FEMALE STROBILI INCIDENCE IN A MINNESOTA POPULATION OF BLACK SPRUCE: HERITABILITY AND CORRELATION WITH HEIGHT GROWTH[1]

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Abstract.--Significant family variation in female strobili incidence, ripeness-to-flower and production were found in a Minnesota black spruce (*Picea mariana* (Mill.) B.S.P.) population tested at four locations. Heritability estimates indicated that gain in early flowering from selection would be possible. Height growth through age 12 years was positively correlated (genetic and phenotypic) to female strobili production between ages 10 and 12 years.

Additional Keywords: flowering, fruitfulness, reproductive-vegetative relationship, genetic variation.

In forest tree recurrent selection programs the difference between selection age and flowering age is important to understand and manage. Depending on the species and program, selection may occur well before the mean age of first flowering. The greater the time between selection and flowering (breeding) the lesser the advantage of early selection. Given a fixed selection age, two approaches are possible in managing the flowering age: (1) apply cultural practices that stimulate early flowering or (2) apply selection pressure for increased early flowering. Cultural practices which effectively stimulate early flowering have been developed (Greenwood et al. 1987, Pharis et al. 1987), but may be too costly for some applications. The feasibility of management through selection depends on the heritability of early flowering traits and their genetic correlation with economic traits such as growth rate.

To investigate the genetic control of early flowering in black spruce and its correlation with height growth, female strobili and height growth data were collected, in four wind-pollinated family tests, and analyzed. The specific objectives of this paper were to estimate the heritability of female strobili incidence, ripeness-to-flower and female strobili production and the genetic correlation of strobili production with tree height and height increments.

Previous research with forest tree species indicated that flowering traits were moderately to highly heritable and negatively correlated to height and/or diameter growth (Schmidtling 1981, Eis et al. 1965). Most flowering research in *Picea* has concentrated on understanding the physiology of reproductive bud initiation and development and developing cultural practices to decrease time-to-flower (Pharis and Ross 1986, Ho 1988, Ross 1985, Marquard and Hanover 1984).

MATERIAL AND METHODS

Data for this study were obtained from four black spruce wind-pollinated family tests, which resulted from a Minnesota statewide single tree seed collection in 1974 (Hyun 1982, Nelson 1988). The tests were established in a greenhouse and transplanted to four nurseries in 1975. At the end of the 1977 growing season, family selection for 3-year height was conducted in three

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nurseries based on data from all four nurseries. Of the 300 families tested, 200 were selected and transplanted to three field locations (DNR, Blandin and Potlatch) in the spring of 1978. The fourth field test (CFC) was also planted in 1978 and consisted of trees from all 300 families. All field sites were located in Minnesota: DNR (Department of Natural Resources), eastern; Blandin, north central; and Potlatch and CFC (Cloquet Forestry Center) both northeastern.

Sets-in-reps, randomized complete block experimental designs were used at each field location. At DNR, Blandin and Potlatch, 50 families were randomly assigned to each of four sets and trees were planted in 3-tree non-contiguous plots in six replications. At CFC, each set contained 75 families and trees were planted in 4-tree non-contiguous plots in three replications. Spacing at each location was 6 x 6 ft and single border rows of excess stock were planted at Blandin and CFC.

The presence of female strobili (yes=1, no=0) was recorded for each tree at each location the spring before the 11th growing season (incidence, age 10 years from seed). At DNR, Blandin and CFC, the presence of female strobili and/or year-old cones were also recorded the spring before the 13th season (incidence, ages I I and 12). Ripeness-to-flower (yes=l, no=0) was determined for each tree by evaluating strobili presence at ages 10 through 12. Trees showing evidence of female strobili in at least one of these three years were considered "ripe-to-flower" (Schmidtling 1981).

In addition to recording age 11 and 12 incidence data at CFC, trees were classified by the estimated number of female strobili with the following scheme:

Occurrence class	Number observed
0	0
1	1 - 10
2	11 - 50
3	> 50.

