Table 3. — Average height (in feet), crown score, stem straightness score and percent fusiform fust infection for nine test locations.

County	State	Avg. Height	% Rust infection	Avg. crown score	Avg. straightness score
Jackson	La.	17.65	50.03	3.3	3.0
Shelby	Ala.	12.06	3.18	3.7	3.2
Bullock	Ga.	11.39	16.38	2.9	2.6
Rhea	Tenn.	11.11	3.96	3.4	3.4
Halifax	N.C.	10.61	3.88	3.5	3.5
Columbus	N.C.	10.49	15.76	3.8	3.2
Murray	Ga.	9.85	2.41	3.4	3.3
Kershaw	S.C.	8.27	14.84	—	—
Tyrrell	N.C.	7.79	1.47	3.5	3.8

eines 1968 groß angelegten Experiments zum Studium von Genotyp-Umwelt Interaktion und genotypischer Stabilität bei ***Pinus taeda*** behandelt. Der Versuch soll u. a. über geeignete genotypische Stabilitätsparameter, über Heterosis von Nachkommenschaften weit entfernter Eltern, die Verfälschung von Voraussetzungen des genetischen Gewinns durch Genotyp-Umwelt Interaktion und über die genotypische Stabilität von Nachkommenschaften frei abgeblühter Bäume und von Kreuzungen zwischen und innerhalb von Populationen Aufschluß geben.

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Genotype x Environment Interaction and Genotypic Stability in Loblolly pine

II. Genotypic stability comparisons*

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Introduction

Loblolly pine is the leading commercial forest species in the Southeastern United States. Its natural range extends from Maryland through the Carolinas to Georgia and northern Florida in the east and westward to east Texas. In recent years, there has been a marked trend of accelerated activity in forest production in this region with loblolly pine receiving much of the attention. It has become a stated objective of the large industrial forest land owners and the United States Forest Service that the projected accelerated regeneration be done only with genetically improved trees (ZOBEL 1975). This, together with the facts that (i) loblolly pine has a wide natural range, (ii) some of the forest land owners operate in large areas covering diverse environments, (iii) a very heavy exchange of research ideas and breeding materials has been instituted amongst the widespread membership of the co-operative tree improvement programs and (iv) intensive culturalpractices of site preparation and fertilization are becoming more widely accepted, makes it imperative that the tree breeder ensure that selected genotypes have the widest adaptability along with superior volume production if he is to avoid 'genetic slippage' due to genotype X environment interactions. A practical handle on adaptability can be achieved through genotypic stability analyses. The investigation reported here was carried out to determine the stability of performance of groups of loblolly pine genotypes across several locations. The specific objectives of the investigation were:

1. To compare parameters of genotypic stability useful in tree breeding.
2. To compare the stability of wide crosses compared with local crosses.

Literature Review

Ever since the introduction of the analysis of variance technique in the 1920's, plant breeders have reported statistically significant genotype X location, genotype X year or genotype X location X year interactions. For a long time such interactions were considered intractable and the routine has been to reduce them through experimental designs or to scale them out prior to analyses (BREESE 1971). Experimental and theoretical studies of genotypic stability has advanced in two divergent directions: one followed by those interested in the underlying genetic mechanisms and the other followed by plant breeders seeking practical measures of stability.

The genetic approach can be traced to LERNER'S (1954) development of the concept of genetic homeostasis. GRANT (1963) made the distinction between phenotypic plasticity and physiological homeostasis. He pointed out that plants largely rely on phenotypic plasticity while animals rely on physiological homeostasis for their stability in changing environments. Of particular interest in this category are the studies of JINKS and MATHER (1955) which showed that the extent to which a genotype interacts with the environ-

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ment is a highly heritable character. These ideas have been advanced by Allard and Bradshaw (1964) into population fitness categories. They added the concepts of 'individual buffering' which corresponds to Grant's phenotypic plasticity and 'population buffering' which can be viewed as increased efficiency through the utilization of diverse microniche's. Experimtal evidence has accumulated in support of the hypothesis that the more heterogenous and heterozygous the breeding population, the more stable it is to changes in environmental conditions (Allard 1961, Eberhart 1969, Scott 1967). In the present study with loblolly pine, experimental testing of this hypothesis will be obtained by comparing the stability of wide crosses with stability of local crosses.

