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Genetics of wood characters of black spruce (Picea mariana (Mill.) B.S.P.) in Newfoundland, Canada

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Summary

The variation and relative control of genotype and environment over 11 wood characters in black spruce *(Picea mariana* (Mill.) B.S.P.) were studied to identify populations with superior pulping qualities. A four- and three-level cluster sampling scheme was adopted and the statistical and genetic analyses comprised analyses of variance, Bonferroni t-tests, repeatability calculations and multiple regressions.

Trees, discs and populations rank from highest to lowest as sources of variation in most characters. Within trees, the trend varies with character. There are weak north-south trends in relative densities, alcohol-benzene and sodium hydroxide solubilities and fibre length and wall thickness. Regression analyses of the squares of longitude and altitude show a negative and a positive influence respectively on sodium hydroxide solubility. Temperature and precipitation appear most frequently in different combinations in other regression equations. Repeatability values are good estimates of heritabilities. All characters except fibre wall thickness have high heritability ($R \geqslant 0.30$). The environmental factors studied have a significant influence on the non-genotypic portion of variation in all characters except fibre and lumen diameters (tangential section) and alcohol-benzene solubility. Populations 11, 16 and 19—23 have superior pulping qualities.

Key words: Heritability, Hierarchical analyses of variance, Multiple regression analyses, Step-wise multiple regression analyses, Genotypic variation, Environmental variation.

Résumé

Les tendances dans la variabilité générale et le conôle relatif du génotype et du milieu de 11 caractéristiques du

bois de l'épinette noire *(Picea mariana* (MILL.) B.S.P.) identifier les populations de cette essence qui se prêtent le mieux à la fabrication de la pâte à papier. Un plan d'échantillonnage en grappes à quatre et à trois niveaux a été adopté, et les résultats ont été soumis à des analyses statistiques et génétiques, y compris celle de la variance,le "t" de BONFERRONI, le calcul de la répétabilité et des régressions multiples.

En ordre décroissant, les arbres, les disques et les populations sont les sources de variation de la plupart des caractères. Chez les arbres la tendance varie selon le caractère. La densité, la solubilité dans un mélange d'alcool et de benzène et dans l'hyroxyde de sodium, la longueur des fibres et l'épaisseur pariétale obéissent à de faibles tendances dans l'axe nord-sud. L'analyse de régression montre une influence négative et positive des carrés de longitude et de l'altitude, respectivement, sur la solubilité dans l'hydroxyde de sodium. La température et la pluviosité apparaissent le plus souvent, en diverses combinaisons, dans les autres équations de régression. La répétabilité donne une bonne estimation de l'héritabilité. Tous les caractères, sauf l'épaisseur pariétale des fibres, possèdent une forte héritabilité ($R \geqslant 0.30$). Les facteurs étudiés du milieu influent notablement sur la variation, non liée au génotype, de tous les caractères sauf le diamètre des fibres et du lumen (coupe tangentielle) et la solubilité dans le mélange alcool et benzène. Les populations 11, 16 et 19 à 23 se pêtent le mieux à la fabrication de la pâte.

Zusammenfassung

Untersuchungen an der Schwarzfichte *(Picea mariana* (MILL.) B. S. P.), hatten ein zweifaches Ziel: Feststellung der Variationstendenzen und der Auswirkung von Genotyp und Umwelt auf 11 Holzmerkmale sowie Kennzeichnung von Beständen mit überlegener Eignung zur Zellstofferzeugung. Es wurde für diese Untersuchungen ein vier- und dreistufiges Klumpenstichprobenverfahren gewählt; die statistische und genetische Auswertung erfolgte mit Hilfe von Varianzanalyse, BONFERRONI-t-test, Wiederholbarkeitsberechnungen und mehrfacher Regressionsanalyse.

Bei den meisten Merkmalen veringert sich das Ausmaß der Variation in der Reihenfolge Baum, Stammscheibe und Bestand. Bei Bäumen schwankt die Tendenz je nach Merkmal. Hinsichtlich relativer Dichte, Löslichkeit in Alkohol/Benzol und Natronlauge sowie Faserlänge und Faserwanddicke wurden schwache Nord-Süd-Tendenzen festgestellt. Die Regressionsanalyse ergab einen negativen Einfluß des Quadrats der geographischen Länge auf die Natronlaugenlöslichkeit, jedoch einen positiven Einfluß des Quadrats der Höhenlage auf dieses Merkmal. In anderen Regressionsgleichungen sind Temperatur und Niederschlag die am häufigsten in verschiedenen Kombinationen auftretenden Parameter. Die Wiederholbarkeitswerte sind gute Schätzwerte für die Erblichkeit. Alle Merkmale mit Ausnahme der Faserwanddicke zeigen eine hohe Erblichkeit ($R \geqslant 0{,}30$). Bei allen Merkmalen, außer Faserdurchmesser, Lumendurchmesser (Fladerschnitt) und Alkohol/Benzol-Löslichkeit haben die von uns untersuchten Umweltfaktoren einen signifikanten Einfluß auf den nichtgenetischen Anteil der Variationen. Die Bestände 11, 16 und 19 bis 23 zeigten sich in ihrer Eignung zur Zellstofferzeugung überlegen.

Introduction

Breeding for wood quality has resulted in economically justifiable improvements in productivity throughout the world. However, the relative economic value of improving various wood properties varies with the species and its end use (NAMKOONG *et al.* 1969; BAREFOOT 1976; VAN BUIJTENEN *et al.* 1974). For example, the genetic improvement of fibre dimensions, relative density and chemical properties which vary at the species as well as infra-species levels and are genotypically as well as environmentally controlled, requires the establishment of the norms, ranges and trends in variation for formulation of a rational genetic improvement program (HALE 1961, 1962; RYDHOLM 1967).

In white pine *(Pinus strobus* L.) relative density varies significantly among provenances, within trees at breast height and at various heights up the bole but not with geographic coordinates of the seed sources (GILMORE and JOKELA 1978). OLESEN (1982) reports that in Norway spruce *(Picea abies* (L.)) tracheid length in the first formed secondary xylem ring is constant along the length of the stem but tracheid diameter increases axially as well as radially. Basic density is constant along the stem length in open grown trees but decreases with stem height in closed stands and shows considerable inter-tree variation. No correlation exists between tracheid length and basic density.

