Genotype-Environment Interaction and Stability in Ten-Year Height Growth of Norway Spruce Clones (Picea abies Karst.)

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Abstract

Norway spruce cuttings of 40 clones were tested on seven contrasting sites in northern Germany. Analysis of variance for ten-year height growth indicate a highly significant clone × site interaction. This interaction may be reduced by selection of stable clones. Several measures of stability were calculated and discussed. Characterization of sites by the method of genetic correlation indicate that most of the interaction is being generated between sites of high and low elevation. Stratification of the area into two planting

zones based on elevation would also reduce the interaction. Whatever method is used, the costs involved must be compared with the increase in genetic gain.

Key words: genotype × site interaction, stability, Norway spruce clones, height growth.

Zusammenfassung

Stecklinge von 40 Fichtenklonen wurden auf 7 unterschiedlichen Standorten in Norddeutschland geprüft. Die Varianzanalyse für das Höhenwachstum im Alter 10 weist eine hochsignifikante Klon × Anbaustandort Interaktion aus. Verschiedene Stabilitätsmaße wurden errechnet und verglichen. Beschreibt man die Standorte mit Hilfe der genetischen Korrelationen, so zeigt sich, daß die stärkste Interaktion zwischen Standorten unterschiedlicher Höhenlage auftritt. Eine Gliederung des Gebietes in zwei Anbauzonen aufgrund der Höhenlage, würde die Interaktion ganz wesentlich reduzieren. Ob man eine Gliederung des Anbaugebietes vornimmt oder Klone mit hoher Stabilität auswählt, muß aufgrund der Kosten im Vergleich zum Zuwachs im genetischen Gewinn entschieden werden.

Introduction

Genotype-environment interaction is the differential response of genotypes to changing environmental conditions. Such interactions complicate testing and selection in tree improvement programs, and result in reduced overall genetic gains. The literature on genotype- environment interactions is extensive. General reviews include Comstock and Moll (1963), Allard and Bradshaw (1974), and Freeman (1973). Reviews within forest tree breeding include Squillace (1970), Shelbourne (1972), Shelbourne and Campbell (1976), Morgenstern (1982), and Skrøppa (1984). Matheson and Raymond (1984) evaluated the importance of genotype-environment interactions on *Pinus radiata* breeding programs in Australia using a criteria of the resulting loss of potential gain.

Genotype-environment interactions can be diminished in two ways: (1) by creating groups of essentially homogeneous environments and selecting cultivars suited to each environment, and (2) by developing stable cultivars which perform dependably over a range of environments. Stability may be achieved by population buffering and by individual buffering (Allard and Bradshaw, 1964). Population buffering involves creating varieties composed of different genotypes adapted to a range of environments. It depends upon the elimination of less fit genotypes from the stand through intergenotypic competition. Individual buffering implies stable performance of individual genotypes and typically depends on heterozygosity, which implies a contribution of non-additive gene effects (Allard, 1961; Rowe and Andrew, 1964; Scott, 1967).

Evidence from crop plants indicate that selection for stability may be effective (Scott, 1967). Non-additive gene effects, however, will be lost in a cycle of sexual reproduction, but may be captured clonal selection and propagation.

Clonal tree improvement programs may be designed to take full advantage of both individual and population buffering. Besides capturing both the additive and non-additive gene effects associated with stability, the composition and number of clones within clonal varieties can be chosen to provide maximum population buffering. In addition, clonal programs enable the development of varieties designed for smaller environmental units, something that is prohibitively expensive for seed-orchard tree improvement programs. Clones can also provide a more sensitive means of detecting genotype-environment interactions and evaluating genotypic stability.

Norway spruce has proved to be a good species for large-scale clonal tree improvement programs. Cuttings from young trees root easily and show good growth and form Kleinschmit *et al.*, 1973; Roulund, 1973, 1979). In addition, serial propagation appears to be effective in maintaining juvenility (St. Clair *et al.*, 1985). As a result several European countries have initiated operational clonal tree improvement programs using early selection and propagation of clones from provenance and progeny trials (Kleinschmit and Schmidt, 1977; Lepistö, 1977; Roulund, 1977; Werner, 1977; Bentzer, 1981; Monchaux, 1982).

As part of the clonal tree improvement program of the Lower Saxony Forest Research Institute, 40 clones were tested on seven contrasting sites in northern Federal Republic of Germany. This material provides an excellent opportunity to assess genotype-environment interaction and genotypic stability among clones used in an actual, ongoing tree improvement program. The objectives of this study are:

(1) to examine the magnitude of genotype-environment interaction in ten-year height growth in Norway spruce clones;
(2) to characterize these clones for stability;
(3) to characterize sites in their contribution to the interaction;
(4) to compare the merits of these sites as general testing environments;
(5) to provide estimates of clonal repeatabilities and genetic gains for a Norway spruce tree improvement program.

