Genetics of Cone Morphology of Black Spruce [Picea mariana (Mill). B. S. P.] in Newfoundland, Canada

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Summary

The paper presents the results of a study conducted to determine the relative role of genotypic and environmental control over characters of cone morphology and seed weight in black spruce *(Picea mariana* (Mill.) B.S.P.) A three-stage cluster sampling scheme was adopted with the sampling stages of populations, trees within populations and cones within trees. Nine characters of cone morphology were measured on each cone and mean 1 000-seed weight was determined for each tree.

Statistical analyses comprised (1) calculation of population means and standard deviations for each character, (2) cone length-cone diameter correlations at the populations and tree levels, (3) hierarchical analyses of variance and (4) comparison of the cone length-cone diameter correlations with similar values obtained six years earlier. Genetic analyses consisted of (1) calculation of repeatability with standard error and confidence limits for each character at the population level as estimates of heritability; and (2) multiple regression analysis for each character. The latter was conducted using the stepwise zig-zag procedure with cone character as the dependent variable and 12 environmental factors together with their squares and first order interactions as independent variables to identify the subset which contributes most to the variation in the character.

Though the means and repeatabilities of all characters vary with populations, no geographic trends can be discerned. Repeatability values have been shown to be good estimates of heritability. All characters are under statistically significant genotypic as well as environmental control and the most important subset of the latter has been identified. Cone length, diameter, and oven dry weight as well as dimensions of the middle scale are under strong, and length and width of the base and tip scale, under weak genotypic control. The earlier indications of pleiotropic control over cone length and diameter is supported. Seed weight is under weak environmental control.

Key words: Picea mariana (Mill.) B. S. P., cone morphology, Heritability, Repeatability, variation, genetic parameters, correlations.

Zusammenfassung

Die Arbeit stellt die Ergebnisse aus einer Untersuchung vor, die durchgeführt wurde, um den relativen Einfluß der genotypischen und der umweltbedingten Kontrolle der Merkmale der Zapfenmorphologie und des Samengewichtes bei *Picea mariana* (Mill.) B.S.P., zu prüfen. Es wurde ein dreistufiges Gruppen-Probeentnahme-Schema benutzt, d. h. auf der Stufe der Population, auf der Stufe von Einzelbäumen innerhalb der Populationen und auf der Stufe der Zapfen innerhalb der Einzelbäume. Dabei wurden 9 morphologische Merkmale an jedem Zapfen gemessen und das mittlere 1000-Korn-Gewicht für jeden Baum bestimmt. Die statistischen Analysen umfaßten

1) die Errechnung der Populationsmittel und der Standardabweichungen für jedes Merkmal,
2) die Zapfenlängen : Zapfendurchmesser-Korrelationen auf dem Populations- und Einzelbaum-Level,
3) die hierarchische Varianzanalyse und
4) den Vergleich von Zapfenlängen : Zapfendurchmesser-Korrelationen mit gleichartigen Werten, die 6 Jahre früher ermittelt worden waren.

Die genetischen Analysen bestanden 1) aus der Wiederholbarkeit mit Standardabweichung und Konfidenzintervallen für jedes Merkmal auf dem Niveau der Population als Schätzung der Heritabilitäten und 2) aus multiplen Regressionsanalysen für jedes Merkmal. Letzteres wurde verwendet, indem stufenweise Zick-Zack-Prozeduren mit dem Zapfenmerkmal als der abhängigen Variablen und 12 Umweltfaktoren zusammen mit ihren Quadraten und an erster Stelle Interaktionen als unabhängige Variablen zur Identifizierung der Ursache benutzt wurden, die am meisten zur Merkmals-Variation beiträgt.

Obwohl die Mittelwerte und Wiederholbarkeiten aller Merkmale mit der Population variieren, können keine geographischen Trends entdeckt werden. Die Wiederholbarkeit zeigte, daß sich die Heritabilität so gut schätzen läßt. Alle Merkmale sind sowohl unter statistisch signifikant genotypischer wie umweltbedingter Kontrolle, wobei die wichtigsten Ursachen der letzteren identifiziert wurden. Zapfenlänge und -durchmesser und Trockengewicht sowie Ausmaße der mittleren Zapfenschuppe waren unter strenger, Länge und Breite der Basis und Spitzenschuppe unter leichter genotypischer Kontrolle.

Frühere Anzeichen der pleiotropischen Kontrolle über Zapfenlänge und -durchmesser wurden unterstrichen.

Das Samengewicht steht unter leichter Umweltkontrolle.

Introduction

Black spruce *(Picea mariana* (Mill.) B.S.P.) is a very important North American species, because of its excellent pulpwood, wide distribution, site diversity, relatively high tolerance to insect pests and diseases and relative ease in artificial regeneration. Intensive research on the genetics of black spruce has been in progress in North America during the past 20 years. Genetics of cone morphology and seed comprises an important part of this study because floral structures have been shown to be under stronger genetic control than growth characters (Stebbins 1950).

Considerable work has been done, in the past 30 years, on the geographic variation in the characters of cone morphology of serveral coniferous species and on the relative significance of genotypic and environmental control on these characters.

Intensive literature review of the past 100 years has shown that environmental, genetic and physiological factors together play an important role in determining a forest tree's potential for seed quality, by determining its flowering threshold, intensity and periodicity of flowering and seed fertility (Andersson 1965). Character of seed quality appear to be under strong genetic control. However, no information is available in this review on possible correlation between the characters of seed quality and those of cone morphology. Andersson's review also shows that the genotype has a dominating influence on cone length and cone weight in Norway spruce *(Picea abies* (L). Karst).

Lester (1968), in a study of the variation pattern of the characters of cone morphology of balsam fir *(Abies balsamea* (L). Mill.), demonstrated approximately equal contribution of populations, trees within populations and cones within trees within populations to the variation in cone length. The predominant sources of variation for other characters were populations and trees within populations. This suggests a combined control of genotypic and environmental factors on characters of cone morphology.

Balut (1969) reported that length, diameter and shape of cones of Polish larch *(Larix decidua* Mill. var. *polonica)* were distributed normally within individual trees in a stand and within the whole stand. This indicates approximately equal contribution of trees and position within trees to the total variation. He also found that in seven Polish and one Alpine population the mean values of the cone parameters were sufficiently different for separation of *L. polonica* as a species from *L. decidua* but the variation within the former species could not be used for distinguishing ecotypes and races.

