Swedish University of Agricultural Sciences
Faculty of Forestry
Uppsala, Sweden

NORDIC GROUP OF FOREST TREE BREEDERS

Proceedings from a conference on genotype×environment interaction, Uppsala 23–27 August 1982

Contributors

Invited papers
Tore Skrøppa
Dag Lindgren
Urban Gullberg
Kenneth Lundkvist

Volontary paper
Katarina Lindgren

Studia Forestalia Suecica
No. 166 · 1984

ISSN 0039-3150
ISBN 91-576-1847-X

Contents

MS. accepted 14 November 1983

Tofters tryckeri ab, Östervåla 1984

A CRITICAL EVALUATION OF METHODS AVAILABLE TO ESTIMATE THE GENOTYPE × ENVIRONMENT INTERACTION

TORE SKRØPPA

Norwegian Forest Research Institute
1432 ÅS-NLH, Norway

Abstract

Skrøppa, T. 1984. *A critical evaluation of methods available to estimate the genotype × environment interaction.* Studia Forestalia Suecica 166, 3–14. ISSN 0039-3150, ISBN 91-576-1847-X.

Methods to analyse genotype × environment interactions in forest tree breeding experiments are discussed and evaluated based both on empirical data and statistical and biological considerations. The joint regression analysis is a valuable technique for analysis, but has its limitations for generalizations and biological interpretations. It is shown that different stability parameters can give different rankings of stability and also that the choice of scale can influence the results of the analysis. When experiments are planted at few sites, differences between performance at pairs of sites can be plotted to identify genotypes with aberrant performance. The analysis based on genetic correlations between pairs of sites is good for characterizing test environments. It is argued that whenever possible main environmental factors should be identified and be used in the interpretation of the statistical analyses.

Key words: genotype × environment interaction, joint regression analysis, stability, genetic correlation, selection.
ODC 232.12:181.

Tore Skrøppa, Norwegian Forest Research Institute, 1432 Ås-NLH, Norway.

Introduction

Genotype × environment interactions are present if the ranking of genetic entries changes from one environment to another. A large number of statistical methods have been proposed for the analysis of such interactions. The objective of this paper is to review some of these methods and discuss their applicability in the analysis of forest tree breeding experiments performed to select families or individuals (clones) for inclusion in a specific breeding population. The genetic entries can be viewed as random selections within populations which are adapted to the breeding zone. Thus, provenance trials are not considered as they involve a combination of random effects and fixed effects varying along latitudinal or altitudinal gradients. "Genotype" is used as a collective term to denote either an individual or different types of families. By "environment" is denoted all factors or combination of factors that can influence tree growth.

With forest trees genotype × environment interactions have most frequently been studied at the provenance level (Morgenstern & Teich, 1969; Mergen et al., 1974; Rehfeldt, 1979), but have also been found between families (Johnstone & Samuel, 1978) and between clones (Shelbourne, 1974). Recent reviews of genotype × environment interactions and their implications in forest tree breeding have been given by Shelbourne (1972), Shelbourne & Campbell (1976), and Barnes et al. (1982).

An example

In 1970, a 21×4 factorial crossing design was performed in Opsahl Norway spruce seed orchard which comprises clones from altitudes 450–880 m in south-eastern Norway (Dietrichson & Haug, 1976). The full-sib families were planted in 1975 at nine different sites in Oppland County at altitudes ranging from 600 to 900 m. The experimental design was single-tree plots with 20 replicates. A few of the sites have suffered a rather high mortality due to causes like drought the year of planting, competition with grass, and sheep grazing, but also due to frost damage. In 1979 the sitewise mortality ranged from 12% to 49%.

Here, a subset of 10 out of the 21 maternal parents are chosen, and the height data from measurements in 1979 at age nine years from seed for the plants from the corresponding 40 full-sib families will be used to illustrate and evaluate the different methods to study genotype × environment interactions. The results obtained here may not be representative for the whole experiment as only a subset is analysed and should not be generalized. Only analyses based on maternal half-sib families will be presented.

Statistical models. Analysis of variance

It is convenient to consider the following basic model for a phenotype as being of the form

$$P = \mu + G + E + GE + \varepsilon$$

where

P = phenotypic value
μ = general mean
G = genotypic effect
E = environmental effect
GE = genotype × environment interaction effect
ε = random error

To be more specific, if Y_{ijk} is the measured value of the i-th genetic entry in replicate k at site j, the model can be rewritten as

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + B_{jk} + \varepsilon_{ijk}$$

where B_{jk} is the effect of replicate k at site j.

If the residual variation can be considered reasonably homogeneous between environments, this model leads to the familiar analysis of variance which is shown in Table 1 for the example. All effects are treated as random, and the significance of the various sources of variation are indicated by p-values. The analysis is only approximate as Barlett's test for testing homogeneity between variances was significant at the 1% level. The effects were still significant after a logaritmic transformation. Inspection of the two-way table of half-sib family means at the nine sites reveals that the indicated interaction also is "true" in Burdon's (1977) sense as it alter the ranking of genotypes between environments.

Table 1. *Analysis of variance for the example*

Source	DF	MS	F	p-value
Half-sib families	9	3341.44	8.85	0.0001
Sites	8	31530.40	83.51	0.0001
Half-sib families × sites	72	377.56	1.48	0.005
Replicate within sites	171	592.12	2.33	0.0001
Error	4319	254.52		

This ANOVA should be the first step in the analysis of genotype × environment interactions.

The joint regression analysis. Stability

The basic idea with this method is to express the interactions $(GE)_{ij}$ as a linear function of an environmental index I_j and a deviation δ_{ij} from the regression line (Finlay & Wilkinson, 1963; Eberhart & Russel, 1964; Hinkelman, 1974)

$$(GE)_{ij} = \beta'_i I_j + \delta_{ij}$$

In most cases I_j is taken to be the environmental effect E_j and the model becomes

$$Y_{ijk} = \mu + G_i + \beta_i E_j + \delta_{ij} + B_{jk} + \varepsilon_{ijk}$$

where

$$\beta_i = 1 + \beta'_i$$

Usually, the environmental effect is set equal to the deviation of the site mean from the total mean, and β_i is estimated as the slope in a regression analysis by

$$b_i = \Sigma_j \bar{Y}_{ij}.(\bar{Y}_{.j.} - \bar{Y}_{...})/\Sigma_j(\bar{Y}_{.j.} - \bar{Y}_{...})^2$$

The interaction sum of squares can now be broken into two components, as indicated in Table 2 (Mandel, 1961; Hinkelman, 1974).

Table 2. *Breakdown of the interaction sum of squares*

Source	df	MS	F	p-value
Among slopes	9	744.24	2.91	0.002
Deviations	63	325.17	1.28	0.085

It is obvious that an interaction exists if not all β_i are equal. The F-value in Table 2 tests this hypothesis

$$H_0{:}\beta_1 = \beta_2 = \ldots = \beta_{10} = 1$$

In the example, this hypothesis is rejected; it is reason to believe that the half-sib families behave differently as the environmental conditions change. The same conclusion was reached based on a weighted regression analysis, using the reciprocals of the within-site family mean variances as weights. Then it becomes important to characterize the behaviour of each half-sib family. This can be done in several ways.

Finlay & Wilkinson (1963) proposed to measure the stability of each genetic entry by its estimated regression coefficient b_i. A value close to 1 indicates average stability, a high value low stability, and a low value high stability. As this stability concept does not tell anything about the performance level, they proposed to plot the regression coefficient against the entry mean yield over all invironments.

A plot of the half-sib family mean heights against the site means together with the estimated regression lines is shown in Fig. 1 for four families. The next figure (Fig. 2) presents the plot of regression coefficients against the total half-sib family mean heights. Families 8 and 9 are the two best-growing families. They also have the steepest regression lines and should, according to Finlay & Wilkinson (1963), be the most unstable families, and in particular adapted to high-yielding environments. Family 3 is the poorest-growing family with a high stability.

Eberhart & Russel (1966) proposed to supplement the regression coefficient with a second stability parameter, the mean square deviations from the regression line for each individual genetic entry. A low deviation mean square indicates a good fit to the linear model. Similar measures were proposed by Tai

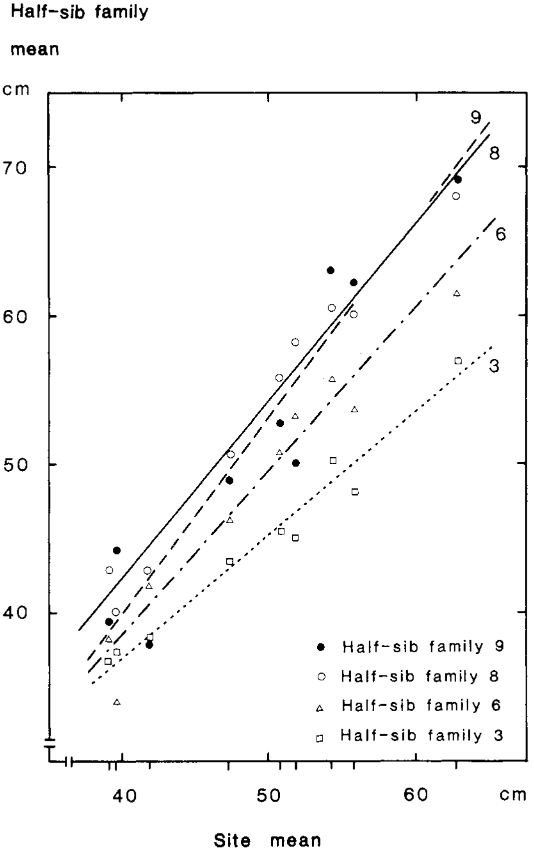

Fig. 1. Plot of half-sib family means against site means and estimated regression lines for four half-sib families.

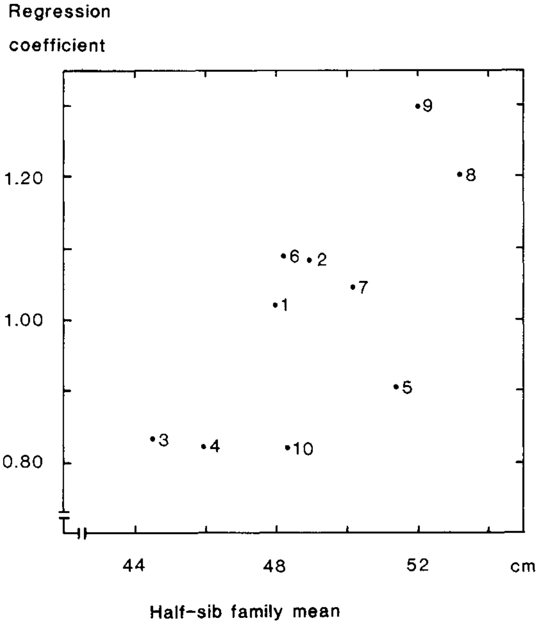

Fig. 2. Plot of regression coefficients against overall half-sib family means.

