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ABSTRACT

Two sets of Norway spruce progeny tests of Czechoslovakian and Bulgarian origin were evaluated for early height growth and survival to provide information on genetic variances and feasibility of selection. Variances due to family differences were significant for both sets of progenies. Progenies from Bulgarian provenances were genetically more variable than those from Czechoslovakian provenances. Provenance variation within a limited geographical area was negligible. The heritability estimates for 5 and 6 year height of Czechoslovakian progenies was low (0.04) but for 10-year height was moderate (0.18). Higher heritability estimates were obtained for Bulgarian progenies, i.e., 0.45 for height and 0.34 for survival. Family x environment interactions were significant for Czechoslovakian progenies, and amounted to about half the family component by age 10. One possible approach for genetic improvement of Norway spruce in the Region would be to use existing provenance plantations as a source of materials for selection and breeding.

RESUME

La croissance précoce en hauteur et la survie d'épinettes de Norvège d'origines tchécoslovaque et bulgare obtenues dans deux séries de tests de descendance ont été analysées du point de vue des variances génétiques et des possibilités de sélection. Les variances dues à des différences familiales sont significatives pour les deux séries de descendants. La variabilité génétique est plus élevée pour les descendances bulgares. Sur un territoire limité, la variation est négligeable. Dans le cas des descendances tchécoslovaques, les estimations de l'héritabilité sont faibles (0,04) pour la hauteur à 5 et 6 ans mais modérées (0,18) pour celle à 10 ans. Chez les descendances bulgares, l'héritabilité serait plus élevée: 0,45 pour la hauteur et 0,34 pour la survie. Les interactions famille-milieu sont significatives chez les descendances tchécoslovaques, la part du milieu comptant pour environ la moitié de celle de la famille vers l'âge de 10 ans. Pour l'amélioration génétique de l'épinette de Norvège dans la région, on pourrait recourir aux plantations existantes de provenance pour le matériel de sélection et de reproduction.

INTRODUCTION

Norway spruce (Picea abies (L.) Karst.) is native to central and northern Europe and is the most widely planted exotic conifer in northeastern North America (Fowler and Coles 1979). The species has been planted on a small scale in the Maritimes Region of Canada since the early 1900's (Hughes and Loucks 1962). More recently extensive provenance tests have been established in the Maritimes (Holst 1963; Fowler and Coles 1979) and elsewhere (Krutzsch 1974; Baldwin et al. 1973; and many others).

Norway spruce is highly variable genetically at the geographic or provenance level. Variation in seed germination, phenology, and frost hardiness, height and diameter growth, crown form, cone characteristics, and isozymes have been reported (for more detailed reviews see Fowler and Coles 1979). Norway spruce also exhibits genetic variability at the individual tree level with respect to flushing and control of dormancy (Mergen et al. 1964; Worrall and Mergen 1967), competitive ability (Stern 1966), branching characteristics (Schmidt 1952; Nanson 1971) and wood properties (Mergen et al. 1964).

The purposes of this report are: (1) to estimate the genetic and environmental components of variability from open-pollinated progenies; (2) to provide heritability information for use in future improvement programs; and (3) to examine the genetic variation between the provenances of a limited geographic range.

MATERIALS AND METHODS

Plant Materials and Planting

The materials included in this study are from a series of provenance tests established in the Maritimes by George MacGillivray (retired) of Maritimes Forest Research Centre (MFRC) in cooperation with Mark Holst (retired) of Petawawa National Forestry Institute (PNFI). Results of these provenance tests have been reported in detail by Fowler and Coles (1979). Two of these tests provide the individual family information presented in this report.

Czechoslovakian progenies: Seeds from 20 open-pollinated families derived from 10 individual trees from each of two provenances, Hojna Voda and Rabstyn (Table 1) were sown in a nursery at the Acadia Forest Experiment Station (AFES), New Brunswick and raised as 2+2 stock. The seedlings were planted in two locations at AFES and Marydale, Nova Scotia, in the spring of 1970. At each location, a randomized block design with 10 replications of 10-tree row plots planted at 1.8 x 1.8 m spacing was used. Total height was measured in the fall of 1975 (5 years from planting) at AFES and in 1976 (6 years) at Marydale and in 1980 (10 years) at both locations. Observations on survival and white pine weevil (Pissodes strobi Peck.) damage were also recorded.