Materials and Assessment

Propagation procedures and the breeding scheme of the Norway spruce program of the Lower Saxony Forest Research Institute have been described earlier in Kleinschmit *et al.* (1973); Kleinschmit (1974), and Kleinschmit and Schmidt (1977). As part of this program, rooted cuttings are serially propagated on a three-year cycle. Selection based on nursery and field performance occurs at each repropagation. Cuttings of the 40 clones used in this study were tertiary cuttings (third cycle of vegetative propagation) rooted in spring 1974 and grown for three years in the nursery. The clones originated from different provenances of outstanding performance. The top provenance was Westerhof, therefore seedlings of a tested stand of this provenance serve as a base for comparison. The clones were selected at age 4 due to growth potential and entered clonal tests. According to the results of these clonal tests selection occured between each repropagation. Therefor these 40 clones are the result of truncation selection. Clones are assumed not to differ in maturation. During spring 1977, cuttings were planted at seven contrasting sites in northern Germany *(Figure 1)*. Heights to the 1983 whorl were measured with a height pole during summer 1984. Thus, height growth was after ten growing seasons, ie. seven years after planting at the test site.

The seven sites were chosen to represent the range of sites in which Norway spruce clones from this program are expected to be planted. Three sites are located in the low coastal plains of northern Germany, while the other four sites are located in country of higher elevation further south *(Table 1)*. The three low-elevation sites are warmer and drier than the heigher-elevation sites. Medingen is the

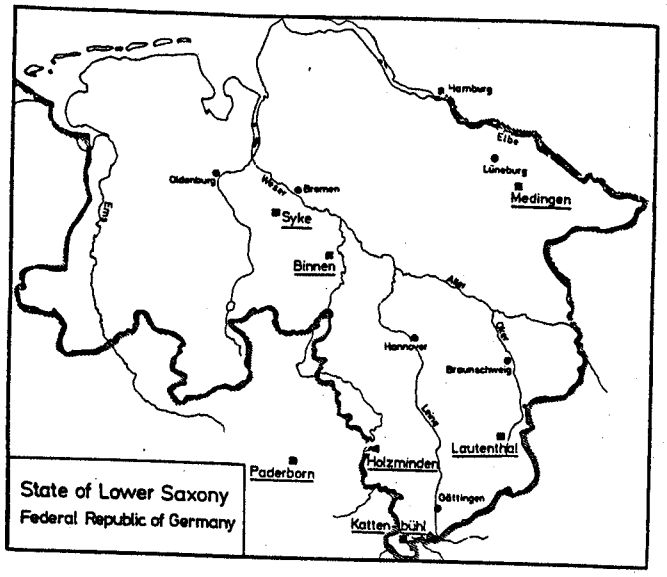

Fig. 1. — Map of northern Federal Republic of Germany showing location of tests sites as indicated by ■.

warmest and driest site, being further from the ocean than Syke and Binnen. Lautenthal is located in the Harz mountains and is the coldest and wettest site. Soil and nutrient conditions were similar in the four higher-elevation sites, but vary from a nutrient-rich, loamy soil at Syke, to a less fertile site with a somewhat sandy soil at Medingen, to a nutrient-poor, sandy site at Binnen.

The experimental design at each site was a randomized complete block design with 40 clones replicated in each of 20 blocks in single-tree plots. In addition to the 40 clones, each block contained nine 3-0 seedlings from the provenance Westerhof. Westerhof is considered an excellent provenance for planting in northern Germany (DIETRICHSON *et al.*, 1976), and may be used to evaluate gains achieved so far from clonal selection as compared to seedlings.

Statistical Analysis and Concepts

Analysis of variance was done for all sites combined using the statistical model

$$Y_{ijk} = \mu + C_i + S_j + CS_{ij} + \varepsilon_{ijk} \qquad (1)$$

where Y_{ijk} = ten-year height growth of the k^{th} ramet of the i^{th} clone at site j

μ = overall mean

C_i = effect of the i^{th} clone

S_j = effect of the j^{th} site

CS_{ij} = interaction between the i^{th} clone and the j^{th} site

ε_{ijk} = error term.

Block effects within sites were not considered in this part of the study, owing to the unbalanced nature resulting from dead or missing trees. The form for the analysis of variance is given in *Table 2*. All effects were treated as random. Estimated variance components were used to calculate phenotypic variance, broad-sense heritability, repeatability of clonal means, and genetic gain. Formulas used include (see SHELBOURNE and THULIN, 1974):

Table 1. — Elevation, temperature and rainfall at seven test sites.

site	elevation (m)	mean temperature (°C)		mean rainfall (mm)			physical soil structure	comments
		year	growing season	year	growing season	nutrient status		
Syke	39	8.4	14.5	741	346	good	very good	Deep loam soil with good nutrient status
Medingen	5o	8.5	15.6	6o6	296	mean	good	Sandy soil with some finer components
Binnen	4o	8.5	14.9	67o	32o	poor	poor	Sandy soil with poor nutrient status and poor drainage below 6o cm
Paderborn	34o	7.8	13.8	1134	514	mean	very good	Loam soil with some sand components
Kattenbühl	35o	7.5	13.3	8oo	38o	mean	good	Sandy soil with loam upper horizon
Holzminden	445	7 5	13.4	9oo	42o	mean	good	Sandy soil with some finer components
Lautenthal	575	5.9	12.o	1344	55o	mean	mean	Loam soil with some sand components