Table 3. *Half-sib family means and stability parameters*

Half-sib family	$\bar{Y}_{i\cdot}$	b_i	St. dev. of b_i	Mean square deviation	Eco-valence, %	S_{1i}	S_{4i}
8	53.2	1.20	0.07	2.22	7.05	1.67	1.49
9	52.0	1.30	0.17	14.45	28.40	3.28	2.91
5	51.4	0.90	0.12	7.13	10.87	2.14	1.75
7	50.2	1.04	0.13	8.15	11.29	2.28	1.89
2	49.0	1.08	0.07	2.59	4.13	2.50	1.87
6	48.4	1.09	0.09	4.54	7.00	2.47	1.99
10	48.3	0.82	0.12	6.98	12.62	3.56	2.87
1	48.0	1.02	0.08	3.36	4.65	1.94	1.56
4	46.1	0.82	0.09	3.93	8.61	1.92	1.57
3	44.6	0.83	0.06	1.80	5.37	1.00	0.82

Table 4. *Ranks of the half-sib families at different sites*

Half-sib family	Total rank	Rank at site 1	2	3	4	5	6	7	8	9
8	1	1	3	1	6	1	2	3	2	2
9	2	4	1	6	1	2	1	10	4	1
5	3	2	2	3	3	4	5	2	1	7
7	4	3	4	2	7	7	7	4	3	3
2	5	8	6	5	4	6	3	7	9	4
6	6	5	7	4	10	8	4	5	5	8
10	7	10	9	7	2	3	6	1	6	6
1	8	6	5	8	9	5	9	6	7	5
4	9	7	8	9	5	9	10	8	10	10
3	10	9	10	10	8	10	8	9	8	9

(1971) and Hinkelmann (1974), while Hanson (1970) combined the regression coefficient and the deviation from regression into one single stability measure.

Wricke (1962) proposed the concept ecovalence, which is the contribution from each genotype to the interaction sum of squares. In statistical terms, measured as a fraction of the total interaction sum of squares, the ecovalence equals

$$\Sigma_j(\bar{Y}_{ij\cdot} - \bar{Y}_{i\cdot\cdot} - \bar{Y}_{\cdot j\cdot} + \bar{Y}_{\cdots})^2/\Sigma\Sigma_{ij}(\bar{Y}_{ij\cdot} - \\ - \bar{Y}_{i\cdot\cdot} - \bar{Y}_{\cdot j\cdot} + \bar{Y}_{\cdots})^2$$

The mean heights, regression coefficients, their standard deviations, deviation mean squares from regression, and ecovalences are shown in Table 3 for the ten half-sib families.

The stability parameters presented above are based on the original measurements. Hühn (1979) wanted to avoid the problems involved in comparing measurements with different error variances and proposed several stability parameters based on the ranks of the entries in each separate environment. He considered a genotype to be stable if its ranks between the different environments are as similar as possible. Denote by r_{ij} the rank of genetic entry i in the environment j. Here the two parameters S_{1i} and S_{4i} (Hühn's notation) will be considered, where

$$S_{1i} = 2\sum_{j<j'} |r_{ij} - r_{ij}|/n(n-1)$$

$$S_{4i} = (\frac{1}{n}\sum_j (r_{ij} - \frac{1}{n}\sum_j r_{ij})^2)^{1/2}$$

The first parameter expresses the average rank differences between all pairs of environments, while the second is the standard deviation of the ranks of each genotype.

The total rank of each of the ten half-sib families and their ranks at the nine sites are presented in Table 4, and the two stability parameters are shown in the last two columns of Table 3. They show a good correspondence with a rank correlation coefficient of $r = 0.94$ (Table 5), and are also significantly correlated to the mean square deviation from regression. The latter is also highly correlated to the ecovalence.

Table 5. *Rank correlation coefficients between different stability parameters*

Stability parameters	b_i	Mean square deviation	Eco-valence	S_{1i}	S_{4i}
$\bar{Y}_{i\cdot}$	0.74*	0.41	0.39	0.27	0.32
b_i		0.14	−0.01	0.19	0.26
Mean square deviation			0.81**	0.65*	0.81**
Ecovalence				0.43	0.61
S_{1i}					0.94**

Significance at 5% and 1% level is denoted by * and **, respectively.

Evaluation of the joint regression analysis

Statistical considerations

Several statistical objections have been raised against the joint regression technique. A first comment is that the environment index, represented by the total environmental mean, represents only an estimate of the true environmental effect and thus is subject to error (Freeman & Perkins, 1971). This fact will cause the estimated regression coefficients to be biased, but their ranking will not be disturbed (Hardwick & Wood, 1972). A second bias results from the presence in the environmental index of the genotypic values which are to be regressed on it (Freeman & Perkins, 1971; Freeman, 1973), but the bias will, as shown by Wright (1976), only be present in the case of random genotypic effects. It is possible to omit the regressed genotype from the environmental index or make modifications in the estimation procedure, but the practical significance of such modifications seems to be small (Snoad & Arthur, 1975).

A frequent experience in the analysis of replicated experiments is that error variances are not homogeneous between sites. In the ordinary least squares regression analysis equal weights are given to the genotypic means. A more appropriate method would be a weighted regression analysis. In the example analysed here the reciprocals of the variances of the family means were used as weights, but without any changes neither in the absolute values of the regression coefficients nor in their errors. Hühn (1980) tried a number of different weights in an example with 20 varieties of winter-wheat planted at 10 locations and found nearly identical rank-orders of the varieties both for the regression coefficients and for the deviation mean squares. It seems that a weighted regression analysis is necessary only in cases with extreme differences in accuracy between the genotypic means from different locations. Other possibilities for the environmental index have been discussed: mode, median, maximum-yield and minimum-yield of each environment (Hühn, 1980). It is, however, reasonable to believe that these parameters will give a less precise characterization of the environment than the total mean. In the case of a separate set of standards interactions between the standards and the environments play a crucial part, particularly since the set of standards has to be small compared to the total number of genotypes tested.

Significance testing in the joint regression analysis depends upon even more assumptions than is usual in the analysis of variance, as pointed out by Freeman (1973). He also recommends that the significance of regression coefficients should be tested based on individual error terms rather than against pooled deviations. An important point is to be aware of the conditional nature of the statistical inferences being drawn (Freeman, 1973; Hill, 1975). Thus, marginal means, both environmental and genotypic, are to be regarded as fixed. Extrapolation of a demonstrated linearity to other environments should be based on experimental evidence, by identification of the responses of the genotypes to environmental factors. It is easier to justify generalizations if the test sites can be considered as random selections within different strata of similar environments. The number of test sites should not be too small; at least five is recommended. Attention should also be paid to the observed environmental range. The joint regression analysis is not appropriate in a situation like that indicated on Fig. 3.

As long as these requirements are met, the joint regression analysis should be valid statistically.

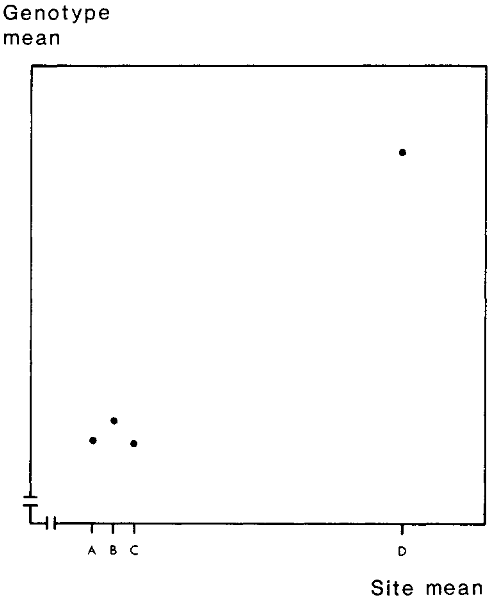

Fig. 3. An example where the joint regression analysis is not an appropriate method.

Biological considerations

A given genotype's reaction to changing environmental conditions can appropriately be described by physiological response functions, which generally are non-linear (Namkoong, 1978). Nevertheless, the linear regression technique has in many instances adequately described the behaviour of genotypes over a range of environments (see Hill, 1975, for a large number of references). The reason for this is that a linear model fits well to some parts of a response curve and thus can "explain" a substantial portion of its variation (Hardwick & Wood, 1972; Namkoong, 1978), even if systematic deviations exist. This linearization is highly dependent on the environments sampled and makes extrapolations risky.

Knight (1970) showed that low yields caused by either sub-optimum or super-optimum conditions in the same environmental factor can not be distinquished, and that changes in ranking at low yields are difficult to detect by regression or deviation from regression. When several environmental factors influence yield it is not possible to know which is the limiting factor(s), and genotypes will be ranked based on different physiological responses. This is particularly the case in field experiments with forest trees, in which several environmental factors may limit growth. Consider an example with two families 1 and 2 planted at four sites A, B, C, and D (Fig. 4). The two last sites are productive, whilst site A and B have low total means; A because of late frost, and B because of early frost. If family 2 is late flushing with a late growth cessation, and family 1 is the opposite, the results may be as indicated in Fig. 4. Here both families will be ranked as equally stable based on the regression coefficient as well as on the deviation from regression. It is also clear that the environmental index expressed by the site mean depends very much on the genetic composition of the families tested, whether they are late frost resistant, early frost resistant, or a mixture of both categories. The example clearly shows the need for characterizing each planting site by its critical environmental factors, and also that several characters should be analyzed together to assess adaption and yield, not only mean yield itself.

The linear regression model will in many instances give a satisfactory fit also in forest genetic experiments and thus is a valuable technique for the analysis. The important thing is to be aware of its limitations for biological interpretations and for generalizations.

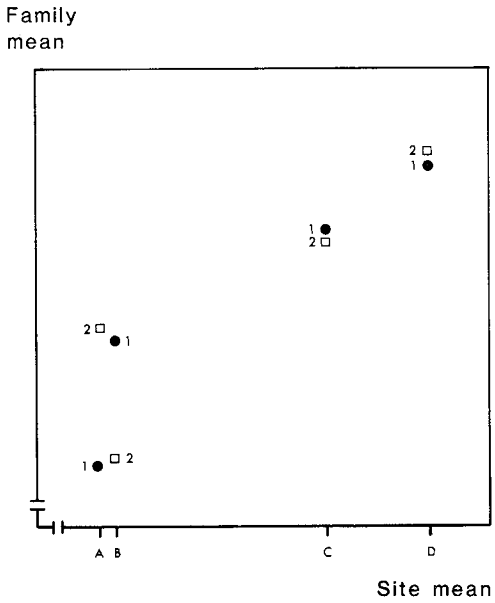

Fig. 4. A constructed example with two families planted at four sites. Late (spring) frost and early (autumn) frost are the reasons for low values at sites A and B, respectively.

Discussion of the stability parameters

According to the regression coefficient criterion of Finlay & Wilkinson (1963) the best-growing families in our example, 8 and 9, are most unstable, whilst the families 3, 4 and 10 have above average stability. By the deviation from the regression line criterion halfsib family 8 is very stable, and by the ecovalence it is somewhere in between. Thus, the different parameters can give different rankings of the stability, even if some of them are highly correlated (Table 5). Similar empirical results were found by Becker (1981), who based his comparisons on data from extensive yield trials with various crops. It can be shown by mathematical relations that the ecovalence and the deviation from regression should be highly correlated. The two parameters based on ranks are similarly strongly related.

Consider the significance of the different parameters as measures of stability. The regression coefficient reflects that portion of genotypic stability associated with the capacity of a genotype to perform relatively better in a unfavourable than in a favourable environment (Hanson, 1970). If genotypes with high b_i's are rejected, the yield at the poor sites are increased at the expense of the yield at the good sites. A genotype tends to be stable if its response function is similar to the mean response. The second parameter measures the deviations from the regression line. A high value tells that a straight line does not represent the performance well. It may be that the genotype studied shows a substantial response difference compared to the other genotypes being tested. The ecovalence reflects the capacity of a genotype to yield more consistently among environments than other genotypes (Hanson, 1970). The two measures based on ranks express changes in the ranking of genotypes between environments. In all cases, stability is defined relative to the other genotypes being tested and relative to the test environments.