Although the genetics of black spruce *(Picea mariana* (MILL.) B.S.P.) have been studied during the past 20 years, very little work has been done on its wood characters. The weigthed mean relative density of 10 trees from Petawawa, Ontario, Canada was found to be 0.436 and the ethyl ether and 1% sodium hydroxide solubilities were 1.08—1.65% and 10.70—13.01% respectively, depending upon position of the sample within the stem (CLERMONT and SCHWARZ 1951). The unweighted mean relative density of 33 trees from Maine, New Hampshire, New York, Michigan, Wisconsin and Minnesota, U.S.A. was 0.384 ± 0.028 (BENDSTEN 1974). Similarly, fibre lengths in a black spruce tree were 900—3 700 μ and 3 200—3 800 μ in radial and axial directions respectively (RYDHOLM 1967). Subsequent studies of among tree differences (LADELL 1971) showed black spruce wood to be unusually uniform with reference to age. Adult characteristics are exhibited early in the tree's life. The changes after the 10th ring in some characters, and after the 15th or 20th ring in others, are minor compared with those taking place in the rings closest to the pith. The core of anomalous wood with changing characters is small and of little practical significance in mature trees. The radial ranges of fibre length, fibre diameter, lumen diameter and fibre wall thickness were 2 400—3 300 μ, 22.1—27.8 μ, 17.6—22.3 μ and 2.3—2.8 μ respectively at 25% height from the base. These characters had higher mean values in the radial than the tangential sections.

No information is yet available on the geographic trends in variation of wood properties of black spruce or the influence of genotypic and environmental factors on them. Consequently, a project for intensive study of the genetics of important characters of black spruce was intiated at the Newfoundland Forest Research Centre in 1973, and is the subject of this paper.

Material and Methods

Sampling Procedure

A four- and three-level cluster sampling procedure was adopted in which 23 populations were selected across insular Newfoundland as primary sampling units. Of these 21 were the same as or very close to the populations used in the regional black spruce provenance study (KHALIL 1975, 1981, (1984). *(Table 1, Fig. 1).* This sampling provided adequate north-south and coastal-inland distribution to represent most of the climatic and edaphic conditions in Newfoundland. Out of the 10 randomly selected dominant and codominant trees, spaced about 50 m apart to minimize consanguinity, two were selected in each of 21 pop-

Table 1. — Location of populations.

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
23	49.38	56.97	137	

* Rowe (1972).

ulations for the present study. Because of their location in the most valuable forest section, 25 and 5 trees respectively were selected from populations 22 and 23 respectively. The sample trees were over 90 years in age. Trees of that age are mature in Newfoundland (Ker 1976). A 5 cm thick disc was taken from the tree bole at 30 cm above ground level and at intervals of one-tenth of total height thereafter for a total of 10 discs. In a few cases all the 10 discs were not available for all the tests. A thin wedge, running from pith to cambium, was obtained from each disc as a representative sample of the disc. This was justified by the uniform nature of wood of mature trees (Ladell 1971). Separate portions of the wedge were macerated and microtomed to allow study of the radial and tangential cells and to do relative density and solubility tests in 1:2 mixture of 95% ethyl alcohol-benzene and 1% sodium hydroxide solution. The maceration consisted of 0.5 g air-dry thin wood sticks being placed in 15 ml of 30% hydrogen peroxide-glacial acetic acid for 24—48 hours at 60 °C; washed in distilled water for 24 hours, and shaken to separate the fibres. The fibres were stained with 2% safranin 0 and mounted in 50% glycerin on a slide for microscopic examination using the calibrated stage micrometer. The other tests were performed according to Anon. (1959, 1976, 1978), and Smith (1965). Ten fibres were sampled for all of characters Y_1—Y_7.

The Data

The following characters were studied on the material of each disc:

Fibre length (Y_1); Fibre diameter (radial section) (Y_2); Lumen diameter (radial section) (Y_3); Fibre wall thickness (radial section) (Y_4); Fibre diameter (tangential section) (Y_5); Lumen diameter (tangential section) (Y_6); Fibre wall thickness (tangential section) (Y_7); Unweighted mean oven-dry relative density (Y_8); Weighted mean oven-dry relative density (Y_9); Alcohol-benzene

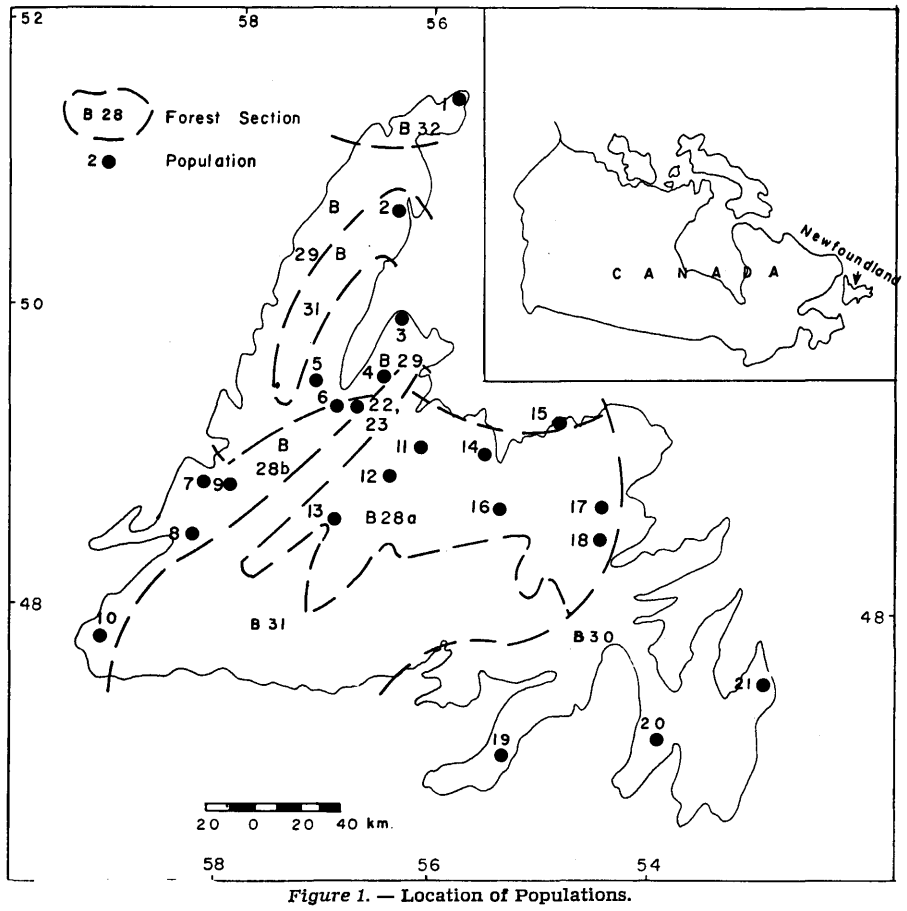

Figure 1. — Location of Populations.

