Ann. Rev. Plant Physiol. 7: 191–214 (1956). — Weetman, G. F.: Nitrogen relations in a black spruce (Picea mariana Mill.) stand subject to various fertilizer and soil treatments. Pulp and Paper Res. Inst. Canada. Woodl. Res. Index No. 129, 112 p. (1962). — White, P. A.: The computation of eigenvalues and eigenvectors of a matrix. J. Soc. Industr. Appl. Math. 6: 393—437 (1958). — Williamson, M. H.: An ecological survey of a Scottish herring fishery. Part IV: Changes in the plankton during the period 1949 to 1959. Bull. Mar. Ecol. 5: 208—229 (1961). — Withrow, R. B., (ed.): Photoperiodism and related phenomena in plants and animals. Am. Assoc. Adv. Sci. Pub. 55, 903 p. (1959). — Wright, J. W., and Bull, W. I.: Geographic variation in European black pine — two-year results. For. Sci. 8: 32—42 (1962). — Yeatman, C. W.: Geographie variation in jack pine (Pinus banksiana Lamb.) seedlings. Ph. D. thesis, Yale Univ., 231 p. (1966 a). — Yeatman, C. W.: Germinant size of jack pine in relation to seed size and geographic origin. In: U. S. For. Serv. Res. Paper NC-6: 28–36 (1966 b). — Youngberg, C. T.: Effect of soil fertility on the physical and chemical properties of tree seed. J. For. 50: 850–852 (1952).

Genetic Variation in Seedlings of Picea mariana (Mill.) BSP.

II. Variation Patterns

By E. K. Morgenstern1)

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Introduction

The genetic processes of mutation, recombination, migration, isolation and selection change the frequency of genes in natural populations and lead to the development of certain variation patterns. For each species this pattern is complex in origin but may be explained in a simplified manner by assuming that natural selection is the dominant genetic process. By making this assumption, the pattern can be related to environmental factors, and it is then possible to define the factors which are most important. This approach has been taken in Part I of this paper (Morgenstern 1969).

The combined effect of all genetic processes must be measured in a different manner. The expected subdivision of the species can be investigated by means of hierarchal sampling and analysis of variance. Thus the total variance can be divided into the components associated with populations (among regions), subpopulations (among stands within regions), half-sib families (among single-tree progenies within stands), and within half-sib families (among replications of the same single-tree progenies). The study was continued in this way and the results are given in the present paper.

Methods

Experiments

The four experiments carried out in this study dealt with germination and early development, survival and dry-matter production under drought conditions, and growth and phenology. Details of the experimental procedure were outlined elsewhere (Morgenstern 1966, 1969). Thirteen physiological and morphological characters are considered in this paper to test certain black spruce populations for the presence of a clinal or clinal and ecotypic variation pattern.

Criteria for Classification

Clinal variation (Huxley 1938) is defined as a gradation in measurable characters of organisms. It is thought that this type of variation may develop after an initial disruptive selection (Mather 1953) in the base population migrating from the centre of origin of a species, which is then followed by stabilizing selection and gene exchange among adjacent populations over the species range (Haldane 1948, Fisher 1950).

Ecotypic variation (Turesson 1922) is marked by an abrupt pattern change resulting from disruptive selection within populations where habitats are discontinuous and from stabilizing selection within subpopulations. Therefore, both clinal and ecotypic variation are similar in that they are forms of adaptive genetic variation, but they differ in the underlying evolutionary mechanisms. Thus their distinction is important (Stern 1964). Furthermore, it must be recognized that subpopulation differences may also arise in non-adaptive fashion by migration from different refugia (Bouvarel 1959), random drift in small populations (Wright and Bull 1963), and inbreeding (Mayr 1963).

The variation pattern found in this study will be classified in the following manner: If the population component of variance is larger than the subpopulation and family component, variation will be considered clinal. If the subpopulation component is larger than the population and family component, variation will be considered ecotypic regardless of the genetic processes involved. Direct comparisons of the variance components can also be made provided that a similar sampling system has been used (Stern 1964, Squillace 1966).

Statistical Analysis

The statistical analysis was based upon the model

$$Y_{ijkl} = \mu + p_i + s_{ij} + f_{ijk} + w_{ijkl}$$

where Y_{ijkl} represents the plot mean of a particular character measured in replication 1 of the k-th family in the j-th subpopulation and the i-th population; μ the overall mean of the experiment; p_i, s_{ij}, and f_{ijk} the effects of the i-th population, j-th subpopulation in population i, and k-th half-sib family in the j-th subpopulation of population i, respectively; and w_{ijkl} the within-family deviation including error and the effect of replication 1. Although randomized block and modified lattice square designs were used in the physical layout of experiments, the preceding model assumes a completely randomized structure. This simplified the presentation of results and the calculation of mean square coefficients, without resulting in large disadvantages. All experimental units were considered ran-

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1) Research Scientist, Department of Fisheries and Forestry, Petawawa Forest Experiment Station, Chalk River, Ontasio, Canada. Second paper based upon a dissertation for the degree of Dr. rer. nat. submitted in 1966 to the Mathematisch-Naturwissenschaftliche Fakultät, Universität Hamburg, Germany. The larger part of the experimental work was performed at Institut für Forstgenetik und Forstpflanzenzüchtung, Bundesforschungsanstalt für Forst- und Holzwirtschaft, Schmalenbeck, Germany.