Stability analyses have followed three trends in development for practical application. Firstly, there are those techniques aimed at determining individual contributions to the genotype × environment interactions sums of squares in analysis of variance. This group includes the method introduced by Plaisted (1959) where individual genotypes are eliminated from the general analysis one at a time and the resulting reductions in genotype × environment interaction variance is taken as their proportionate contributions. A similar method was advanced by Wricke (1962) whereby the individual contribution to the total genotype × environment interaction sums of squares are calculated. Wricke called this stability measure *ecovalence* and it is simply $\Sigma_j gl^2_{ij}$. The ecovalence has been calculated in the present study. Skukla (1972) considered a similar parameter which he called *stability variance*. This can be expressed as $\Sigma_j(gl_{ij} + \bar{e}_{ij})^2$ where $\bar{e}_{ij}$ is the mean random error effect associated with measurement of the i^th^ genotype in the i^th^ environment (Freeman 1973).

The second class of techniques involve regression analyses. The principle was first discussed by Yates and Cochran (1938) but received little attention until its development and application by Finlay and Wilkinson (1963). A similar technique was developed by Eberhart and Russell (1966) who also proposed a second stability parameter — the deviations from linear response. In these regression analyses, an environmental index measured as the mean of all genotypes at a given environment is used. However, Hardwick and Wood (1972) have proposed that factors of the environment that are important physiologically to the species being studied be used instead of the index. In the present study, a regression method of the type developed by Eberhart and Russell has been used.

The third class of practical analytical techniques involve extensions of the regression concept. Regressing the mean of a genotype on the mean of all genotypes at a location (of which it is a constituent) introduces a forced covariance that complicates interpretation. To avoid this, Tai (1971) has used structural analysis to calculate a pair of stability parameters in his studies with potatoes. This method has been explored for use in this study. A technique that makes use of Euclidian distances to derive 'relative genotypic stability' and 'comparative genotypic stability' was proposed by Hanson (1970).

These genotype stability concepts have received very little attention in forest tree breeding despite the fact that this is an area where they should prove very beneficial. The regression and ecovalence stability parameters have been applied by Morgenstern and Teich (1969) to data from an experiment with Jack pine provenances grown in 12 locations. Recently, Shelbourne (1972) reviewed the literature and commented on the potential use of these stability analyses in tree breeding.

When genotypes are grown in several environments, some show stable performance like in case 1 (b = 0) in the *figure 1* where b is the regression coefficient. This is the case when the genotypes are completely unresponsive to changes in environments. Such genotypes are not desirable in breeding programs because they cannot take advantage of the improved environments. Other genotypes show performance like in case 2 (b = 1) where the added performance in better environments is proportional to improvement in environmental quality. In this discussion, such genotypes will be regarded as having average stability. Cases 3 (b > 1) and 4 (b < 1) represent genotypes that have below average and above average stability of performance respectively. Relative to the average value of b = 1, genotypes that have b > 1 will perform better than average in better environments but less than average in poor environments. Conversely, genotypes with b < 1 will perform less well in better environments but better in poor environments. Therefore, depending on whether one is breeding for

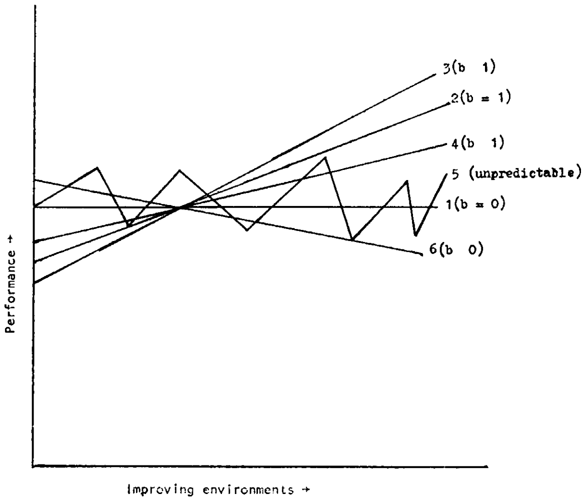

Figure 1. — Graphical representation of genotypic stability types: explanation in the test.