Table 2. — Analysis of variance format for ten-year height of clones with sites combined (assuming fully random model).

source	df	expected mean squares
clones	c-1	$\sigma_e^2 + t\sigma_{cs}^2 + st\,\sigma_c^2$
sites	s-1	$\sigma_e^2 + t\sigma_{cs}^2 + ct\,\sigma_s^2$
clone x site	(c-1)(s-1)	$\sigma_e^2 + t\sigma_{cs}^2$
error	cs(t-1)	σ_e^2

Note: c = number of clones; s = number of blocks; t = effective number ramets per clone per site; σ^2_c = variance due to differences among clones; σ^2_s = variance due to differences among sites; σ^2_{cs} = variance due to interaction of clones and sites; σ^2_e = within-site variance.

$$\sigma_p^2 = \sigma_c^2 + \sigma_{cs}^2 + \sigma_e^2 \qquad (2)$$

$$\sigma_{\bar{p}}^2 = \sigma_c^2 + \frac{\sigma_{cs}^2}{s} + \frac{\sigma_e^2}{st}$$

$$h_B^2 = \frac{\sigma_c^2}{\sigma_p^2}$$

$$R_{\bar{c}} = \frac{\sigma_c^2}{\sigma_{\bar{p}}^2}$$

where σ_c^2, σ_{cs}^2 and σ_e^2 are estimated variance components (Table 2)

σ_p^2 = phenotypic variance

$\sigma_{\bar{p}}^2$ = phenotypic variance of clonal means

h_B^2 = broad-sense heritability

$R_{\bar{c}}$ = repeatability of clonal means

s = number of sites

t = mean number ramets per clone per site

Genetic gain was calculated in two ways (Falconer, 1981). First, gain is calculated as $\Delta G = i\sigma_p R_{\bar{c}}$ where i is the intensity of selection. In this study, it is assumed to equal 1.596 which corresponds to selection of five clones out of 40 (Becker, 1984). Second, the selection differential D is determined from the difference of the mean of the top five clones and the overall mean. Genetic gain is then calculated as $\Delta G = D \cdot R_{\bar{c}}$.

As the clone × site variance component increases relative to clonal variance, the repeatability of clonal means decreases, and thus, genetic gains are reduced. One solution is to select clones with high stability. Several statistical techniques have been proposed to characterize stability.

The most common approach, known as joint regression analysis, regresses the yield of each genotype upon some environmental index (Finley and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968; Skrøppa, 1984). In terms of the model presented above:

$$CS_{ij} = \beta_i l_j + \delta_{ij} \qquad (3)$$

where β_i = departure of the linear regression coefficient of the i^{th} clone from the overall linear regression coefficient

l_j = environmental index of the j^{th} site

δ_{ij} = deviations from the regression line of the i^{th} clone at the j^{th} site.

If the environmental index is taken to be the mean yield of all genotypes in that environment, then l_j becomes the site effect S_j and the model can then be rewritten as:

$$Y_{ijk} = \mu + C_i + (1 + \beta_i) S_j + \delta_{ij} + \bar{\varepsilon}_{ijk}$$

The interaction sums of squares can then be partitioned into two components, the sum of squares due to differences in individual regression lines with (c - 1) degrees of freedom, and the sum of squares due to deviations from the regressions with (c - 1) (t - 2) degrees of freedom (Freeman and Perkins, 1971).

Finlay and Wilkinson used the estimated regression coefficient b_i (where b_i estimates $1 + \beta_i$) to measure stability and relative adaptability. A variety with a value near one was considered to be of average stability and equally adapted to good and poor sites. A variety with a value greater than unity was of low stability and better adapted to good sites. A variety with a value less than unity was of high stability and better adapted to poor sites. Eberhard and Russell (1966) proposed the use of an additional stability parameter, the mean squares deviations from the regression for each genotype, as measured by S^2_{di}; a stable variety was defined as one with bi = 1.0 and $S^2_{di} = 0$.

The use of the mean of all genotypes as the environmental index has been criticized on statistical grounds (Freeman and Perkins, 1971; Hardwick and Wood, 1972). However, provided that the numbers of genotypes and environments are reasonably large and the environmental range is sufficient, linear regression using the mean of all genotypes should be biologically valid (Fripp and Caten, 1971; Fripp, 1972; Hühn, 1980; Skrøppa, 1983).

The technique of Finlay and Wilkinson (1963) and Eberhart and Russell (1966) is used in this study to characterize genotypic stability. In addition, Wricke's (1962) ecovalence and S_{1i} from Hühn (1979) are calculated. Ecovalence is the contribution of each genotype to the interaction sums of squares, and is given by $\sum_j (Y_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{...})^2$, a low value indicating greater stability. S_{1i} is the average change in rank between all pairs of environments for genotype i, that is $S_{1i} = \frac{2\sum_j \sum_{j'} | r_{ij} - r_{ij'} |}{n(n-1)}$. It is one of six stability parameters based on rank changes as developed by Hühn. A genotype which ranks similarly in different environments is considered stable and has a low value for S_{1i}.