In forest tree breeding we want to select for superior and stable performance over a wide range of sites. A desired genotype is one that yields close to the optimum level of productivity of each site, which in most cases will have to be described by the mean of either a subset or of the whole set of entries. The parameters discussed above distinguish certain types of undesired or atypical behaviour, but genotypes should not be characterized as unstable only because they have high parameter values (Easton & Clements, 1973). The breeder should base his choice upon inspection of mean yields and significant rank changes, supplemented by a possible interpretation of atypical behaviour of candidate genotypes based on other characters and on environmental variables.

Choice of scale

In the example analysed environmental errors were found to be heterogeneous between sites. This effect was somewhat reduced by a logaritmic transformation, but did not disappear and the interaction effect was significant also after the transformation. According to Falconer (1981), the main reasons for making scale transformations are: to make the distribution normal; to make the variance independent of the mean; and to remove or reduce interactions. Thus, a transformation is done to simplify or make possible the statistical analysis of the data. The choice of scale will, however, in many instances influence the results of the analysis of interactions, particularly the joint regression analysis. If a logaritmic scale is being used, then genotypic differences at high values are minimized, and differences at low values maximized. On an arithmetic scale exceptional high values will have a greater influence on the mean yield and the regression coefficient, so that the mean yield and regression coefficient for a genotype are positively correlated (Knight, 1970). This seems to be the case in the example analysed here ($r = 0.74$, Table 5).

The transformation may also somewhat alter the relative ranking of the genotypes based on other stability parameters, as shown by the estimates from logaritmic heights presented in Table 6. The choice of scale can sometimes be motivated by the underlying biological model; whether it should be arithmetic or geometric. If it is not the case, then the most appropriate scale will be the natural units of measurements as long as a valid statistical analysis can be done. When analysing data from selection experiments the scale should easily be translated into units that are relevant for assessing genetic gain. But it may be wise to perform a statistical analysis based both on the original measurements and the transformed values. If the conclusions differ, then a more thorough examination is necessary.

Table 6. *Half-sib family means and stability parameters of transformed heights*

Half-sib family	$\bar{Y}_{i\cdot}$	b_i	St. dev. of b_i	Mean square deviation	Eco-valence, %	S_{1i}	S_{4i}
8	3.90	1.12	0.09	0.0020	6.86	2.06	1.83
9	3.88	1.18	0.17	0.0067	21.19	3.06	2.54
5	3.87	0.86	0.10	0.0026	9.11	2.72	2.18
7	3.84	1.00	0.12	0.0033	9.26	2.36	1.95
2	3.82	1.13	0.11	0.0030	10.35	2.69	2.11
6	3.79	1.16	0.11	0.0028	11.05	2.64	2.04
10	3.81	0.86	0.11	0.0027	8.98	3.06	2.45
1	3.81	1.05	0.08	0.0017	4.88	1.56	1.26
4	3.76	0.89	0.14	0.0048	14.11	2.56	2.42
3	3.73	0.87	0.06	0.0009	4.23	1.14	0.99

Experiments planted at few sites

A typical forest genetic experiment is planted at one, two, or three sites. This is particularly the case with the older trials which are very important to-day. Those trials can give us information about genetic differences in growth and quality beyond the juvenile stage, and can provide estimates of juvenile-mature correlations.

When an experiment is planted at one single site the observed results are valid only for that site. Generalization to other types of environments should not be done unless additional information can tell that interactions are small in the environmental range considered. Genetic entry means will generally be biased by interactions, and the one-site ranking of entries is doubtful as a basis for the selection of genetically improved material to be planted over a wide range of environments. A single experimental plantation cannot provide any evaluation of genotype×environment interactions.

An experiment replicated at two sites allows for a statistical test of interactions by the ordinary *F*-test. If this is found significant, plots can be made to see which genotypes are responsible for the interactions. Ekberg et al. (1983) propose to plot the differences between the individual entry means at each site, corrected for site effects, against their total means from the two sites. They expressed the differences in units of the standard deviation. The same technique can be applied when an experiment is replicated at three or four sites, providing three or six plots, respectively.

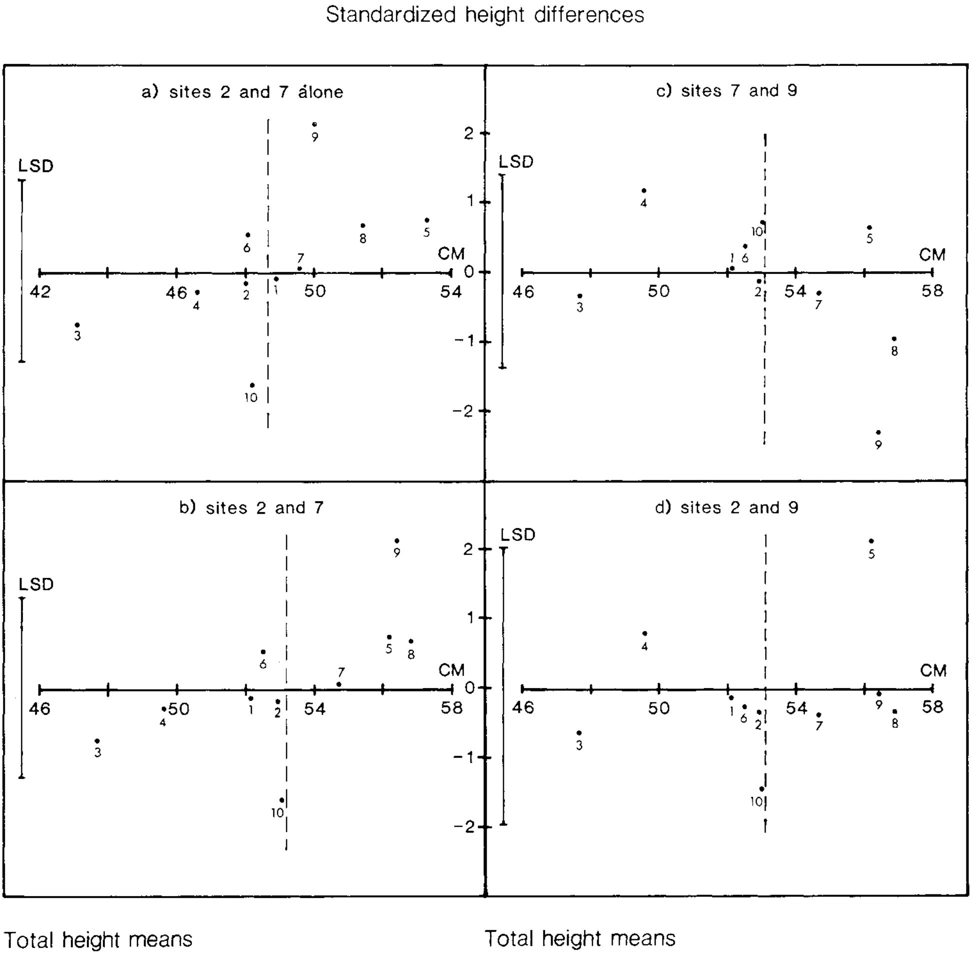

Fig. 5. Plots of standardized height differences for pairs of sites against overall half-sib family means. In (a) sites 2 and 7 are considered as one experiment and in (b), (c), and (d) all three sites 2, 7, and 9 are analysed together. The dotted vertical line represents the overall mean, whilst the line on the left hand side shows the least significant difference (LSD).

Significant differences can be identified by the LSD test (Snedecor & Cochran, 1972) or by more conservative multiple comparison methods (Scheffé, 1959). It is also possible to calculate differences in ranks between two, three, or four sites, but such methods are less sensitive than the analyses based on the measurement data.

To illustrate the plots the three sites 2, 7, and 9 are sampled from the set of sites in the example. Firstly, sites 2 and 7 are considered as one experiment and, secondly, all three sites are analysed together. Significant effects for half-sib families and significant interactions were found in both cases. For each pair of sites the differences between the family means were divided by their standard deviation and were plotted against their means from the two sites (Fig. 5a) and against their means from the three sites (Fig. 5b, c, d). The standardization has no practical significance when comparing two sites only, but will be helpful when several plots are to be considered simultaneously. The plots show that half-sib families with an aberrant height growth between sites can be identified, and in the case of three sites, the site with inconsistencies can be found. An example is family 9 at site 7. The same information can of course be obtained by comparing the columns of ranks for sites 2, 7, and 9 in Table 4.

Genetic correlations

Burdon (1977) studied genotype × environment interactions by chacterizing environments rather the genotypes. This can be done by examining the matrix of genetic correlations between pairs of test sites. Thus, it can be found which environments are out of line with the rest. Based on the formula for correlated response

$$\triangle G_{y.x} = ih_x \sigma_{Ay} r_{Axy}$$

expected response at site y when the selection is performed at site x, can be calculated. If the genetic entries are half-sibs, then

h^2_x = heritability of half-sib family means at site x
σ^2_{Ay} = additive genetic variance at site y
r_{Axy} = correlation between half-sib family means at sites x and y

The matrix of gain expectations at one site after selection in another will tell which sites are good for selection. In Table 7 this matrix is presented for the example, assuming that clones are selected for an open-pollinated seed orchard. The first thing to note is the negative estimate of the additive genetic variance at site 4. Thus, selection at this site will not predict any gain at other sites, neither will there be any expected gain at this site when selection is performed at another. With a few exceptions, the best test site will be the planting site itself (diagonal values). Sites 5 and 7 are not very good as indicated by the low heritability values. The best sites for selection would be 2, 3, or 9; they also have the highest heritability estimates. Selection based on the overall means has the highest expected gain at all planting sites.

This method focuses experimental sites rather than genotypes. Its main use is in deciding which environment gives the best screening of genotypes. The gene-

Table 7. *Expected genetic gains when selection is performed at site x and the seed orchard progenies are planted at site y and from overall selection, in units of the selection intensity i*

Planting site y	Selection site x									Overall selection	σ^2Ay
	1	2	3	4	5	6	7	8	9		
1	2.38	3.29	3.04	0	0.17	1.68	0.10	1.61	2.05	4.46	20.79
2	3.17	5.41	3.39	0	0.31	2.86	0.09	2.36	3.37	6.85	45.83
3	2.26	2.60	4.38	0	0.18	1.33	0.27	1.87	2.10	4.65	28.62
4	0	0	0	0	0	0	0	0	0	0	−6.25
5	0.38	0.67	0.47	0	0.08	0.56	0.06	0.37	0.65	1.13	1.44
6	1.59	2.79	1.70	0	0.25	4.27	−0.14	0.79	3.21	4.72	35.40
7	0.14	0.13	0.57	0	0.04	−0.24	0.13	0.30	0.10	0.48	1.93
8	1.41	2.11	2.20	0	0.13	0.71	0.17	1.74	1.43	3.18	13.25
9	2.22	3.75	3.01	0	0.33	3.61	0.08	1.75	4.34	6.31	40.83
h^2x	0.26	0.40	0.41	0	0.03	0.36	0.05	0.24	0.34	0.56	

tic analysis should be followed by studies of environmental factors at each site, aiming to find which type of sites are well suited and which are not, for selection experiments. It may be found that some particular accidents are the reasons for aberrant results at some sites. The method also seems to be good for analyzing provenance tests planted at many sites for the purpose of delineating plantation or breeding zones or to study genotype × environment interactions. The method supplements the regression and stability analyses and can explain some of the interactions, but it can not be used for the ranking of genotypes, which is the main purpose of selection experiments.

Multivariate analyses

Interactions in the two-way table consisting of the performances of many genotypes in several environments can be tested by special tests for non-additivity (Mandel, 1971; Corsten & van Eljnsbergen, 1972). The tests are based on a principal component analysis which tries to reduce the dimension of the interactions. This method has not been much used in the analysis of genotype × environment interactions, and it is not quite clear how it can be used in selection experiments to assess stability. It has been suggested that this method will be useful when regression on the environmental mean shows wide deviations from linearity (Freeman, 1973).