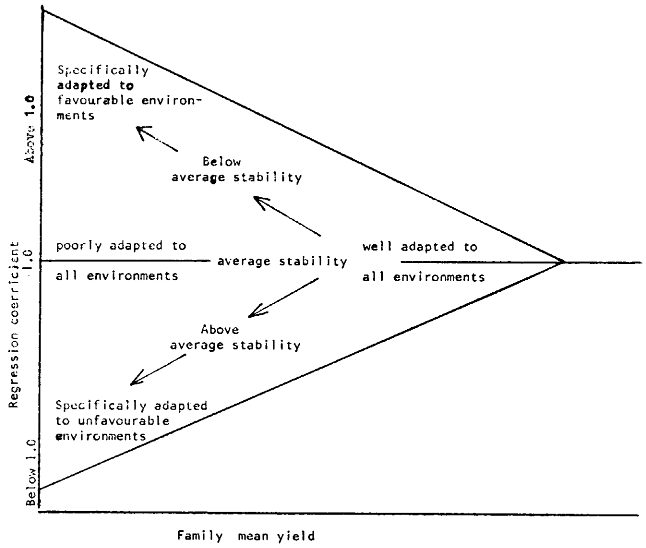

Figure 2. — Family regression coefficients plotted against family mean performance; explanation in text (After Finlay and Wilkinson, 1963).

poor or good environments, he can choose genotypes with stability case 4 and case 3 respectively. Some genotypes show unpredictable performance across environments as shown for case 5. Such genotypes should be avoided in any breeding programm. Lastly, genotypes can perform worse in better environments as shown in case 6 ($b < 0$). While this last case is unlikely to occur for most traits that tree breeders work with, it has been observed in cultural improvements aimed at increasing flower production in seed orchards (Schultz 1971).

The phenotypic regressions described above were transformed into adaptability concepts by Finlay and Wilkinson (1963) as shown on *figure 2.*

The technique for assessing genotypic stability consists of growing a number of genotypes in a number of environments, quantifying the environments by computing the average expression of all genotypes at each environment and estimating linear regression of the value of each genotype on the mean values for environments (Breese 1971). This is the method as it was first proposed by Finlay and Wilkinson (1963). It is illustrated graphically in *Figure 3.* The mean of all genotype at an environment is used as a biological index of environmental quality.

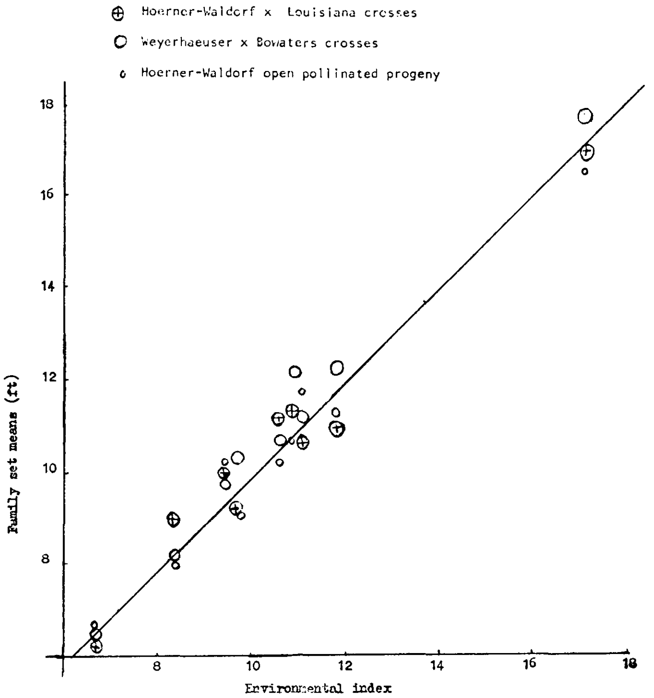

Figure 3. — Graphical presentation of the relationship between family set means and environmental index (mean of all genotypes at the particular environment).