Roche (1969) has recognized clinal variation in cone-scale morphology in white-Engelmann, white-Sitka and white-black spruce complexes in British Columbia, Canada. The clines range from pure white spruce *(Picea glauca* (Moench) Voss) to pure Engelmann *(P. engelmannii* Parry), Sitka *(P. sitchensis* (Bong.) Carr.), or black spruce, as a result of introgressive hybridization, in which the hybrids occupy regions intermediate between those of the pure species. The hybrids have intermediate cone scale forms like other characters. This indicates genetic control over the characters of cone scale morphology in these species.

Later work on white spruce in Newfoundland by Khalil (1974) has provided satisfactory evidence to show that most characters of cone morphology are under strong control of the genotype of the individual trees and are only weakly controlled by environmental gradients.

Cone size has been found to decrease with increasing distance from the apex of the tree in Douglas fir *(Pseudotsuga menziesii* (Mirb.) Franco) (Winjum and Johnson 1964), red pine *(Pinus resinosa* Ait.) (Lyons 1956), Scots pine *(P. sylvestris* L.) (Sarvas 1962, Hadders 1971) and Norway spruce (Messer 1958). Yao (1971) reports that in Douglas fir all levels of sampling, regions, sub-regions, provenances and trees are statistically significant contributors of variation in seed weight and cone scale length and width. These parameters increase clinally from low to high altitude and from north to south.

Very little work has been done on the genetics of cone morphology of black spruce. Preliminary work (Khalil 1975) has shown that the largest proportion of the variation in cone length and diameter occurs among cones within trees within populations and is due to the genotype of the male and the female parent, which appear to have the largest degree of control over them. A small degree of ecotypic environmental control was also found over these characters. In a later study all important characters of cone morphology were examined to quantify the genotypic and environmental control on their variation for an adequate understanding of their genetics. The present paper reports the results of this study.

Table 1. — Location of seed sources.

Location	Lat. (°N)	Long. (°W)	Alt. (m)	Forest section*
1	51.48	55.70	15	B. 32 - Forest Tundra
2	50.53	56.07	15	B. 31 - Newfoundland-Labrador Barrens
3	50.10	56.17	152)	B. 29 - Northern Peninsula
4	49.45	56.47	61)	
5	49.42	57.25	107)	
6	49.23	57.28	122)	B. 28b - Corner Brook
7	48.80	58.07	183)	
8	48.50	58.28	107)	
9	48.87	57.93	274)	
10	47.88	59.08	46)	
11	49.18	56.10	183)	B. 28a - Grand Falls
12	48.83	56.48	183)	
13	48.45	57.00	304)	
14	49.02	55.43	61)	
15	48.37	54.42	30	B. 29 - Northern Peninsula
16	48.67	55.23	122)	B. 28a - Grand Falls
17	48.70	54.45	91)	
18	48.40	54.21	61)	
19	47.02	55.23	91)	B. 30 - Avalon
20	47.22	53.88	61)	
21	47.50	52.87	152)	
22	49.38	56.97	137	B. 28b - Corner Brook

*Rowe (1972)

Material and Methods

Sampling Procedure

A three-stage cluster sampling procedure was adopted in 1973 in which twenty-two populations were selected across insular Newfoundland as primary sampling units. Of these, 21 were the same or very close to the populations whose seed had been used in the regional black spruce provenance study (Khalil 1975, 1981). These populations are located in five forest sections (Rowe 1972) as shown in *Table 1* and *Fig. 1.* They provide adequate north-south and coastal-inland distribution to maximize the number of climatic and edaphic conditions sampled. Ten dominant and codominant trees spaced about 50 m apart to minimize consanguinity were randomly selected in each population. Over 200 current year's cones were collected from the previous year's portion of the stem to minimize within tree variation. A random sample of 20 cones was obtained from each tree's cones after seed extraction.

The Data

Measurements were made on the following variables of each cone:

1. Cone length) After soaking the) cones in warm water for one hour,
2. Cone diameter at the widest point) followed by heating) at 50° C for two) hours to close the) cone scales.
3. Oven-dry weight of cone after heating overnight at 105° C.
4. Length of a cone scale from the base of the cone.
5. Width of the scale in (4) at the widest point.
6. Length of a randomly selected cone scale from the middle of the cone.
7. Width of the scale in (6) at the widest point.
8. Length of a cone scale from the tip of the cone.

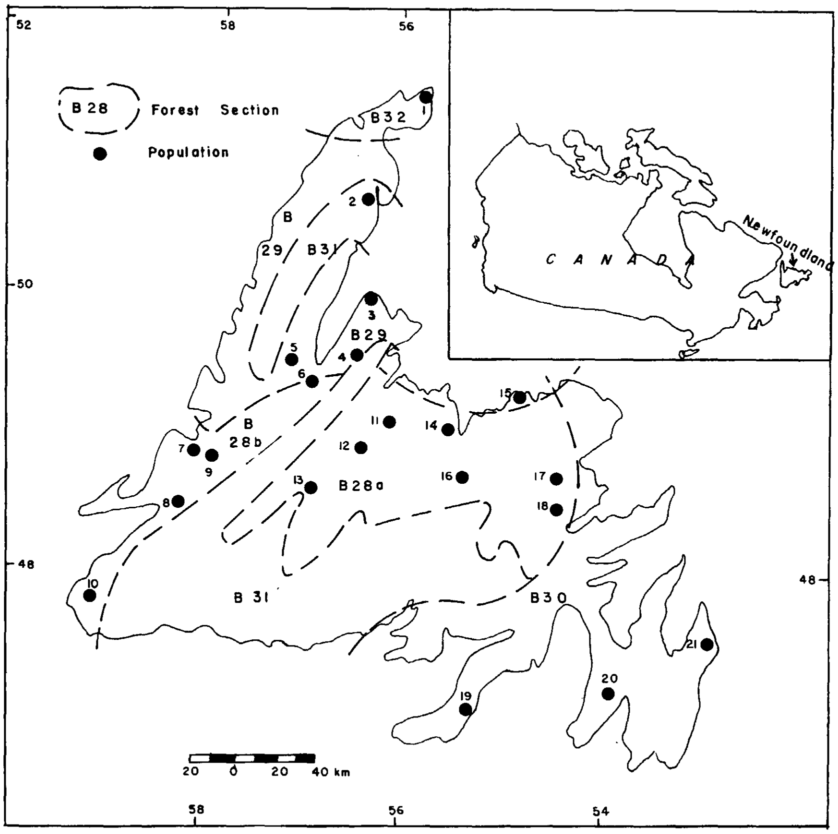

Fig. 1. — Location of Populations.