Bulgarian progenies: The Bulgarian progenies are from seed of open-pollinated collections

Table 1. Information on provenances from which progenies were derived

Provenance number[a]	Origin of provenances	Latitude °N	Longitude °E	Elevation m	Height[b] cm	Survival[b] %
988 to 997	Hojna Voda, Czechoslovakia	48.7	14.7	800-940	107	87
998 to 1007	Rabstyn, Czechoslovakia	49.8	17.3	650	104	88
1384 to 1993	Pouchtinaka, Rila Mts., Bulgaria	42.3	23.6	1000	67	79
1394 to 1403	Bistritza, Rila Mts., Bulgaria	42.3	23.6	1400	68	77
1404 to 1413	Gvardeiska, Rila Mts., Bulgaria	42.3	23.6	1600-1650	66	76
1424 to 1433	Lopouha Central, Rhodopes Mts., Bulgaria	41.7	24.7	1000	63	76
1434 to 1438	Ardachla Central, Rhodopes Mts., Bulgaria	41.6	24.7	1450	70	74

[a] Accession number at the Maritimes Forest Research Centre, Fredericton, New Brunswick.
[b] Five-year data at Acadia Forest Experiment Station from Fowler and Coles (1979).

from 10 trees in each of four provenances and from five trees of one provenance (Table 1). The seedlings were raised as 2+2 stock at AFES. One test of the 45 families was established in the spring of 1972 at AFES with 10 replicates of four-tree square plots at 1.8 x 1.8 m spacing. Total height, survival, and weevil damage were recorded in the fall of 1977 when the seedlings were 5 years from planting.

Analytic Procedures

For the Czechoslovakian progenies, analyses of variance for heights were performed using the model:

$$Y_{hijkl} = \mu + L_h + R_{hi} + P_j + F_{jk} + LP_{hj} + LF_{hjk} + e_{hijkl},$$

where

Y_{hijkl} = height of the l^{th} progeny of the k^{th} family from the j^{th} provenance grown in the i^{th} replicate of the h^{th} location,

μ = overall mean,

L_h = h^{th} location effect,

R_{hi} = l^{th} replicate effect within h^{th} location,

P_j = j^{th} provenance effect,

F_{jk} = k^{th} family effect within the j^{th} provenance,

LP_{hj} = interaction effect between the h^{th} location and the j^{th} provenance,

LF_{hjk} = interaction effect between the h^{th} location and jk^{th} family, and

e_{hijkl} = random error effect.

Data for 5 years at AFES and 6 years at Marydale are combined in this analysis. Approximate tests of significance from the least squares solutions were performed by comparing expected mean square coefficients.

Variance components due to provenances (σ^2_P), families (σ^2_F), interactions between locations and provenances (σ^2_{LP}) and families (σ^2_{LF}), and error (σ^2_e) were estimated. The variance component due to families was interpreted as one-quarter of additive genetic variance (σ^2_A). Thus, narrow sense heritabilities were estimated as follows:

$$h^2 = \frac{4\sigma^2_F}{\sigma^2_P + \sigma^2_F + \sigma^2_{LP} + \sigma^2_{LF} + \sigma^2_e}$$

Variance components as a percentage of total variance were calculated for each component to examine relative magnitude. The negative estimates of variance components were considered as zero, and were excluded from the calculations. In addition, correlations among observed characters in each location were computed.

Similarly, for the Bulgarian progenies, analyses of variance for 5-year height and survival were performed using the model:

$$Y_{ijkl} = \mu + R_i + P_j + F_{jk} + RP_{ij} + e_{ijk},$$

where

R_i = i^{th} replicate effect,

RP_{ij} = interaction effect between the i^{th} replicate and the j^{th} provenance,

and all the other terms are as defined previously. Heritabilities for each character were estimated as

$$h^2 = \frac{4\sigma^2_F}{\sigma^2_P + \sigma^2_F + \sigma^2_{RP} + \sigma^2_e}$$

where σ^2_{RP} is variance component due to replicates by provenances interactions. Simple linear correlation between height and survival was computed.

RESULTS

Czechoslovakian Progenies

Height, survival, and weevil damage by progeny are summarized in Table 2. Significant differences between locations were found for both 5- and 6-year and 10-year heights. Mean plantation height increased from 106 cm to 1.9 m over the 5-year period at AFES while the increase at the Marydale plantation was from 132 cm to 2.9 m in the 4-year period (Table 2). Mean family heights at age 5 ranged from 98 to 116 cm at AFES, while those at Marydale, at age 6, ranged from 113 to 151 cm. At 10 years, mean family height ranged from 1.7 to 2.2 m at AFES and from 2.5 to 3.4 m at Marydale. The differences between provenance means were not significant.