Several multivariate statistical techniques are available for the analysis of many genetic entries over several sites: principal component analysis; factor analysis; cluster analysis; pattern analysis. Such methods can group genotypes performing similarly in several environments or classify the environments into clusters that minimize the within-cluster interactions. As a basis for the grouping several measures are available, one possibility is the matrix of genetic correlation coefficients calculated by Burdon's method. The usefulness of these methods for the grouping of test environments is doubtful, as the number of test sites in forest genetic experiments usually is low. It is more likely that the methods could be valuable for the grouping of genotypes, particularly if several different characters are to be considered simultaneously in the selection. It is possible in some of these analyses to give the characters different weights. One problem is that it difficult to relate these methods to the quantitative genetic models and the selection parameters. It is therefore recommended that such multivariate methods should be evaluated for use in selection, and studies should be made to link the multivariate analyses to the quantitative genetic models.

Discussion of the example

Significant genotype × environment interactions are found in this example, and the joint regression analysis indicates response differences between half-sib families when they are compared at low-yielding and high-yielding sites. Inspection of Table 4, however, reveals that the largest changes in ranks occurred at sites 4, 5, and 7. At site 4 the estimate of the additive variance component is negative, and at the two other sites the heritability values are very low (Table 7). Thus, the major interactions are found on sites which had large experimental errors or where little genetic variation was expressed. Site 4 also has a mortality of 49%. The practical significance of the interactions therefore seems to be small.

We have seen that most of the different analyses have thrown some light on the interactions. The full interpretation can only be given when we know which environmental factors are causing low yield and/or high mortality. It should also be assessed how representative the environments are for the breeding zone.

Final discussion

Based on the results from selection tests we want to divide the set of genetic entries into two groups; one group for further breeding and the other group to be culled. Changes in ranking between members within each group have no practical significance. More important are extreme rank changes between genotypes from site to site. It seems that most methods or a combination of several methods can identify single genotypes with such aberrant performance. If a larger part of the genotypes are involved in interactions, a revision of the breeding zones may be needed. To identify the environmental factors causing the interactions, however, is more difficult and requires measurements of important environmental characteristics. It is perhaps not realistic to expect to explain and be able to utilize interactions caused by more than a single environmental factor with a predictable influence (Barnes et al., 1982).

Usually little information about genotype × environment interactions is available when the breeding populations are to be set up. Several strategies are then possible. One choice is to make wide zones and breed for general adaptability over a range of sites. This requires a stability parameter as selection criterion. If large interactions later turn up problems may arise. Another possibility is to start with a larger number of separate breeding populations and select for specific adaptability in each particular zone. The different populations can always be combined if later results indicate that it can be done. This leaves a flexibility that one never has with the first alternative. A third possibility is to combine the above strategies in long term breeding, selecting at one site in the first generation and in the next breed trees selected from different environments. With all alternatives, studies of genotype × environment interactions should be done to design an optimal breeding strategy.

Most of the statistical methods discussed are univariate, analysing one character at a time. In forest genetic experiments, yield usually relates to height growth at a juvenile age. However, most frequently a larger number of characters are of importance, i. e. survival, flushing, growth cessation, and quality traits. It is possible that some parts of the genetic variation (i. e. non-additive effects) interact with the environment while other parts (i. e. additive effects) do not. Multivariate statistical methods taking into account both the correlation between characters and the interactions between genotypes and sites can be used for analysis. With many traits, however, the analyses become complicated and difficult to interprete. Characters showing little interactions with environmental factors can more precisely be evaluated under standardized conditions than in field tests (Dormling, 1980). Accordingly, properly designed experiments to study genotype × environment interactions should be established to find out whether they need special attention or not in the breeding. Such experiments will also help identifying the type of site conditions that are optimal for the ranking of families or clones.

References

Barnes, R. D., Burley, J., Gibson, G. L. & Garcia De Leon, J. P. 1982. Genotype × environment interactions in tropical pines and their effects on the structure of breeding populations. 22 pp. Paper presented at the IUFRO Joint Meeting of Working Parties on Genetics about breeding strategies including multiclonal varieties, Sensenstein, Federal Republic of Germany.

Becker, H. C. 1981. Correlations among some statistical measures of phenotypic stability. *Euphytica 30,* 835–840.

Burdon, R. D. 1977. Genetic correlations as a concept for studying genotype × environment interactions in forest tree breeding. *Silvae Genet. 26,* 168–175.

Corsten, L. C. A. & Van Eijnsbergen, A. C. 1972. Multiplicative effects in two-way analysis of variance. *Statistica Neerlandica 26,* 61–68.

Dietrichson, J. & Haug, G. 1976. Resultater fra et avkomforsøk med gran *Picea abies* (L.) Karst. fra Opsahl i Ringebu. *Meddr Norsk inst. skogforsk. 32,* 459–482.

Easton, H. S. & Clements, R. J. 1973. The interaction of wheat genotypes with a specific factor of the environment. *J. agric. Sci. Camb. 80,* 43–52.

Eberhart, S. A. & Russel, W. A. 1966. Stability parameters for comparing varieties. *Crop Sci. 6,* 36–40.

Ekberg, I., Eriksson, G. & Hadders, G. 1983. Growth of intra- and interprovenance families of *Picea abies* (L.) Karst. *Silvae Genetica 31,* 160–167.

Dormling, I. 1980. Vilken roll kommer forskningen i klimatkamrar att spela för den framtida skogsträdsförädlingen. *Sveriges Skogsvårdsförbunds Tidskrift 78,* 153–162.

Falconer, D. C. 1981. *Introduction to quantitative genetics,* 2nd ed. 340 pp. London: Longman.

Finlay, K. W. & Wilkinson, G. N. 1963. The analysis of adaptation in a plant breeding programme. *Aust. J. Agric. Res. 14,* 742–754.

Freeman, G. H. 1973. Statistical methods for the analysis of genotype × environment interactions. *Heredity 31,* 339–354.

Freeman, G. H. & Perkins, J. M. 1971. Environmental and genotype × environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. *Heredity 27,* 15–23.

Hanson, W. D. 1970. Genotypic stability. *Theor. Appl. Genet. 40,* 226–231.

Hardwick, R. C. & Wood, J. T. 1972. Regression methods for studying genotype × environment interactions. *Heredity 28,* 209–222.

Hill, J. 1975. Genotype-environment interactions-a challenge for plant breeding. *J. agric. Sci. Camb. 85,* 477–493.

Hinkelman, K. 1974. Genotype × environment interaction: aspects of statistical design, analysis and interpretation. 32 pp. Paper presented at the 8th International Biometric Conference, Constanta, Romania.

Hühn, M. 1979. Beiträge zur Erfassung der phänotypischen Stabilität. I. Vorschlag einiger auf Ranginformationen beruhenden Stabilitätsparameter. *EDV in Medizin und Biologie 10,* 112–117.

Hühn, M. 1980. Beiträge zur Erfassung der phänotypischen Stabilität. II. Modifikationen des Regressionansatzes durch Verwendung gewogener Regressionsmodelle sowie Änderungen der Bezugsbasis. *EDV in Medizin und Biologie 11,* 113–120.

Johnstone, R. C. B. & Samuel, C. J. A. 1978. The interaction between genotype and site: its influence on tree selection programmes in Britain. 18 pp. Research & Development Paper 122. Forestry Commission.

Knight, R. 1970. The measurement and interpretation of genotype × environment interactions. *Euphytica 19,* 225–235.

Mandel, J. 1961. Non-additivity in two-way analysis of variance. *J. Am. Stat. Assoc. 56,* 878–888.

Mandel, J. 1971. A new analysis of variance model for non-additive data. *Technometrics 13,* 1–18.

Mergen, F., Burley, J. & Furnival, G. M. 1974. Provenance-temperature interactions in four coniferous species. *Silvae Genet. 23,* 200–210.

Morgenstern, E. K. & Teich, A. H. 1969. Phenotypic stability of height growth of Jack pine provenances. *Can. J. Genet. Cytol. 11,* 110–117.

Namkoong, G. 1978. Genotype by environment interactions: Some theoretical considerations. In *Proc. Fifth North American Forest Biology Workshop,* 35–45. Gainesville, Florida.

Rehfeldt, G. E. 1979. Ecological adaptations in Douglas fir *(Pseudotsuga menziesii* var. *glauca)* populations. I. North Idaho and North-east Washington. *Heredity 43,* 383–397.

Scheffé, H. 1959. *The analysis of variance.* 477 pp. New York: John Wiley & Sons.

Shelbourne, C. J. A. 1972. Genotype × environment interaction: its study and its implications in forest tree improvement. In *Proc. IUFRO Genetics—SABRAO Joint Symposia, B-1 (I),* 1–28. Tokyo, Japan.

Shelbourne, C. J. A. 1974. Clonal test with *Picea abies* in Norway—10 to 17 year results. Unpublished report, 38 pp. Norwegian Forest Research Institute, Ås, Norway.

Shelbourne, C. J. A. & Campbell, R. K. 1976. The impact of genotype environment interactions on tree improvement strategies. In *Proc. IUFRO Joint Meeting Working Parties on Populations and Ecological Genetics,* 73–93. Bordeaux, France.

Snedecor, G. W. & Cochrane W. G. 1972. *Statistical methods,* 6th ed. 593 pp. Ames, Iowa: The Iowa State University Press.

Snoad, B. & Arthur, A. E. 1976. The use of regression techniques for predicting the response of peas to environment. *Theor. Appl. Genet. 47,* 9–19.

Tai, G. C. C. 1971. Genotypic stability analysis and its application to potato regional trials. *Crop. Sci. 11,* 184–190.

Wricke, G. 1962. Über eine Metode zur Erfassung der Ökologischen Streubreite in Feldversuchen. *Z. Pflzücht 47,* 92–96.

Wright, A. J. 1976. Bias in the estimation of regression coefficients in the analysis of genotype × environment interaction. *Heredity 37,* 299–303.

Acknowledgement. Thanks are due to G. Haug and J. Dietrichson for the permission to use data from the factorial Norway spruce crossings as an example.

PREDICTION AND OPTIMIZATION OF GENETIC GAIN WITH REGARD TO GENOTYPE × ENVIRONMENT INTERACTIONS

DAG LINDGREN

Department of Forest Genetics and Plant Physiology
S-901-83 UMEÅ, Sweden

Abstract

Lindgren, D. 1984. *Prediction and optimization of genetic gain with regard to genotype × environment interactions.* Studia Forestalia Suecica 166, 15–24. ISSN 0039-3150, ISBN 91-576-1847-X.

A tree breeder has to make decisions prior to full rotation time. A formula suggested by Lambeth seems to be useful for predicting the effect of selecting for height in young age. Based on the formula and other considerations it was suggested that as a rule of thumb for Scandinavian conditions, decisions should be made when the trees are 3–5 m high (in Lappland 2–4 m).

Experimental results on genotype × environmental interactions in progeny-testing conifers were discussed. Some data on cereals were also presented and discussed. Often the variance component due to genotype × environment interaction is rather low compared to that of the genetic entries. The reduction of genetic gain due to a limited number of test localities was analysed. A model for the Swedish progeny-testing programme for Scots pine suggested that the best use of limited resources is to utilize test results from 3–4 localities. Considering the risk that a locality suffer damage and the area of use of breeding material it was recommended to use at least five localities, although the theoretical losses incurred in using fewer localities are minimal.

The concept of "testing orchards" was discussed. It might be profitable, but there are no good data for a quantitative discussion.