A slight deviation from the method above was proposed by Eberhart and Russell (1966). Their altered method uses the mean of all genotypes at an environment minus the mean over all environments as the environmental index.

Statistical Models and Data Analysis

For the regression coefficient parameter, the model of Eberhart and Russell was used as follows:

$$\bar{X}_{ij} = \bar{X}_{i.} + b_i\,(\bar{X}_{.j} - \bar{X}_{..}) + d_{ij}$$

where $\bar{X}_{ij}$ is the family mean of the i^{th} family at the j^{th} environment ($i = 1,2,\ldots, m$, $j = 1,2,\ldots, p$), $\bar{X}_{i.}$ is the mean of the i^{th} family over all environments, b_i is the regression coefficient that measures the stability of the i^{th} family across the environments, $\bar{X}_{.j}$ is the mean of all families at j^{th} location, $\bar{X}_{..}$ is the mean of all the families over all environments and d_{ij} is the deviation from linear response. The following model was used for Tai's structural analysis method:

$$X_{ijk} = mu + g_i + l_j + (gl)_{ij} + b_{jk} + e_{kij}$$

where X_{ijk} is the phenotypic value of the i^{th} family in the k^{th} replicate in the j^{th} environment, mu is the mean of all families over all environments, g_i is the effect of the i^{th} family, l_j is the effect of the j^{th} environment, $(gl)_{ij}$ is the effect of the interaction between the i^{th} family and the j^{th} environment, b_{jk} is the effect of the k^{th} replicate in the j^{th} environment and e_{ijk} is the random error deviate on the i^{th} family in the k^{th} replicate in the j^{th} environment.

The interaction term, can be partitioned into two components:

$$(gl)_{ij} = \alpha_i l_j + d_{ij}$$

Computationally, α and λ parameters were calculated using mean squares from appropriate analysis of variance *(table 4)* as follows:

$$\alpha_i = \frac{\Sigma[\bar{X}_{.j.} - \bar{X}_{...})\,(B)]/(p - 1)}{(MSL - MSB)\,mr}$$

and

$$\lambda_i = \frac{\Sigma(B)^2 - \alpha_i\Sigma[\bar{X}_{.j.} - \bar{X}_{...})\,(B)]/(p - 1)}{(m - 1)\,MSE/mr}$$

where $B = (\bar{X}_{ij.} - \bar{X}_{.j.} - \bar{X}_{i..} + \bar{X}_{...})$ and r is the harmonic mean of the number of replication per location, MSL is the mean square for locations, MSB is the mean square for replications within environment MSE is the pooled error mean square. The steps involved in the calculation of α_i and λ_i are detailed in *appendix 1.*

The ecovalence is calculated as follows:

$$\Sigma_i gl_{ij}{}^2 = \Sigma_j\,[X_{ij} - (X_{i.}/p) - X_{.j}/m) - (X_{..}/pm)]^2$$

where Σ_j stands for sum over j, X_{ij} is the height growth of the i^{th} family at location j, $X_{i.}$ is the sum of height growth values over all locations, $X_{.j}$ is the sum of height growth for all families at location j,$X_{..}$ is the grand total height

Table 4. — Pooled analysis of variance for height growth used in the calculation of Tai's α and λ stability parameters

Source of variation	DF	SS	MS	
Environment	72	9335.54	129.66 **[a]	(MSL)
Reps within environments	301	1627.19	5.4059**	(MSV)
Families within sets	70	2054.42	29.3488**	(MSB)
Families (sets) × environment	112	727.51	6.50 **	(MSVL)
Polled Error	1198	3409.76	2.846	(MSE)

[a] Significant at the .10% probability level.

