

# Genetic Variation and C-Effects in Black Spruce Seedlings under Two Nutrient Regimes

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## Summary

In a short-term black spruce (*Picea mariana* (MILL.) B.S.P.) progeny test genetic variation and C-effects in several early traits were evaluated under two fertilizer regimes. For this purpose, seed lots were raised from 55 ramets representing 19 clones growing in a northern Ontario clonal seed orchard. The family means in number of cotyledons ranged from 3.9 to 4.7 and varied significantly among families, accounting for 11% of the total variance. Family variation was also highly significant in the number of branches per seedling after three months. Under the low and high fertilizer regime, 11% and 12% of the total variance, respectively, were due to families. No variance was associated with ramets within families in the number of cotyledons and branches. Height variation due to ramets and families after three and four months was highly significant. Early heights were also closely correlated with ramet mean seed weights suggesting that these C-effects were caused by maternal effects manifested in seed weight differences. After five months, only family variation was significant. Heritability estimates for number of cotyledons was 0.44 and ranged for heights from 0.42 to 0.00, decreasing with age and increased fertilizer level. Genetic and phenotypic correlations between seedling traits are also reported.

*Key words:* *Picea mariana* (MILL.) B.S.P., clonal seed orchard, progeny testing, heritability, genetic correlations.

## Introduction

Black spruce (*Picea mariana* MILL. B.S.P.) is an economically important species in eastern Canada, yielding high quality pulp for newsprint and fine papers. Accordingly, genetic and tree breeding studies with this species are underway. In an earlier work, MORGENSTERN (1969b) reported geographic variation to be predominantly clinal along a north-south gradient in several physiological and morphological traits in young seedlings. Recently, BOYLE (1985) and PARK and FOWLER (1988) confirmed these findings with older trees. While these authors investigated provenance variation, BOYLE (1987) estimated family variation using a diallel cross. He found that differences in general combining ability accounted for most variance among seed parents. Thus, potential gains can be achieved through selection and subsequent crossing of proven superior genotypes.

First generation progeny tests are usually established with seedlings raised from open-pollinated seed collected from the original selections growing in natural stands. An alternative to tests using seed from the original parents is the use of open-pollinated seed collected from established seed orchards. This may have the advantage that all seed orchard entries are subjected to a common pollen pool

and the progeny test reflects more closely the actual genetic make-up of the future seed orchard crop.

This type of progeny test with seed from clonal orchards can be established by bulking seeds from different ramets within a clone (family). However, the bulking of seed from different genetically identical mother trees is based on the assumption that non-genetic (environmental) effects are identical among progeny of the same family. Often, environmental effects vary from ramet to ramet and thus can lead to C-effects (LERNER, 1958) manifested as ramet-within-clone variation. For example, rootstocks in grafts are known to affect reproductive phenology, yield and quality of seed (SAX, 1958; SCHMIDTLING, 1973), therefore potentially increasing environmentally-induced ramet-within-clone variation. Microsite differences among ramets of the same clone may also affect seed weight, which can lead to increased within-family variation. Furthermore, topophytic effects associated with the original ortet may also vary among ramets within a clone and can contribute to within-family variation in the offspring. While C-effects have been mainly evaluated in vegetatively reproduced relatives (LIBBY and JUND, 1962; WILCOX and FARMER, 1968), the importance of such effects in sexually reproduced relatives in forest trees has not been studied yet. The presence of C-effects in seed from a clonal seed orchard may falsify the genetic gain realized from seed orchards.

In this study open-pollinated seed was used to estimate C-effects expressed as progeny variation among ramets of the same clone. Therefore, C-effects are confounded with possible unequal male parent contributions to individual ramets due to a non-uniform pollen pool resulting in a potential overestimation of C-effects.

The objectives of this study were to evaluate family and ramet-within-family variation in a seed crop from a clonal orchard where significant ramet-within-clone variation has been reported in cone, seed and germination properties VERHEGGEN and FARMER, 1983; STOEHR and FARMER, 1986). Genetic correlations among various seedling properties were investigated as well.

## Materials and Methods

### Seed Origin and Collection

Between 30 and 50 current year's cones were collected in mid-September 1983 from two ramets of two clones and three ramets of 17 black spruce clones growing in the Matawin seed orchard (48°23' N and 90°03' W) in northwestern Ontario, Canada. The orchard was established between 1966 and 1972 by the Ontario Ministry of Natural Resources with scions from superior phenotypes growing between latitudes 48° and 50° N and longitudes 88° and 91° W. The scions were bench-grafted to nursery-grown white spruce (*Picea glauca* MOENCH. VOSS.) seedlings and after three years outplanted at a spacing of 3.6 m × 3.6 m in into blocks containing 12 clones with 12 ramets each. Arrangement of the ramets within blocks was random with the

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condition that ramets of the same clone could not be adjacent. A total of 61 black spruce clones were planted in 18 blocks. A pollen contamination barrier of mature jack pine (*Pinus banksiana* LAMB.) surrounded the orchard.