Overall survival 6 years from planting was slightly better at Marydale (93%) than at AFES (88%); however, there was little difference between the provenances within each location. Mean survival of families at AFES ranged from 78 to 95%, while those at Marydale ranged from 87 to 97%.

Damage by the white pine weevil was a problem only at AFES. Overall weevil damage at AFES was 6 and 8% at 5 and 10 years from planting, respectively. Differences among families in respect to weeviling were large, however, there was no significant relationship among families in percent weeviling at 5 and 10 years.

Analyses of variance indicated that the families-within-provenances and the location x

Table 2. Average performance of Czechoslovakian progenies

Seedlot number MS.	5 years from planting at AFES				6 years from planting at Marydale			10 years from planting at: AFES			Marydale			Combined	
	Survival (%)	Height (cm)	Rank	Weevil damage (%)	Survival (%)	Height (cm)	Rank	Height (m)	Rank	Weevil damage (%)	Height (m)	Rank	Weevil damage (%)	Height (m)	Rank
Hojna Voda Source															
988	85	99	17	0	95	144	2	1.8	15	14	3.4	1	0	2.6	3
989	88	110	5	2	93	119	19	1.9	12	2	2.6	19	0	2.2	17
990	89	112	3	8	91	151	1	2.2	1	12	3.3	2	4	2.7	1
991	78	109	6	5	96	142	3	2.0	6	6	3.2	4	0	2.6	3
992	85	109	6	5	93	132	10	2.0	6	16	2.8	13	0	2.4	12
993	88	100	15	13	94	120	18	1.7	18	18	2.8	13	0	2.2	17
994	82	107	8	12	96	131	13	1.9	12	4	2.8	13	4	2.3	16
995	92	104	12	9	95	131	13	1.8	15	4	3.0	7	0	2.4	12
996	89	103	14	11	93	132	10	2.0	6	16	3.0	7	2	2.5	9
997	92	114	2	9	97	134	7	2.0	6	3	3.0	7	0	2.6	3
Mean	87	107	–	7	94	134	–	1.9	–	10	3.0	–	.05	2.5	–
Rabstyn Source															
998	95	112	3	5	94	132	10	2.2	1	4	3.0	7	0	2.6	3
999	89	105	9	4	94	137	5	2.1	4	12	3.1	5	2	2.6	3
1000	88	104	12	4	92	133	9	1.9	12	4	2.8	13	0	2.5	9
1001	85	99	17	8	87	141	4	2.1	4	6	3.3	2	2	2.7	1
1002	86	105	9	8	95	128	15	2.0	6	4	2.9	11	0	2.4	12
1003	89	105	9	6	94	137	5	2.0	6	4	2.8	13	0	2.4	12
1004	95	116	1	4	92	121	17	2.2	1	3	2.9	11	2	2.6	3
1005	82	98	19	5	90	113	20	1.7	18	8	2.5	20	0	2.1	20
1006	84	98	19	7	88	122	16	1.7	18	4	2.7	18	0	2.2	17
1007	86	100	15	6	94	134	7	1.8	15	12	3.1	5	0	2.5	9
Mean	88	104	–	6	92	130	–	2.0	–	6	2.9	–	.04	2.5	–
Overall	88	106	–	6	93	132	–	1.9	–	8	2.9	–	.05	2.5	–

Table 3. Variances of heights derived from the Czechoslovakian progenies

Variance component for	Height at age 5-6[a]		Height at age 10	
	VC	VC%	VC	VC%
Provenance (P), σ^2_P	2.62	0.22	-0.003	0.0
Families in P (F), σ^2_F	12.32*	1.01	0.025*	4.49
Location x P, σ^2_{LP}	-4.92	0.0	-0.001	0.0
Location x F, σ^2_{LF}	30.10*	2.48	0.013*	2.33
Error, σ^2_e	1169.71	96.29	0.519	93.18
Total variances	1214.75	100.00	0.557	100.0
Heritabilities	0.04		0.18	

a/ Total heights measured at age 5 at AFES and at age 6 at Marydale and combined in the analysis.
* Significant at P = 0.05.

