ODC 165.3:174.7 *Picea glauca* (Moench) Voss

Inheritance of Budbreak and Correlation with Early Height Growth in White Spruce (Picea glauca) from New England

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ABSTRACT

Variation in budbreak date among 37 half-sib families of white spruce in a replicated one-parent progeny test plantation in southern Maine was only 5 days. Differences in the mean date of budbreak between years were greater than those between families, but the genetic correlation between date of budbreak in different years was .661. Heritability estimates ranged from.228 to .814, depending on the year and method of calculation. In each of 2 years, heritabilities estimated for family selection were higher than those for mass selection of individual trees in the plantation, but family selection for late budbreak would result in genetic gains of less than 1.5 days if more than the two latest families were selected. Selections for late budbreak and rapid early height growth were not compatible; genetic correlations between date of budbreak and height elongation for the same year were large and negative.

INTRODUCTION

LATE BUDBREAK (flushing) is an important selection criterion for genetic improvement of white spruce *(Picea glauca* (Moench) Voss) in the North Central and Northeastern United States and in Canada (Nienstaedt and King 1969; Nienstaedt and Teich 1972). Early spring frost damage to white spruce planted in the open is avoided or is greatly reduced in trees with late budbreak.

Budbreak depends on temperature and the genetic constitution of a tree; it is under strong genetic control in white spruce. Progeny tests of white spruce in Wisconsin yielded heritability estimates for date of budbreak ranging from 0.28 to 0.70 (Nienstaedt and Teich 1972). Yeatman and Venkatesh (1974) reported a heritability of 0.91 from observations of five mature white spruce and their half- and full-sib progenies growing in Ontario, Canada. Nienstaedt and King (1969) showed in clonal selections that late budbreak and fast growth are positively correlated, and that simultaneous selection for late budbreak and superior growth is possible.

Despite these encouraging results, there are questions that remain unanswered. First: Is flushing in white spruce from the Northeast United States under strong genetic control? Second: Can selection for late budbreak be effectively applied to ongoing improvement programs for white spruce in which initial selection has been based entirely on rapid growth?

I attempted to answer these questions by recording budbreak date and measuring early height growth of half-sib families of white spruce—a one-parent progeny test for a plus-tree selection program in the Northeast—that are growing in a replicated plantation in southern Maine.

MATERIALS AND METHODS

The progeny test plantation contained 37 half-sib families. The female parents were plus trees in Maine and New Hampshire selected for sustained rapid growth rate and good form by cooperators in the Northeast Spruce-Fir Tree Improvement Program. Seed was collected from the parent trees in 1967 or 1968, and was sown in the New Hampshire State Nursery in the fall of 1970.

The 3-0 seedlings were planted in the field in 1974; the plantation site was an open field. The study design was a randomized complete-block with 4-tree row plots in each of 10 blocks; trees were planted at 8- by 8-foot spacings.

Height growth, both total height and current year height elongation, was measured in the late summer or early fall of 1974, 1975, and 1976, the end of the fourth, fifth, and sixth growing seasons.

I recorded budbreak date for individual trees in the springs of 1975 and 1976. In each year the trees were observed (every other day) from the beginning of budbreak until the last tree in the plantation had flushed. The date of budbreak was defined as the day when buds in the uppermost branch whorl showed green needles under the cap of bud scales; data was recorded as the number of days after April 27—the day before the first tree flushed in 1976.

Each set of data was analyzed separately using a least-squares analysis with unequal subclass numbers for plot means (Harvey 1960), and an analysis of variance for individual-tree values. Family and error variance components were estimated from the mean square for all variables.

Genetic, phenotypic, and environmental correlations between date of budbreak and height growth were obtained from cross-product analysis (Falconer 1960).

To estimate the effectiveness of selection for budbreak date and early height growth, two heritabilities were calculated from each analysis of variance. The first, or individual-tree heritability, is appropriate for estimating gain from mass selection among randomly placed seedlings in small test plantings. For the plot mean analysis, heritability was estimated using methods by Kriebel and others (1972):

$$h_I^2 = \frac{4\,\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_p^2 + \hat{\sigma}_w^2}$$

where:

$\hat{\sigma}_f^2$ = family variance

$\hat{\sigma}_p^2$ = plot error variance

$\hat{\sigma}_w^2$ = within-plot error variance.