Using the occurrence class and age 10 incidence data, a flowering index was calculated by summing class values from age 10 to 12. This index, with a range of 0 (no strobili) to 7 (strobili each year and greater than 50 at ages 11 and 12), was used to quantify female strobili production at CFC.

Total heights of each tree were measured at ages 7 and 10 at each location and again at age 12 at DNR, Blandin and CFC. Height increments (12-10, 12-7 and 10-7) were calculated for trees at CFC only. Details of the height growth analysis can be found in Nelson (1988).

Analyses of variance and F-tests were computed within and across locations (Table 1). Traits and locations involved in these analyses were;

Trait	Locations	Pooled Analysis Locations
age 10 incidence	All	DNR, Blandin, Potlatch
age 12 ripeness	DNR, Blandin, CFC	DNR, Blandin
flowering index	CFC	none.

CFC data were not included in the pooled analyses since many ramifies were in ant erent sets witn respect to the other plantings.

For each trait analyzed, individual tree heritabilities were calculated as follows;

Within location

$$h^2 = 4*\sigma^2_{f(s)} / (\sigma^2_{f(s)} + \sigma^2_{\varepsilon} + \sigma^2_{\delta}) \text{ or}$$

Across locations

$$h^2 = 4*\sigma^2_{f(s)} / (\sigma^2_{f(s)} + \sigma^2_{lf(s)} + \sigma^2_{\epsilon} + \sigma^2_{\delta}) ,$$

where $\sigma^2_{f(s)}$ = estimated family-in-set variance component, $\sigma^2_{lf(s)}$ = estimated location x family-in-set interaction variance component, and σ^2_{ϵ} and σ^2_{δ} = estimated experimental and within plot error variance components, respectively. Binomial-scale heritability estimates were transformed to continuous-scale estimates by;

$$h_c^2 = h_b^2 * ((1-p) / (i^2 p)) ,$$

where p = proportion of trees with female strobili (i.e. incidence) and i = standardized mean of trees with strobili on the continuous scale (Dempster and Lerner 1950). This transformation eliminates the measurement error variance associated with binomial measures of continuous variables and results in heritability estimates that are independent of incidence (Falconer 1981).

Table 1. Analysis of variance format and expected mean squares for within and across locations analyses.

Source	Coefficients of Expected Mean Squares								
Within location									
	σ^2_w	σ^2_e	$\sigma^2_{f(s)}$	σ^2_{r*s}	σ^2_s	σ^2_r			
Rep	1	k		fk		sfk			
Set	1	k	rk	fk	rfk				
Rep*Set	1	k		fk					
Family/Set	1	k	rk						
Error	1	k							
Within	1								
Across locations									
	σ^2_w	σ^2_{eB}	$\sigma^2_{l*f(s)}$	$\sigma^2_{f(s)}$	σ^2_{eA}	σ^2_{l*s}	σ^2_s	$\sigma^2_{r(l)}$	σ^2_l
Location	1	k	rk		fk	rfk		sfk	rsfk
Rep/Loc	1	k			fk			sfk	
Set	1	k	rk	lrk	fk	rfk	lrfk		
Loc*Set	1	k	rk		fk	rfk			
Error[A]	1	k			fk				
Family/Set	1	k	rk	lrk					
Loc*Fam/S	1	k	rk						
Error[B]	1	k							
Within	1								

Note: Error and Error[B] are experimental errors
Error[A] is Rep/Loc*Set interaction
k, r, f, s and l = numbers of trees per plot, replications, families, sets and locations, respectively

Within the CFC location, additive genetic and phenotypic correlation coefficient estimates were computed between the flowering index and each total height and height increment variable with the following formulae:

Additive genetic

Phenotypic

$$r_{A:Y,X} = \sigma_{f(s):X,Y} / \surd\{\sigma^2_{f(s):X} * \sigma^2_{f(s):Y}\} \text{ and}$$

$$r_{P:X,Y} = \sigma_{X,Y} / \surd\{\sigma^2_X * \sigma^2_Y\} ,$$

where $\sigma_{f(s)}$ = estimated family-in-set covariance component and $\sigma^2_{f(s)}$ = estimated family-in-set variance component.