Table 4. Correlations among characters from the Czechoslovakian progenies

	Characters	1	2	3	4	5	6	7	8	9	10
1	Survival, AFES[a]	1	.49*	.01	.10	-.06	.45*	.04	.30	-.15	.05
2	5-year height, AFES		1	-.09	.38	.14	.72**	.05	.39	-.34	.23
3	Weevil damage (1975), AFES			1	.08	.08	-.11	-.08	-.18	.15	.33
4	Survival, N.S.[b]				1	.16	.02	.12	.10	.01	-.13
5	6-year height, N.S.					1	.47*	.86**	.80**	.19	.38
6	10-year height, AFES						1	.42	.74**	-.16	.49*
7	10-year height, N.S.							1	.86**	.28	.24
8	10-year height, combined location								1	.05	.30
9	Weevil damage (1980), AFES									1	.04
10	Weevil damage (1980), N.S.										1

a/ Acadia Forest Experiment Station, New Brunswick.
b/ Marydale, Nova Scotia.
* Significant at P = 0.05.
** Significant at P = 0.01.

family interactions were the significant sources of variation for both 5- and 6-year and 10-year heights. The variance for families increased from 1.01 to 4.49% in the 5-year period (Table 3). The magnitude of the location x family interactions variance did not change substantially during this period although it was even greater than family variance for 5 and 6-year height. Most of the variation, however, was due to genetic/environmental errors (σ^2_e) amounting to 96.29 and 93.18%, respectively. Heritability estimates for 5 and 6-year and 10-year heights were 0.04 and 0.18, respectively (Table 3).

Several significant correlations were obtained among the characters observed (Table 4). Heights at 5 or 6 years and at 10 years at each location were significantly correlated. Heights between the two locations at the same age were not correlated implying genotype x environment interactions. At AFES, survival was positively correlated with 5- and 10-year height.

Bulgarian progenies

Mean family height ranged from 54 to 85 cm with an overall mean of 68 cm (Table 5).

Table 5. Five-year height and survival of 45 open-pollinated families from five Bulgarian provenances

MS No.	Survival (%)	Height (cm)
Pouchtinaka Source		
1384	70	77
1385	83	74
1386	78	65
1387	88	58
1388	88	78
1389	75	80
1390	68	64
1391	89	69
1392	78	59
1393	85	77
Mean[a]	79	67
Bistritza Source		
1394	70	75
1395	83	67
1396	85	65
1397	85	71
1398	75	85
1399	78	78
1400	78	62
1401	56	63
1402	80	71
1403	69	63
Mean	77	68
Gvardeiska Source		
1404	80	65
1405	85	83
1406	88	55
1407	83	72
1408	85	76
Gvardeiska Source Continued		
1409	63	58
1410	75	79
1411	88	61
1412	36	71
1413	70	57
Mean	76	66
Lopouka Central Source		
1424	73	66
1425	70	69
1426	72	58
1427	68	65
1428	83	66
1429	80	73
1430	78	54
1431	83	69
1432	92	59
1433	63	59
Mean	76	63
Ardachla Central Source		
1434	65	75
1435	78	78
1436	88	77
1437	75	66
1438	75	54
Mean	74	70
Grand Mean		77

[a] Means by provenance from Fowler and Coles (1979).
Correlation coefficient between height and survival: r = 0.1.

Table 6. Variances of 5-year height and survival derived from Bulgarian progenies

Variance components for	Height VC	Height VC%	Survival VC	Survival VC%
Provenance (P), σ_P^2	-1.10	0.0	-0.0006	0.0
Families in P (F), σ_F^2	55.54*	11.26	0.0049*	7.98
Replicate x P, σ_{RP}^2	2.53	0.52	-0.0020	0.0
Error, σ_e^2	435.05	88.22	0.0565	92.02
Total variances	493.12	100.00	0.0614	100.00
Heritabilities	0.45		0.32	

* Significant at P=0.05.

Survival of trees varied from 36 to 92% with a grand mean of 77% (Table 5).

Significant differences between replicates and families were found for both 5-year height and survival (Table 6). Variance due to family differences (σ_F^2) was 11.37 and 8.5% of the total variance for height and survival, respectively. Variance due to provenances (σ_P^2) was negligible for both characters. Again, the largest components of variance were genetic/environmental errors which amounted to 88.7 and 91.50% of the total variance for height and survival, respectively. Narrow sense heritabilities were estimated as 0.45 for height and 0.32 for survival (Table 6). The correlation between height and survival was non-significant (r = 0.10).

DISCUSSION

Differences in height and survival among provenances from both Czechoslovakia and Bulgaria are not significant. On the other hand, family differences are an important source of variability, especially in the Bulgarian material. It follows that genetic variability within a limited geographical area may be due to individual tree rather than stand differences. Genetic/environmental error components of variance are the largest source of variability for all analyses. These components of variance include within-plot error variance and other possible interactions which the linear models did not define. If competition effects are absent, the within-plot error variance includes genetic variance among the members of the same progeny (Cockerham 1963). Although precise partitioning of genetic/environmental error variance into these components was not carried out, it appears that within-plot error variance was large. This is in agreement with results from many progeny tests of forest tree species, e.g., Hanover and Barnes (1967) and Kriebel et al. (1972). Relatively large genetic/environmental error variance, indicating a substantial amount of combined genetic and environmental effects on progeny, are less predictable than additive genetic effect and more difficult to utilize in a breeding program.