For the individual-tree analysis, heritability was estimated by:

$$h_I^2 = \frac{4\,\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_e^2}$$

where:

$\hat{\sigma}_f^2$ = family variance

$\hat{\sigma}_e^2$ = error variance.

The second, or family heritability, is appropriate for estimating gain from selection among half-sib families if 4 seedlings per plot and 10 replicates of each family plot are used to judge the potential of each family. For the plot mean analysis, heritability was estimated by:

$$h_f^2 = \frac{\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + 10^{-1}\,\hat{\sigma}_p^2 + 40^{-1}\,\hat{\sigma}_w^2}$$

For the individual-tree analysis family heritability was estimated by:

$$h_f^2 = \frac{\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + 40^{-1}\,\hat{\sigma}_e^2}$$

RESULTS AND DISCUSSION

Differences in budbreak among white spruce of as many as 21 days were reported by Nienstaedt and Teich (1972); this figure is near the range of variation for the seedling material in this study. The range of budbreak in family means was quite small (Table 1). In 1975, the earliest and latest families differed by less than 4 days; in 1976, the difference was only 5 days. Differences between individual trees were greater than those between families, 12 days in 1975, and 19 days in 1976.

Differences in mean budbreak between 1975 and 1976 for both families and individual trees

Table 1.—*Overall mean and ranges for date of budbreak of half-sib families and individual trees in 1975 and 1976*

Budbreak year	Mean [a]	Range	
		Individuals	Family means
	Days		
1975	23.1	12	3.5
1976	8.3	19	5.1

[a] Days from April 27 in each year.

are almost entirely functions of early spring temperature. Differences in budbreak of up to 2 weeks from year to year are normal (Nienstaedt and King 1969). In 1976, an unusually warm period in early April—including a week with daytime temperatures in the high 90's—was responsible for budbreak as early as April 28; in 1975, the earliest individual trees did not break bud until May 16.

Heritability estimates for date of budbreak ranged from .228 to .814, depending on the year and the method of calculation (Table 2); the estimates for date of budbreak were somewhat higher in 1976 than in 1975. In both years, heritabilities for family selection were higher than those for mass selection of individual trees.

Heritability estimates for total height were high; they approached or were greater than 1.0 in 1974, 1975, and 1976. However these values are not reported here because they would be useless in predicting response to selection. Overestimates of heritability for early height growth in half-sib progeny tests are common. The assumption that all progeny within families are half-sibs and that differences between families account for only 1/4 of the additive genetic variance may be one source of overestimation. Another could be the presence of maternal effects.

Heritability estimates for height elongation decreased with age; the tendency for heritability to decrease with age has been noted in many species. The high heritability in 1974 may have been caused by the uniformity of growth in all trees in the first year after transplanting. In 1975 and 1976, heritability estimates for height elongation were approximately equal to or slightly lower than those for budbreak.

My heritability estimates for flushing are close to those of Nienstaedt and King (1969), but they are lower than 0.91 reported by Yeatman and Venkatesh (1974). The estimates by Nienstaedt and King were derived from controlled-cross progeny of parent material selected for extreme differences in date of budbreak. My estimates are probably more conservative, and probably would have been higher had there been a wider array of genotypes in the plantation.

The heritability estimates are large enough to permit effective selection for late budbreak, but selection in the progeny test plantation would not be effective because of the lack of variation. Family selection at any intensity greater than 5 percent, even with a high heritability, would result in gains of less than 1.5 days. Individual-tree selection, despite a lower heritability, is slightly more promising; but selecting those trees that flushed on the last day in each year would result in an average gain of only 3.9 days. Even if such intense selection were possible, this gain would not be significant in avoiding frost.

Date of flushing is influenced by juvenility, and flushing is progressively later with advancing age (Nienstaedt and King 1969). So it is possible that the differential between families would become greater, and that opportunities for selection at an advanced age would improve.

Table 2.—*Heritability estimates for date of budbreak and early height growth of half-sib progenies of white spruce*

Growth character and year	Plot mean analysis		Individual tree analysis	
	Individual heritability	Family heritability	Individual heritability	Family heritability
Budbreak				
1975	.420 ± .206	.647	.228	.708
1976	.461 ± .212	.652	.396	.814
Height elongation				
1974	1.153 ± .285	.867	.811	.911
1975	.395 ± .198	.604	.241	.720
1976	.280 ± .178	.507	.296	.762

Additional measurements of flushing date in this plantation will be made to investigate this possibility.