Appendix 1. — An Example to show the steps for calculation of three genotypic stability parameters. Family Set 4 = Hoerner-Waldorf O.P. in *Table 1* is used in this example.

	Locations									
	6	3	4	1	9	8	7	2	5	
X_{4j}	9.09	11.71	10.54	16.32	6.51	8.05	9.83	11.11	10.26	$\bar{X}_4 = 10.38$
$X_{.j.}$	9.71	11.05	10.87	17.26	6.58	8.30	9.38	10.83	10.58	$\bar{X}_{...} = 10.45$
$\hat{e} = (X_{.j.} - X\ldots)$	—.74	.60	.42	6.81	—3.87	—2.15	—1.07	1.38	.13	
$\hat{e}^2$	.55	.36	.18	46.37	14.62	4.62	1.14	1.90	.02	$\sum e^2 = 70.12$
$\hat{e}f = B$	—.55	—.78	—.26	—.87	0	—.18	.52	.65	.25	
$(\hat{e}f)^2$	.30	.61	.07	.76	0	.03	.27	.42	.06	$\sum (\hat{e}f)^2 = 2.52$
$T = \hat{e}.(\hat{e}f)$	.41	.47	—.11	—5.92	0	.39	—.56	—.90	—.03	$\sum T = 6.25$
$R = \hat{e}.X_{4j.}$	—6.73	7.06	4.43	11.43	—25.19	—17.31	—10.52	15.33	1.33	$\sum R = 79.54$

Tai's α and λ.

$$\alpha_4 = \frac{\sum T/(p-1)}{(MSL - MSB)mr} = \frac{-6.25/8}{26.18} = -.029$$

$$\lambda_4 = \frac{\sum (\hat{e}f)^2 + 181/(p-1)}{(m-1)\,MSE/mr} = \frac{2.52 + .02}{7.03} = .356$$

growth, p and m are the numbers of locations and families respectively.

Results and Discussion

Genotypic stabilities reported here are those of sets of families ie. a group of open-pollinated families from one region, a set of wide crosses e.t.c. The performance in height growth of commercial checks, open-pollinated progeny, within orchard crosses and wide crosses are shown in *Table 1*. It is evident that families tend to retain same relative ranks from location to location which is an indication that genotype × environment interaction may not be very important. The performance of three sets of families, chosen to represent open-pollinated progeny, local crosses and wide crosses, is plotted on *Figure 3*. It is informative that the three sets do not show differences in the extent to which they respond to improving environmental quality, The regression coefficients in *Table 2* are shown to be statistically homogenous according to the analysis of variance on *Table 3*.

Judged by the regression coefficients in *Table 2*, all the 11 sets of families show stabilities well below the average stability of b = 1.0 with the only exception being the Hoerner-Waldorf × Continental family set. This finding is of great practical importance since it indicates that loblolly pine genotypes are specifically adapted to favourable environments. It means, in practical terms, that it pays well to couple genetic improvement work with improved husbandry methods like site preparation and fertilization because the selected genotypes will take advantage of such environmental improvements.

There is greater variation among calculated ecovalence values relative to regression coefficients as shown on *Table 2*. This may suggest that the ecovalence stability parameter is more discrimating than the regression coefficient stability parameter. In general, however, the range of ecovalence values found agree very well with those reported for Jack pine provenances (Morgenstern and Teich 1969).

According to Tai's structural analysis method, the two parameters (α, λ) as tabulated in *Table 2* are used jointly to determine genotypic stability. A perfectly stable genotype has values of (—1,1) for (α, λ) while a genotype of average stability has (0,1) values. The general picture (see *Table 2*) is that the sets of loblolly pine genotypes show average genotypic stabilities. A few sets of families show below average stabilities. This indicates that the family sets are well adapted to all environments.