Table II-1. — Degrees of freedom (DF) and expected mean squares (EMS) in the analyses of variance.

Source of Variation	DF	Experiment No. 1 EMS	DF	Experiment No. 2 and 3 EMS	DF	Experiment No. 4 EMS
Populations	8	$\delta^2_w + 6\,\delta^2_f + 23.20\,\delta^2_s + 70.13\,\delta^2_p$	1	$\delta^2_w + 4\,\delta^2_f + 17.16\,\delta^2_s + 71.35\,\delta^2_p$	8	$\delta^2_w + 4\,\delta^2_f + 21.36\,\delta^2_s + 50.36\,\delta^2_p$
Subpopulation in populations	15	$\delta^2_w + 6\,\delta^2_f + 32.55\,\delta^2_s$	8	$\delta^2_w + 4\,\delta^2_f + 14.12\,\delta^2_s$	14	$\delta^2_w + 4\,\delta^2_f + 20.82\,\delta^2_s$
Half-sib families in subpopulations	94	$\delta^2_w + 6\,\delta^2_f$	27	$\delta^2_w + 4\,\delta^2_f$	98	$\delta^2_w + 4\,\delta^2_f$
Within half-sib families	590	δ^2_w	111	δ^2_w	363	δ^2_w

dom samples from an infinitely large population, thus corresponding to Model II (Snedecor 1956).

The degrees of freedom and expected mean squares of the analysis for all four experiments are given in *Table II-1*. The numbers of subpopulations and families sampled in each population were unequal and therefore coefficients of the mean squares in the column EMS were computed as shown by Anderson and Bancroft (1952). By setting calculated mean squares equal to the expected mean squares, variance components were derived. These components made possible a direct estimate of variation at each level of sampling, and were also used to express the proportion of any level in total variance by means of genetic intraclass correlations (Kempthorne 1957). Variance components are independent of the normal distribution (Steel and Torrie 1960) and freely applicable in the present study.

The utility of significance tests was more limited. They are subject to a number of restrictive assumptions, i. e. normal distribution of errors at each level of sampling, homogeneous variance, and equal coefficients of the mean squares (Snedecor 1956). Not all of these requirements could be met and, therefore, the significance tests made were considered approximations.

Results and Discussions

Variation of Individual Characters

General information on ranges, means, standard deviations and coefficients of variation is summarized in *Table II-2*. The results of the analysis of variance are given in *Table II-3*. The variation of individual characters at the four levels of sampling differed greatly in significance and contribution to total variance. By referring back to the principal component analysis given in *Part I* of this paper (Morgenstern 1969, *Tables I-3, I-5, I-7, I-9)*, these results can now be more fully explained and understood.

Germination rate. — Variation in germination rate was largest among families which accounted for 27.5 percent of total variance, smaller among subpopulations accounting for 15.3 percent, and smallest among populations with 10.8 percent. Significant differences were only associated with families and subpopulations. The subpopulation differences were related to soil moisture regime of the place of seed origin *(Table I-3)* which in turn probably influenced nitrogen availability and seed nutrition. Seed nutrition appeared to have been more favourable on dry and fresh sites than on moist and wet sites. Much of the variance among subpopulations may therefore be environmental in origin. But the variation among families will be genetic to a greater extent because of reduced site variation within the area occupied by the single trees of a subpopulation. A similar situation was described by Greathouse (1966) who showed that in *Pseudotsuga menziesii* germination rate differed significantly even when the mother trees were growing on relatively uniform sites in seed orchards. Similarly, Schell (1960) found a consistent germination rate in seed collected from individual *Picea abies* trees in different years, which appeared to depend upon thickness of the seed coat, but there was no correlation of rapid germination with fast growth up to age 20. It is conceivable that both rapid and slow germination possess selective value in different ecological situations, and that such contrasting qualities are maintained in a population by opposing selective forces, thus leading to polymorphisms (Ford 1964).