Key words: Pinus sylvestris L., tree breeding, age, test localities, varieties × environments, interactions, variance components, test orchard, juvenile-mature correlation.
ODC 232.12:181.

Dag Lindgren, Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden.

Introduction

Methods for predicting genetic gain are essential for comparing the options which a forest tree breeder has to consider. Existing measurable experiments seldom comprise the alternatives most appealing today, but may still contribute information on some essential parameters. A small improvement of genetic gain has a considerable impact measured as effect on Gross National Product and employment, even if it is not experimentally measureable. Decisions must still be made based on existing—but usually meager—information. Thus the forest tree breeder has to rely on theoretical conclusions for his practical decisions.

Selection will be made based on tests grown under other conditions than those in which the material will be practically utilized. Thus the influence of genotype × environment interaction on genetic gain has to be dealt with to develop tools to compare different alternatives.

In this paper the following aspects are discussed:

- The influence of mature-juvenile correlation, which can be considered as a special case of interaction with the environment.
- The influence of the number of test localities within a well-defined breeding zone.
- The concept of a test orchard.

Genotype × environment interactions in relation to choice of experimental localities have been discussed e.g. by Patterson & Silvey (1980), Burdon (1977) and literature cited by them.

Mature-juvenile correlation

Forest tree breeders are not keen on the idea of waiting a full rotation period to make decisions. Lambeth (1980) compiled mature-juvenile correlations from several studies representing different species, site indici and general growing conditions. The study presents good evidence that the phenotypic correlation for height of individual trees between two ages (*r*) may be satisfactorily estimated by the equation:

$$r = 1.02 + 0.308\, ln\, Q \qquad (1)$$

Q = the quotient between early and late age (since planting).

Lambeth points out that values obtained a few years after planting may be highly misleading, and that the deviating values occur mainly before 2 meters height is reached. He also states that for many studies, genetic and phenotypic correlations are roughly equal in genetic tests on forest trees. Although it has not been satisfactory proven, it is often assumed that the gain in a juvenile selection is approximately proportional to the mature-juvenile correlation.

The function is demonstrated in Figure 1.

Lambeth finds that the same function gives a good fit even if the late age is not mature; thus the age-dependence of the juvenile-mature correlation may be estimated before full rotation.

To investigate whether the formula is also applicable to Scandinavian conditions, points are illustrated in Figure 1 from an investigation with Norway spruce (*Picea abies*) cuttings (Skrøppa, 1981), (values at lower age excluded because of low height) and grafted clones of Scots pine (*Pinus sylvestris*) (von Euler, F. 1982, unpubl. Kvalitet i ett tallympförsök. Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå. Internal report 46). It seems as if formula (1) often gives a lower estimate than the experimentally obtained, but the points do not seem more spread than the points Lambeth used.

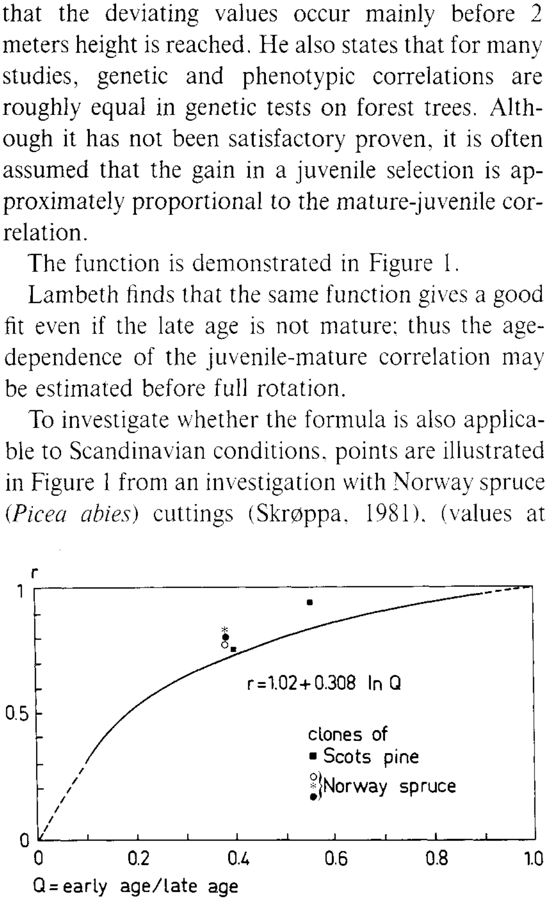

Fig. 1. The correlation (r) between height development at early and late age (counted from planting) is predicted rather well by a formula suggested by Lambeth (1980). Some new experimental points for clones obtained for Norway spruce by Skrøppa (1981) and for Scots pine by von Euler (1982) are included to demonstrate the fit of experimental values. The correlation is not reliable predicted, when young height is below 2 meters.

Thus, until better experimental evidence appears, it is suggested that Lambeth's function be used in designing breeding programmes in Scandinavia. However, when survival is highly important, the function probably underestimates the possibilities of making decisions at young ages.

Optimal moment for decision-making in field trials

Waiting with decisions may mean loss in genetic gain per time unit and a longer delay until genetic improvements reach practical forestry.

Lambeth's function makes it in principle possible to advise an optimal age for making decisions concerning which genotypes to include in the next cycle of crossings. There is a time lag between measurement and the planting of the next cycle. This is necessary because of evaluation, decision-making, crossings and plant production.

The genetic gain per time unit will be proportional to *r* divided by time between cycles, thus:

$$E = (1.02 + 0.308\, ln\, Qe)/(Qe + a) \qquad (2)$$

where *a* is the time lag between measurement and planting of experiments belonging to the next cycle and *Qe* the age at measurement for decision as a fraction of the full rotation time. The optimal age for decision making is the age giving the maximal value of *E*. This is dependent on the time lag *a*.

In Figure 2 the optimum age for making decisions is demonstrated as a function of the time lag between cycles. The time lag will be in the range of 2–10 years. A surprisingly narrow range of optimum age for decision-making is indicated in the order of 0.13–0.20 of full rotation time (Lambeth carried out similar calculations). This often means that the trees are 2–5 meters at optimal selection age.

Besides a mechanical consideration of the results of the rather uncertain formula, factors listed below should be considered as regards waiting a longer or shorter time with decisions.

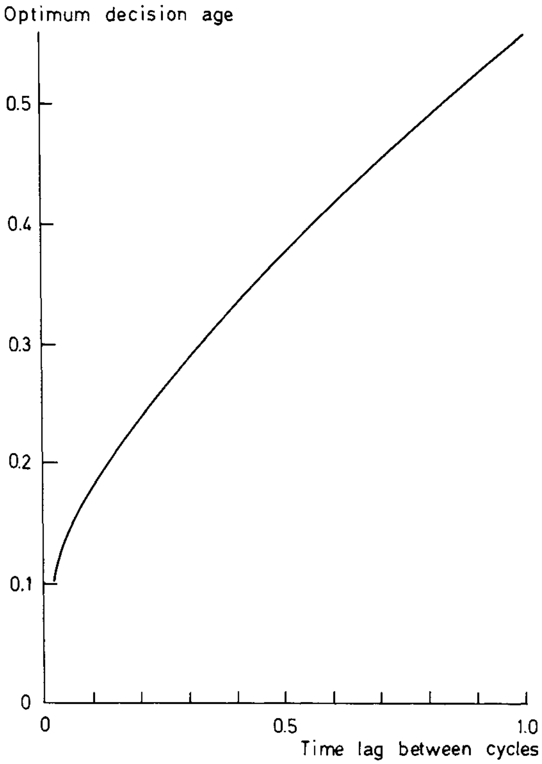

Fig. 2. The curve demonstrates at what age (measured as fraction of full rotation) maximal genetic gain per time unit is obtained. The gain increases as 1.02 + 0.308 *ln* (age), but it is a necessary time lag between cycles for evaluating measurements, decision-making, making crosses and producing plants. The longer the time lag, the higher the optimum decision age. As the time lag in Sweden seldom will be any considerable fraction of the rotation time, it usually seems optimal to make decisions before 20% of the rotation time.

Reasons for making later decisions

- During the first part of the rotation time most of the biomass production is in needles and branches, and only after around 10% of the rotation times does the production of valuable stem wood start to be important (cf. Albrektsson, 1980).
- During the first part of the rotation time the ecological space is not fully utilized. Efficiency in speed of establishment and filling of the space does not necessarily predict efficiency in a limited ecological space.
- Some quality characters are difficult to evaluate on young trees. The bottom log is the most valuable part of a tree, and on a 4–5 m high tree the quality of the future log may be predicted with a reasonable accuracy.
- Certain types of injuries may occur first at a certain size (e.g. snow break or consequences of exposure above snow cover).
- Sexual maturity is necessary if crosses are intended.
- The potential genetic gain may be comparatively large in the first cycle of breeding.
- Each cycle means a reduction of genetic base and diversity.
- Shorter cycles mean larger costs per time.

Reasons for making earlier decisions

- The information in Figure 1 indicates that Lambeth's formula underestimates mature—juvenile correlation.
- Practical, psychological and administrative advantages. Continuity in personnel, organizations and recordkeeping.
- Physical size of tree makes it more difficult to measure and cross.
- No considerations of the effects of competition and thinning are necessary.
- Heritability may be greater at a juvenile stage than at a mature stage, and the genetic juvenile—mature correlation larger than the phenotypic correlation.
- Testing costs may be reduced by denser spacing.

Recommendation

Considering all the facts, I think a good guideline for Scandinavian conditions is that decisions concerning choice of genetic material within species should be made when the trees are 3–5 m high. For Scots pine in Lappland, survival is a limiting factor, and decisions could be made earlier, but not before the trees have been exposed above snow cover some years,—thus at 2–4 m.

Calculating correlated response considering genotype × environment interactions

Wright (1976, formula 10) gives a formula for correlated response:

$$E(\Delta G) = i\sigma_g^2/\sqrt{\sigma_g^2 + (\sigma_f^2 - V(\sigma))/L + \sigma_e^2/nL} \quad (3)$$

$E(\Delta G)$ = expected gain (response to selection)
i = selection intensity
σ_g^2 = variance for differences between genetic entries
σ_f^2 = variance for genetic entries × localities
σ_e^2 = variance for error attached to individual plot or plant observation
$V(\sigma)$ = variance of phenotypic standard deviation
L = number of environments
n = number of replications

Two applications of this formula are presented in this paper. Phenotypic standard deviation in this connection is assumed to be constant, thus $V(\sigma) = 0$ (this assumption is discussed later).

$K = \sigma_f^2/\sigma_g^2$
$B = \sigma_e^2/\sigma_g^2$

After division of the numerator and the denominator of formula (3) by σ_g it takes the form:

$$E(\Delta G) = i\sigma_g/\sqrt{1 + K/L + B/Ln}$$

If the experimental error of the entry values on an individual site is small ($\sigma_e^2 \rightarrow 0$ or $n \rightarrow \infty$) the formula is simplified to:

$$E(\Delta G) = i\sigma_g/\sqrt{1 + K/L}$$

Tested on an infinite number of localities ($L \rightarrow \infty$) the gain is $i\sigma_g$.

The relation between the gain possible if the genetic entries were tested on all possible localities compared to a random sample of these possible localities can be expressed as a "loss factor": $1/\sqrt{1 + K/L}$. The relation is graphically demonstrated in Figure 3.