Table 3. — Expected mean squares and degrees of freedom.

Source of variation	Characters with four sampling levels: Expected mean squares	Expected d.f.	Characters with three sampling levels: Expected mean squares	Expected d.f.
Populations	$\sigma^2 + k_1\sigma_T^2 + F(P_i^2)$	P-1	$\sigma^2 + k_3\sigma_T^2 + F(P_i)^2$	P-1
Trees within Populations	$\sigma^2 + k_2\sigma_T^2$	$\sum_{i=1}^{23} (T_i-1)$	$\sigma^2 + k_4\sigma_T^2$	$\sum_{i=1}^{23}(T_i-1)$
Discs within Trees within Populations	$\sigma^2 + F(D_i^2)$	$\sum_{i=1}^{23}\sum_{j=1}^{t_i} (D_{ij}-1)$	σ^2	$\sum_{i=1}^{23}\sum_{j=1}^{t_i} (D_{ij}-1)$
Fibres within Discs within Trees within Populations	σ^2	$\sum_{i=1}^{23}\sum_{j=1}^{t_i}\sum_{k=1}^{d_{ij}} (F_{ijk}-1)$		
Total		$\sum_{i=1}^{23}\sum_{j=1}^{t_i}\sum_{k=1}^{d_{ij}} F_{ijk}-1$		$\sum_{i=1}^{23}\sum_{j=1}^{t_i} D_{ij}-1$

F indicates "a function of".
k_1-k_4 = Coefficients of variance components which are complicated functions of the number of trees, discs and fibres in the analysis of the character concerned.
σ^2 is a mixture of fixed (populations and discs) and random (trees and fibres) effects.

solubility percent (Y_{10}); Sodium hydroxide solubility percent (Y_{11}).

Fibre wall thickness was calculated from fibre and lumen diameters. The weighted mean oven-dry relative density was obtained by weighting the oven-dry relative density (Ford-Robertson 1971) of each disc by its surface area.

Statistical Analyses

The arithmetic mean and standard deviation of each character in each population were calculated for ranking and Bonferroni t-test, and multiple regression analyses.

Hierarchical Analyses of Variance — Populations, trees within populations, discs within trees and fibres within discs represented the four hierarchical sampling levels. Analyses of variance over populations were performed for all characters, using four sampling levels for characters Y_1—Y_7 and three characters Y_8—Y_{11}. The mixed model consisted of populations and discs being fixed and trees and fibres being random effects. The equation in Steel and Torrie (1980) p. 159 was used for three-level sampling with addition of the term "E_{ijkl}" for effect of fibres (random). The expected error mean squares and the appropriate error terms used are shown in *Table 3.*

Due to the unequal numbers at sampling levels 2 and 3 the numerical values of the coefficients of various variance components varied from line to line in the analyses of variance table. This resulted in the calculation of a synthetic F-test for fibre length at the population level, with synthetic denominator degrees of freedom (Steel and Torrie 1980, pp. 163—164). For other variables the coefficients of variance components were similar enough to justify use of trees within populations as the appropriate denominator. The error term (fibres within discs within trees within populations) was the appropriate denominator for the F-tests for discs within trees within populations for all characters. The use of unequal number analysis technique did not require missing values estimates.

Hierarchical analyses of variance were performed for all characters for population 22, using three and two sampling levels for characters Y_1—Y_7 and Y_8—Y_{11} respectively, to study the distribution of variation among the sampling levels, and calculation of repeatability of each character as an estimate of its heritability. These analyses were also based on the mixed model in which tree and fibre effects were random and disc effects were fixed.

Ranking and Bonferroni T-tests — These tests were performed according to Douglas (1979) for all characters to make all possible pair-wise comparisons between populations and between forest sections B.28a, B.28b, B.29, B.30 and B.32 (Rowe 1972), using *Equation (1).* If the value of the contrast (C) was less than the test statistic (B) the null hypothesis H_0: C = 0; H_a: C ≠ 0 was not rejected.

$$B = t_{P,n,f}\left[\text{EEMS}\left(\sum_{i=1}^{m}\frac{c_i^2}{r_i}\right)\right]^{\frac{1}{2}} \quad \ldots\ldots\ldots\ldots\ldots (1)$$

where B = Value of the test statistic with which the value of each constant C* is compared; $t_{P,n,f}$ = tabulated value of t for an overall probability of P for n contrasts and f Experimental Error degrees of freedom; EEMS = Experimental error Mean Square; m = Number of means; r_i = Number of observations.

*C = $\sum c_i\bar{x}_i$, where $\bar{x}_i$ ist the mean value of population i and c_i is constant, such that $\sum c_i = 0$.

Repeatability — The repeatability of each character for population 22 was calculated as an estimate of its heritability to determine the magnitude and statistical significance of genotypic control on these characters. *Equation*

$$\hat{R} = \frac{\hat{\sigma}_T^2}{\hat{\sigma}_e^2 \quad \hat{\sigma}_T^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

where $\hat{R}$ = Estimated repeatability, $\hat{\sigma}_T^2 = \frac{MS(T)^{*2} - \text{Error } MS^{*3}}{K}$; $\hat{\sigma}_e^2$ = Error MS^{*3}; K = coefficient of $\hat{\sigma}_T^2$ in MS(T).

*2 M.S. of trees.
*3 M.S. of Discs within Trees.