Germination percent. — Variation was largest among families which accounted for 50.7 percent of total variance; it was much smaller and not significant at the level of subpopulations and populations which contributed 5.4 and 0 percent, respectively. Germination percent was best related to vigour *(Table I-3)* and, as such, similar to germination rate. However, the correlation with soil moisture regime was weaker which may explain the non-significance of subpopulation differences. Because of the measures

Table II-2. — Ranges, means, standard deviations, and coefficients of variation for thirteen characters rated in four experiments.

Exp. No.	Character	No. of families	Unit	Range[1]	Mean[2]	Standard deviation	Coefficient of variation
1	Germination rate	118	Rate index[3]	.111—.761	.439	.081	18.4
1	Germination percent	118	Percent[4]	8.13—90.00	53.68	12.13	22.6
1	Survival percent	118	Percent[4]	20.70—90.00	62.54	7.80	12.5
1	Cotyledon number	118	Number	3.6—5.7	4.24	.30	7.1
1	Hypocotyl length	118	mm	3.5—12.5	8.27	1.26	15.2
1	10-months height	118	cm	6.8—19.9	14.28	1.41	9.9
2	Survival index	37	Rate index[3]	.255—.641	.458	.052	11.4
3	Total dry weight	37	mg	.0111—.0387	.0225	.0046	20.4
4	Prolepsis, year 1	121	Percent[4]	5.74—31.95	8.81	3.92	44.4
4	Growth cessation, year 1	121	Days[5]	239—311	278	14.0	5.0
4	Growth initiation, year 2	121	Days[5]	111—134	121	3.6	3.0
4	Growth cessation, year 2	121	Days[5]	203—309	278	18.7	6.7
4	Total height, year 2	121	cm	2.2—19.0	11.31	2.82	24.9

[1] Based on plot means.
[2] General mean of the experiment.
[3] Sum of seedlings per plot counted every second day, divided by the product of number of counts times the largest number observed (Bartlett 1937).
[4] Arcsin transformation (Snedecor 1956).
[5] Days of the year, e. g. Day 239 is August 27, 1964.

Table II-3. — Mean squares (MS)[1] and percentages of total variance (V%)[2] based upon variance components. (1) and (2) refer to figures based upon measurements of 1- and 2-year-old seedlings, respectively. Variance components are given in *Table II-4.*

Experiment and Character	Source of Variation							
	Populations		Subpopulation		Families		Within Families	
	MS	V%	MS	V%	MS	V%	MS	V%
Exp. No. 1								
Germination rate	151666	10.8	81433***	15.3	24199***	27.5	5311	46.4
Germination percent	1229.9	0	1360.9	5.4	901.7***	50.7	113.7	43.9
Survival percent	969.3	2.4	696.8*	5.1	322.3***	10.0	186.4	82.5
Cotyledon number	3.4192**	30.6	.7819***	12.6	.2484***	27.0	.0387	29.8
Hypocotyl length	6208**	25.7	1373**	8.8	543***	25.4	114	40.1
10-months height	2380	1.0	1998	2.2	1426***	15.6	663	81.2
Exp. No. 2								
Survival index	10719	0	18368	12.2	8965***	25.4	3407	62.4
Exp. No. 3								
Total dry weight	24342	5.8	8179	0	8464***	41.7	2024	52.5
Exp. No. 4								
Prolepsis (1)	325.43*	14.3	113.18***	13.2	33.09***	13.6	17.22	58.9
Growth cessation (1)	11095***	83.6	78	0.4	53*	1.4	38	14.6
Growth initiation (2)	598***	60.6	27**	4.2	11***	7.6	5	27.6
Growth cessation (2)	20402***	90.0	94	0.4	53*	0.7	40	8.9
Total height (2)	39216***	62.2	585	0	625**	4.3	412	33.5

[1] Significance levels: * 5 percent, ** 1 percent, *** .1 percent.
[2] If variance component negative, V% listed as 0.

taken to improve seed uniformity by collection, extraction, empty-seed removal by alcohol flotation, cold-moist treatment and fungicide application, much of the remaining variation must have been caused by damage prior to collection, such as by insects, or by differences in embryo development. Andersson (1965) has shown that embryo development in *Picea abies* differs among populations as a result of summer temperatures. But Simak and Gustafsson (1954) found that in *Pinus silvestris* the relative frequency of embryo types changes little when seed develops on mother trees and their grafts in different climatic regions, indicating that genetic factors were involved. Orr-Ewing (1957) has shown that in *Pseudotsuga menziesii* embryo development is inhibited by inbreeding. Similar situations may exist in *Picea mariana.*

Survival percent. — The largest part of the variation, i. e. 82.5 percent, was contributed by the within-family component, indicating that error and replication effects were most important. In this case the replication effect dominated and was clearly observed when the germinant seedlings were attacked by damping-off fungi during a period of warm, humid weather. The second largest component of variance (10.0 percent) was contributed by families; this was followed by subpopulations (5.1 percent) and populations (2.4 percent). The importance of family differences is in agreement with the earlier analysis *(Table I-3)*, showing that survival percent was most closely related to vigour

Although vigour was weakly related to soil moisture, and could conceivably differ with age and environment of the parent tree (Busse 1931), the role of non-adaptive, genetic factors, such as inbreeding (Righter 1945, Dieckert 1964) must again be considered.

