between growth rate of parental selections of balsam fir and the 11-year height of their progeny growing in a half-sib progeny test plantation at LW,VT. Vertical and horizontal lines represent arbitrary standards for mass and family selection respectively.

Table 4. Height of progeny of mass-selected and average balsam fir parents growing in half-sib progeny test plantations in Lake Willoughby, VT (age 11) and Dover-Foxcroft, ME (age 9).

Plantation	Parental Phenotype	No. of Families	Height Average (cm)	Height Family Range (cm)
LW, VT				
	Average	12	226	177-259
	Selected	29	227	205-259
D-F, ME				
	Average	2	164	157-170
	Selected	15	156	131-177

Table 5. Eleven year height of progeny of mass-selected and average balsam fir parents from a stand in Weston, VT growing in the Lake Willoughby, VT half-sib progeny test.

U VMI	Parental Phenotype	Height cm	Height % of mean
154	Average	234	104
155	Selected	224	99
157	Selected	221	98

DISCUSSION AND CONCLUSIONS

Genetic variation in growth rate and branching characteristics in balsam fir is substantial and, despite statistically significant interactions between family and environment, considerable improvement in the growth and quality of balsam fir Christmas trees can be expected through family selection. In fact, it seems possible to shorten Christmas tree rotations by 1 to 2 years through family selection for growth rate, while simultaneously improving form by selecting for a large number of internodal buds and branches per whorl. Without the necessary information on age-age growth correlations, it is not yet possible to project the effectiveness or impact of family selection for growth rate through a pulpwood rotation. Also, since components of genetic variation attributable to stand and family-within-stand could not be separated in this study, it is not possible to contrast the relative merits of family vs. stand and family selection. However, if data on the distribution of genetic variation in balsam fir from the Lake States (Lester, et al., 1976b) are applicable to New England, it would appear that a considerable proportion of the family variation observed in this study may actually be attributed to stand of origin. Studies currently underway will quantify the distribution of genetic variation in balsam fir from New England.

The low parent-progeny growth rate correlations and lack of differences in growth rate between progeny of selected and average parents clearly indicate that mass selection for growth rate in balsam fir was ineffective. Similar results have been reported for white spruce (*Picea glauca* [Moench.] Voss) (Khalil, 1975; Ying and Morgenstern, 1979) and black spruce (*Picea mariana* [Mill.] B.S.P.) (Morgenstern, 1974), which are common associates of balsam fir in northern forest regions.

Although there is considerable genetic variation in growth rate among balsam fir trees, it is apparently not possible to identify genetically fast-growing trees in the wild even with adjustments for age (Snyder, 1969) and corrections for the stand environment via the comparison-tree selection method (Morgenstern et al., 1975). Whether the ineffectiveness is due to the selection procedures or criteria employed, the structure of balsam fir populations, or a substantial environmental influence on parental growth rate is not known. Ledig (1974) has noted that if comparison and candidate trees are related, the effectiveness of comparison-tree selection may be reduced. Although the familial relationship between comparison and candidate trees in this study is obviously not known, there was nearly a 300% difference in mean annual increment between extreme parental selections which was not reflected in growth rate of the progeny and, therefore, must be attributed to environmental influences. Although more sophisticated selection procedures may somewhat improve the efficiency of mass selection, it doesn't appear that the selection method *per se* was responsible for the ineffectiveness of selection noted in this study. Despite uncertainity with regard to selection methods, results of this study clearly indicate that casual ocular selection for growth rate among balsam fir trees in the wild, as is commonly practiced by many Christmas tree growers and nurserymen, will not result in the production of fast-growing progeny. In addition, a mass selection method' that might be expected to improve the efficiency of selection for growth rate in balsam fir is likely to be time-consuming and costly.

Family selection appears to be the most effective and economical approach toward improving growth rate as well as other characteristics in balsam fir. Selection among and within open-pollinated families in large, carefully designed progeny tests should result in considerable genetic gain per unit time and cost. In fact, Snyder (1969) reported three times greater gain from half-sib family than phenotypic selection in longleaf pine (Pinus palustris Mill.), even when parent-progeny growth rate correlations were significant. In establishing such progeny tests for balsam fir, parental phenotype should be ignored or minimally considered, at least with respect to growth rate, so that a greater number of families can be sampled per unit of seed collection time and the selection differential for family selection can be increased. Contrary to popular belief, phenotypic selection can be very expensive. For instance, in this study, it took several cooperators 5 years to select and collect seed from 30 trees (only 30 of the 41 trees were selected for growth rate) and 16 years to reliabily select the best families for Christmas tree production. Clearly, genetic gain would be greater if parental phenotype had been ignored, seeds were collected from three to four times the number of parents and family selection were practiced for the best of 100 to 120 families. If existing age-age correlations from provenance tests prove reliable for half-sib progeny tests, family selection for Christmas tree production may perhaps be feasible *as early as* 3 to 5 years after establishment of progeny tests. In addition, such tests would provide needed theoretical information on the distribution of genetic variation among and within stands and would provide opportunity for additional gain through individual-tree selection.

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