(2) was used for repeatability estimates and *Equations (3)—(5)* for confidence limits of these estimates at the 0.05 level (Becker 1968, Bogyo and Becker 1963, Swiger *et al.* 1964). If the confidence limits included zero the null hypothesis H_0: R = 0, H_a: R≠ 0 was not rejected.

Multiple Regression Analyses — These analyses were performed to identify the sub-set of geographic and climatic factors which, singly or in combination, contribute most to the variation in each character. The factors for each population which together with their squares and first order interactions were used as independent variables were:

The standard error of $\hat{R}$, S.E. ($\hat{R}$) is defined as:

$$\text{S.E. } (R) = \left[\frac{2(F_{i..}-1)(1-\hat{R})^2 [1 + (K_2-1)\hat{R}]^2}{K_2^2(F_{i..}-T_i)(T_i-1)} \right]^{\frac{1}{2}} \quad \ldots\ldots\ldots\ldots (3)$$

where $F_{i..}$ = Number of fibres in all discs in all trees in location i; K_2 = Coefficient of σ_T^2 from analysis of variance computer output; T_i = Number of trees in location i.

$$\text{Confidence limits of } \hat{R} = \text{C.L.}(\hat{R}) = P_r \left[1-M_{\alpha/2} \leqslant R \leqslant 1-M_{1-\alpha/2} \right] = 1-\alpha \quad \ldots(4)$$

where P_r = Probability; M = Coefficient of $\hat{\sigma}_T^2$ in the Expected M.S.(T); α = the appropriate significance level; and

$$M_r = \frac{K_1 \text{ (Error M.S.) } F_r}{\text{(Trees M.S.) + (Error M.S.)}(K_1-1)F_r} \quad \ldots\ldots\ldots\ldots (5)$$

where F_r = Tabulated value of F-distribution at significance level r which is equal to $\alpha/2$ or $1-\alpha/2$.

latitude (X_1); longitude (X_2); altitude (X_3); mean number of days from January 1 to date of last spring frost (X_4); mean number of frost-free days (X_5) mean number of days from January 1 to date of commencement of growing season (mean daily temperature remained below 5 °C) (X_6); mean number of growing days (mean daily temperature remained above 5 °C) (X_7); mean temperature in May-September period (X_8); mean precipitation in May-September period (X_9); average maximum July temperature (X_{10}); mean number of degree-days above 5 °C (X_{11}); day length on June 21 (X_{12}). The step-wise regression with forward selection procedure was used (Draper and Smith 1981) with the model shown in *Equation (6).*

$$Y_k = \beta_o + \sum_{i=1}^{12} \beta_i X_i + \sum_{i=1}^{12} \beta_{i+12} X_i^2 + \sum_{i<j} \beta_{i+24} X_i X_j + \epsilon \quad \ldots\ldots\ldots\ldots (6)$$

where Y_k = Observed value of the dependent variable k; β_o = the intercept, β_i = the partial regression coefficient of the ith independent variable (i=1, ..., 12) X_i = ith independent variable, X_j = X variable with a larger subscript than X_i, ϵ = random error component.

The lack of fit mean squares was tested by an F-test, using the trees/populations mean squares as the denominator and the lack of fit mean squares as the numerator to determine the step at which to stop, i.e. the step when the F-value was nonsignificant at the 0.05 level. The contribution of the independent variables to the regression equation was estimated by calculating the coefficient of determination (R^2) according to *Equation (7).*

$$R^2 = \frac{\text{Total SS - Residual SS at cut-off stage}}{\text{Population SS}} \quad \ldots\ldots\ldots\ldots (7)$$

Results and Discussion

Estimates of Character Parameters

Considerable variation in all characters occurred among populations but no geographic trends were observed *(Table 2).* The analyses show some trends and elucidate the relative role of the genotype and the environment in controlling these characters.

Hierarchical Analyses of Variance

The results of the analysis of variance over populations are summarized in *Table 4.* As the F-tests have been performed with two sets of error terms the significance of a sampling level can be considered only with reference to the level used as the error term. Thus, populations are significant with reference to the trees within populations at various levels for all characters excent fibre and lumen diameters in tangential sections and alcohol-benzene solubility percent. This indicates the significant influence of environmental factors in controlling the characters studied.

For characters with four sampling levels both trees within populations and discs within trees within populations are significant sources of variation with reference to fibres within discs within trees within populations. For characters with three sampling levels trees within populations are significant at the 0.05 level with reference to discs within trees within populations. This indicates that within populations the variation among trees is higher than that within trees and that variation among discs within trees is higher than that within discs. The sampling procedure adopted for sampling within populations minimized the contribution of micro-environmental factors (like competition, crown size and soil nutrients) to the among tree variation, and that of position of the sample on the tree to the within tree variation. The high significance of variation among trees within populations and among discs within trees "in spite of the above efforts to minimize them" shows that most of the variation is due to the genotype of the male and female parent which appears to have the largest degree of control over wood characters in black spruce. Thus, these characters are controlled genotypically as well as environmentally.

Analyses of variance within population 22 *(Table 5)* and comparison of means of characters by discs within trees gives useful information about the distribution of variation among and within trees. As both trees and discs within trees were tested with the error term, fibres within discs within trees, the F-values for all sampling levels are comparable. Both trees and discs within trees are significant sources of variation in all characters (0.005 level), except unweighted mean oven-dry relative density for which discs within trees is nonsignificant (0.05 level). This shows significant among- and within-tree variation in all characters except unweighted mean oven-dry relative density. The contribution of discs to variation is also larger than that of trees, except for unweighted oven-dry relative density, and sodium hydroxide solubility percent where the reverse is true. These results indicate heterogeneity of trees in the axial direction with respect to all characters, except unweighted mean oven-dry relative density. The resultant trends are summarized below in which discs are numbered consecutively from the base to the top of the tree.

Fibre length *Fibre diameter* (radial section) *Lumen diameter* (radial section)	}	The highest value occurs at disc 4 and decreases progressively both below and above that disc.
Fibre wall thickness (radial section)	—	Disc 8 has the highest value; the values of all other discs are not considerably different from each other.
Fibre diameter (tan-	—	The values decrease progres-

Table 2. — Parameters of characters.