Cotyledon number and hypocotyl length. — There was large and significant variation at all three levels, populations contributing most of it (30.6 and 25.7 percent). Next was the variation among families which accounted for 27.0 and 25.4 percent. Subpopulations came last, with 12.6 and 8.8 percent, respectively. The results agree in general with the earlier analysis where the relationship to latitude and seed weight was demonstrated *(Table I-3).* In spite of indications that in some species the heritability of seed weight is low, e. g. in *Pinus resinosa* (Fowler 1964), it is not possible to conclude that cotyledon number and hypocotyl length, being closely related to seed weight, are also weakly inherited. Studies in *Pseudotsuga menziesii* show that the narrow-sense heritability of cotyledon number was .53 when seed weight was nearly equal (Sorensen 1966) and .42 when calculated on the basis of the pollen parent (Sziklai 1966). Heritability estimates of cotyledon number and hypocotyl length based on this study would not be reliable and should better be made from seed grown in a common environment.

Ten-months height. — Within-family variation dominated with 81.2 percent of the total. The family variation with 15.6 percent was the only remaining group that was large and significant. Initial germination percent determining differences in spacing and competition was the underlying factor *(Table I-3).* Thus a great deal of variation was introduced by the test environment and this submerged most genetic differences.

Survival index and total dry weight. — The variation within families accounted for 62.4 and 52.5 percent of the total, but the variation among families (25.4 and 41.7 percent) was significant as well. Although seed size, root size and soil moisture of origin were contributing factors, plant size, an expression of vigour and growth rate, was most important *(Tables I-5, I-7).* Therefore, both the concentration of differences at the family level and the correlation with vigour tend to indicate that neither adaptation to soil moisture regime nor preconditioning of the seed may have been very important. Inbreeding is again one of the possible explanations, another one being a differentiation in growth rate caused by differences in phasic development (Weck 1954, Stern 1960).

Prolepsis. — Much of the variation (58.9 percent) was contributed by the within-family component, implying that the environmental proportion of variance was large. Schmidt-Vogt (1964), likewise, found that in *Picea abies* provenances grown in the nursery, prolepsis may be easily modified by soil factors. On the other hand, significant portions of the variation in this study were also associated with populations (14.3 percent), families (13.6 percent), and subpopulations (13.2 percent). Seed weight and day length at the place of origin were the most important related variables *(Table I-9).* The regional pattern of variation, indicated by the population component, is in agreement with Rudolph (1964) who showed that prolepsis is more frequent in *Pinus banksiana* sources from southern latitudes, and with Hoffmann (1965) who demonstrated higher frequencies in *Picea abies* provenances from lower elevations. Probably such differences among populations are adaptive and indicate the effect of natural selection by climate upon this character.

Growth initiation. — Variation was largest among populations, which accounted for 60.6 percent of total variance, followed by families (7.6 percent) and subpopulations (4.2 percent). Spring temperature at the place of seed origin was the most important single variable explaining the population differences *(Table I-9).* Soil moisture regime, which depended primarily upon topographic position and therefore was associated with local climate, was correlated at the 5-percent significance level with growth initiation *(Table I-8),* but this effect, actually caused by the correlation of soil moisture regime and latitude, diminished when soil moisture was extracted as an independent factor in principal component analysis *(Table I-9).* It is clear, therefore, that variation at the subpopulation level is not important. Variation at the family level could reflect a polymorphic state. Conceivably, the variability of individual trees within a stand is beneficial to the species in an environment which is heterogeneous in time, i. e. would assist regeneration during different stages of stand development in the open and in shade (Stern 1964). Early and late flushing individuals have long been described in the genus *Picea* (Rubner 1960) and the high heritability of flushing time has been demonstrated (Nienstaedt 1963, Langner and Stern 1964).

Growth cessation, first and second year. — Populations accounted for 83.6 and 90.0 percent, subpopulations for 0.4 percent in both years, and families for 1.4 and 0.7 percent of total variance, respectively. Day length of the native habitat was the primary factor controlling this response, and temperature a secondary one *(Table I-9).* The within-family variance was small (14.6 and 8.9 percent), showing that error and replication effects were unimportant. Growth cessation, more than any other response investigated, is an adaptive character for which a high heritability may be expected.