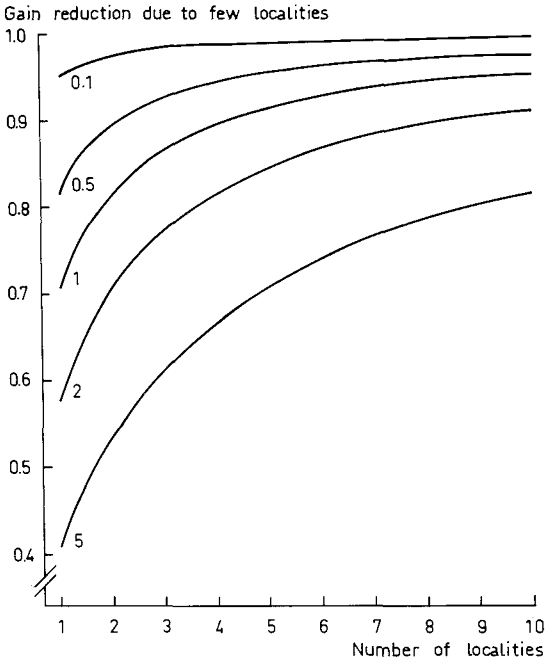

Fig. 3. A decrease in possible gain occurs when a genetic entry is tested on a less than infinite number of localities. This is visualized in the figure. The curves correspond to different values of *K*, the quotient between the variance components of interaction genetic entries × localities and the genetic entries.

Experiences from cereals in agriculture

Agricultural breeding often includes two steps—the tests made by the breeder and official testing of the candidate varieties before marketing. There is, in contrast to forestry, a lot of field data available covering many years and localities. The idea that the forester has something to learn from the agriculturist seems justified. Therefore experiences from cereal testing is presented. Although there are much data, there is generally a lack of compilation, evaluation and general conclusions from the data.

Patterson & Silvey (1980) analysed grain yield obtained in trials of recommended varieties in the United Kingdom during 1968–1976 at different centres (different fields within the centres in different years).

The following values were found:

	Spring barley	Winter wheat
Coefficient of variation for varieties[1]	0.034	0.059
K^2	3.4	1.4

[1] The square root of the component of variance divided by the average. This way of expressing variance components will be used.

[2] Depending on differences between investigations and presentations, the definition of *K* is not quite consistent. The definition is given for each case as the variance components concerned.

K is calculated as a quotient of variance components (varieties × centres + varieties × years + varieties × centres × years)/varieties.

By considering the variance components in the examples, Patterson and Silvey reached the following conclusions:

- It seems preferable to spend resources on testing over many years. The variance for the difference between two varieties of barley is twice as large if tested on 25 centres for 2 years compared to 10 centres for 5 years.
- Increasing the number of test centres beyond 10 only increases the genetic gain by some parts in a thousand, at least in a certain test procedure for barley.

Aastveit (1982) presented figures for grain yield during 3–4 years from Östlandet, Norway. The following results were obtained:

	K
Two-row barley	8.9
Early oats	2.6
Late oats	4.8

K is calculated as a quotient of variance components: (varieties × years + varieties × fields)/varieties.

Based on calculations from these data, Aastveit notes little gain in using more than 15–20 fields, but it is important to use results obtained over many years.

Interaction found in progeny tests of forest trees

Pinus taeda (Owino et al., 1977) variance component constitutes to my knowledge the most extensive experimental analysis on genotype × environment interaction in forest trees. The origin of the parents and the twelve test plantations covered the following states in the southeastern US: Louisiana, Alabama, Tennessee, Georgia, Texas, South Carolina and North Carolina. The parents could be grouped according to origin. Field assessments were done at the end of the fourth growing season.

K = families × localities/families variance components

Three sets with controlled crosses and one with open pollination gave the following data for fusiform rust score on three of the locations:

$K = 0.1;\ 1.0;\ \rightarrow \infty$ (negative between family component); 0.8.

The variance components for height for sets of experiments using different mating designs were given, and based on these values *K* was calculated as *gca* × localities/*gca* (*gca* means general combining abilities). It was possible to divide the types of crosses according to the origin of parents into three categories. The following *K*-values were calculated:

Type of cross	*K*-values
Local	0.4; 0; 0; 0.03
Intermediate between local and wide	0; 1.2; $\rightarrow \infty$
Wide	0.9; 0.09; $\rightarrow \infty$

The interactions were found to be large enough to cause considerable upward biases of gain prediction (60–100%).

Pinus virginiana. (Rink & Thor, 1976). Tree volume was measured at age five on half-sib families from 13 natural stands which were planted at five localities in Tennessee and Alabama. *K* was estimated as the following quotient between variance components:

K = (localities × stands + localities × families within stands)/
(between stands + families within stands)
= 0.11.

Pinus sylvestris: Krusche et al., (1980) compared height of open pollinated progenies originating from one provenance after 11 years at two localities in northern Germany:

Table 1. *Variance components (expressed as coefficient of variation or related to σ_{gca}^2) for two progeny-tests*

Source of variation	Coefficient of variation 101 Dömle	 104 Svartnäs
Between gca	0.025	0.035
Between trees within a full-sib family and locality	0.314	0.211
Interaction *gca* × localities	0.036	0.032
K = *gca* × localities/*gca*	2.10	0.849
B = variance components between trees/*gca*	175.9	36.2

K = families × localities/families = 0.06.

Johnstone, et al., (1978) analysed height at age 6 years for three sets of open-pollinated progenies at five nearby sites in the area Inverness-Aberdeen and an additional site northeast of Cambridge:

K = families × localities/families for the three sets = 0.9; 1.2; and 0.014, respectively.

Johnsson (1972) analysed the height of 10-year-old full-sib families originating from clones of the pine seed orchard at Ekebo. The material was tested at two localities situated in Småland. At one locality there were two experiments situated close to each other. The data given below were calculated from Johnsson's data by the author. (The adjacent experiments were regarded as different localities).

Cause of variation	Coefficient of variation for the variance component
Between gca (general combining ability)	0.0973
Interaction gca × localities	0.0265
K = gca × localities/gca	0.07
B = between trees/gca	3.0

Wilhelmsson & Lindgren (personal communication and material presented at excursion) analysed two sets of progeny tests with full-sib families (denoted 101 Dömle and 104 Svartnäs according to the name of the corresponding seed orchards). The series comprised a total of nine localities in middle Sweden at latitudes 59°–61°N. The estimates arrived at are presented in Table 1 (variance components are expressed as coefficients of variation).

According to the model, if additional costs per tested clone and experimental error in individual values are negligible, it seldom seems justified to test materials on more than two localities. Some values of K reported for conifers are:

K	0–0.1	0.11–1	1.1–3	> 3	Sum
No of cases	9	7	3	3	22

The cases where K is above 3 are probably a reflection of low genetic variance, and in these cases it is probably not justified to spend money on testing on many localities.

That the genotype × environment interaction is as low as it is in many experiments may be due to the fact that breeding materials often are not tested in a satisfactorally large range of environments.

The optimal number of localities

A simple optimization model

The agricultural case

It is assumed that a value of a variety is estimated without experimental error on an individual site. There is an economical constraint that the number of tested varieties (N) times the number of test localities (L) is 500. There is no additional cost for additional varieties or localities. (These might be regarded as rather unrealistic simplifications). Various years and localities are regarded as equivalent. The aim of the testing is to maximize the value of the best variety.

The genetic gain of selection based on the testing is according to the formula:

$$E(\Delta G) = i\,\sigma_g/\sqrt{1 + K/L} \qquad (4)$$

The loss by testing on too few localities as a function of K and L may be studied in Figure 3. i is set as the selection intensity of choosing the best out of $500/L$ varieties. The number of test localities (L) maximizing $E(\Delta G)$ is the following:

	Optimal number of test localities (L)
$K < 0.39$	1
$K \simeq 0.6$	2
$K \simeq 1$	3
$K \simeq 2$	5
$K \simeq 3$	7
$K \simeq 5$	10

Under this simplified model is seems justified to assume that testing 50 cereal varieties on 10 localities is preferable to testing 10 cereal varieties on 50 localities.

The forestry case

The simplified-model assumptions are somewhat different. The economical constraint is still $NL = 500$. The goal of selecting the best variety is changed to selecting the 20 best progeny-tested clones for use in a future seed orchard.

The meaning of i changes to the selection intensity obtained via selecting the 20 best of $500/L$ progeny-tested clones.

In this case the optimal values of L become:

	Optimal number of test localities (L)
$K < 1.05$	1
$K \simeq 2$	2
$K \simeq 4$	3
$K > 6$	more than 3

However, for progeny-testing the model may be oversimplified. A considerable part of available resources is spent on selection, grafting and crosses of trees to be progeny-tested, and thus the cost-dependence of the number of entries is not negligible. Trees are expensive test organisms, and it seems doubtful that it is optimal use of resources to test a progeny with so many trees that the experimental error becomes insignificant.

A model for optimization of progeny testing forest trees

The method of optimization is related to that presented by Lindgren (1977). A genetic goal is set. Constraints are defined. Available resources are expressed monetarily, and costs for different components are defined. Experimental data are used in formulae predicting correlation between experimentally obtained and true values.

Genetic goal: Design a test that ranks the genotypes superior for *gca* on top. Choose the number of localities to maximize the gain.

Costs: Each locality costs 8 000 monetary units (m.u.), and each measurable tree costs 10 m.u. (The monetary units refer to Swedish kronor, price level 1978, but it is the *relations* between costs that matter, not the actual levels).

Testing method; genetic constraint: Polycross or common testers. To simplify, no specific combining ability is assumed. (Lindgren, 1977, described how to deal with specific combining ability.)

Economic constraint: A total of 136 000 m.u. are available for progeny-testing 200 genotypes. Thus, L (number of localities) and n (number of trees per tested genotype and locality) must be chosen to fit:

$$136\,000 = 8\,000\,L + 2\,000\,Ln \qquad (5)$$

Thus, $n = 68/L - 4$

For example, 17 measurable trees on each of 4 measurable localities fit. This is close to the intention of the present Swedish progeny-testing programme.

Formula: The genetic gain expected by testing n trees per progeny on a random choice of L localities is given by formula (3). The expectation with an infinite number of trees on all possible localities is $i\sigma_{gca}$, and formula (3) is divided by that value:

$$1/\sqrt{1 + B/nL + K/L} \qquad (6)$$

This is a factor expressing the testing loss with a limited number of trees and a limited number of test localities.

Experimental: In Figure 4 the factor (6) is demonstrated as a function of L under the contraint $n = 68/L - 4$ for the experimental data described above from progeny-testing Scots pine clones in the seed orchards Dömle and Svartnäs. The data from Johnsson (1972) described above were also used for calculation. Table 2 is a compilation.

Table 2. *Optimal number of test localities and consequencies of using only one locality*

Progeny test (Seed orchard)	Optimal number of localities according to the model	Loss by using only one locality (per cent) compared to optimal number
Ekebo	4	2
Svartnäs	4	11
Dömle	3	9

Comments

- Three independent sets of experimental materials with extremely different values for the genetic variance components all indicated that 3–4 localities are the optimal number.
- The loss resulting from using fewer localities than the optimal number is not large.

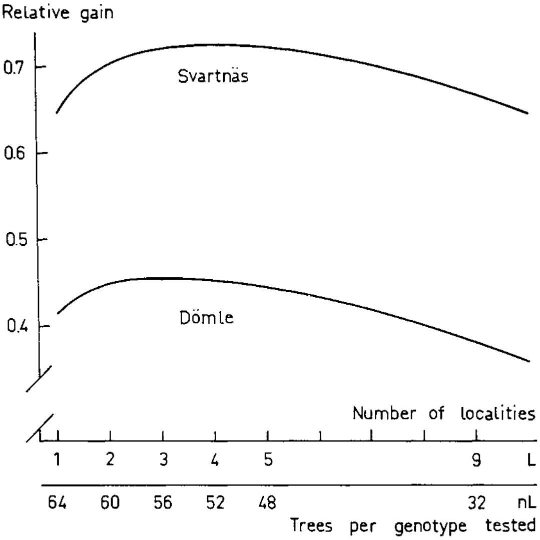

Fig. 4. The loss in genetic gain due to the testing of a limited number of trees on a limited number of localities under an economical constraint. Curves for two sets of genetic parameters obtained through two different progeny tests are demonstrated. There is an optimum number of localities, which seems to be rather independent of the genetic parameters.