The contribution of environments in generating interactions was studied using a method developed by Burdon (1977). He considers heights in different environments as separate traits and calculates the genetic correlations between heights at pairs of environments. Gain for selection at one site with planting at another is determined from the formula for correlated response to selection (Falconer, 1981). Estimated correlations can then be used to indicate which sites are most similar to one another (in terms of showing least interaction), and a matrix of expected gains can indicate which sites are best for testing.

The formula for expected gain at site y based on clonal selection at site × can be written as:

$$\Delta G_{y \cdot x} = i\sqrt{R_{\bar{c}x}}\ \sigma_{cy}\ r_{xy} \qquad (4)$$

where i = intensity of selection

$R_{\bar{c}x}$ = repeatability of clonal means at site x

σ^2_{cy} = clonal component of variance at site y

r_{xy} = correlation between clonal means at sites x and y.

Variance components and repeatability of clonal means were estimated from analyses of variance done separately for each site. The statistical model considered effects due to clone, block and error. Clone × block interaction was confounded with the error term since single-tree subclasses were used. All twenty blocks were included.

Calculations were carried out in Göttingen on the UNIVAC-computer 1110 of the "Gesellschaft für wissenschaftliche Datenverarbeitung" and on the TA 1600/30 of the Lower Saxony Forest Research Institute, using SPSS, Harvey and own programs.

Result and Discussion

Overall means and analysis of variance

All effects, including clone × site interaction, where highly statistically significant ($p < 0.001$) in the overall analysis of variance *(Table 3)*. Site means decreased with increasing elevation and decreasing temperatures *(Table 4)*. Syke was the top-ranked site with a mean ten-year height of nearly three meters, 2.3 times better than the bottom-ranked site, Lautenthal. Differences between the three low-elevation sites may be related to soil structure and nutrient availability.

Table 3. — Analysis of variance for ten-year height (meters) of 40 clones at seven sites.

source	df	MS	F	variance components magnitude	%
clones	39	6.52	9.08***	0.048	13.0
sites	6	209.91	292.29***	0.305	82.0
clone x site	234	0.72	1.80***	0.019	5.0
error	4524	0.40		0.399	

Note: *** indicates highly significant, $p < .001$; variance component percentage is from total excluding error variance.

Overall clonal means ranged from 1.66 meters for Clone 189 to 2.69 meters for Clone 37. Clone 37 was particularly outstanding, ranking first at five out of seven sites.

The significant clone × site interaction indicates that clones perform differently between sites. Of greater in-

Table 4. — Mean 10-year heights for 40 clones and seedlings of provenance Westerhof at seven sites (in meters).