Total height. — Much of the variation was associated with populations (62.2 percent) and a much smaller portion (4.3 percent) with families. The within-family variation, with 33.5 percent, was also relatively large. Day length and temperature of the place of origin, determining primarily the duration of growth, were the principal underlying factors *(Table I-9),* but the sizable within-family component and direct observations indicate that soil variation in the experiment also played a role. The portion of genetic variance will therefore be lower than for growth cessation.

Variation Patterns

When the variation of individual characters at each level of sampling is expressed as a proportion of total variance excluding within-family variance components, genetic intraclass correlations are obtained *(Table II-4).* These intraclass correlations show certain regularities associated with developmental stages. During germination and early development in the greenhouse under normal and drought conditions, the column-average of 8 characters measured in the first three experiments is largest for families, V(F), which account for 65 percent of total variance. The prevalence of family differences reflects the dominant role played by individual trees in seed development and in subsequent progeny vigour. During growth in the nursery, measured by total height and 4 phenological characters in the fourth experiment, the population variance, V(P), is leading with an average of 82 percent. This reflects the primary importance of geographic origin in further plant development. A similar dominance of family differences in germination

Table II-4. — Components of variance and genetic intraclass correlations. The first three genetic intraclass correlations have been combined into two groups (Group 1: Exp. No. 1, 2, 3; Group 2: Exp. No. 4) and averaged to obtain one approximate figure for each of the two developmental stages considered.

Experiment and Character	Components of Variance			Genetic Intraclass Correlations (Percent)			
	Populations V(P)	Subpopulation V(S)	Families V(F)	$\frac{V(P)}{V(P) + V(S) + V(F)}$	$\frac{V(S)}{V(P) + V(S) + V(F)}$	$\frac{V(F)}{V(P) + V(S) + V(F)}$	$\frac{V(S)}{V(S) + V(F)}$
Exp. No. 1							
Germination rate	1236	1758	3148	20	29	51	36
Germination percent	.01	14.11	131.34	0	10	90	10
Survival percent	5.42	11.51	22.64	14	29	57	34
Cotyledon number	.0398	.0164	.0350	44	18	38	32
Hypocotyl length	73	25	72	43	15	42	26
10-months height	8	18	127	5	12	83	12
Exp. No. 2							
Survival index	0	666	1389	0	32	68	32
Exp. No. 3							
Total dry weight	223	0	1610	12	0	88	0
				138/8 = 17	145/8 = 18	517/8 = 65	
Exp. No. 4							
Prolepsis (1)	4.17	3.85	3.97	35	32	33	49
Growth cessation (1)	218.77	1.20	3.63	97	1	2	25
Growth initiation (2)	11.33	.78	1.42	84	6	10	35
Growth cessation (2)	403.23	1.97	3.30	98	1	1	37
Total height (2)	766	0	53	94	0	6	0
				408/5 = 82	40/5 = 8	52/5 = 10	

was found in *Pinus elliottii* by Squillace (1966) and of population differences in phenological characters of *Betula japonica* and *B. maximowicziana* by Stern (1964).

On the basis of these results conclusions can now be drawn regarding the variation pattern of black spruce. The first hypothesis to be tested is that variation is clinal in response to selection by continuous ecological factors such as day length and regional temperatures, while the second is that genetic variation is not only clinal but also ecotypic in consequence of discrete factors such as local climate and soil moisture regime.

The hypothesis of clinal variation is supported by much evidence in this study. The proportion of population variance was largest for cotyledon number, hypocotyl length, prolepsis, initiation and cessation of growth and total height (*Table II-4*). Because it exceeded both the subpopulation and family variance, the variation of these characters is clinal as defined earlier in this paper.

In contrast, there is little evidence for ecotypic variation. The proportion of subpopulation variance exceeded that of populations for germination rate, survival percent and survival index, but it was smaller than that of families. As a result none of the characters exhibited ecotypic variation on the basis of the criteria adopted for this study. This is in agreement with Fowler (1966) who found no evidence of ecotypic variation in Ontario black spruce in a greenhouse experiment.

In evaluating these results, the following limitations of this study must be considered: The pattern found is not independent of sampling. It depends upon the number of regions included, and with many regions and high temperature gradients, the population component of variance will be large. Similarly, the concentration of subpopulation samples within a 20-kilometer radius imposes restrictions upon sampling of soils moisture regimes and local climates. Furthermore, sampling should take account of yearly fluctuations in flowering and seed crops (Sarvas 1962). Another problem is that the pattern found depends upon the characters selected, the age of testing (Wilusz 1966), the genotype × environment interactions and error involved. No doubt verification is required by additional experimentation with this little-known species.