	Fibre Length (μ)			Cell Diameter (μ) (Radial)			Lumen Diameter (μ) (Radial)			Cell Wall Thickness (μ)(Radial)			Cell Diameter (μ) (Tangential)			Lumen Diameter (μ) (Tangential)			Cell Wall Thickness (μ)(Tangential)			Unweighted Oven Dry Relative Density			Weighted Oven Dry Relative Density			Alcohol Benzene Solubility %			1% NaOH Solubility %		
Rank	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)	Population	Mean	S.D. (±)
1	16	3148	588	17	12.39	2.07	17	9.75	2.17	6	1.50	0.42	17	12.81	2.28	1	10.19	1.83	2	1.58	0.46	3	0.4990	0.0728	3	0.5185	0.0403	3	3.6335	1.3471	3	20.5563	4.2136
2	17	2922	509	1	12.33	2.02	1	9.70	2.13	2	1.47	0.44	13	12.76	2.20	17	10.14	2.17	3	1.57	0.39	2	0.4800	0.0474	4	0.4790	0.0325	14	3.6195	2.3704	14	20.0210	2.7868
3	1	2876	482	5	12.25	2.56	13	9.67	2.50	5	1.44	0.35	1	12.70	1.92	11	10.03	2.13	6	1.55	0.40	4	0.4695	0.0336	2	0.4775	0.0290	15	3.1910	2.7760	20	19.8526	2.2009
4	5	2813	547	13	12.08	2.51	16	9.50	1.89	3	1.43	0.40	12	12.66	1.66	13	10.00	2.08	5	1.54	0.39	8	0.4535	0.0374	8	0.4585	0.0134	11	3.1290	1.0134	21	19.0954	2.9501
5	11	2772	627	16	11.91	1.97	11	9.44	1.89	4 18	1.40	0.33 0.36	11	12.65	2.20	12	9.83	1.62	4	1.51	0.42	15	0.4525	0.0429	15	0.4530	0.0283	2	3.1174	0.9264	13	18.9000	2.2971
6	18	2734	576	7	11.89	2.34	5	9.37	2.43	9	1.35	0.33	8	12.38	1.94	15	9.79	2.11	8	1.45	0.39	6	0.4440	0.0307	11	0.4495	0.0035	18	3.0230	1.3535	10	18.7789	4.5800
7	12	2711	526	18	11.81	2.18	7	9.33	2.15	1 17	1.32	0.44 0.35	18	12.35	1.81	18	9.68	1.75	12	1.42	0.30	10	0.4420	0.0349	6 13	0.4400	0.0226 0.0014	20	2.9133	0.7582	12	18.6526	1.6922
8	8 14	2651	535 456	11	11.72	1.95	14	9.29	1.81	12	1.29	0.30	15	12.30	2.15	10	9.59	1.77	7 9	1.40	0.33 0.33	11 13	0.4365	0.0410 0.0366	18	0.4370	0.0099	7	2.9005	1.4327	11	18.5000	1.0477
9	6	2607	540	6	11.62	2.15	15	9.18	1.99	7	1.28	0.29	10	12.28	1.95	14	9.51	1.43	13	1.38	0.35	17	0.4360	0.0582	17	0.4362	0.0580	6	2.8900	0.6523	18	18.4105	2.2857
10	4	2595	544	15	11.60	2.11	21	9.15	1.96	8	1.26	0.28	7	12.18	2.07	8	9.48	1.87	10	1.35	0.42	21	0.4345	0.0435	21	0.4325	0.0092	13	2.8025	0.8527	17	18.2421	1.3981
11	3	2594	565	22 23	11.51	2.25 2.06	23	9.10	1.96	22	1.21	0.25	5 6	12.08	2.55 2.17	7	9.38	2.01	18	1.34	0.37	16	0.4320	0.0309	10	0.4300	0.0325	8	2.7320	0.6656	16	18.0947	1.9063
12	13	2540	837	14	11.46	1.93	22	9.08	2.14	13,15 16,23	1.20	0.26, 0.40 0.32, 0.25	3 4	12.05	2.71 2.13	16	9.17	1.88	17	1.33	0.40	18	0.4310	0.0380	16	0.4275	0.0064	17	2.6940	0.7793	23	18.0857	2.4032
13	9	2534	546	21	11.42	2.09	18	9.02	2.20	10	1.17	0.27	14	11.93	1.54	23	9.07	1.65	11	1.31	0.32	12	0.4225	0.0213	12	0.4235	0.0035	12	2.6855	1.5219	15	17.9722	1.3830
14	10	2497	593	4	11.35	2.25	10	8.97	1.72	20	1.16	0.25	16	11.70	1.91	6	8.99	2.21	16	1.27	0.28	9	0.4180	0.0375	9	0.4205	0.0374	10	2.6695	1.1725	8	17.9389	2.1066
15	2	2495	428	10	11.32	1.81	19	8.87	1.93	19	1.15	0.35	9	11.59	1.99	5	8.98	2.36	1	1.26	0.58	1	0.4165	0.0168	1	0.4195	0.0064	21	2.6647	0.7228	1	17.5667	1.5636
16	15	2488	610	8	11.30	1.97	8	8.78	1.99	11 21	1.14	0.25 0.22	23	11.53	1.74	20	8.94	1.98	15	1.25	0.30	20	0.4155	0.0465	22	0.4173	0.0306	1	2.6295	0.7657	19	17.5222	1.6735
17	22	2318	465	12	11.28	1.79	12	8.71	1.77	14	1.09	0.20	2	11.38	2.28	3	8.91	2.65	22	1.24	0.28	22	0.4148	0.0389	23	0.4108	0.0185	22	2.5830	1.0474	4,6	17.0167	0.9237 1.1467
18	23	2241	495	19	11.17	2.02	6	8.62	2.35				20	11.27	2.08	21	8.83	1.84	23	1.23	0.25	23	0.4126	0.0226	7 20	0.4030	0.0000 0.0679	5	2.4970	0.8442	7	17.0118	2.3523
19	7	2215	527	9	10.94	2.03	4	8.54	2.13				21	11.13	1.83	9	8.79	2.07	14	1.21	0.26	7	0.4040	0.0215	14	0.3995	0.0148	16	2.2595	0.7666	22	16.8058	1.6002
20	21	2148	558	3	10.48	1.98	9	8.23	2.02				22	11.05	1.75	22	8.58	1.68	20	1.16	0.24	5	0.3975	0.0274	5	0.3990	0.0354	19	2.2590	0.6253	2	16.7222	1.2374
21	20	2141	432	2	9.96	1.51	3	7.62	2.21				19	10.67	1.92	4	8.56	2.05	21	1.15	0.24	14	0.3950	0.0504	19	0.3540	0.0226	9	2.2550	1.1789	5	16.4105	1.1967
22	19	2039	395	20	9.90	2.20	20	7.58	2.19							19	8.38	1.82	19	1.14	0.25	19	0.3810	0.0348				4	2.1960	0.5884	9	15.3944	1.8128
23							2	7.01	1.77							2	8.23	2.25										23	2.1400	0.6258			
Mean		2553			11.44			8.89			1.27			11.98			9.26			1.35			0.4315			0.4316			2.7598			18.0682	
S.D.		275			0.65			0.71			0.12			0.60			0.58			0.14			0.0276			0.0332			0.4095			1.1476	