clone	Syke mean	rank	Medingen mean	rank	Binnen mean	rank	Paderborn mean	rank	Kattenbühl mean	rank	Holzminden mean	rank	Lautenthal mean	rank	overall mean	rank
37	3.71	1	3.29	2	2.77	6	2.56	1	2.50	1	2.16	1	1.81	1	2.69	1
123	3.52	6	3.36	1	3.04	2	2.37	3	2.46	2	2.12	2	1.55	2	2.63	2
95	3.51	7	2.91	6	3.01	3	2.22	8	2.29	5	1.66	15	1.44	7	2.43	3
41	3.52	5	3.02	4	2.87	4	2.11	15	1.89	23	1.97	3	1.44	8	2.40	4
107	3.59	2	2.82	9	3.05	1	2.20	9	1.98	16	1.71	10	1.09	33	2.35	5
143	3.02	20	2.51	20	2.83	5	2.26	7	2.44	3	1.86	5	1.35	13	2.32	6
103	3.49	8	2.62	14	2.59	8	2.01	23	2.36	4	1.75	9	1.33	16	2.30	7
152	3.55	3	2.86	8	2.15	19	2.41	2	2.12	7	1.65	17	1.23	25	2.28	8
188	3.20	10	3.02	3	2.22	13	2.28	5	2.10	8	1.62	23	1.47	4	2.27	9
197	3.53	4	2.76	10	2.65	7	2.26	6	1.82	28	1.47	30	1.31	17	2.26	10
125	2.78	27	2.67	13	2.38	10	2.08	16	2.06	10	1.87	4	1.47	6	2.19	11
45	3.20	11	2.46	24	2.44	9	1.92	27	1.96	18	1.81	7	1.50	3	2.18	12
26	3.19	12	2.86	7	2.15	18	2.08	17	2.04	11	1.66	16	1.31	19	2.18	13
101	3.10	14	2.92	5	2.40	10	1.96	25	1.89	24	1.46	32	1.25	22	2.14	14
46	3.37	9	2.61	15	2.18	16	1.79	34	2.26	6	1.43	34	1.15	31	2.11	15
90	2.91	21	2.50	22	2.00	27	1.98	24	1.98	15	1.84	6	1.38	12	2.08	16
87	3.09	16	2.68	12	2.06	23	1.89	28	1.98	14	1.69	12	1.20	28	2.08	17
50	3.15	13	2.57	18	2.21	14	2.04	20	1.72	34	1.69	13	1.08	35	2.06	18
18	2.90	22	2.71	11	2.09	20	2.02	21	1.74	33	1.62	20	1.35	14	2.06	19
42	3.09	17	2.58	16	1.78	33	2.02	22	1.89	22	1.81	8	1.19	29	2.05	20
142	2.83	24	2.38	26	2.36	12	2.07	18	1.75	32	1.63	19	1.23	26	2.04	21
9	2.79	26	2.31	31	2.04	24	2.35	4	1.85	27	1.59	25	1.29	19	2.03	22
4	3.09	15	2.21	34	2.06	21	1.82	32	2.06	9	1.62	20	1.26	20	2.02	23
145	3.04	18	2.27	32	1.68	37	2.11	14	1.94	19	1.70	11	1.38	11	2.02	24
15	2.69	31	2.58	16	1.91	30	2.04	19	2.01	13	1.47	31	1.34	15	2.01	25
88	2.54	35	2.34	28	2.15	17	2.13	13	1.93	20	1.61	24	1.25	23	1.99	26
110	2.75	28	2.47	23	1.86	32	1.80	33	1.86	26	1.64	18	1.47	5	1.98	27
115	2.65	35	2.33	30	1.91	28	2.17	10	2.03	12	1.51	27	1.24	24	1.96	28
113	2.80	25	2.51	21	1.47	40	2.16	11	1.97	17	1.37	36	1.43	10	1.96	29
94	2.73	30	2.54	19	1.68	38	2.14	12	1.72	35	1.68	14	1.09	34	1.94	30
98	2.75	28	2.12	37	2.06	22	1.96	26	1.88	25	1.56	26	1.03	37	1.91	31
116	3.03	19	2.45	25	2.02	26	1.71	37	1.77	31	1.33	38	1.02	38	1.90	32
104	2.48	37	2.13	36	1.91	29	1.84	30	1.92	21	1.62	22	1.17	30	1.87	33
196	2.48	38	2.05	38	2.19	15	1.88	29	1.78	29	1.45	33	1.21	27	1.86	34
181	2.69	32	2.34	29	1.76	35	1.83	31	1.69	37	1.47	29	1.05	36	1.83	35
173	2.88	23	2.35	27	1.87	31	1.79	35	1.64	38	1.43	34	0.86	40	1.83	36
66	2.60	33	2.22	33	1.68	36	1.58	38	1.69	36	1.32	39	1.43	9	1.79	37
112	2.57	34	2.01	39	1.64	39	1.56	39	1.78	30	1.35	37	1.15	32	1.72	38
11	2.19	40	2.16	35	2.03	25	1.73	36	1.55	39	1.24	40	0.92	39	1.69	39
189	2.42	39	1.86	40	1.77	34	1.53	40	1.30	40	1.51	28	1.26	21	1.66	40
overall clonal means	2.97		2.54		2.18		2.02		1.95		1.63		1.28		2.09	
seedling means	2.24		2.09		1.84		1.74		2.22		1.41		1.08		1.81	

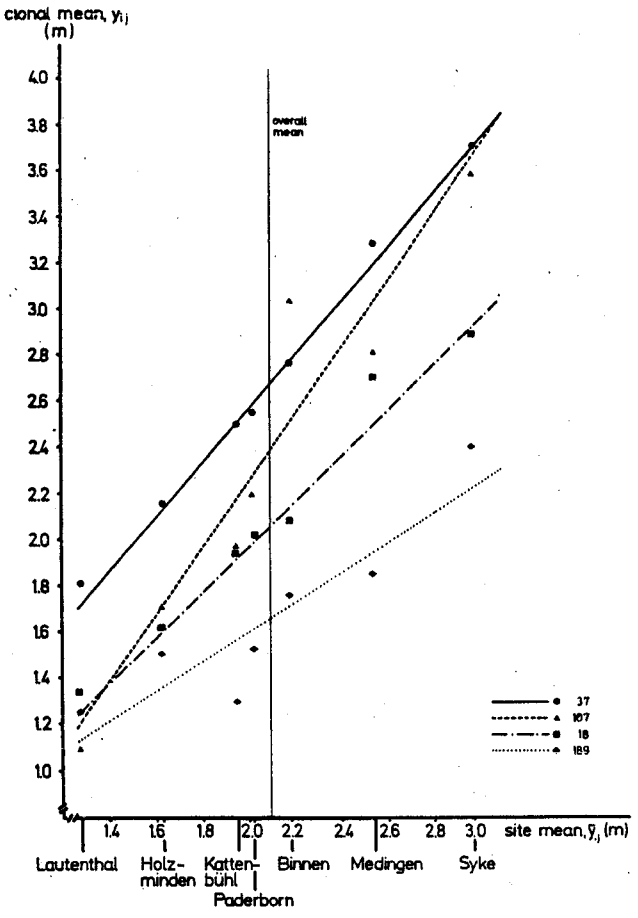

Fig. 2. — Plot of clonal means for four clones against site means with corresponding regression lines.

terest than statistical significance is the importance of the interaction in reducing gains. The magnitude of the interaction component was less than half that of the clonal variance component *(Table 3)*.