In spite of these limitations, many of the results are consistent with ecological observations and population genetic theory. Most subpopulations included in this study were not isolated but were found in a continuous series from wet through moist and fresh to moderately dry sites. Yet isolation is an important condition required to accumulate gene differences (Ford 1964). In the large populations sampled in the central part of the species range, selection must be expected to operate for general performance in all niches (Carson 1959), particularly in a fluctuating environment (Baker 1964, Bradshaw 1964). The boreal environment of black spruce is fluctuating as a result of past glaciation and migrations, present manipulation of water levels by beaver, and the change of moisture, temperature and light following forest fires and succession. It is therefore possible that black spruce is more generally adapted to the more regular temperature and light cycles of its major regions, but less specialized for the fluctuating conditions of local habitats.

Applications

Aside from theoretical questions, the results of this study are applicable in regeneration, seed control, and a breeding and selection program.

Regeneration could take advantage of the differentiation in early vigour associated with half-sib families and subpopulations. Because germination rate, germination percent, and survival percent of germinant seedlings increased with seed weight and were slightly higher in progenies originating on fresh and moderately dry sites, seed collection could take advantage of these differences regardless of the heritability of these characters. Germination rate appears to be a juvenile character not related to rapid growth at later stages (Schell 1960), but the differences found may ensure survival during the first year when available moisture is most critical (Place 1955, Eis 1965).

Seed control is a related problem. The clinal pattern of variation, particularly in phenological characters, could be best met by a continuous system of seed control, permitting transfer for a specified maximum distance north or south from the place of origin, such as devised by Prof. O. Langlet for Sweden (Lindquist 1951). But the regional system now used in Ontario, based on Hills (1955), may be more practical, without resulting in large disadvantages. Most of Hill's regions encompass about two to three degrees of latitude, i. e. a distance which seed could be moved at equal elevation according to Vincent (1965). Nevertheless, mainly because of differences in temperature gradients, Vincent's European results are not necessarily applicable everywhere in North America, and more specific experiments are required.

The experimental results indicated possibilities for the planting of provenances north of their region of origin in order to prolong their growth period. In the nursery experiment at Schmalenbeck, provenances from 60° N grew for about 3 months while those from 43° N grew for 6 months. These southern sources were frost hardy, and exceeded the growth of most *Picea abies* provenances of equal age from a large collection raised in the same nursery. Areas with mild fall temperatures would favour this approach.

In a breeding program the prevailing pattern of clinal variation could be utilized for interprovenance hybridization. By crossing individuals of a northern with those of a southern population, frost hardiness and fast growth might be combined (Nilsson 1964). This should be easiest if individuals from moderately distant populations are crossed to decrease problems resulting from coadaptation and epistasis (Stern 1964).

For the planning of a selection program, the intraclass correlations given in *Table II-4* could serve as a basis. Selection for attributes related to germination should be practiced primarily at the family-level, although environmental influences, affecting seed nutrition, are also involved. Selection for phenological attributes should generally be carried out at the population level where 84 to 94 percent of total variance is concentrated. If only one population or region is available, selection at the level of subpopulations or stands is also promising. This is seen in the last row figures in *Table II-4*, giving the subpopulation variance, V(S), as a percentage of the total variance, V(S) + V(F). The variance available for selection would then range from 0 to 49 percent. Furthermore, it is realized that if the half-sib-family variance is additive variance and free of inbreeding effects, the figures should be multiplied by 4 since only ¼ of the additive genetic variance is recovered in a half-sib progeny test (Falconer 1960, Namkoong 1966). Selection among single trees is therefore again more promising than indicated by these figures. Giving due weight to the limitations of this study, particularly the manner of sampling and testing, different alternatives in a selection program may be considered.

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Summary

1. The degree of subdivision was investigated in thirteen characters. Analysis of variance was employed and variance components were calculated for populations (among regions), subpopulations (among stands within regions), half-sib families (among single-tree progenies within stands), and within half-sib families (among replications). The genetic intraclass correlations, derived from variance components, were used to interpret the variation pattern.

2. For 6 characters related to germination and drought resistance, the family variance, expressed as a percentage of the total, was largest; for 7 mainly phenological and morphological characters the population variance was largest; the variance of subpopulations was small and never exceeded both the family and population variance. On the basis of the criteria adopted for this study, variation is therefore essentially clinal.

3. Applications were discussed. The large population variance is important for seed control, the introduction of southern sources, and interprovenance hybridization. The small subpopulation variance carries much weight only if selection is restricted to one region. The family variance could be utilized particularly to increase germination percent, survival, and drought resistance at early stages.

Résumé

Titre de l'article: *Variation génétique des semis de Picea mariana. II. Modes de la variation.*

1. Le degré de subdivision fut étudié par treize caractères. L'analyse de variance et les composantes de la variance ont été calculées pour les populations (entre les régions); les sous-populations (entre les peuplements à l'intérieur des régions); les familles de descendance uniparentale (entre les descendances des individus à l'intérieur des peuplements); et entre les familles de descendance uniparentale (parmi les répétitions).