9. Width of the scale in (8) ~~at~~ the widest point.
10. In addition, weight of 1 000 oven-dried seeds was determined for each tree.

Statistical Analyses

1. *Cone length — Cone diameter correlations* — Simple correlation coefficients between cone length and cone diameter were determined at two levels of sampling, over cones for each tree within each population and over trees within each population. Correlation coefficients at the population level were compared for the 1967 and 1973 samples using the procedure of Steel and Torrie (1980). As 21 simultaneous comparisons were made the appropriate level of significance, γ, had to be used for the test of each population to achieve an overall significance level of α. The value of γ was calculated from equation (1):

$$\alpha = 1-(1-\gamma)^k \quad \text{---} \quad (1)$$

where α is the desired level of significance = 0.05 and k is the number of independent comparisons = 21. The value of γ so obtained was 0.00244. The critical point in a standard normal distribution corresponding to this probability in a two-tailed test is 3.031 (Douglas and Chopra 1978). The value of Z_i for each population was calculated, using equation (2):

$$Z_i = \frac{z_{i1} - z_{i2}}{(\sigma^2_{i1} + \sigma^2_{i2})^{\frac{1}{2}}} \quad \text{-----------------------------------} \quad (2)$$

where Z_i or z_i are Fisher's transformations for population i such that Z_i or $z_i = 0.5 \ln \frac{1 + r_i}{1 - r_i}$ (ln is the natural logarithm, base e, r_i is the sample correlation coefficient for population i (Steel and Torrie 1980)

Z_i = Calculated value for population i
z_{i1}, z_{i2} Values of z for population i in 1967 and 1973 respectively
$\sigma^2_{i1}, \sigma^2_{i2}$ = Variance of population i in 1967 and 1973 respectively and equals $\frac{1}{n_i - 3}$, where n is the number of observations.

2. *Parameters of cone characters* — Mean and standard deviation of each character in each population were calculated to study the distribution of these parameters among populations. The populations were arranged in arrays to detect geographic trends.

3. *Hierarchical analyses of variance* — Three hierarchical sampling levels were recognized, i.e. populations, trees within populations and cones within trees within populations. Three- and two-level hierarchical analyses of variance were performed for characters 1—9 and 10 respectively.

These analyses were on the mixed model with population effects fixed and trees and cones effects random, represented by Equations (3) and (4) for characters of cone morphology and seed weight respectively:

$$Y_{ijk} = \mu + \alpha_i + \tau_{ij} + \varepsilon_{ijk} \quad \text{-----------------------------------} \quad (3)$$

where Y_{ijk} = Measurement of the kth cone on the jth tree in the ith population
μ = Over-all mean
α_i = Effect of the ith population (fixed)
τ_{ij} = Effect of the jth tree in the ith population (random)
ε_{ijk} = Uncontrolled environmental and genetic deviations attributable to individual cones

$$Y_{ij} = \mu + \alpha_i + \epsilon_{ij} \text{ --- } (4)$$

where Y_{ij} = Seed weight of the jth in the ith population and other symbols have the same meaning as in equation (3).

4. *Repeatability* — Repeatability with standard error and confidence limits were calculated for characters 1—9 as estimates of their heritability to determine the magnitude, statistical significance and variation of genotypic control on these characters. Formulas (5), (6), (7) and (8) were used for these calculations (Becker 1968, Bogyo and Becker 1963 and Swiger *et al.* 1964):

$$\hat{R} \ \frac{\hat{\sigma}^2_T}{\hat{\sigma}^2_E + \hat{\sigma}^2_T} \text{ --- } (5)$$

where $\hat{R}$ = Estimated repeatability

$$\hat{\sigma}^2_E = \text{M.S. } (C/T)^{*1}$$

$$\hat{\sigma}^2_T = \frac{\text{M.S. } (T)^{*2} - \text{M.S. } (C/T)^{*1}}{k}$$

where k is the coefficient of $\hat{\sigma}^2_T$ in M.S. (T) = 20

$$\text{S.E. } (\hat{R}) = \left[\frac{2(ct-1)^2 \ (1-\hat{R})^2[(1 + (k-1)\hat{R}]^2}{ctk^2(ct-t)(t-1)}\right]^{\frac{1}{2}} \text{ --------------------- } (6)$$

where S.E. $(\hat{R})$ = Standard error of $\hat{R}$

c = Number of cones per tree
t = Number of trees per population
k = Coefficient of $\hat{\sigma}^2_\tau$ in E.M.S. (T) = 20

$$K_r = \frac{k\text{M.S. } (C/T)F_r}{\text{M.S. } (T) + \text{M.S. } (C/T)(k-1)F_r} \text{ -------------------- } (7)$$

where K_r = Upper or lower confidence limit
k = Coefficient of $\hat{\sigma}^2_\tau$ in E.M.S. (T) = 20
F = Tabulated F value
r = $\alpha/2$ or $(1-\alpha)/2$ for lower and upper confidence limits respectively, where α is the significance level = 0.05.

$$P[1-K_{\gamma/2} \leq R \leq 1-K_{(1-\gamma)/2}] = 1-\gamma \text{ --------------------- } (8)$$

where P = probability, and other symbols have the same value as in equations (1), (6) and (7).

The value of γ was obtained from equation (1). This value was used instead of α for reasons explained under correlations. If the confidence limits calculated above included 0 the null hypothesis H_0: R = 0 vs. H_a: R # 0 was not rejected.

5. *Multiple regression analyses* — These analyses were performed to identify the sub-set of geographic and meteorological variables, singly or in combination, which contribute most to the variation in each character and which can be used as predictors. The geographic and meteorological factors for each population which were used as independent variables are listed below:

X_1 = Latitude
X_2 = Longitude
X_3 = Altitude
X_4 = Mean number of days from January 1 to the date of the last spring frost
X_5 = Mean number of days from January 1 to the date of the first fall frost
X_6 = Mean number of frost-free days
X_7 = Mean number of days from January 1 to the date of the commencement of growth (mean temperature > 5° C)
X_8 = Mean number of days from January 1 to the date of the end of the growing season (mean temperature < 5° C)
X_9 = Mean number of growing days (temperature > 5° C)
X_{10} = Average mean temperature from May to September
X_{11} = Mean precipitation from May to September
X_{12} = Average maximum July temperature
X_{13} = Mean number of degree-days above 5° C
X_{14} = Day length on June 1

The stepwise zig-zag regression procedure (Blair, Brown and Wilson 1971; Wilson 1975) was used in two ways. The linear form was used first (equation 9):

$$Y_k = \beta_o + \sum_{i=1}^{14} \beta_i X_i + \varepsilon \text{ --------- } (9)$$

where Y_k = Observed value of the dependent variable k, β_0 = the intercept; β_i = the partial regression coefficient of the ith independent variable (i = 1 . . . . 14); X_i = ith independent variable (i = 1 . . . . 14); ε = random error component.