Number o test localities in practical breeding

Relevance of the model

It may be doubted if the approach of calculating a variance component for genotype × environment interaction is the best possible approach (cf. Burdon, 1977). The conditions for an analysis of variance may not be fullfilled, and it is technically difficult to make the analyses in a correct way.

The assumption $V(\sigma) = 0$ in connection with formula (3) is not completely fullfilled. All theory is correct if K is defined:
$K = (\sigma_f^2 - V(\sigma))/\sigma_g^2$ instead of σ_f^2/σ_g^2, but few data are available on $V(\sigma)$. The effect would be that all experimental values of K are lower than given.

There are more factors to consider than are possible to express in the model.

Risk of loss

The experience in Sweden is that 40% of the localities are not suitable for evaluation due to damage. If the probability is independent between locations, the probability that at least a certain number of localities remains is expressed in Table 3.

If 4 localities are established, it is rather probable that only 2 will remain, which is somewhat suboptimal and it cannot be excluded that only one will remain, which is not acceptable, as the interaction cannot then be estimated.

On the other hand reduction of possible gain seems to be low even if all localities except one are lost.

Steps can be taken to increase the probability of success, such as fencing and chemical treatment against rodents, and the success rate will probably be higher in future Swedish test plantations.This has consequences for the reliability of the tests in relation to actual forestry conditions. The risk of loss justifies a higher number of localities than the optimum given by the model.

The range of use of breeding materials

The purpose of a test of breeding materials on several sites may be regarded as delimiting the use of particular breeding materials, and not only a ranking of them for some particular area. This justifies a larger number of test localities distributed over a range of edaphic and geographic factors.

Recommendation

In routine Swedish progeny testing it seems an optimal use of resources to have at least five test localities.

Table 3. *The probability that a certain number of test localities remains as a function of the number of established ones, assuming the risk of losing an individual locality is 0.4*

Remaining localities	Established localities					
	1	2	3	4	5	6
1 or more	0.60	0.84	0.94	0.97	0.99	1.00
2 or more	–	0.36	0.65	0.82	0.91	0.96
3 or more	–	–	0.22	0.48	0.68	0.82

Testing orchard

In many programmes the testing of breeding materials is done in environments and conditions not typical for practical forestry. Such testing orchards may include e.g. the following characteristics:

- close to experimental stations
- smooth, accessible sites with small environmental variation
- good site preparation
- bigger plants
- dense spacing
- fencing and other protective features
- removal of competitive vegetation.

By these features the costs per measured tree and/or the residual between plant variance may be reduced. In this way the statistical error may be reduced and the correlation at a certain cost increased. In Figure 4 the relative gain would be 1 if an infinite number of trees were tested on an infinite number of localities. Evidently there is a good potential to increase the correlation, and the fact that it is only one test locality does not result in a severe loss. However, the testing orchard is not a "sample"; a further reduction factor—basically, the correlation between the results under testing orchard conditions and under field conditions—is introduced. It is essential that the possible size of that correlation is evaluated, but considering the often rather low genotype × environment interactions, it seems quite possible that the correlation is high enough to make the testing orchard an interesting alternative to field testing.

By fertilization, using a site with a good site index and other actions, the rotation time in the testing seed orchard may be reduced, and thus the correlation according to Figure 1 increased at a fixed physical age. This increase in correlation may be larger than the loss in the correlation due to deviation from field conditions.

There are no good data, either with regard to variance components and correlations or to economics, for evaluating the quantitative merits. Such data ought to be produced.

In Scots pine there is some evidence that provenances (Persson, 1977) and clones (Fries, A., 1982. Genotyp-miljösamspel i ett tallympförsök. Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Progress report 3; Hellström, C. 1982. Reagerar tallkloner olika på förband och gödsling? Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Progress report 1) rank in the same order, equally well in dense as in wide spacing. Progenies seem to rank similarly in big plots and in single tree plots (Johnsson, 1972). Thus the risk of making mistakes by ignoring the interaction between genotypes in selection seems rather small for Scots pine.

Note added in proof: It has been pointed out by Rowland Burdon that the interpretation of $V(\sigma)$ and of the condition when it equals 0, could be improved. Readers are therefor cautioned against the uncritical application of these results.

References

Aastveit, A. H. 1982. *Synspunkter på omfanget av verdiprøvning av sorter,* 10. Department of mathematics and statistics. Agricultural University of Norway.

Albrektsson, A. 1980. Relations between tree biomass fractions and conventional silvicultural measurements. *Ecol. Bull. 32,* 315–327. Stockholm.

Burdon, R. D. 1977. Genetic Correlation as a Concept for Studying Genotype × Environment Interaction in Forest Tree Breeding. *Silvae Genetica 26,* 168-175.

Burdon, R. D. 1975. Compression wood in *Pinus radiata* clones on four different sites. *New Zealand J. For. Sci. 5,* 152–164.

Johnsson, H. 1972. Avkommeprövning av en tallfröplantage baserad på tioåriga avkommor. *(Institute of Forest Improvement. Annual report 1972),* 140–159.

Johnstone, R. C. B. & Samuel, C. J. A. 1978. The interaction between genotype and site: its influence on tree selection programmes in Britain. *Forestry Commission Research & Development Paper 22.* 18 pp. Presented at Eight World Forestry Congress 1978, Jakarta, Indonesia.

Krusche, D., Das, B. L. & Stephan, B. R. 1980. Results of a Progeny Test with *Pinus sylvestris* and Estimation of Genetic Gains from different Selection Methods. *Silvae Genetica 29,* 122–129.

Lambeth, C. C. 1980. Juvenile-Mature Correlations in *Pinaceae* and Implications for Early Selection. *Forest Sci. 26,* 571–580.

Lindgren, D. 1977. Genetic gain by progeny testing as a function of mating design and cost. *Third World Consultation on Forest Tree Breeding,* 1223–1235. ISBN 0643-0225-97. Canberra.

Namkoong, G. 1979. Introduction to quantitative genetics in forestry, *USDA Forest Service Technical Bulletin No. 1588.*

Owino, F., Kellison, R. C. & Zobel, B. J. 1977. Genotype × Environment Interaction and Genotypic Stability in Loblolly pine. V. Effects of genotype × environment interactions on genetic variance component estimates and gain predictions. *Silvae Genetica 26:4,* 131–134.

Patterson, H. C. & Silvey, V. 1980. Statutory and Recommended List Trials of Crop Varities in the United Kingdom. *J. R. Statist. Soc. A. 143,* 219–252.

Persson, A. 1977. Proveniensförsök med tall. Forskningsverksamheten 1977. *Skogshögskolan. Inst. f. skogsgenetik. Rapporter och uppsatser 26,* 17–25.

Rink, G. & Thor, E. 1976. Variance components and gains in volume growth of Virginia Pine (*Pinus virginiana* Mill.). *Silvae Genetica 25,* 17–22.

Skrøppa, T. 1981. Some results from a 20-year-old cutting experiment with Norway spruce. *Department of Forest Genetics, Swedish University of Agricultural Sciences. Research Notes 32,* 105–116.

Wright, A. J. 1976. The significance for breeding of linear regression analysis of genotype environment interactions. *Heredity 37,* 83–93.

CHARACTERIZING ENVIRONMENTS IN SWEDISH FORESTRY IN ORDER TO MINIMIZE THE EFFECTS OF GENOTYPE × ENVIRONMENT INTERACTION

URBAN GULLBERG

Department of Forest Genetics
S-750 07 UPPSALA, Sweden

Abstract

Gullberg, U. 1984. *Characterizing environments in Swedish forestry in order to minimize the effects of genotype × environment interaction.* Studia Forestalia Suecica 166. 25–34. ISSN 0039-3150. ISBN 91-576-1847-X.

The methods which will minimize the effects of genotype × environment interaction in forest tree breeding were analysed. The possibilities with characterizing the environment were especially considered and the present knowledge about conifers important to Swedish forestry (*Picea abies* (L.) Karst., *Pinus sylvestris* L. and *Pinus contorta* Dougl.) was reviewed.

It was contended that forest tree breeding could handle interaction without developing broad genotypes, that is, individual genotypes that cover a wide range of environments. On the contrary it was proposed that narrow genotypes ought to be used either in mixtures or separately depending on the environmental causes of interaction.

Swedish tree breeding has a zonation based on the idea that interaction is caused by bad synchronization between the genotype's growth rhythm and the seasonal rhythm. There is evidence that there are such effects in both spring and autumn, but it was questioned whether they are of any importance in the spring. A revision of the zonation was suggested since shortcomings with respect to genetic units so far used, environmental causes studied and cost/benefit analyses made, were found.

Key words: Picea abies, Pinus sylvestris, Pinus contorta, genotype × environment interaction, Sweden, environment. ODC 232.12.181.

Urban Gullberg, Department of Forest Genetics, Swedish University of Agricultural Sciences, P. O. Box 7027, S-750 07 Uppsala, Sweden.

Introduction

Genotype × environment interaction causes genotypes to be ranked differently in different environments. The set of genotypes that is best in one environment is not necessarily the best elsewhere and this implies an obstacle to the breeding.

The breeder could circumvent interaction by breeding for broad genotypes that are high-yielding in a wide range of environments or for many narrow genotypes together covering the same range. As long as the causes of interaction are known it is possible to define a set of environmental conditions in which to screen for the wanted genotypes and naturally it will be easiest to find the narrow genotype. At the same time it will be necessary to develop many more narrow than broad genotypes. If the causes are unknown the screening must be based on criteria that are supposed to give stability, e.g. high degree of heterozygosity. A successful selection in this situation will certainly be more difficult than when the causes of interaction are known. In this review, however, we emphasize the problems of interaction when the environmental causes could be explained and disregard the problems with general stability independent of environmental conditions.

When looking at the interaction problem on the variety level, that is on a composition of genotypes, the breeder has three principal options. One option is to use broad genotypes the others depend on narrow genotypes used separately or in mixture. Figure 1 summarizes when these options could be used. Broad

Type of variety \ Environmental cause	Unpredictable	Predictable
Homogenous	- broad genotypes	- broad genotypes - narrow genotypes used separately
Mixed	- broad genotypes - narrow genotypes used in mixture	- broad genotypes - narrow genotypes used in mixture - narrow genotypes used separately

Fig. 1. Options for producing varieties in different breeding situations.

genotypes cover a wide range of environmental conditions. To achieve this type of variety wide ranging tests and the existence of stable genotypes are required. The wide range of environments covered by the broad genotype could also be dealt with by a variety composed of a mixture of narrow genotypes together covering the range in question. This alternative requires that mixtures could be used successfully. Finally several varieties could be developed each specified to a part of the range. This alternative, however, requires that the environmental conditions constituting such a part of the range could be predicted before cultivation. The two last options are favoured by good possibilities to split the breeding population in many narrow and different genotypes. In forestry the utilization of clonal mixtures or full-sib families instead of conventional seed orchards are such possibilities. Intensive selection from the breeding population will also make it possible to create many different genotypes.