Cones from the 55 individual ramets were stored as separate seed lots in sealed glass jars at 4° C. In early January 1984, seeds were extracted as outlined by SAFFORD (1974) and dewinged. Mean ramet seed weights were determined as described by STOEHR and FARMER (1986) before seeds were stratified for 14 days at 4° C.

#### Test Establishment

The progeny test was established in a greenhouse with 16 hrs. of light (extended with sodium vapour lights during winter and spring) at approximately 25° C and 8 hrs. of darkness at 15° C. The test was conducted using a split-plot design by dividing each of four blocks into two main plots, each receiving either 25 ppm (0.1 g/l of water) or 200 ppm (0.9 g/l of water) of 20-20-20 N-P-K soluble fertilizer. Seedlings grown under the high fertilizer regime received fertilizer with every watering, while seedlings under the low fertilizer regime received fertilizer only during alternate waterings. In each main plot, each ramet was represented by four seedlings in one Tinus container box (i.e., one experimental unit), which was filled with a 1:1 mixture of peat-vermiculite.

#### Data Collection and Analyses

The number of cotyledons per seedling was counted in two randomly selected main plots after the seed coats

dropped and prior to the installment of the fertilizer treatment. Three months after test establishment, the number of branches longer than 1.0 cm were counted on each seedling. Height measurements were taken after three, four and five months. For cotyledon and branch number counts, a total of 17 families represented by three ramets each were evaluated. For height measurements in additional two families with two ramets each were included. All data were subjected to nested analyses of variance. The outline of the analyses of variance for heights and branches is given in Table 1. As the term "Ramets/Fa" (Table 1, 4 and 5) represents the variation due to ramets within a family, its magnitude is an estimate of C-effects. Additional analyses of variance were carried out for the two fertilizer regimes separately to obtain variance components without the overriding effects of the fertilizer treatment.

Phenotypic and genetic correlations between measured traits were calculated for the two fertilizer treatments separately. The correlation analyses were based on 51 ramet means (17 families × 3 ramets per family) as not all traits were measured on all seedlings. Genetic correlations were calculated as described by BECKER (1985):

$$r_G \text{ of trait A and trait B} = \text{cov}_F / \sigma_A \cdot \sigma_B$$

where  $r_G$  = genetic correlation

$\text{cov}_F$  = family covariance between traits A and B

$\sigma_A$  = standard deviation of trait A

$\sigma_B$  = standard deviation of trait B

Table 1. — Expected mean squares for the analyses of variance for heights and number of branches for a black spruce progeny test of a clonal seed orchard.

Source of Variation	Expected Mean Squares <sup>1</sup>
Blocks ( $B_1$ )	$\sigma^2_S + 4\sigma^2_E + 8\sigma^2_{B \times R} + 8a\sigma^2_{B \times F \times R} + 8ab\sigma^2_B$
Fertilizer ( $F_1$ )	$\sigma^2_S + 4\sigma^2_E + 16\sigma^2_{F \times R} + 16a\sigma^2_{F \times F \times R} + 16ab\sigma^2_F$
B × F	$\sigma^2_S + 4\sigma^2_E + 4\sigma^2_{B \times F \times R} + 4a\sigma^2_{B \times F \times F \times R} + 4ab\sigma^2_{B \times F}$
Families ( $F_{ak}$ )	$\sigma^2_S + 4\sigma^2_E + 32\sigma^2_R + 32a\sigma^2_{F \times R}$
B × F × R	$\sigma^2_S + 4\sigma^2_E + 8\sigma^2_{B \times R} + 8a\sigma^2_{B \times F \times R}$
F × F × R	$\sigma^2_S + 4\sigma^2_E + 16\sigma^2_{F \times R} + 16a\sigma^2_{F \times F \times R}$
B × F × F × R	$\sigma^2_S + 4\sigma^2_E + 4\sigma^2_{B \times F \times R} + 4a\sigma^2_{B \times F \times F \times R}$
Ramets/Fa ( $R_{(k)_1}$ )	$\sigma^2_S + 4\sigma^2_E + 32\sigma^2_R$
B × R	$\sigma^2_S + 4\sigma^2_E + 8\sigma^2_{B \times R}$
F × R	$\sigma^2_S + 4\sigma^2_E + 16\sigma^2_{F \times R}$
Residual <sup>2</sup>	$\sigma^2_S + 4\sigma^2_E + 4\sigma^2_{B \times F \times R}$
Within-Plot Error	$\sigma^2_S$

<sup>1</sup>) Coefficient a = 2.9 due to unbalanced design in analyses for heights (BECKER, 1985), for number of branches a = 3; b = 19 for height analyses, for number of branches b = 17.