The multiple correlation coefficients, residual mean squares and the lack of fit tests indicated that the first order prediction equations did not adequately represent the correlation between the dependent and the independent variables. The analyses were repeated using prediction equation (10), which includes only 12 geographic and meteorological factors, their squares and first order interactions:

$$Y_k = \beta_o + \sum_{i=1}^{12} \beta_i X_i + \sum_{i=1}^{12} \beta_{i+12} X_i^2 + \sum_{i<j} \beta_{i+24} X_i X_j + \varepsilon \text{ ---------------- } (10)$$

The various symbols in this equation have the same meaning as in equation (9) and X_j indicates an X-variable with a larger subscript than X_i. Independent variables X_5 and X_8 were eliminated on account of being linear combinations of other independent variables. This reduced the number of independent variables from 119 to 90.

The analysis of variance of the regression was of the form shown in *Table 2.*

The lack of fit mean squares was tested by an F-test, using T/P mean squares as the denominator and the lack of fit mean squares as the numerator, to determine the step at which to stop. The contribution to the regression equation by the independent variables tested was estimated by calculating R^2 according to Equation (11).

$$R^2 = \frac{\text{Total S.S. - Residual S.S. at cutoff stage}}{\text{Population S.S.}} \text{ ------------------ } (11)$$

Results and Discussion

Cone Length — Cone Diameter Correlations

Of the 220 correlation coefficients at the trees within populations level only 11 are non-significant (0.05 level). All correlations at the populations level are statistically significant (0.01 level) *(Table 3).* All populations in which the sample trees were selected from the same site in both years have a non-significant Z-value except populations 10, 11 and 19 in which there is significant difference (0.05 level) *(Table 4).* Current data are inadequate to explain these deviations. The remaining results, however, show that cone length and cone diameter are affected equally by environmental changes caused by changes in meteorological conditions between the years of sampling, so that

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$(C/T)^{*1}$ = Cones within trees
$(T)^{*2}$ = Trees within populations

Table 2. — Analysis of variance of regression.

Source of variation	Degress of freedom
Population (P)	21
Regression	q*
Lack of fit	21 - q*
Error	4 378
Trees within populations (T/P)	198
Cones within trees within populations (C/TP)	4 180
Total	4 399

q* - Number of Xs in the regression equation.

Table 3. — Correlation coefficients of cone length-cone diameter.

Population	Range	Mean
1	0.5209* - 0.8577**	0.7108**
2	0.7458** - 0.9445**	0.7710**
3	0.6261** - 0.9267**	0.8790**
4	0.4249* - 0.9051**	0.8093**
5	0.4143* - 0.9075**	0.8182**
6	0.6291** - 0.9423**	0.6748**
7	0.5037* - 0.9219**	0.7846**
8	0.2019^{NS} - 0.9125**	0.5822**
9	0.3032^{NS} - 0.8318**	0.5599**
10	0.2182^{NS} - 0.8081**	0.6380**
11	0.0342^{NS} - 0.8365**	0.3233**
12	0.3097^{NS} - 0.8938**	0.5725**
13	0.5027* - 0.9439**	0.6156**
14	0.3911* - 0.8290**	0.6650**
15	0.2205^{NS} - 0.7603**	0.3213**
16	0.4932* - 0.9551**	0.3799**
17	0.3983* - 0.7369**	0.3532**
18	0.3191^{NS} - 0.8154**	0.5799**
19	-0.1015^{NS} - 0.7897**	0.5966**
20	-0.0723^{NS} - 0.7189**	0.4906**
21	0.4659* - 0.8563**	0.7499**
22	0.3410^{NS} - 0.8626**	0.6435**

** - Statistically significant (overall 0.01 level).
* - Statistically significant (overall 0.05 level).
NS - Statistically non-significant (overall 0.05 level).

Table 4. — Comparison of correlation coefficients.

Population	Correlation Coeff. 1967	Correlation Coeff. 1973	Z	Remarks
1	0.79	0.71	1.6559^{NS}	
2	0.84	0.77	1.8050^{NS}	
3	0.88	0.88	0^{NS}	
4	0.76	0.81	1.1757^{NS}	
5	0.81	0.82	-0.2677^{NS}	
6	0.75	0.67	1.4578^{NS}	
7	0.80	0.78	0.4785^{NS}	
8	0.80	0.58	3.9197*	Populations different from those of 1967
9	0.91	0.56	8.0407*	
10	0.87	0.64	5.1668*	
11	0.70	0.32	4.8140*	
12	0.76	0.57	3.1337^{NS}	
13	0.77	0.62	2.6541^{NS}	
14	0.65	0.66	0.1574^{NS}	
15	0.85	0.32	8.3086*	
16	0.59	0.38	2.4949^{NS}	
17	0.60	0.35	2.9290^{NS}	
18	0.77	0.58	3.2162^{NS}	
19	0.84	0.49	6.1572*	
20	0.84	0.75	2.2308^{NS}	
21	0.86	0.64	4.8097^{NS}	
22		0.60	-	Population not sampled in 1967

* - Statisticall significant (over-all 0.05 level)
NS - Statistically non-significant (over-all 0.05 level)

their correlations do not change. This suggests partial genotypic and partial environmental control over these characters. It also supports the earlier indication of pleiotropic genetic control in the genotypic component of variation (Khalil 1975).

Parameters of Cone Characters

The results are summarized in *Table 5*. There is considerable variation among populations in all characters (*Table 6)*, but ranking of populations in arrays did not show any geographic trends. The analyses which follow elucidate the relative role of the genotype and the environment in controlling these characters.

Hierarchical Analyses of Variance

Though all the three levels of sampling are statistically significant sources of variation in all characters (0.005 and 0.05 levels) trees within populations and cones within trees within populations are the most important contributors (*Table 6*).