Summary of Bonferroni T-Tests (0.05 level).
Fibre length — Forest Section B.28a > B.30.
Cell wall thickness (radial) — Forest Section B.28a > B.29 > B.30
B.28b > B.30.
Cell wall thickness (tangential) — Forest Section B.29 > B.30.
Unweighted oven-dry relative density-Population 3 > 19, 22.
Unweighted oven-dry relative density-Population 3 > 19, 22, 23.
1% NaOH solubility % — Population 3 > 9.

Table 4. — Summary of analyses of variance.

Source of variation	Fibre length			Fibre diam. (Radial)			Lumen diam. (Radial)			Fibre wall thickness (Radial)			Fibre diam. (tangential)		
	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F
Populations	22	17 618 700	2.19*	22	128.5059	2.61***	22	98.0387	2.26**	22	4.4757	3.61***	22	82.1422	1.12NS
Trees within Populations	48	7 217 400	3.42***	49	49.2521	30.39***	49	43.4077	27.88***	49	1.2414	14.46***	49	73.4746	31.42***
Discs within Trees within Populations	568	2 109 170	20.20***	625	26.0311	16.06***	625	23.7213	15.24***	625	0.3515	4.09***	625	28.2877	12.10***
Fibres within Discs within Trees within Populations	5 749	104 428		6 273	1.6207		6 273	1.5570		6 273	0.0859		6 273	2.3383	
Total	6 387			6 969			6 969			6 969			6 969		

Lumen diam. (tangential)			Fibre wall thickness (tangential)			Unweighted mean oven-dry R.D.			Weighted mean oven-dry R.D.			Alcohol-benzene solubility (%)			Sodium hydroxide solubility (%)		
D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.	F
22	98.0596	1.34NS	22	3.1006	2.68***	22	0.0130	2.41**	22	0.0021	2.33***	22	3.8917	1.23NS	22	35.9325	2.76***
49	73.0993	34.18***	49	1.1554	17.27***	49	0.0054	5.34***	49	0.0009		49	3.1662	2.72***	49	13.0379	3.75***
625	27.6846	12.95***	625	0.4074	6.09***	468	0.0010		468			633	1.1621		570	3.4722	
6 273	2.1386		6 273	0.0669													
6 919			6 919			539			539			704			641		

*** = Statistically significant (0.005 level).
** = Statistically significant (0.01 level).
NS = Statistically nonsignificant (0.05 level).

Table 5. — Summary of analyses of variance in population 22.

Source of variation	Trees			Discs within trees			Fibres within discs within trees	
Character	D.F.	M.S.	F	D.F.	M.S.	F	D.F.	M.S.
Fibre length	24	4 581 290	2.69***	169	1 703 440	17.44***	1 744	97 683
Fibre diameter (radial)	24	40.0520	1.75*	223	22.8419	19.46***	2 232	1.1741
Lumen diameter (radial)	24	41.4972	1.97***	223	21.0893	19.55***	2 232	1.0788
Fibre wall thickness (radial)	24	1.3907	5.43***	223	0.2562	3.80***	2 232	0.0675
Fibre diameter (tangential)	24	103.5439	2.96***	223	34.9670	15.19***	2 232	2.3013
Lumen diameter (tangential)	24	106.4815	3.37***	223	31.5983	15.21***	2 232	2.0779
Fibre wall thickness (tangential)	24	1.822	3.76***	223	0.3141	5.69***	2 232	0.0552
Unweighted mean oven-dry relative density	24	0.0051	7.36***	Discs 8	0.0005	0.77NS	Discs x Trees = Error	
Alcohol-benzene solubility percent	24	3.3273	8.75***	9	12.30	32.36***		
Sodium hydroxide solubility percent	24	85.16	10.84***	9	14.84	5.04***		

Note: The F-values were calculated after accounting for missing cells and the degrees of freedom associated with them.

gential section) sively from disc 1 to disc 10.

Lumen diameter (tangential section) — Discs 1 and 2 have the highest values. The values decrease progressively from disc 3 to 10.

Fibre wall thickness (tangential section) — Disc 2 has the highest value. The distribution of the other discs for the trait shows no trends, but the mean value of this character over populations shows the same trend as for lumen diameter (tangential section).

Unweighted mean oven-dry relative density — Disc 9 has the highest value but all other discs have practically the same value.

Alcohol-benzene solubility percent, *Sodium hydroxide solubility percent* — The values, highest at disc 10, decline progressively to disc 3 and rise again in discs 1 and 2.

Results based on the means over all the 23 populations are very similar to those above. Thus, these trends can be taken to apply to the black spruce of Newfoundland.

Ranking and Bonferroni T-Tests

Significant differences between pairs of populations are exhibited only for unweighted and weighted mean oven-dry relative densites and sodium hydroxide solubility percent. The results show a weak north to south reduction in the means of these characters *(Table 2)*. General comparisons between pairs of forest sections show a reduction from north to south in the means of fibre length, fibre wall thickness (tangential section), unweighted mean oven-dry relative density and sodium hydroxide solubility percent. The highest values for fibre wall thickness (radial section) are in central Newfoundland; reductions occur in both northern and southern directions. This is an indication of low environmental influence on these characters, which is the result of their low value in natural selection. These results support those of the analyses of variance.