The phenotypic correlation between date of budbreak in 1975 and that in 1976 was close to zero, but the genetic correlation of .661 is significantly positive. This uniform family response to different environmental conditions is further evidence of the strong genetic control of budbreak in white spruce. The ranking of families for budbreak date changed little from one year to the next, while the ranking of individual trees fluctuated from year to year. The family that had the second latest budbreak date in 1975 had the latest budbreak in 1976, and the earliest family in 1975 was the second earliest in 1976. In all, 25 families changed less than 10 positions in ranking from one year to the next, and 14 of these families changed less than 5 positions. The strong positive genetic correlation between budbreak dates in 1975 and 1976 is somewhat surprising when the range of only 5 days between all families is considered.

Selection for late budbreak in this plantation would be selection against rapid height growth. Correlations between date of budbreak and height growth in both years were low or were negative (Table 3); correlations between date of budbreak and height elongation were close to zero or were negative. More importantly, for simultaneous selection, the genetic correlations between date of budbreak and height elongation for the same year are large and negative, especially in 1976. Overall, the correlation between budbreak and height growth was more strongly negative in 1976 than in 1975.

These negative correlations do not agree with the findings of Nienstaedt and King (1969), who reported a correlation of .605 between flushing and mean height growth; they also found that late flushing clones were 42 percent taller than early flushing clones. However the correlations between flushing and height growth were negative in progenies from several of these clones (Nienstaedt 1972).

There may be an explanation for the negative correlations that I obtained. If it is assumed that late budbreak and rapid growth are positively correlated, then the initial selection of parents for rapid growth may have resulted in the concurrent selection for late budbreak. All of the families in the progeny test would be late flushing, explaining the lack of variation in flushing date, and all of the correlations would

Table 3.—*Phenotypic, genetic, and environmental correlation coefficients between date of budbreak and early height growth of half-sib progenies of white spruce*

Budbreak year [a]	Growth character and year	Phenotypic correlation r	Genetic correlation r	Environmental correlation r
1975	*Height elongation*			
	1974	−.073	.093	−.238
	1975	−.363	−.688	−.060
	Total height			
	1974	.103	.157	.028
	1975	−.010	−.084	.131
1976	*Height elongation*			
	1975	−.063	−.523	.456
	1976	−.272	−.943	.300
	Total height			
	1975	−.056	−.206	.279
	1976	−.164	−.410	.624

[a] Correlation coefficients between budbreak date in 1975 and in 1976 are .071, .661, and −.440 for phenotypic, genetic, and environmental correlations, respectively.

be within a small, select group. Nienstaedt and King (1969) found that within-group relations between flushing and clonal elongation and mean growth rate were unclear, and, in some instances, they were negatively correlated.

At this stage it would be difficult to establish whether the negative correlation between height growth and budbreak date applies generally to white spruce as a species, or whether the correlations represent only a within-sample relationship. However the simple correlation for date of budbreak and height growth rate for all of the individual trees in the plantation for both years was .053, or no correlation. And these trees varied by almost 20 days in date of budbreak. Also, the correlation between budbreak date and height growth elongation was negative in 32 of the 37 families in 1975, and in 26 families in 1976.

This relationship between budbreak date and height growth rate in white spruce may require further clarification. Until then, I believe that a negative or no correlation between these two traits in seedling material should be assumed for selection in improvement programs where initial selection has been based exclusively on growth rate.

CONCLUSIONS

Although the strong genetic control of budbreak date in white spruce was confirmed, high heritabilities were not sufficient to ensure adequate genetic gains from a selection program. Selection for late budbreak in progeny test plantations where initial parental selections were made only for rapid growth rate may not be successful due to lack of variation and low selection differentials. The low selection differential coupled with the negative correlation between budbreak date and height growth rate suggest that these two traits be considered mutually exclusive, and that any improvement programs in the Northeast should be for only one trait or the other. The choice would depend on the general and local climates at the proposed planting sites, and on whether frost avoidance or rapid height growth rate is more important in those climates.

Finally, the early budbreak pattern in 1976—due to unseasonable spring temperatures—suggests that in some years, even the latest flushing genotypes might suffer considerable frost damage in southern New England, where it is considered extremely risky to plant a vegetable garden before the last day of May.

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