For cone length and cone diameter the variation distribution pattern is similar to that for the 1967 data (Khalil 1975), i.e. a small contribution of the inter-populations and a large contribution of the intra-population component, which is equally divided between trees within populations and cones within trees within populations. This shows that years and the environmental changes associated with them are not important in determining variation in these two characters. These results also confirm similar conclusions arrived at by correlation analyses and stated earlier.

The relatively small control of the environment over these characters is confirmed by the above results. In spite

Table 5. — Parameter of cone characters.

Pop-ulation	Cone length (cm) Length ± S.D.	Cone diameter (cm) Diam. ± S.D.	Oven-dry cone wt. (g) Wt. ± S.D.	Length of base scale (cm) Length ± S.D.	Width of base scale (cm) Width ± S.D.	Length of middle scale (cm) Length ± S.D.	Width of middle scale (cm) Width ± S.D.	Length of tip scale (cm) Length ± S.D.	Width of tip scale (cm) Width ± S.D.
1	2.55 ± 0.49	1.38 ± 0.23	1.41 ± 0.55	0.51 ± 0.10	0.40 ± 0.10	0.92 ± 0.12	0.73 ± 0.10	0.70 ± 0.11	0.41 ± 0.08
2	2.59 ± 0.32	1.32 ± 0.13	1.31 ± 0.43	0.83 ± 0.11	0.86 ± 0.08	1.03 ± 0.11	0.84 ± 0.09	0.81 ± 0.13	0.51 ± 0.10
3	2.71 ± 0.40	1.32 ± 0.14	1.33 ± 0.47	0.83 ± 0.13	0.83 ± 0.12	1.04 ± 0.13	0.86 ± 0.09	0.83 ± 0.17	0.52 ± 0.10
4	2.37 ± 0.28	1.37 ± 0.18	1.32 ± 0.45	0.79 ± 0.10	0.80 ± 0.11	1.08 ± 0.13	0.89 ± 0.11	0.78 ± 0.14	0.46 ± 0.09
5	2.44 ± 0.33	1.30 ± 0.16	1.24 ± 0.43	0.72 ± 0.11	0.70 ± 0.12	1.10 ± 0.11	0.86 ± 0.13	0.79 ± 0.14	0.45 ± 0.09
6	2.39 ± 0.29	1.35 ± 0.13	1.35 ± 0.36	0.79 ± 0.09	0.80 ± 0.09	1.13 ± 0.13	0.90 ± 0.09	0.81 ± 0.11	0.43 ± 0.07
7	2.34 ± 0.33	1.32 ± 0.15	1.18 ± 0.37	0.75 ± 0.11	0.76 ± 0.14	1.03 ± 0.14	0.85 ± 0.09	0.76 ± 0.13	0.44 ± 0.08
8	2.23 ± 0.25	1.27 ± 0.12	1.09 ± 0.33	0.74 ± 0.10	0.76 ± 0.10	0.96 ± 0.13	0.82 ± 0.11	0.77 ± 0.11	0.48 ± 0.08
9	2.76 ± 0.28	1.42 ± 0.12	1.77 ± 0.47	0.85 ± 0.10	0.87 ± 0.09	1.13 ± 0.11	0.93 ± 0.08	0.85 ± 0.11	0.54 ± 0.09
10	2.51 ± 0.30	1.29 ± 0.14	1.29 ± 0.38	0.74 ± 0.12	0.76 ± 0.11	1.00 ± 0.15	0.84 ± 0.12	0.79 ± 0.13	0.51 ± 0.10
11	2.55 ± 0.25	1.37 ± 0.10	1.48 ± 0.31	0.81 ± 0.12	0.81 ± 0.12	1.06 ± 0.13	0.89 ± 0.10	0.85 ± 0.11	0.51 ± 0.08
12	2.56 ± 0.39	1.40 ± 0.21	1.51 ± 0.39	0.85 ± 0.09	0.82 ± 0.10	1.13 ± 0.10	0.85 ± 0.09	0.81 ± 0.13	0.45 ± 0.08
13	2.50 ± 0.35	1.38 ± 0.12	1.48 ± 0.49	0.80 ± 0.10	0.82 ± 0.11	1.08 ± 0.12	0.91 ± 0.10	0.85 ± 0.13	0.53 ± 0.08
14	2.58 ± 0.31	1.37 ± 0.12	1.56 ± 0.43	0.80 ± 0.11	0.77 ± 0.10	1.08 ± 0.11	0.87 ± 0.08	0.82 ± 0.11	0.50 ± 0.09
15	2.27 ± 0.22	1.36 ± 0.15	1.29 ± 0.30	0.76 ± 0.11	0.76 ± 0.11	1.00 ± 0.11	0.87 ± 0.10	0.79 ± 0.12	0.48 ± 0.09
16	2.56 ± 0.24	1.37 ± 0.11	1.50 ± 0.29	0.79 ± 0.10	0.77 ± 0.10	1.04 ± 0.15	0.88 ± 0.07	0.83 ± 0.13	0.51 ± 0.08
17	2.49 ± 0.24	1.35 ± 0.12	1.47 ± 0.32	0.80 ± 0.11	0.79 ± 0.10	1.09 ± 0.11	0.92 ± 0.08	0.88 ± 0.11	0.54 ± 0.09
18	2.73 ± 0.29	1.39 ± 0.13	1.67 ± 0.46	0.85 ± 0.10	0.86 ± 0.09	1.13 ± 0.11	0.91 ± 0.09	0.85 ± 0.11	0.54 ± 0.09
19	2.49 ± 0.36	1.40 ± 0.13	1.58 ± 0.46	0.70 ± 0.10	0.74 ± 0.11	1.03 ± 0.12	0.89 ± 0.09	0.77 ± 0.12	0.49 ± 0.08
20	2.49 ± 0.20	1.37 ± 0.09	1.40 ± 0.28	0.78 ± 0.09	0.81 ± 0.08	1.01 ± 0.11	0.80 ± 0.08	0.76 ± 0.13	0.46 ± 0.08
21	2.13 ± 0.26	1.26 ± 0.11	1.01 ± 0.30	0.77 ± 0.10	0.80 ± 0.08	0.94 ± 0.11	0.82 ± 0.08	0.72 ± 0.12	0.45 ± 0.08
22	2.62 ± 0.28	1.31 ± 0.11	1.54 ± 0.40	0.91 ± 0.12	0.90 ± 0.09	1.18 ± 0.11	0.86 ± 0.10	0.93 ± 0.13	0.50 ± 0.08

Table 6. — Summary of analyses of variance.