The most significant finding in this section is that wide crosses, local crosses and open-pollinated progeny do not differ significantly in stability of performance across the range of environmental conditions tested. It must be emphasized, however, that sets of families rather than individual families were studied. Genotypic stabilities observed may therefore be of the 'population buffering' type rather than of the 'physiological homeostasis' type for individual families within sets.

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Summary

Three genotypic stability parameters were used to compare sets of families namely, the regression coefficient Der Regressionskoeffizient nach Eberhardt and Russell (1966). Das Parameterpaar nach Tai (1971) und die Ökovalenz (1971) and thirdly the ecovalence parameter Wricke (1962). Judging by the regression coefficients, all the family sets exhibited below average genotypic stabilities indicating that the genotypes are specifically adapted to high site class environments.

Key words: Pinus taeda, adaptation analysis.

Zusammenfassung

Der Regressionskoeffizient nach Eberhard and Russell (1966). Das Parameter nach Tai (1971) und die Ökovalenz nach Wricke (1962) wurden benutzt, um Baumgruppen von *Pinus taeda* verschiedener Standorte auf spezifische Anpassung zu testen. Danach zeigten alle Familien unterdurchschnittliche genotypische Stabilität.

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Table 1. — Mean height growth (in feet) by family sets and location.

Source of seed	Location									
	1	2	3	4	5	6	7	8	9	$\overline{X}_{i.}$
Commercial check	—	10.44	10.59	—	10.86	9.51		6.76		10.25
Westvaco O.P.	—	—	11.65	—	10.90	—	7.64	6.84	—	10.12
Weyerhaeuser O.P.	16.87	12.14	—	10.51	10.68	10.91	7.52	8.14	7.44	10.46
Hoerner-Waldorf	16.32	11.11	11.76	10.54	10.26	9.91	9.83	8.05	7.51	10.38
Weyerhaeuser × Weyerhaeuser	17.31	12.63	11.36	10.76	9.63	10.06	—	—	6.71	10.53
Hoerner-Waldorf × Hoerner-Waldorf	17.47	11.89	11.49	11.54	11.02	9.51	—	10.30	8.92	11.71
Hoerner-Waldorf × Weyerhaeuser	17.20	12.85	10.66	10.88	10.82	9.47	10.54	7.96	7.68	10.19
Hoerner-Waldorf × Union Camp	17.64	11.86	10.91	10.63	10.55	10.01	10.43	8.74	8.00	10.53
Hoerner-Waldorf × Kimberly-Clark	18.04	12.45	11.51	11.12	10.67	10.56	11.23	8.43	7.32	10.29
Hoerner-Waldorf × Westvaco	17.34	12.52	11.40	11.12	10.53	10.62	7.93	9.39	7.50	10.82
Hoerner-Waldorf × Continental Can	16.20	10.20	10.60	10.12	9.47	9.47	10.04	7.69	7.88	10.11
Weyerhaeuser × Bowaters	17.62	12.43	—	12.07	10.53	10.23	9.77	8.08	7.39	10.90
Weyerhaeuser × Continental Can	17.25	10.97	10.35	10.31	10.46	10.21	9.83	8.51	7.45	10.34
Weyerhaeuser × Champion	—	—	—	9.64	10.33	—	—	7.95	7.71	9.32
Weyerhaeuser × Continental Can	16.57	13.02	10.40	11.68	10.96	9.91	11.83	6.70	7.80	10.06
Weyerhaeuser × Texas	18.22	12.32	11.00	10.57	10.40	10.11	7.63	9.32	7.13	10.52
Hoerner-Waldorf × Texas	17.92	11.54	11.03	12.56	10.52	10.63	8.31	9.23	6.61	10.81
Hoerner-Waldorf × Continental Can	16.99	10.87	10.60	11.34	11.13	10.12	9.93	8.91	7.18	10.56
$\overline{X}_{.j}$	17.65	12.06	11.39	11.11	10.61	10.49	9.83	8.27	7.79	