RESULTS

Analyses involving the DNR, Blandin and/or Potlatch locations utilized data on 190 (46 to 49 families per set) of the 200 nursery-selected families. These families were represented at each field location by surviving trees in at least three (of six) replications. At CFC, all 300 families were represented in at least two (of three) replications and were included in the analyses.

Incidence of female strobili and ripeness-to-flower location means and ranges in family means are listed in Table 2. At age 10, flowering was observed at all locations although some families at DNR, Blandin and CFC did not flower that year. Large increases in incidence between ages 10 and 12 were observed at Blandin and CFC. Most of the CFC increase occurred at age 11 (28 to 57 percent), while the increase at Blandin was gradual (15 to 30 to 54 percent). Ripeness-to-flower and age 12 incidence means showed that a small proportion of the flowering trees at age 12 at DNR had not previously flowered, while at Blandin and CFC a high proportion had.

Table 2. Location means and family mean ranges of female strobili incidence, ripeness-to-flower and total height in four black spruce wind-pollinated family tests.

	DNR	Blandin	Potlatch	CFC
Age 10				
incidence (%)	34	15	39	28
family range (%)	0 - 83	0 - 64	6 - 86	0 - 89
mean height (m)	2.17	1.61	1.87	1.83
Age 11				
incidence (%)	36	30	--[a]	57
Age 12				
incidence (%)	44	54	--[a]	68
ripeness (%)	53	57	--	71
family range (%)	0 - 100	0 - 100	--	22 - 100
mean height (m)	2.93	2.45	--	2.52
ripeness=0	2.52	1.98	--	1.74
ripeness=1	3.30	2.82	--	2.85

[a] age 11 and 12 data were not available at Potlatch

Results of the analyses of variance and F-tests show that within and across locations the differences in family means were statistically significant for all traits analyzed (Table 3, age 10 and Table 4, age 12). Significant location by family interaction was detected for age 10 incidence (Table 3). Spearman rank-correlation estimates of family means between the pairs of locations were positive and significant (DNR-Blandin, .32; DNR-Potlatch, .26; Blandin-Potlatch, .30), although relatively small for practical application. The location by family interaction was not significant for age 12 ripeness-to-flower (Table 4). For this trait, the rank-correlation was larger (.43) indicating greater stability of family rankings of ripeness than incidence.