Source of variation	Expected mean squares	Degrees of freedom		Cone length		Cone diameter		Oven-dry cone wt.		Length of tip scale		Width of tip scale		Length of middle scale		Width of middle scale		Length of base scale		Width of base scale		Seed weight	
		formula	Actual	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F	Var %	F
Populations	$\sigma^2_\varepsilon + c\sigma^2_\tau + ct\sigma^2_\alpha$	p-1	21	21.36	4.35 (0.005)	8.99	1.68 (0.05)	17.62	3.54 (0.005)	14.94	3.86 (0.005)	16.29	6.52 (0.005)	24.02	5.26 (0.005)	18.10	3.97 (0.005)	34.69	16.10 (0.005)	45.72	21.21 (0.005)	22.29	2.71 (0.005)
Trees within populations	$\sigma^2_\varepsilon + c\sigma^2_\tau$	p(t-1)	198	46.33	30.27 (0.005)	50.59	26.41 (0.005)	46.91	27.92 (0.005)	36.52	15.89 (0.005)	23.56	8.27 (0.005)	43.04	27.54 (0.005)	42.96	23.30 (0.005)	20.31	9.54 (0.005)	20.32	12.64 (0.005)	77.71	
Cones within trees within populations	σ^2_ε	pt(c-1)	4 180	32.31		40.42		35.47		48.54		60.15		32.94		38.94		45.00		33.96			
Total		ptc-1	4 399	100.00		100.00		100.00		100.00		100.00		100.00		100.00		100.00		100.00		100.00	

The figures in parentheses in the F-columns indicate the level of significance of the F-value.

of the large environmental differences created by the meteorological and edaphic conditions of the sites of the 22 populations the contribution of the latter to the total variation is small.

The dominant and co-dominant status of the selected trees and their occurrence over a small and relatively homogeneous site within each population ensured minimization of the contribution of micro-environmental factors, like competition, crown size and soil nutrients to the among-trees within-populations variation. The effect of the position in the crown was minimized by sampling only the previous year's portion on the stem. The existence of a large proportion of the variation among trees and cones within populations in spite of the above attempts to minimize them shows that most of this variation is due to the genotype of the male and female parent, which appear have the largest degree of control on cone morphology in black spruce. This result agrees with the results of ANDERSSON (1965), ROCHE (1969) and KHALIL (1974).

Repeatability

Table 7 summarizes the results. Test of significance shows that all repeatability values are statistically significant (0.05 level), except length of base scale in population 6 and width of tip scale in populations 6 and 18 which are barely non-significant. Repeatability, which is expressed by the conceptual formula $R = (\sigma^2_G + \sigma^2_{EG})/\sigma^2_P$ is an estimate of heritability. This estimate is upward biased by the factor σ^2_{EG}/σ^2_P, where σ^2_{FG} is general environmental variance, i.e. the environmental variance contributing to the between-individuals component and caused by permanent or non-localized circumstances, and σ^2_P is phenotypic variance. The numerator has been minimized by reducing the area of the primary sampling units as much as possible consistent with the need to minimize inbreeding, and by collecting the cones only from the last year's portion of the stem. Hence, the repeatability values are good estimates of heritability. Significant values for heritability for these characters indicate strong genotypic control over them.

Table 8 shows the ranking of the populations by repeatability of different characters. Although repeatability of every character varies with the population, these arrays do not indicate any geographic trends. Population 10 has the highest repeatability for six characters and very high repeatability for the other three. These results show the degree of inbreeding in the different populations studied. Populations with a high repeatability of several characters are more outbred than those with low repeatability.

Mean repeatability over populations was calculated for each character. Cone length, cone diameter, cone oven-dry weight and length and width of the middle scale have high repeatability ($R > 0.4$) and length and width of the base and tip scales have low heritability ($R \leq 0.4$).

Multiple Regression Analyses

Populations have been shown to be significant source of variation in all characters, indicating geographic and meteorological factors, which characterize their locations, to exercise at least partial influence on the characters. Multiple regression analyses have identified the subset of these factors, singly or in combination, which contributes most to the variation in each character and which can be used as predictors. *Tables 9* and *10* present the regression relationships and tests of their lack of fit respectively.

Table 7. — Repeatability with standard error of characters.