Les relations génétiques intraclasses provenant des composantes de la variance furent employées dans l'interprétation du mode de la variation.

2. La variance de la famille, exprimée en tant que pourcentage de l'ensemble fut la plus grande pour 6 caractères se rapportant à la germination et à la résistance à la sécheresse, tandis que la variance de la population fut la plus grande pour 7 caractères surtout phénologiques et morphologiques. La variance des sous-populations fut petite et ne dépassa jamais la variance de la famille ou de la population. Ainsi, suivant les critères utilisés pour cette étude, il s'ensuit que la variation est essentiellement clinale.

3. On peut dès lors établir des conclusions d'ordre pratique: l'amplitude de la variance de la population souligne l'importance d'un contrôle des semences, de l'introduction de sources sudistes, et d'un hybridation entre les provenances. La variance inférieure de la sous-population peut revêtir une plus grande importance à condition que la sélection soit restreinte à une région. Finalement, la variance de la famille peut être utilisée principalement dans le but d'augmenter le pourcentage de germination, de survivance et de résistance à la sécheresse durant les premiers stades de développement.

Literature Cited

Andersson, E.: Cone and seed studies in Norway spruce (*Picea abies* [L.] Karst.). Studia Forestalia Suecica 23, 214 p. + App. (1965). — Anderson, R. L., and Bancroft, T. A.: Statistical theory in research. McGraw-Hill, New York, 399 p. (1952). — Baker, H. G.: Hybridization in the evolution of weeds. Tenth Intern. Bot. Congr., Edinburgh 1964. Abstr. Nr. 305, p. 134 (1964). — Bouvarel, P.: Race ou variation clinale. Rev. For. Franç. 1959: 463—464. — Bradshaw, A. D.: Inter-relationship of genotype and phenotype in a varying environment. Scott. Plant Breedg. St. Rec. for 1964: 117—125 (1964). — Busse, J.: Einfluß des Alters der Mutterkiefern auf ihre Nachkommenschaft. Mitt. Deutsch. Dendrol. Ges. 43: 61—74 (1931). — Carson, H. L.: Genetic conditions which promote or retard the formation of species. *In:* Cold Spring Harbor Symp. Quant. Biol. 24: 87—105 (1959). — Dieckert, H.: Einige Untersuchungen zur Selbststerilität und Inzucht bei Fichte und Lärche. Silvae Genet. 13: 77—86 (1964). — Eis, S.: Development of white spruce and alpine fir seedlings on cut-over areas in the central Interior of British Columbia. For. Chron. 41: 419—431 (1965). — Falconer, D. A.: Introduction to quantitative genetics. Oliver and Boyd, Edinburgh, 365 p. (1960). — Fisher, R. A.: Gene frequencies in a cline determined by selection and diffusion. Biometrics 6: 353—361 (1950). — Ford, E. B.: Ecological genetics. Wiley, New York, 335 p. (1964). — Fowler, D. P.: Effects of inbreeding in red pine, *Pinus resinosa* Ait. I. Introduction, Natural Variation. Silvae Genet. 13: 170—177 (1964). — Fowler, D. P.: Pine and spruce breeding at the Southern Research Station, Maple, Ontario. Proc. Tenth. Meetg. Comm. For. Tree Breedg. Canada, Vancouver, 1966, Part II: 37—45 (1966). — Greathouse, T. E.: Inheritance of germinative energy and germinative capacity in Douglas-fir. *In:* U. S. For. Serv. Res. Paper NC-6: 60—62 (1966). — Haldane, J. B. S.: The theory of a cline. J. Genetics 48: 277—284 (1948). — Hills, G. A.: Field methods for investigating site. Ontario Dept. of Lands and Forests, Site Res. Manual No. 4, 120 p. (1955). — Hoffmann, K.: Bedeutung des Augusttriebes für den Fichtenanbau im Pleistozän der DDR. Soz. Forstwirtsch. 5: 204—207 (1965). — Huxley, J.: Clines: an auxiliary taxonomic principle. Nature 142: 219—220 (1938). — Kempthorne, O.: An introduction to genetic statistics. Wiley, New York, 545 p. (1957). — Langner, W., and Stern, K.: Untersuchungen über den Austriebstermin von Fichten und dessen Beziehungen zu anderen Merkmalen. Allg. Forst- u. Jagdztg. 