The large genotype x environment (GE) interactions within the Czechoslovakian progenies result in ranking changes of family means and a poor correlation between the two test plantations. It should be noted that this component of variance for 5- and 6-year height is confounded with family x year and family x location interactions. GE interactions are not uncommon in forest trees, especially when seed is moved far from its native environment. Large GE interactions, the magnitude of which can be as great as or greater than the genotype component in forest trees, have been reported from several provenance tests (Morgenstern and Teich 1969; and Squillace 1970). The pattern of GE interactions in this experiment results from changes in ranking of family means as well as from relative differences in performance of the families in different environments. The proportion of GE interactions component relative to family component was 2.5 at age 5 and 6, but decreased to 0.5 by age 10. When the GE interaction component reaches half or more of the genotype component of variance then GE interaction is likely to have a serious effect on gains from conventional selection and testing (Shelbourne 1972). It is therefore necessary to select families for specific environments, and heritability estimates should be applied only to the population and breeding zone from which the estimates were derived.

Heritability estimates are commonly used to predict genetic gains in tree breeding programs (Namkoong et al. 1966). Based on the above results, mass selection for height in the Bulgarian populations is expected to be effective whereas selection in the Czechoslovakian populations is not, although the heritability did increase between 5-6 years and 10 years. In fact, prediction of gain through selection is rather academic because of the general inaccessibility of the original populations for further selection.

Developing a breeding program for tree improvement in a planting zone or region is governed by many factors. Choice of species is an obvious one. The long-term suitability of Norway spruce in the Maritimes Region has not yet been established. In general, early height growth of Norway spruce is superior to native red (*Picea rubens* Sarg.) and white (*P. glauca* (Moench) Voss) spruces but inferior to black (*P. mariana* (Mill.) B.S.P.) spruce (Fowler and Coles 1979). There are, however, indications that volume growth may exceed that of all native spruces (Hawley and Lutz 1943; Ashman 1958; and MacArthur 1964). Survival of Norway spruce compares favorably to that of the native spruces.

Areas of "best" provenances of Norway spruce have been identified and recommendations made for their use in the Maritimes Region (Fowler 1979). One possible approach for the genetic improvement of Norway spruce in the Maritimes would be to use the many existing provenance trials as a source of materials which can be improved through selection. A total of 1243 provenances from 21 countries has been established in one or more of 17 test locations in the Maritimes Region since 1961. This approach has the advantage that; a) selection could be made in the Region where the trees are to be used; b) the selected trees would have attained at least some degree of maturity; and c) the selection would be under local political control. The major disadvantage is that the number of trees from the better provenances is limited and thus the intensity of selection would be low. Development of a breeding population from these selected parents should be the next step for improvement of the species.

CONCLUSIONS

Two sets of Norway spruce progeny tests involving 65 open-pollinated families were evaluated for early height growth and survival in an attempt to provide information on genetic variances and feasibility of selection.
The following conclusions were supported:

1. In general, progenies derived from Bulgarian provenances were genetically more variable in height than those from Czechoslovakian provenances. Variance due to family differences was an important component of height and survival for both sets of progenies. However, variances due to genetic/environmental errors provided the largest component indicating substantial genetic/environmental influences on individual trees. Provenance variation in a limited area was negligible.

2. The heritability estimate for 5 and 6-year height of Czechoslovakian progenies was low (0.04) which indicates that progress through early selection may be limited. The heritability estimate for 10-year height was moderate (0.18). Large heritability estimates were obtained for Bulgarian progenies, (0.45 for height and 0.32 for survival), indicating that selection would be effective.

3. For the set of Czechoslovakian progenies, the family x location interaction was more than twice the family component of variance at age 5-6 but the interaction was only half the family component at age 10. The GE interactions remain significant, and, therefore, breeders are cautioned to use genetic parameters of the populations in relation to a specific breeding zone for which the estimates were derived. Size and pattern of genotype x environment interactions involving Bulgarian progenies have yet to be used to provide realistic estimates of heritability.

4. Survival of Norway spruce was not correlated with height, except for Czechoslovakian progenies at AFES. Differential survival between two test locations for the Czechoslovakian families may indicate that Norway spruce is exacting in its site requirements.

5. A possible approach for the genetic improvement of Norway spruce in the Region would be to utilize the existing provenance plantations as a source of materials for future selection and breeding.

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