Population	Cone length		Cone diameter		Oven-dry cone weight		Length of base scale		Width of base scale		Length of middle scale		Width of middle scale		Length of tip scale		Width of tip scale	
	R	SE	R	SE	R	SE	R	SE	R	SE	R	SE	R	SE	R	SE	R	SE
1	0.6615	0.1105	0.6366	0.1145	0.4463	0.1263	0.2284	0.0991	0.2668	0.1071	0.5089	0.1261	0.2970	0.1124	0.3366	0.1180	0.2008	0.0926
2	0.5756	0.1219	0.4999	0.1263	0.5437	0.1244	0.4380	0.1261	0.2490	0.1030	0.5789	0.1216	0.3324	0.1175	0.5925	0.1202	0.4926	0.1265
3	0.6521	0.1121	0.6066	0.1186	0.5743	0.1220	0.4391	0.1261	0.6424	0.1136	0.6233	0.1164	0.5106	0.1260	0.6996	0.1033	0.5027	0.1263
4	0.4833	0.1266	0.7122	0.1008	0.6091	0.1183	0.5348	0.1249	0.7147	0.1001	0.6597	0.1108	0.7169	0.0996	0.5646	0.1229	0.3672	0.1215
5	0.6148	0.1175	0.6490	0.1126	0.6499	0.1124	0.3642	0.1212	0.4958	0.1264	0.4384	0.1261	0.5169	0.1258	0.2163	0.0964	0.2264	0.0987
6	0.5327	0.1250	0.3680	0.1215	0.4115	0.1249	0.0823	0.0566	0.2066	0.0940	0.4956	0.1264	0.4955	0.1264	0.1925	0.0905	0.0834	0.0570
7	0.6072	0.1185	0.5359	0.1249	0.6044	0.1188	0.3130	0.1148	0.4313	0.1258	0.5474	0.1242	0.3142	0.1150	0.4480	0.1263	0.1397	0.0756
8	0.4272	0.1257	0.3401	0.1185	0.4439	0.1262	0.1709	0.0828	0.3241	0.1164	0.4202	0.1253	0.5618	0.1231	0.4140	0.1250	0.3510	0.1198
9	0.6290	0.1156	0.6063	0.1186	0.6320	0.1152	0.2680	0.1073	0.2936	0.1118	0.6520	0.1121	0.5743	0.1220	0.2569	0.1052	0.2750	0.1086
10	0.7424	0.0936	0.7155	0.0999	0.7542	0.0907	0.4873	0.1266	0.5137	0.1259	0.7580	0.0897	0.7712	0.0862	0.5849	0.1210	0.5239	0.1255
11	0.5454	0.1243	0.4835	0.1256	0.4840	0.1266	0.2776	0.1091	0.5421	0.1245	0.6941	0.1044	0.6443	0.1133	0.3030	0.1210	0.1559	0.0805
12	0.6305	0.1154	0.6701	0.1090	0.6676	0.1095	0.1143	0.0676	0.3691	0.1216	0.4763	0.1266	0.3609	0.1208	0.3588	0.1206	0.1603	0.0817
13	0.7013	0.1030	0.5698	0.1224	0.6937	0.1045	0.2538	0.1045	0.3899	0.1234	0.5605	0.1232	0.6599	0.1108	0.2988	0.1127	0.1952	0.0912
14	0.5818	0.1213	0.3054	0.1137	0.5373	0.1248	0.2288	0.0992	0.1140	0.0675	0.5797	0.1215	0.5342	0.1250	0.2051	0.0937	0.2675	0.1072
15	0.6017	0.1192	0.5226	0.1255	0.6154	0.1175	0.2216	0.0976	0.2933	0.1118	0.3836	0.1229	0.4368	0.1260	0.2733	0.1083	0.2207	0.0974
16	0.5311	0.1251	0.3614	0.1209	0.3750	0.1222	0.2171	0.0965	0.1617	0.0821	0.4034	0.1244	0.5363	0.1248	0.5388	0.1247	0.1192	0.0692
17	0.2786	0.1092	0.3367	0.1181	0.2997	0.1128	0.1527	0.0795	0.1517	0.0792	0.4087	0.1247	0.5050	0.1262	0.2356	0.1007	0.2191	0.0970
18	0.6173	0.1172	0.6555	0.1115	0.6808	0.1070	0.2914	0.0971	0.3443	0.1190	0.6377	0.1143	0.5411	0.1248	0.2934	0.1118	0.0990	0.0625
19	0.6401	0.1140	0.6021	0.1191	0.5988	0.1195	0.2171	0.0965	0.1871	0.0891	0.6112	0.1180	0.6113	0.1180	0.3248	0.1165	0.1273	0.0718
20	0.4168	0.1252	0.2489	0.1035	0.3670	0.1214	0.2485	0.1035	0.1064	0.0650	0.6511	0.1123	0.3714	0.1219	0.5102	0.1260	0.1551	0.0802
21	0.4766	0.1266	0.3975	0.1240	0.5322	0.1251	0.3903	0.1235	0.2315	0.0998	0.6486	0.1126	0.2730	0.1082	0.4904	0.1265	0.1278	0.0720
22	0.5260	0.1254	0.6336	0.1150	0.6612	0.1106	0.4378	0.1261	0.5113	0.1260	0.7023	0.1027	0.5776	0.1217	0.5478	0.1241	0.2964	0.1123

Table 8. — Ranking of populations by repeatability of various characters.

	Population (by character)								
Rank	Cone length	Cone diameter	Oven-dry cone wt.	Length of base scale	Width of base scale	Length of middle scale	Width of middle scale	Length of tip scale	Width of tip scale
1	10	10	10	4	4	10	10	3	10
2	13	4	13	10	3	22	4	2	3
3	1	12	18	3	11	11	13	10	2
4	3	18	12	2	10	4	11	4	4
5	19	5	22	22	22	9	19	22	8
6	12	1	5	21	5	20	9	16	22
7	9	22	9	5	7	21	8	20	9
8	18	3	15	7	13	18	22	21	14
9	5	9	4	18	12	3	18	7	5
10	7	19	7	11	18	19	16	8	15
11	15	13	19	9	8	14	14	11	17
12	14	7	3	13	9	2	5	12	1
13	2	15	2	20	15	13	3	1	13
14	11	2	14	14	1	7	17	19	12
15	6	11	21	1	2	1	6	13	11
16	16	21	11	15	21	6	15	18	20
17	22	6	1	16	6	12	20	15	7
18	4	16	8	19	19	5	12	9	21
19	21	8	6	8	16	8	2	17	19
20	8	17	16	17	17	17	7	5	16
21	20	14	20	12	14	16	1	14	18
22	17	20	17	9	20	15	21	6	6

For the dependent variables Y_4 and Y_5 the test was terminated at step 23 after including 10 independent variables in the equation, even though the F-values were statistically significant (0.005 level). Termination occurred because with 22 separate values of the X-vector available the subsequent choice of additional Xs would be very highly dependent upon the particular set of data observed. As the lack of fit test is conservative and becomes progressively so with additional inclusion of X-variables to the equation, these equations for Y_4 and Y_5 in all probability can be accepted with 10, or even fewer, X-variables.

The independent variables included in regression equations vary widely in number as well as in the subset chosen for inclusion in the above equations. This is to be expected because the models of this type are quite data dependent. However, it can be stated with confidence that for all characters the geographic and climatic variables are highly correlated with the characters and that these equations can be used to predict the average values of these characters.

Table 10 lists the values of mean repeatabilities and coefficients of determination from regression analyses of all characters. Repeatability values provide an estimate of heritability or genotypic control over the characters. Though they are means over populations, they do not include the influence of inter-population differences in environmental factors. The remaining variation is under the influence of such differences in environmental factors. The coefficients of determination represent the proportion of this variation produced by the subset of environmental factors tested in the respective regression equations. The subsets tested in each regression equation are the major contributors to the non-genetic portion of the variation.

Conclusions

The following conclusions are available from this study:

1. Although these is considerable variation in cone characters among populations no geographic trends are discernible.
2. The repeatability values obtained in this study are good estimates of heritability.
3. All characters are under both genotypic and environmental control.
4. An estimate has been obtained of the relative role of the genotype and the subset of geographical and climatic factors which contribute most to the variation in each character.
5. Cone length, cone diameter, oven-dry cone weight and length and width of the middle scale are under strong genotypic control. Length and width of base and tip scales are under weak genotypic control.

Table 9. — Summary of multiple regression relationships of geographic and meteorological factors with characters of cone morphology.