135: 53—60 (1964). — Lindquist, B.: Forstgenetik in der schwedischen Waldbaupraxis. Übers. v. J. Räder-Roitzsch u. I. Pein. Neumann, Radebeul, 167 p. (1951). — Mather, K.: The genetical structure of populations. Symp. Soc. Exp. Biol. 7: 66—95 (1953). — Mayr, E.: Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass. 797 p. (1963). — Morgenstern, E. K.: Genetische Variation von *Picea mariana* (Mill.) B. S. P. Dissertation, Math.-Naturw. Fak. Univ. Hamburg, 77 p. (1966). — Morgenstern, E. K.: Genetic variation in seedlings of *Picea mariana* (Mill.) BSP. I. Correlation with ecological factors. Silvae Genetica 18: 151—161 (1969). — Namkoong, G.: Inbreeding effects on estimation of genetic additive variance. For. Sci. 12: 8—13 (1966). — Nienstaedt, H.: Late flushing white spruce clones show less spring frost injury. *In:* Annual Report. Lake States For. Exp. Sta., For. Serv., U. S. Dept. of Agriculture, p. 5 (1963). — Nilsson, B.: Studier av avkommor efter korsning mellan gran av svensk och mellaneuropeisk proveniens. *In:* Föreningen Skogsträdsförädling Årsbok 1963, p. 1—23 (1964). — Orr-Ewing, A. L.: A cytological study of the effects of self-pollination on *Pseudotsuga menziesii* (Mirb.) Franco. Silvae Genet. 6: 179—185 (1957). — Place, I. C. M.: The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canada Dept. North. Aff. and Nat. Resources, For. Br. Bull. 117. 87 p. (1955). — Righter, F. I.: *Pinus:* the relationship of seed size and seedling size to inherent vigour. J. For. 43: 131—137 (1945). — Rubner, K.: Die pflanzengeographischen Grundlagen des Waldbaues. 5th ed. Neumann, Radebeul, 620 p. (1960). — Rudolph, T. D.: Lammas growth and prolepsis in jack pine in the Lake States. For. Sci. Monograph 6, 70 p. (1964). — Sarvas, R.: Investigations on the flowering and seed crop of *Pinus silvestris.* Comm. Inst. Forest. Fenniae 53 (4): 1—198 (1962). — Schell, G.: Keimschnelligkeit als Erbeigenschaft. Silvae Genet. 9: 48—53 (1960). — Schmidt-Vogt, H., (ed.): Forstsamengewinnung und Pflanzenanzucht für das Hochgebirge. BLV Verlagsgesellschaft, München, 248 p. (1964). — Simak, M., and Gustafsson, Å.: Fröbeskaffenheten hos moderträd och ympar av tall. Meddel. f. Statens Skogsforskningsinst. 44 (2): 1—83 (1954). — Snedecor, G. W.: Statistical methods. 5th ed. Iowa State College Press, Ames, Iowa, 534 p. (1956). — Sorensen, F.: Inheritance of cytoledon number in Douglas fir. For. Sci. 12: 175—176 (1966). — Squillace, A. E.: Geographic variation in slash pine. For. Sci. Monograph 10, 65 p. (1966). — Steel, R. G. D., and Torrie, J. H.: Principles and procedure of statistics. McGraw-Hill, New York, 481 p. (1960). — Stern, K.: Plusbäume und Samenplantagen. Sauerländer's Verlag, Frankfurt a. M., 116 p. (1960). — Stern, K.: Herkunftsversuche für Zwecke der Forstpflanzenzüchtung, erläutert am Beispiel zweier Modellversuche. Züchter 34: 181—219 (1964). — Sziklai, O.: Variation and inheritance of some physiological and morphological traits in Douglas-fir. *In:* U. S. For. Serv. Res. Paper NC-6: 62—67 (1966). — Turesson, G.: The species and the variety as ecological units. Hereditas 3: 100—113 (1922). — Vincent, G.: Zertifizierung von Forstsaatgut und seine standortsgemäße Übertragung. 14th Intern. Seed Testing Congr., Munich 1965. Preprint 12, 7 p. (1965). — Weck, J.: Forstliche Zuwachs- und Ertragskunde. 2nd ed. Neumann, Radebeul, 160 p. (1954). — Wilusz, W.: The influence of stand age on the quality of 50-year old *Pinus silvestris* progeny. Arboretum Kornickie (Kornik, Poland) 11: 259—266 (1966). — Wright, J. W., and Bull, W. I.: Geographic variation in Scotch pine. Results of a 3-year Michigan study. Silvae Genet. 12: 1—25 (1963).

Unterscheidung von Pappelklonen

I. Die Variation einzelner Merkmale

Von Hans H. Hattemer*)

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Allgemeines

Vorbemerkungen

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*) Institut für Forstgenetik und Forstpflanzenzüchtung in Schmalenbeck der Bundesforschungsanstalt für Forst- und Holzwirtschaft sowie Lehrstuhl für Forstgenetik und Forstpflanzenzüchtung der Forstlichen Fakultät der Universität Göttingen in Hann. Münden.