<sup>2</sup>) For F-tests, the B × F × R interaction is assumed to be zero.

Table 2. — Summary of results of measured traits in short-term black spruce progeny test.

Trait	Fertilizer	Unit	Mean	Range in Family Mean
Number of Cotyledons <sup>1</sup>		Number	4.4	3.9 - 4.7
Number of Branches at three Months	low	Number	3.4	2.6 - 3.9
	high		4.9	3.7 - 5.8
Height at three Months	low	cm	8.1	7.5 - 8.8
	high		9.2	8.7 - 10.5
Height at four Months	low	cm	11.8	10.9 - 12.5
	high		19.5	17.8 - 20.9
Height at five Months	low	cm	12.6	11.2 - 13.8
	high		32.0	29.6 - 33.9

<sup>1</sup>) Cotyledons counted prior to installment of fertilizer treatment.

The covariances between traits were obtained from the mean-corrected cross products in the Manova procedure of SAS (SAS Institute, 1987).

### Results and Discussion

The mean number of cotyledons per seedling was 4.4 and ranged from 3.9 to 4.7 among individual families (Table 2). These values are comparable to those obtained by MORGENSTERN (1969b) in a progeny test with 118 families having a mean of 4.2 and a family range of 3.6 to 5.7. The analysis of variance (Table 3) revealed significant ( $p < 0.01$ ) variation among families, accounting for 11% of the total variation. No significant variance was associated with ramets

within families. Narrow sense heritability for number of cotyledons was 0.44 (Table 5), an estimate lower than the value of 0.53 reported by SORENSEN (1966) for Douglas fir (*Pseudotsuga menziesii* (MIRB.) FRANCO). According to MORGENSTERN (1969b), heritability estimates for cotyledon number should be based on seedlings raised from seed originating in a common environment. Thus, seed orchard seed probably yields reliable estimates for this trait.

Strong fertilizer effects are evident in our data. Number of branches and heights at all ages increased under the high fertilizer regime. The fertilizer treatment not only caused faster growth but also affected the crown form of the seedlings by increasing branching (Table 2). After three

Table 3. — Analysis of variance for number of cotyledons per seedling in 17 open-pollinated progenies of black spruce clones.

Source	df	Mean Square (MS)	F-ratio <sup>1</sup>	Variance Components
Block (B)	1	0.061	N/A	0
Family (F)	16	1.490	5.5**	.05
BxF	16	0.311	0.9	0
Ramet/Fa (Ra)	34	0.270	0.8	0
Residual <sup>1</sup> (Res)	34	0.333		0
Within-plot Error	306	0.410		.40
Total	407			

<sup>1</sup>) Form of F-ratios: Family:  $F = MS_F / MS_{Ra}$   
 Ramets:  $F = MS_{Ra} / MS_{Res}$   
 BxF:  $F = MS_{BxF} / MS_{Res}$

<sup>2</sup>) Residual includes variation due to experimental error and BxRa/F interaction.

\*\*) significant at 1% level.

Table 4. — Summary of analyses of variance of black spruce progeny heights at three ages and numbers of branches at three months of age.

Source	df	Height at Seedling Age			Number of Branches	
		3 Months MS	4 Months MS	5 Months MS	df	MS
Block (B)	3	5.1	93.5	312.6	3	13.3
Fertil. (F)	1	545.2*	26137**	156665**	1	838.1**
BxF	3	36.0	278.1	544.5	3	7.9
Family (Fa)	18	16.4**	33.3**	67.9**	16	20.0**
BxFa	54	1.9	8.8	20.0	48	1.3
FxFa	18	1.5	10.7	26.9	16	2.3
BxFxFa	54	0.7	6.1	19.3	48	1.6
Ramets/Fa (Ra/Fa)	36	3.6**	11.4**	22.4	34	2.0
BxRa/Fa	108	1.5	7.5	19.3	102	1.6
FxRa/Fa	36	1.1	6.7	28.8	34	1.8
Residual <sup>1</sup>	108	1.6	6.5	15.9	102	1.7
Within-plot						
Error <sup>2</sup>	1320	1.2	4.8	16.4	1224	1.2
Total	1759				1631	

<sup>1</sup>) Residual includes variation due to experimental error and BxFxRa/Fa interaction.