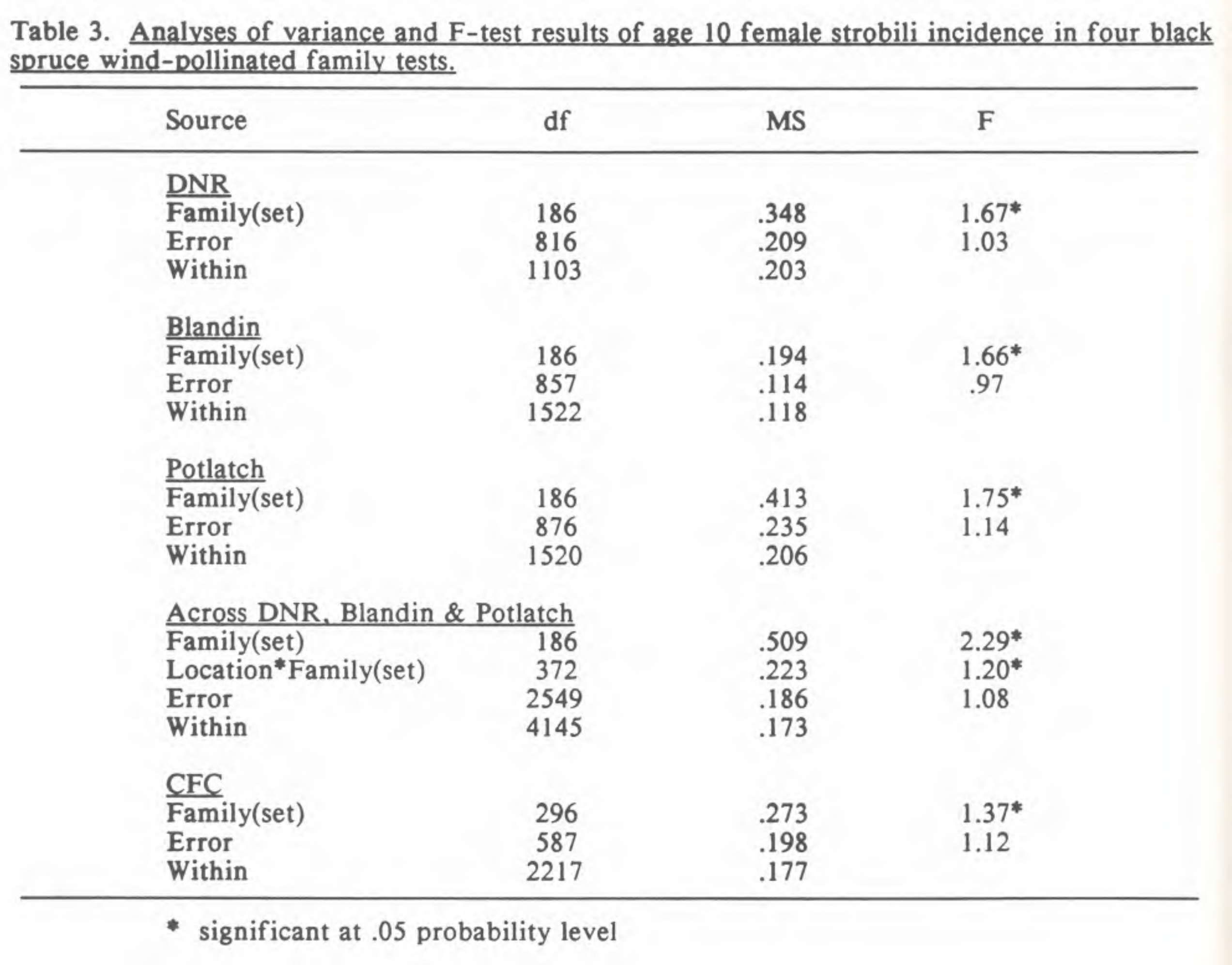

Table 3. Analyses of variance and F-test results of age 10 female strobili incidence in four black spruce wind-pollinated family tests.

Source	df	MS	F
DNR			
Family(set)	186	.348	1.67*
Error	816	.209	1.03
Within	1103	.203	
Blandin			
Family(set)	186	.194	1.66*
Error	857	.114	.97
Within	1522	.118	
Potlatch			
Family(set)	186	.413	1.75*
Error	876	.235	1.14
Within	1520	.206	
Across DNR, Blandin & Potlatch			
Family(set)	186	.509	2.29*
Location*Family(set)	372	.223	1.20*
Error	2549	.186	1.08
Within	4145	.173	
CFC			
Family(set)	296	.273	1.37*
Error	587	.198	1.12
Within	2217	.177	

* significant at .05 probability level

Individual tree heritability estimates are listed in Table 5, including estimates for total tree height. The continuous-scale estimates ranged from .19 at CFC for age 12 ripeness to .44 at Blandin for age 10 incidence. Height heritability estimates were smaller than estimates for incidence or ripeness, suggesting that the additive genetic control of the underlying distributions of female strobili incidence and ripeness are stronger than that for height growth.

The mean flowering index was 2.31 with a range in family means from 1.00 to 5.22. The flowering index distribution was heavy left-tailed, so prior to further analysis the index values (Y) were transformed to the /[Y+.5] scale (Steel and Torrie 1980). Differences among flowering index family means were significant and the estimated individual tree heritability was .22 (Tables 4 and 5).