Repeatability

All repeatability values are statistically significant at the 0.05 level *(Table 6)*. Repeatability, which is expressed by the conceptual formula $R = (\sigma^2_G + \sigma^2_{EG})/\sigma^2_P$P*, is an estimate of heritability, which is upward biased by the factor σ^2_{EG}/σ^2_P. The numerator, σ^2_{EG}, is the environmental variance contributing to the between-individuals component and is caused by permanent and non-localized circumstances. This factor has been minimized in this study by maximizing the homogeneity of the samples at all sampling levels. Hence, the repeatability values in this study are good estimates of heritability with very little upward bias. Significant values of repeatability indicate strong genotype control on the character concerned.

On the basis of these results characters have been classified subjectively into those with high ($\geqslant 0.30$) and low ($R < 0.30$) heritability. All characters, except fibre wall thickness (radial and tangential sections), have reasonably high heritability. This indicates a good opportunity for genetic improvement of these characters by selection and breeding.

Multiple Regression Analyses

It has been shown above that geographic and climatic factors have a partial influence on the expression of most characters. The use of multiple regression analyses has allowed identification of the subset of these factors which, singly or in combination, contribute most to the variation in each character. *Table 6* presents these equations and

* R, σ^2_G, σ^2_{EG} and σ^2_P are repeatability, genotypic variance, general environmental variance and phenotypic variance respectively.

Table 6. — Relative role of genotype and environment in controlling variation in characters.

Character	Role of Genotype: Repeatability	Confidence limits: Lower	Confidence limits: Upper	Remarks	Role of Environment: Regression equation	Coefficient of determination
Fibre length (Y_1)	0.3723	0.2619	0.5377	High repeatability	$\hat{Y}_1 = 3289.8924 - (0.2222 \times 10X_6X_8) + (0.8448X_7X_{10})$	0.4437***
Fibre diameter, radial section (Y_2)	0.2503	0.1658	0.3965	High repeatability	$\hat{Y}_2 = 11.7452 - (0.4020 \times 10^{-2}X_4X_8) + (0.7443 \times 10^{-2}X_1X_{10})$	0.4420***
Lumen diameter, radial section (Y_3)	0.2742	0.1840	0.4260	High repeatability	$\hat{Y}_3 = 8.2208 - (0.2630 \times 10^{-2}X_4X_8) + (0.2144 \times 10^{-2}X_6X_{10})$	0.3007***
Fibre wall thickness, radial section (Y_4)	0.1651	0.1041	0.2821	Low repeatability	$\hat{Y}_4 = -0.5811 + (0.2700 \times 10^{-2}X_2X_{12}) - (0.7115 \times 10^{-2}X_8X_{12}) + (0.3837 \times 10^{-3}X_7X_{10}) - (0.6719 \times 10^{-4}X_9X_{12})$	0.6037***
Fibre diameter, tangential section (Y_5)	0.3072	0.2097	0.4651	High repeatability	$\hat{Y}_5 = 9.4718 + (0.5726 \times 10^{-2}X_{10}X_{12})$	0.1631NS
Lumen diameter, tangential section (Y_6)	0.3362	0.2329	0.4980	High repeatability	$\hat{Y}_6 = 6.1924 - (0.4358 \times 10^{-4}X_4X_9)$	0.2007*
Fibre wall thickness, tangential section (Y_7)	0.1706	0.1079	0.2900	Low repeatability	$\hat{Y}_7 = 0.7825 + (0.8694 \times 10^{-3}X_1X_{12}) - (0.4991 \times 10^{-4}X_8X_9)$	0.4356**
Unweighted mean oven-dry relative density (Y_8)	0.4686	0.3099	0.6550	High repeatability	$\hat{Y}_8 = 0.0232 - (0.4064 \times 10^{-4}X_8X_9) + (0.8335 \times 10^{-4}X_7X_{10}) + (0.4356 \times 10^{-4}X_2X_6) + (0.8865 \times 10^{-6}X_3X_5)$	0.4170***
Weighted mean oven-dry relative density (Y_9)	-	-	-	—	$\hat{Y}_9 = -0.0538 - (0.3809 \times 10^{-4}X_8X_9) + (0.9202 \times 10^{-4}X_7X_{10}) + (0.5036 \times 10^{-4}X_2X_6)$	0.3478***
Alcohol-benzene solubility percent (Y_{10})	0.4367	0.2922	0.6199	High repeatability	$\hat{Y}_{10} = -3.8284 + (0.8500 \times 10^{-3}X_1X_7)$	0.1550NS
Sodium hydroxide solubility percent (Y_{11})	0.6042	0.4578	0.7583	High repeatability	$\hat{Y}_{11} = 34.1623 - (0.5332 \times 10^{-2}X_2^2) + (0.2577 \times 10^{-4}X_3^2)$	0.4899***

*** Statistically significant (0.005 level).
** Statistically significant (0.01 level).
* Statistical significant (0.05 level).
NS Statistically nonsignificant (0.05 level).

also shows the order of appearance of independent variables, which indicates their relative importance.

The independent variables acting singly affect only the sodium hydroxide solubility percent, which is negatively correlated with the square of longitude and positively correlated with the square of the altitude, each at fixed values of the other. The independent variables in the other regression equations vary in number as well as in the subset chosen for inclusion, although factors of temperature and precipitation appear most frequently in various combinations. This is to be expected because models of this type are quite data-dependent. For most characters the geographic and climatic factors are highly correlated with the character. The exceptions are fibre and lumen diameters in tangential sections and alcohol-benzene solubility percent for which populations are a nonsignificant source of variation *(Table 4)*. The results of variance and regression analyses support each other and indicate lack of significant influence by geographic and climatic factors on the above three characters.

Table 6 also lists the values of repeatability and coefficient of determination for regression analyses for each character. Repeatability values provide estimates of heritability or genotypic control. The remaining variation is the result of environmental factors. The coefficients of determination of regression equations represent the proportion of this variation produced by the subset of the geographic and climatic factors included in the respective regression equations. This subset represents the major contributors to the non-genotypic portion of the variation. However, it is important to note hat these equations do not fully account for the non-genotypic variation in these characters. When the stepwise regression equations were advanced to stage 20 with 20 different combinations of X-values the coefficients of determination reached their maximum values of 0.9164—0.9999 indicating that they completely influence the non-genotypic part of variation. The equations presented in *Table 6* represent only the most important independent variables.