<sup>2</sup>) Within-plot error df for four and five months reduced due to mortality to 1318 and 1308, respectively.

\*) significant at 5% level

\*\*\*) significant at 1% level

months under the low fertilizer regime, seedlings in some families had already set a terminal bud and stopped growing in height. In contrast, under the high fertilizer regime, all seedlings grew vigorously beyond the age of five months. It is noteworthy to point out that no statistically significant family  $\times$  fertilizer and ramet  $\times$  fertilizer interactions in height and number of branches were observed (Table 4), indicating that individual families performed equally in relative terms under both fertilizer treatments.

Family variation in the number of branches was highly significant (Table 4), accounting for 11% and 12% of the total variance under the low and high fertilizer regime, respectively (Table 5). Heritability values were comparable between treatments and ranged from 0.45 to 0.51. No significant variance was associated with ramets within families. In contrast, highly significant variation due to ramets was observed in three and four-months heights (Table 4). There are indications that these C-effects may be caused by mean seed weight differences among ramets within families. In a companion study (STOEHR and FARMER, 1986), highly significant differences in mean seed weights among ramets within clones were observed. Here, high phenotypic correlations were detected between mean heights of ramet progeny and mean ramet seed weights at three months (Table 6). This relationship weakened after four months and disappeared after five months, when ramet effects

were no longer statistically significant (Table 4). Thus, indirect evidence indicates that the ramet influence upon early growth may involve maternal effects. This dependence of early seedling growth on initial seed weight is well documented for black spruce (MORGENSTERN, 1969a) and for other conifers (e.g. PERRY, 1976; RIGHTER, 1965) and may be even stronger and longer-lasting in species with heavier seeds.

In this study, C-effects could not be separated from potential paternal effects caused by a non-homogenous pollen cloud. Only through controlled pollinations can the two sources of within-family variation be separated. However, as open-pollinated orchard seed is generally used for reforestation, our approach reflects this operational use of seeds. Despite the potential overestimation of C-effects, the results of our study suggest that C-effects are not persistent and the separation of seed from different mother trees within a clone is not warranted for progeny testing. This lack of ramet effects is in sharp contrast to highly significant ramet-within-clone variation in seed germination in seed germination percent and energy, cone length and volume, number of seed per cone, percent filled seed per cone and seed weight observed in another study of the same ramets (STOEHR and FARMER, 1986).

Highly significant family variation was observed in height at all ages (Table 4), but decreased in magnitude

Table 5. — Percent of components of variance and heritability estimates of several seedling traits for black spruce families growing under two fertilizer regimes.

Trait	Fertilizer Level	Source of Variation					Within Plot ( $\sigma^2_W$ )	Heritability*
		Block ( $\sigma^2_B$ )	Family ( $\sigma^2_F$ )	B x F ( $\sigma^2_{B \times F}$ )	Ramet/F ( $\sigma^2_R$ )	Error ( $\sigma^2_E$ )		
Cotyledon								
Number		0	11.0	0	0	0	89.0	.44±.19
Number of Branches	low	4.7	10.7	0	0	8.0	76.6	.45±.19
	high	1.6	12.5	0.2	2.0	5.1	78.6	.51±.21
Height at three months	low	7.5	9.8	0.8	3.2	0.4	78.3	.42±.18
	high	4.3	8.1	0	3.3	8.1	76.2	.34±.16
Height at four months	low	3.9	4.6	1.6	4.2	11.1	74.6	.19±.12
	high	5.4	1.7	0	0.5	2.6	89.8	.07±.08
Height at five months	low	1.8	7.3	1.5	1.8	10.3	77.3	.30±.15
	high	2.3	0	0.4	1.6	4.3	91.4	.00

\*) Heritability =  $4\sigma^2_F / (\sigma^2_F + \sigma^2_{B \times F} + \sigma^2_R + \sigma^2_E + \sigma^2_W)$

Table 6. — Genetic (above diagonal) and phenotypic (below diagonal) correlation coefficients for some variables measured at two fertilizer levels in progeny test of black spruce seedlings from seed orchard clones.