Table 4. Analyses of variance and F-test results of age 12 ripeness-to-flower and flowering index in four black spruce wind-pollinated family tests.

Source	df	MS	F
DNR, ripeness			
Family(set)	186	.405	1.81*
Error	816	.224	.99
Within	1103	.227	
Blandin, ripeness			
Family(set)	186	.400	1.74*
Error	857	.230	1.11
Within	1522	.208	
Across DNR & Blandin, ripeness			
Family(set)	186	.556	2.24*
Location*Family(set)	186	.249	1.10
Error	1673	.227	1.05
Within	2625	.216	
CFC, ripeness			
Family(set)	296	.270	1.26*
Error	587	.214	1.20*
Within	2217	.178	
CFC, flowering index			
Family(set)	296	.657	1.51*
Error	587	.435	1.26*
Within	2217	.346	

* significant at .05 probability level

Additive genetic and phenotypic (simple) correlation estimates between the flowering index (transformed) and tree heights and height increments are listed in Table 6. All correlations were positive and the phenotypic correlations were substantially larger than the genetic. This suggests that the propensity for abundant, early flowering (10-12 years) and rapid height growth are positively correlated and some of this correlation is additive genetically based. Thus, selection for early height growth (ages 7 to 12) in this black spruce population will have a positive effect on early female strobili production.

DISCUSSION AND CONCLUSIONS

It appears that expression of early female strobili traits is under moderately strong additive genetic control in black spruce of Minnesota origin. Estimated heritabilities of the three flowering traits studied were similar and consistently greater than heritabilities of total height. Ripeness-to-flower was more stable over locations than single-year incidence and as a result may be a better selection trait for decreasing flowering age.

Additive genetic correlations between early female strobili production and total tree heights and height increments were positive, indicating that selection for total height or height increment will result in correlated gain in reproductive earliness. Assuming early selection (age 10) is appropriate, then the correlated gain in reproductive earliness would be valuable in terms of further shortening the generation interval and decreasing the time from selection to commercial seed production. Additionally, male strobili incidence must be assumed to act similarly to or more favorably than female incidence.

Table 5. Individual tree heritability estimates of female strobili incidence, ripeness-to-flower, flowering index and total height in and across four black spruce wind-pollinated family tests.

	DNR	Blandin	Potlatch	DBP[a]	CFC
Age 10					
Incidence					
h^2 binomial	.23	.19	.22	.16	.15
h^2 continuous	.38	.44	.36	.27	.27
Height					
h^2	.23	.23	.15	.10	.16
Age 12					
Ripeness					
h^2 binomial	.24	.22	--[b]	.21	.11
h^2 continuous	.38	.35	--	.33	.19
Flowering index					
h^2					.22
Height					
h^2	.21	.17	--	.11	.16

[a] age 10, across DNR, Blandin and Potlatch
age 12, across DNR and Blandin
[b] age 12 data were not available at Potlatch

Table 6. Additive genetic and phenotypic correlation estimates between the flowering index and total height and height increments in the CFC black spruce wind-pollinated family test.

	Height (years)					
Correlation	7	10	10-7[a]	12	12-10[a]	12-7[a]
Flowering index						
Genetic	.24	.41	.44	.41	.38	.43
Phenotypic	.66	.78	.75	.78	.58	.75

[a] height increment over years indicated

Positive correlations between female strobili production over the age 10 to 12 interval and height growth in this interval or the previous interval (7 to 10), suggest that flowering does not have a negative impact on growth in either a phenotypic or genetic sense. This finding appears to be species and possibly population and site specific, since Schmidtling (1981) has found growth and flower production in loblolly pine (Pinus taeda) to be negatively correlated. Continued evaluations of the developmental relationships between flowering and growth are needed, since we are uncertain about the long-term effects that early, abundant flowering and rapid height growth have on final yield.

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