Identification of Superior Populations

The most suitable characters for selection of superior populations for pulping quality of wood are fibre length, weighted mean oven-dry relative density, fibre wall thickness (radial and tangential sections), alcohol-benzene solubility percent and sodium hydroxide solubility percent. High values of the first two and low ones of the last four characters should be used for this appraisal. Superior populations for pulping should be selected from *Table 2*, restricting the choice to the fourth quartile for fibre length and weighted mean ovendry relative density, and to the first quartile for the other four characters. The actual choice would depend upon a judicious combination of these characters. As the requirements with reference to the combination of these characters differ with the type of paper to be manufactured it is not possible to set standards for combination which can be used in selecting superior populations. However, fibre length, weighted mean oven-dry relative density and fibre wall thickness can be considered of primary importance, and alcohol-benzene and sodium hydroxide solubility percent, of secondary importance. On this basis populations 11, 16, 19, 20, 21, 22 and 23 appear superior *(Table 1)*. When these or adjoining populations are chosen for breeding purposes a decision should be made on the relative importance of the above six characters. Then mass or family selections of the proper selection intensity should be made in order to achieve the required genetic gain.

Conclusions

1. Repeatability values are good estimates of heritability with minimum bias.
2. The pattern of distribution of variation between sampling levels indicates significant genotypic control on all characters and significant environmental control on all except fibre and lumen diameters (tangential sections) and alchol-benzene solubility.
3. Fibre length, fibre and lumen diameters (radial and tangential), unweighted oven-dry relative density, solubility in alcohol-benzene and sodium hydroxide are under strong genotypic control and fibre wall thickness (radial and tangential sections) under weak genotypic control. Trees are heterogenous axially with respect to all characters except unweighted oven-dry relative density. Trends vary with character.
4. Of the geographic and climatic factors tested only sodium hydroxide solubility is correlated negatively with the square of longitude and positively with the square of altitude each with fixed values of the other. Other characters are partially correlated with a variable number of geographic and climatic factors in various combinations, of which temperature and precipitation are the most frequent components.
5. There are weak geographic trends as follows:
   i. North to south reduction in unweighted and weighted mean oven-dry relative density, alcohol-benzene and sodium hydroxide solubility, fibre length and fibre wall thickness (tangential).
   ii. Fibre wall thickness (radial section) is greatest in central Newfoundland and becomes less in both northerly and southerly directions.
6. Populations 11, 16, 19, 20, 21, 22 and 23 have superior pulping qualities.

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Umweltbelastung und Anpassungsfähigkeit von Baumpopulationen

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Zusammenfassung

In diesem Land hat die rasche Zunahme der Belastung von Waldökosystemen durch anthropogen bedingten Umweltstreß dazu geführt, daß bereits über die Hälfte des Waldbestandes akute Schäden zeigt und das Ausmaß der Sekundärschäden unübersehbar ist. Die Fachliteratur liefert inzwischen zahlreiche Hinweise dafür, daß die Wirkung von Umweltbelastungen genetisch selektiv ist. Letzteres hat in Verbindung mit den allgemeinen Streßwirkungen von Umweltbelastungen den Verlust genetischer Vielfalt und die damit verbundene Aushöhlung der ohnehin eingeschränkten natürlichen Anpassungsfähigkeit der gegenwärtigen Waldbaumgeneration zur Folge. Diese Anpassungsfähigkeit hat in der Vergangenheit flexible Reaktionen auf Umweltänderungen ermöglicht, und das Überleben bis zur Gegenwart sichergestellt. Die grundlegenden Prinzipien der Anpassung an verschiedene Formen von Umweltänderungen werden ausführlich dargestellt und die Charakteristika von Waldbäumen angesprochen. Bei aller Vielgestaltigkeit genetischer Anpassungsmechanismen bei Waldbäumen kann aufgrund experimentell belegter Erkenntnisse und allgemeingültiger Überlegungen davon ausgegangen werden, daß hohe genetische Vielfalt bzw. Diversität und hohe Heterozygotie notwendige Voraussetzungen für die Erhaltung der Anpassungsfähigkeit von Waldbaumpopulationen und damit für die Stabilität der von ihnen getragenen Ökosysteme sind.

Daher sind alle Maßnahmen und Einflüsse abträglich, welche diese genetischen Voraussetzungen einschränken. Zum einen werden Folgewirkungen forstlicher Maßnahmen, wie etwa die Auswahl von Vermehrungsgut und die Bestandesgründung beschrieben, wobei die besondere Bedeutung der sexuellen Reproduktion für die Erhaltung der Anpassungsfähigkeit hervorgehoben wird. Aus dem Bereich der Züchtung und des Waldbaues resultierende Einschränkungen der Anpassungsfähigkeit können sich in einer Situation ungewöhnlich rasch sich verschlechternder Umweltbedingungen als besonders nachteilig für die Überlebensfähigkeit von Waldbaumpopulationen erweisen. Zum anderen stellen sich zur Zeit die durch Immissionsbelastungen bedingten genetischen Konsequenzen so einschneidend dar, daß eine Neuorientierung herkömmlicher Verfahrensweisen in der Forstpflanzenzüchtung und in den davon betroffenen Teilen des Waldbaues unumgänglich erscheint.

Als Grundlage für die Planung praktischer Maßnahmen wird ein Katalog von grundlegenden Empfehlungen gegeben, um durch wirkungsvollere Nutzung der noch vorhandenen genetischen Vielfalt eine weitestmögliche Erhaltung der natürlichen Anpassungsfähigkeit sicherzustellen. Der gegenwärtige Kenntnisstand läßt den Schluß zu, daß der Primat der sexuellen Reproduktion nicht nur für die Erzeugung von forstlichem Vermehrungsgut zu gelten hat, sondern auch für die Form der Genkonservierung: Die Einlagerung von Samen dient der Erhaltung genetischer Vielfalt ungleich wirksamer, als dies jede Form der Klonkonservierung zu leisten imstande wäre. Genkonservierung ist jedoch nur eine flankierende Maßnahme der absolut vorrangigen Erhaltung der Anpassungsfähigkeit von