Low Fertilizer Level:						
	BNO	COT	MSW	HT3	HT4	HT5
BNO <sup>1</sup>		.53*	.55	.16	.19	.01
COT	.26		.71	.50	.25	.10
MSW	.36	.47		.62	.12	.01
HT3	.21	.22	.58		.60	.27
HT4	.08	.03	.23	.69		.85
HT5	.11	.03	.10	.41	.84	
High Fertilizer Level:						
	BNO	COT	MSW	HT3	HT4	HT5
BNO		.73	.69	.39	-.02	-.32
COT	.37		.71	.43	-.20	-.61
MSW	.63	.47		.83	.43	.25
HT3	.41	.21	.70		.72	.48
HT4	.09	.01	.33	.69		1.12
HT5	-.05	-.06	.06	.41	.75	

<sup>1</sup>) BNO = branch number > 1 cm; COT = cotyledon number; MSW = mean seed weight; HT3 = height at 3 months; HT4 = height at 4 months; HT5 = height at 5 months.

\*) phenotypic correlation coefficients > 0.27 or < -0.27 significant at p < 0.05.

with age and increased fertilizer level. At age three months, family variance accounted for 9.8% and 8.1% of the total variation at the low and high fertilizer levels, respectively. At age five months, variation due to families dropped to 7.3% of the total variation under the low fertilizer regime. No variance was associated with families under the high fertilizer level (Table 5). This difference in family variation patterns between the high and low fertilizer treatment may have been caused by the early bud set of seedlings in some families at the low fertilizer level. Thus, family differences in bud set times were reflected in height measurements at the low fertilizer regime at four and five months, increasing family variation in height. In comparison, at the high fertilizer level seedlings had not set bud yet, and therefore, this component of final height was not expressed, resulting in lower family variation in heights.

Heritability estimates for early height growth ranged from 0.42 at three months under the high fertilizer regime to 0.00 at five months under the high fertilizer regime (Table 5). The lower heritability values associated with the high fertilizer level are not only due to lower family variances, but are also related to higher within-plot variation (Table 5). At the low fertilizer level, the magnitude of this within-plot variation was comparable to other (field) progeny tests with *Picea glauca* and *P. engelmannii* PARRY (KISS and YEH, 1988) and Douglas fir (YEH and HEAMAN, 1987).

The heritability estimates obtained in our study may be inflated as the assumption that the variance among open-pollinated families estimates one quarter of the additive genetic variance may not be met in our sample families. There is evidence that in this orchard only five of 12 clones studied produced 72% of the total gametes (O'REILLY *et al.*, 1982). Furthermore, BARRETT *et al.* (1987) estimated the variance effective population size in this orchard and found

that only 7% and 22% of the clones contributed male gametes and female gametes, respectively. Thus, in our sample of assumed half-sib families, several full-sibs were likely present in each family leading to an overestimation of the additive genetic variance (SQUILLACE, 1974) as the covariance among open-pollinated seedlings was assumed to be 0.25.

Genetic correlations were high under both fertilizer regimes between number of branches and seed weight, indicating that seed weight not only influenced early height growth, but also branching habit (Table 6). Mean seed weight was also highly correlated with number of cotyledons, a component of embryo weight and seed weight. Further, cotyledon number was also highly correlated with heights at three months, a possible indication of increased initial plant vigour during seedling establishment. Phenotypic correlations between three-month height and cotyledon number were not significant at either fertilizer level.

The differences in genetic correlations between seed weight and seedling height under the two fertilizer regimes at all ages warrant explanation. Most seedlings under the low fertilizer regime ceased growing after three months (Table 2), presumably due to other genes controlling shoot growth cessation switching on. Therefore, genetic correlations were very low since seed weight is not correlated with cessation time.

Genetic and environmental correlation make up the phenotypic correlation and, therefore, can have opposite signs. Consequently, it is possible that either genetic or environmental correlation coefficient can be larger than 1.0. In our study, we found a genetic correlation of 1.12 between heights at four and five months under the high fertilizer regime. The accompanying phenotypic correlation was 0.75, indicating a negative environmental correlation. FALCONER (1981) states that opposite signs or large differences in genetic and environmental correlations indicate that genetic and environmental sources of variation affect the two traits through different physiological pathways.

A recent report with black spruce showed that early height family performance was highly correlated with growth parameters at age 13 years (WILLIAMS *et al.*, 1987), indicating the potential for early selection. Moreover, there is renewed increased interest in very early (90 to 180 days) evaluation of progeny performance (DANCİK and YEH, 1988).

In this study, we identified family variation in several traits. Variation patterns were influenced by nutritional conditions of the soil. Generally, family variation decreased with age and nutrient level. C-effects (ramet effects within families) were only important in very early height measurements, and were influenced by seed weight differences. Genetic correlation analyses revealed that number of cotyledons and seed weight and the height at three months were highly correlated.

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