Broad sense heritability (h^2_B) overall for 10-year height growth was 0.10, which is relatively low. However, repeatability of clonal means (R_c) overall was 0.89. The genetic gain based on a selection intensity of i = 1.596 is 0.33 m, a gain of 16 percent above the overall mean. If the top five clones are selected and genetic gain calculated based on the observed selection differential, the genetic gain is 0.42 m, 20% above the overall mean. The difference between the two gain estimates results from the outstanding height growth of clones 37 and 123. These gain estimates represent gains to be achieved from further clonal selection, and do not include gains already achieved from past selection.

Stability

The F-value for heterogeneity of regressions from the breakdown of the interaction sums of squares confirms the statistical significance of the clone × site interaction *(Table 5)*. Values for the regression coefficient b_i range from 0.65 t o1.46 *(Table 6)*. The plot of clonal means against site means with the corresponding regression lines for four clones illustrates the differential reactions of clones to changing environments *(Figure 2)*. Clone 18 represents a clone of average stability (b_i = 0.99) as defines by Finlay and Wilkinson (1963). Its performance is relatively equal on poor and good sites. Clone 189 represents a clone of high stability (b_i = 0.65). It performs relatively better on poor sites (although its overall performance is poor). Clone 107 represents a clone of low stability (b_i = 1.46). It performs relatively better on good sites.

Table 5. — Breakdown of interaction sums of squares.

Source	df	MS	F
heterogeneity of regressions	39	1.42	3.56***
deviations from regressions	195	o.58	1.44**

Note: *** $p < .001$; ** $< .01$.

The point is, the regression coefficient measures *relative* performance. In forest tree breeding this information is useful to distinguish genotypes for specific environments, but if all environments tested are in one planting zone, and each represents the same proportion of area to be planted, then this information is irrelevant. Selection on the overall mean is all that is necessary to assure the largest overall gains.

More important to forest tree breeding is the predictability of yield of a genotype in various environments. This concept of stability may be measured by the mean deviations from the regression line, S^2_{di} (Becker, 1981). Clone 107 performs well overall, but is very unstable as measured by S^2_{di} *(Table 6)*. Clone 37 also performs well, but is very stable as measured by S^2_{di}. This is apparent from the deviations of the individual points from the regression line in *Figure 2*.

The conclusions are the same when the other stability parameters, ecovalence and S_{1i}, are considered *(Table 6)*. Clone 37 rates as very stable, and Clone 107 as unstable. Rank correlation between ecovalence and S^2_i is high, and is still good between S_{1i} and S^2_{di}, and S_{1i} and ecovalence *(Table 7)*.

A plot of the stability parameter against the clonal means is useful as an aid to selection *(Figure 3)*. In each figure, clones falling in the lower, right-hand side are prefered. Clone 37 is the best clone no matter which stability parameter is used. Selection of clones based on height and stability can then proceed using a selection index for multiple-trait selection (Sonecypher and Arbez, 1976), but assigning weights based on relative economic value may prove difficult. This would require knowledge of the reduction in gain associated with using unstable versus stable genotypes. The use of independent culling levels, that is, setting an acceptable value for a stability parameter followed by selection based on height, may prove more practical.

Correlated gains among sites

The expected gains from various combinations of testing and planting sites, along with estimates of clonal variance and repeatability of clonal means are presented in *Table 8*. Expected gains at planting sites are generally greatest or close to the greatest, when selection is done at the same site. Where this is not true (Paderborn, Kattenbühl, and Holzminden), the clonal variance is small relative to that at Syke, Medingen, and Binnen. Selection based on overall means results in gains second only to those when selection is done at the same site as planting. When selection is done at a single site for planting at all sites, the best sites for testing, as indicated by the largest gains, were Medingen, Syke and Binnen. These three sites were of higher site index, and had the largest value for repeatability of clonal means and the greatest clonal variances.

Medingen and Syke were the best single sites for testing, largely because of the high correlations with most of the

Table 6. — Stability statistics for 10-year height growth.