$\overline{X}_{..} = 10.45$

Legend:

Location	County	State	Company
1.	Jackson	La.	Continental Gan
2.	Shelby	Ala	Kimberly-Clark
3.	Bullock	Ga	Continental Can
4.	Rhea	Tenn.	Bowaters
5.	Halifax	N.C.	Hoerner-Waldorf
6.	Columbus	N.C.	Georgia Pacific
7.	Murray	Ga.	Bowaters
8.	Kernshaw	S.C.	Westvaco
9.	Tyrell	N.C.	Westvaco

Table 2. Mean height growth over all location for sets of families and genotypic stabilities calculated by EBERHART and RUSSELL's method, WRICKE's method and TAI's method.

Set of family	Mean Height	EBERHART'S Regression Coefficient	WRICKER'S Ecovalence	TAI'S	
				α	λ
Hoerner-Waldorf O.P.	10.38	1.134	1.94	—.029	.356
Hoerner-Waldorf × Weyerhaeuser	10.19	1.226	2.46	.002	.595
Horner-Waldorf × Union Camp	10.53	1.204	.79	—.008	.221
Hoerner-Waldorf × Kimberly-Clark	10.29	1.302	2.09	.028	1.044
Hoerner-Waldorf × Westcavo	10.82	1.121	5.21	.003	.667
Hoerner-Waldorf × Continental Can (Ga.)	10.11	1.073	3.31	—.048	.604
Weyerhaeuser × Continental Can (La.)	10.34	1.201	.85	—.007	.193
Weyerhaeuser × Continental Can (Ga.)	10.06	1.179	10.11	—.013	2.042
Weyerhaeuser × Texas	10.52	1.352	6.87	.031	.861
Hoerner-Waldorf × Texas	10.81	1.285	5.73	.018	1.392
Hoerner-Waldorf × Continental Can (La.)	10.56	1.374	1.85	—.020	.444

Table 3. — Analysis of variance based on average height growth of sets of crosses using the method of Eberhart and Russell.

Source of variation	DF	SS	MS	
Sets	10	6.908	.6908	MS^b_1
Location + (Location × Sets)	88	707.736	8.0424**a	
Locations (linear)	1	667.482	667.482**	
Sets × location (linear)	10	3.182	.3182	MS_2
Pooled deviations	77	37.072	.4814	MS_3

[a] Significant at the .01% probabaility level.

[b] To test the significance of differences among sets of crosses. $F \backsimeq MS_1/MS_3$ was used; to test the significance of differences among the regression coefficients, $F \backsimeq MS_2/MS_3$ was used.

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Supernumerary chromosome distribution in provenances of Picea sitchensis (Bong.) Carr.

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Introduction

Moir and Fox (1972) described the existence of supernumerary (B-) chormosomes in seven provenances of Sitka spruce from the central part of its geographical range. This B-chromosome is typical of supernumerary chromosomes in general in existing as a widespread polymorphism, with variable frequency, both in different individuals and different provenances. It is also heterochromatic, another frequent feature of such chromosomes. Indeed, this last property allows the B-chromosome status of a plant to be determined from non-dividing tissue. Generally, one cannot detect the presence, let alone the frequency, of B-chromosomes in a population for they do not have marked effects upon the external phenotype (exophenotype). However, where effects have been described, they frequently affect characters concerned with the fitness of individuals or populations (See Jones, 1975 for review). Small numbers of B-chromosomes sometimes increase fertility and vigour, e.g. fertility and viability were higher in *Lilium calosum* plants with 1 B than in those with O B'sKimura and Kayano (1961) and Rutishauser (1956) found that seed fertility increased with the presence of up to three euchromatic B-chromosomes of a specific type in the endosperm of *Trillium grandiflorum.* However, deleterious effects of B-chromosomes on the exophenotype have been described rather more frequently. The presence of a single B in