	$\hat{Y}_1$	$\hat{Y}_2$	$\hat{Y}_3$	$\hat{Y}_4$	$\hat{Y}_5$	$\hat{Y}_6$	$\hat{Y}_7$	$\hat{Y}_8$	$\hat{Y}_9$	$\hat{Y}_{10}$
Const.	4.943	1.569	15.101	2.092	3.973	3.829	2.946	2.967	2.736	1.514
X_6	0.0476									
X_{10}			-1.509							
X_{11}			$0.389\text{x}10^{-2}$							
X_2^2									$-0.635\text{x}10^{-4}$	
X_3^2	$0.639\text{x}10^{-5}$	$0.117\text{x}10^{-5}$	$0.163\text{x}10^{-4}$	$0.0894\text{x}10^{-5}$	$0.845\text{x}10^{-5}$	$0.487\text{x}10^{-5}$	$0.304\text{x}10^{-5}$	$0.397\text{x}10^{-5}$	$0.487\text{x}10^{-5}$	
X_6^2	$-0.192\text{x}10^{-3}$									
X_7^2						$-0.107\text{x}10^{-3}$		$-0.757\text{x}10^{-4}$		
X_9^2								$-0.533\text{x}10^{-4}$		
X_{10}^2								0.022		
X_{11}^2			$0.643\text{x}10^{-4}$							
X_{14}^2									$-0.291\text{x}10^{-2}$	
X_1X_2						$-0.220\text{x}10^{-3}$				
X_1X_3					$0.510\text{x}10^{-3}$					
X_1X_4	$0.753\text{x}10^{-3}$									
X_1X_9	$-0.975\text{x}10^{-3}$			$0.238\text{x}10^{-3}$						
X_1X_{11}					$0.124\text{x}10^{-3}$					
X_1X_{13}						$-0.130\text{x}10^{-4}$				
X_2X_3				$-0.494\text{x}10^{-4}$						
X_2X_4	$-0.134\text{x}10^{-3}$									
X_2X_7			$-0.798\text{x}10^{-3}$							
X_2X_9								$-0.107\text{x}10^{-3}$		$0.145\text{x}10^{-3}$
X_2X_{11}		$-0.108\text{x}10^{-4}$		$-0.104\text{x}10^{-4}$			$-0.946\text{x}10^{-5}$			
X_3X_4			$0.125\text{x}10^{-3}$	$0.819\text{x}10^{-4}$						
X_3X_6								$-0.656\text{x}10^{-5}$		$0.420\text{x}10^{-5}$
X_3X_7				$-0.918\text{x}10^{-4}$	$-0.210\text{x}10^{-3}$					
X_3X_{11}						$-0.298\text{x}10^{-5}$			$-0.492\text{x}10^{-5}$	
X_3X_{12}			$-0.107\text{x}10^{-2}$						$0.327\text{x}10^{-4}$	
X_3X_{13}							$-0.632\text{x}10^{-6}$			
X_4X_7				$-0.562\text{x}10^{-4}$						
X_4X_9										$-0.488\text{x}10^{-4}$
X_4X_{13}	$-0.416\text{x}10^{-4}$								$-0.347\text{x}10^{-6}$	
X_6X_7					$0.375\text{x}10^{-3}$					
X_6X_{10}					$-0.421\text{x}10^{-2}$					
X_6X_{11}	$-0.379\text{x}10^{-4}$									
X_6X_{12}				$-0.710\text{x}10^{-4}$						$-0.172\text{x}10^{-3}$
X_7X_{10}					$0.366\text{x}10^{-2}$					
X_7X_{13}	$-0.369\text{x}10^{-4}$									
X_7X_{14}				$-0.760\text{x}10^{-3}$	$-0.424\text{x}10^{-2}$		$-0.846\text{x}10^{-3}$		$-0.520\text{x}10^{-3}$	
X_9X_{10}				$0.319\text{x}10^{-3}$		$0.262\text{x}10^{-3}$				
X_9X_{13}	$0.681\text{x}10^{-4}$									
X_9X_{14}								$0.165\text{x}10^{-2}$		
$X_{10}X_{11}$			$0.399\text{x}10^{-2}$							
$X_{10}X_{12}$					$0.716\text{x}10^{-3}$					
$X_{10}X_{14}$								-0.029		
$X_{11}X_{13}$								$-0.641\text{x}10^{-6}$		
$X_{11}X_{14}$					$-0.315\text{x}10^{-3}$					

Table 10. — Tests of lack of fit.

Dependent variable (Y)	Step	No. of Xs	Lack of fit				Multiple regression coefficient (R)
			D.F.	M.S.	T/P M.S.	F	
Y_1. Cone length	22 out of 36	10	11	1.8425	1.2023	1.53^{NS}	0.9027
Y_2. Cone diameter	4 out of 35	2	19	0.2696	0.2216	1.22^{NS}	0.5858
Y_3. Oven-dry cone weight	17 out of 32	8	13	2.6054	2.0273	1.28^{NS}	0.8806
Y_4. Length of base scale	23 out of 33	10	11	0.2287	0.0770	2.97***	0.9504
Y_5. Width of base scale	23 out of 32	10	11	0.4436	0.0904	4.91***	0.9374
Y_6. Length of middle scale	9 out of 28	6	15	0.2435	0.1807	1.35^{NS}	0.9039
Y_7. Width of middle scale	5 out of 35	4	17	0.1412	0.1044	1.35^{NS}	0.8462
Y_8. Length of tip scale	9 out of 37	9	12	0.2399	0.1485	1.62^{NS}	0.8721
Y_9. Width of tip scale	12 out of 35	7	14	0.0816	0.0971	1.73^{NS}	0.9072
Y_{10}.1 000-seed weight	5 out of 39	4	16	0.0400	0.0319	1.25^{NS}	0.7937

NS - Statistically non-significant (0.05 level)

*** - Statistically significant (0.005 level)

Table 11. — Relative role of genotype and environment on characters.

Character	Mean repeat ability	Coeff. of determin- ation	Remarks
Cone length	0.5670	0.8148	High repeatability
Cone diameter	0.5207	0.3432	High repeatability
Oven-dry cone weight	0.5537	0.7754	High repeatability
Length of base scale	0.2899	0.9033	Low repeatability
Width of base scale	0.3428	0.8788	Low repeatability
Length of middle scale	0.5335	0.8170	High repeatability
Width of middle scale	0.5065	0.7160	High repeatability
Length of tip scale	0.3975	0.7606	Low repeatability
Width of tip scale	0.2421	0.8230	Low repeatability
Seed weight	Not known	0.6299	

6. Although the heritability of all characters varies with population, there are no geographic trends.
7. The earlier indication of pleiotropic control over cone length and diameter is supported.

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