clone	regression coefficient b_i	rank	mean square dev. S^2_{di}	rank	ecovalence	rank	S_{1i}	rank
37	1.16	12	0.01	1	0.06	2	1.6	1
123	1.22	8	0.20	31	0.30	30	1.6	1
95	1.28	5	0.28	35	0.43	36	4.1	4
41	1.26	6	0.31	37	0.44	37	8.2	15
107	1.46	1	0.40	39	0.80	40	11.9	35
143	0.92	24	0.36	38	0.37	34	8.5	17
103	1.21	9	0.20	30	0.28	29	7.5	11
152	1.34	3	0.12	21	0.34	32	10.6	29
188	1.14	15	0.12	20	0.15	15	7.9	13
197	1.38	2	0.21	33	0.48	38	12.6	37
125	0.80	33	0.05	7	0.13	11	8.8	19
45	0.97	20	0.14	23	0.15	14	11.0	31
26	1.16	13	0.05	5	0.09	7	5.0	6
101	1.23	7	0.12	19	0.22	23	11.4	34
46	1.30	4	0.19	29	0.36	33	14.4	40
90	0.86	29	0.06	9	0.09	6	9.0	20
87	1.11	16	0.06	8	0.08	4	8.5	17
50	1.19	11	0.07	10	0.13	12	10.9	30
18	0.99	18	0.90	12	0.09	5	7.9	13
42	1.04	17	0.21	32	0.21	22	10.0	27
142	0.94	23	0.10	16	0.11	10	7.9	13
9	0.86	30	0.17	27	0.20	21	9.4	24
4	0.98	19	0.17	28	0.17	16	10.5	28
145	0.88	26	0.30	36	0.32	31	11.9	35
15	0.88	27	0.12	18	0.14	13	9.5	25
88	0.77	36	0.08	11	0.18	19	9.1	22
118	0.79	34	0.09	14	0.17	18	11.2	33
115	0.78	35	0.14	22	0.24	26	11.0	31
113	0.87	28	0.50	40	0.53	39	14.1	39
94	0.94	22	0.27	34	0.28	28	12.9	38
98	0.92	25	0.09	13	0.10	8	6.8	8
116	1.21	10	0.02	2	0.11	9	9.0	20
104	0.71	39	0.05	6	0.20	20	7.3	9
196	0.74	38	0.10	17	0.23	25	9.1	22
181	0.96	21	0.04	4	0.05	1	4.0	3
173	1.15	14	0.03	3	0.07	3	7.3	9
66	0.76	37	0.16	25	0.27	27	9.8	26
112	0.81	32	0.10	15	0.17	17	4.4	5
11	0.82	31	0.16	24	0.22	24	5.5	7
189	0.65	40	0.16	26	0.39	35	8.3	16

other sites *(Table 9)*. Medingen shows high correlations with Syke and Binnen, yet still shows good correlations with the high-elevation sites. The estimated gain for selection at Medingen and planting at Paderborn, Kattenbühl, Holzminden and Lautenthal was in three cases greater than for selection at either Syke or Binnen. Medingen may be considered intermediate between the low and high-elevation sites. The least similar sites are Lautenthal and Binnen as indicated by a low correlation of clonal means and low gains from selection and planting between sites.

Table 7. — Rank correlation coefficients between stability parameters.

	b_i	S^2_{di}	ecovalence	S_{1j}
$\bar{Y}_i$	0.69	0.27	0.20	-0.02
b_i		0.20	0.14	0.04
S^2_{di}			0.88	0.43
ecovalence				0.43

Comparison of clones and seedlings

Estimates of gains from further clonal selection have been given. Gains achieved from past clonal selection can be assessed by comparison of seedlings and clones. It is assumed that seedlings used for comparison are representative of populations from which clones were initially selected, and that these seedlings would be used as planting stock if clones were not used.

The mean ten-year height growth of seedlings was 1.81 meters as compared to a mean for clones of 2.09 meters *(Table 4)*. This represents a gain of 15 percent from clonal selection and planting. Clones grew better than seedlings at all test sites except Kattenbühl. All differences were highly significant owing to the large number of degrees of freedom. The reason seedlings were superior at Kattenbühl is unclear. Clones and seedlings may have been treated differently at planting since survival of clones was much worse than survival of seedlings whereas at all other sites survival was about equal for clones and seedlings.

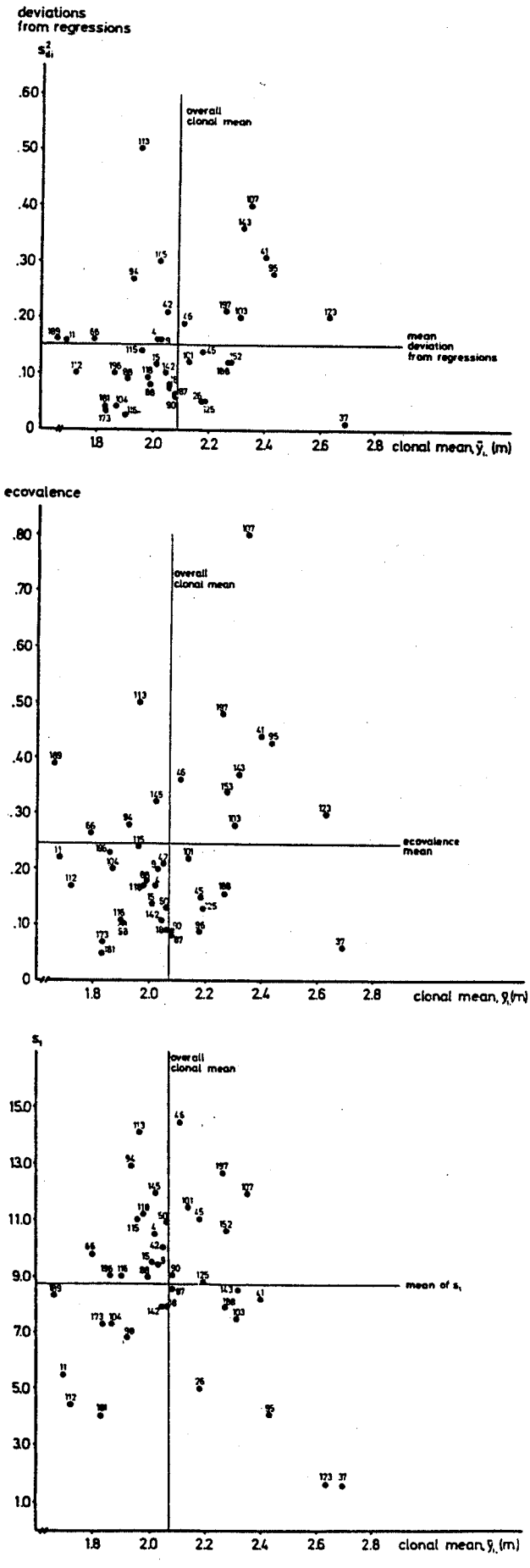

Fig. 3. — Plot of s^2_{di}, ecovalence and s_i against clonal means.

Conclusion

A statistically significant interaction in ten-year height growth exists between Norway spruce clones and their test sites in northern Germany. This interaction may be reduced by dividing the region into two planting zones. This would result in an increase in gain from clonal selection, within each planting zone, but also involves an increase in costs from having two clonal programs as opposed to one.

Characterization of sites by the method of genetic correlations indicates that most of the interaction is being generated between sites of high and low elevation. If the increase in overall gain justifies the increase in costs, stratification of planting zones should proceed based on elevation. Whether one or two planting zones are used, the best sites for testing within each zone may be identified using the method of genetic correlations, taking into account the heritabilities at the respective sites. The next step would be to identify environmental characteristics that determine a good testing site.

Other factors besides height growth may be important to decisions of stratification of planting regions. The Norway spruce clonal program has actually been divided into two zones above and below 300 meters. The two zones are based on differences in crown architecture of trees from different elevations and the relationship to snowbreak damage. Such information would not be available from the present study for many years. Other factors important to the stratification of planting zones may include damage from disease and insects, wind and acid rain.

Interactions may also be reduced by selecting stable clonal varieties within planting zones. A sufficient number of clones within a variety assures some population buffering. Individual buffering can be used by selecting clones that are stable as defined by the stability parameters S^2_{di}, ecovalence, and S_{ji}. Selection for stability within a planting zone involves no increase in cost to the program, but may involve a reduction in gain when clones excluded due to instability were superior in height. The gain from a reduction in clone × site interaction must be compared with the loss from excluding clones with high growth potential.

Identification of specific environmental conditions involved in generating interactions can lead to identification of clones suited to specific environments. Such a fine-tuning of clones and environments would not be possible from a seed orchard approach to tree improvement. Within a clonal program, it would involve considerable record keeping and the increase in costs would need to be weighed against possible gains. Whatever approach is used to handle genotype-environment interactions, economics should be considered.

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Table 8. — Expected genetic gains from clones planted at site y after testing at site x (in meters) intensity of selection assumed to equal 1.396. Estimated clonal components of variance and repeatabilities of clonal means for each site given in margin. Gain for selection at site x with planting at all sites assumes each environment represents equal proportion of area to be planted.

Planting site y	Testing site x								
	Syke	Medingen	Binnen	Paderborn	Kattenbühl	Holzminden	Lautenthal	overall selection	0^2_{ey}
Syke	0.490	0.382	0.339	0.252	0.286	0.269	0.188	0.439	0.112
Medingen	0.354	0.431	0.288	0.274	0.258	0.259	0.220	0.405	0.091
Binnen	0.380	0.350	0.537	0.255	0.293	0.309	0.192	0.464	0.138
Paderborn	0.166	0.195	0.149	0.253	0.164	0.168	0.131	0.228	0.038
Kattenbühl	0.197	0.192	0.179	0.171	0.280	0.180	0.168	0.256	0.044
Holzminden	0.152	0.158	0.155	0.144	0.148	0.256	0.155	0.213	0.033
Lautenthal	0.092	0.117	0.085	0.098	0.120	0.136	0.221	0.151	0.025
Overall planting	0.262	0.261	0.247	0.207	0.221	0.225	0.182	0.329	0.048
R_{rx}	0.77	0.80	0.82	0.66	0.70	0.78	0.84	0.89	

Table 9. — Correlation coefficients between clonal means for ten-year height growth among sites.

	Medingen	Binnen	Paderborn	Kattenbühl	Holzminden	Lautenthal
Syke	0.80	0.70	0.58	0.64	0.57	0.40
Medingen		0.66	0.70	0.64	0.61	0.52
Binnen			0.53	0.59	0.59	0.37
Paderborn				0.63	0.61	0.48
Kattenbühl					0.61	0.57
Holzminden						0.61

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