Environmental causes to genotype × environment interaction that are explainable are of two principal types. Figures 2 to 4, using the illustrations by Knight (1970), describe a situation where there is a continuous change in environmental conditions. In forestry it seems appropriate to use this description on ordinary natural site conditions, that is, on environmental components that largely are predictable. Here a continuous range of environments could be expected as the site index is determined by the average conditions over a long period of years. The problem in this case will probably be to find appropriate site descriptors. The economic effects of interaction (Fig. 4B) which naturally are decisive for the choice of breeding alternative will be different from those where one only considers the environment (Fig. 4A).

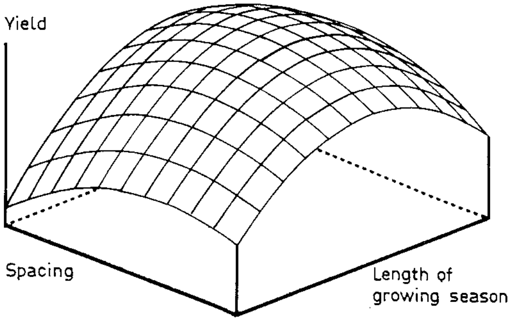

Fig. 2. Response surface showing yield in relation to two environmental variables for one genotype.

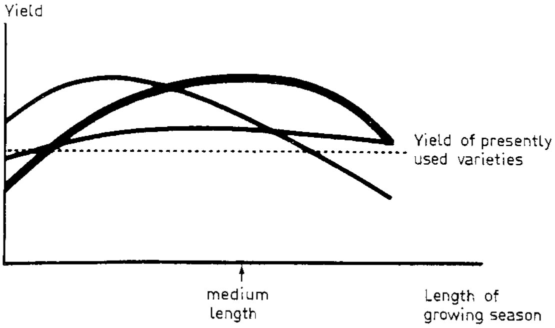

Fig. 3. Response curve showing yield in relation to one environmental variable for three genotypes. The thick line represents a high yielding narrow genotype with its optimum in a medium long season. The other lines represent genotypes that also are of interest under medium long seasons.

The description illustrated in Figure 5, on the other hand, could be used for extreme natural events, i.e. for unpredictable conditions of the type exemplified in the figure. It also covers the possibility of other management regimes than those commonly used, i.e. a predictable environmental cause of interaction. In this situation it is relatively easy to define the environmental classes. It could, however, be a problem to quantify the effects of interaction from these types of events since their probability to occur could be difficult to estimate.

It could be assumed that the breeding situation "homogenous variety—unpredictable environmental causes" (see Fig. 1) is of minor importance in forest tree breeding. One reason is the possibility to use mixed varieties. Less than a quarter of the individuals planted will contribute to more than ninety per cent of the value of the crop, at least in Scandinavian forestry. This means that a variety composed of a mixture of narrow genotypes could be used since those sensitive to some of the environments occurring could be thinned. The argument, however, does not fully apply to situations where there are high plant losses during the establishment phase. Another reason, as Burdon (1977) has pointed out, is that forest environments to a large extent are predictable, be-

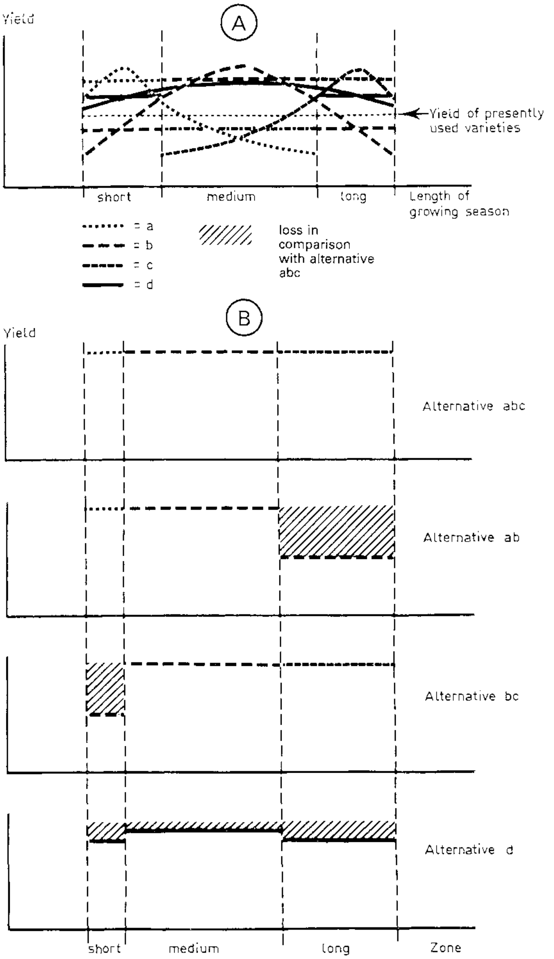

Fig. 4. Response curves and response levels for the four varieties (*a*), (*b*), (*c*), and (*d*). The levels are the average of the curves within a class. In Figure 4B the class widths are determined by the economic importance of the classes. Alternative (*abc*) stands for a breeding programme where the three varieties (*a*), (*b*) and (*c*) are used.

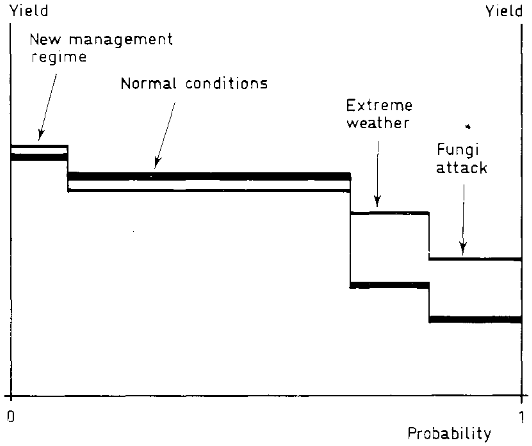

Fig. 5. Response levels for two varieties in normal and extreme conditions. The class width represents the probability of an event.

cause of the long rotation periods that average out year to year variation and thus makes the average conditions important.

It seems probable, considering the argumentation given above, that the emphasis should be on characterization of the environment (Burdon, 1977) rather than on the genotype in forestry, since broad genotypes could be avoided. This is contrary to the situation for annual crops, i.e. the crops for which most of the theory for genotype × environment interaction have been developed, where it is appropriate to select for broad genotypes.

In this paper I have reviewed existing methods for characterizing forest environments with regard to interaction. I have also summarized the principles used when characterizing environments for coniferous trees in Sweden. The general review of the subject concentrated on the studies made by Shelbourne (1972), Campbell (1974*a*, *b*, *c* and 1975), Shelbourne & Campbell (1977) and Burdon (1977, 1978), since they seem to cover the subject appropriately.

Methods for characterizing environments

When characterizing environments one first of all has to judge if the genetic material used is representative for the breeding population in question. The characterization, for example, could be made on genetic materials that do not behave in the same way as that of practical interest, e.g. the test is made with the "wrong" genetic entries. One also has to consider whether the problems caused by difficult environments should be solved by selection within the species, by change of species or by special management.

The methods for characterization of environments consists, in principle, of two steps used iteratively. In one step, the biological, one compiles available information on factors that possibly cause interaction for the species and the region in question. In the other step, the statistical, experiments are laid out and the portion of the genotype × environment interaction these factors explain is estimated. The experiments will probably indicate new factors of importance and thereby initiate further studies of these and a new set of experiments. This process does not have to be too slow if one combines short-term and long-term experiments in an appropriate way.

Present biological explanations as to the occurrence of genotype × environment interaction mainly of the predictable type are presented schematically in Figure 6. Campbell (1974*a*, *b*, *c* and 1979: Shelbourne & Campbell, 1977) when developing a model for provenance transfer of indigenous species, has focused his attention on the combination adaptation-growth rhythm. The environmental factors that he assumes to be of greatest value are those that explain survival or timing of phenological traits i.e. geographic location, occurrence of frosts or site conditions. The combination competition-allocation, that is differences between genotypes in allocation of resources between different organs will result in interaction when there is competition (see Fig. 6), is developed by Grafius (1972). Shelbourne (1972) gives examples where this combination seems to apply in forestry and concludes that genotype-fertilizer interaction is the only example for which information is available.

Causes	Genotypic reactions	
	Rhythm	Allocation
Adaptation to site	★	
Competition with neighbours		★

Fig. 6. Explanations to genotype × environment interaction. The combinations believed to be most probable are indicated.

A statistical method for characterization of environments has been developed by Burdon (1977, 1978). It is based on the concepts of genetic correlation and multi-trait selection index. A site observed for one set of variables could be related to another site observed for another set of variables. The sites could also be related to each other with regard to their capacity to function as selection sites for a breeding zone. This method does not only apply to explainable causes to interaction but could be used to estimate the general stability.

Shelbourne (Shelbourne & Campbell, 1977) outlines experiments that will give information on how to delineate zones. They should, he says, be distributed on many sites covering a wide range of conditions. The genetic entries included in the experiment should be well-defined, preferably clones.

Applications of the characterization

The characterization could be used to group similar environments in breeding zones and indirectly to organize the genetic material used for breeding. It can also be applied when defining test sites for a zone.

Shelbourne (Shelbourne & Campbell, 1977) reviews methods for grouping environments and concludes that Burdon's (1977, 1978) correlation method as well as multivariate methods are useful. In contrast to the statistical methods reviewed by Shelbourne (l.c.), Campbell (Shelbourne & Campbell, 1977) has based the grouping on a population genetic model. His model for transfer of provenances starts by describing "the complex clinal pattern in the species and region of interest". Thereafter he delineates zones by putting an upper limit to differences in environmental factors that explains survival or the timing of phenological traits. These rules come from his basic assumption that natural selection tends to produce an optimum strategy for the allocation of survival resources available to a population. They are intended to apply to the first steps in a breeding program, for instance provenance transfer.

An optimal grouping of environments, however, is not only determined by biological or statistical similarities. As discussed in the introduction (see Fig. 4) it is also affected by factors determining the economic value per unit-area i.e. site index. The magnitude of these factors is shown by Ledig & Porterfield (1982) in their economic analysis of breeding Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws). Thus for Ponderosa pine in Pacific south west, USA, an increase of site index of 50% has the equivalent effect on the economy of a breeding program as doubling the zone size. In both cases the economic break-even point is lowered by a third. The study also shows that an ordinary zone size requires a six per cent gain to reach the economic break-even point. If a nine per cent gain could be achieved the break-even point is reached with half the zone size, that is, an easily obtained goal requires smaller zones.

Finally there could be biological as well as economic constraints on the utilization of the breeding zones obtained by characterizing environments. Thus Campbell (Shelbourne & Campbell, 1977) demands that the provenances used in a breeding zone must originate from the zone. This restriction results from the basic assumption of an optimum strategy of natural populations. However, Campbell (l.c.) also comments on this restriction by noting that artificial regeneration creates conditions different from those occurring naturally and that the restriction therefore gives suboptimal results. Namkoong (1969) also questions the optimality of the local race by stating that "natural selection is for rapid reproduction while tree breeders are concerned with vegetative vigor". He cites several examples of long-term tests where the local race is outgrown by non-local sources.

Economic constraints will occur as soon as the delineations into breeding zones cut across or require a further subdivision of operational units established for management purposes. When characterizing environments for genotype × environment interaction it is consequently important to test the factors that are important for subdivision into operational units, i.e. level of productivity.

General facts about conifer breeding in Sweden

The phenomenon of genotype × environment interaction has a considerable impact on Swedish forest tree breeding since it has caused a subdivision of the country in breeding zones. A zone is defined as the area where the seeds from an open pollinated seed orchard will be used and all together there are 35 such zones. For Norway spruce (*Picea abies* (L.) Karst.) there are 9 zones, for Scots pine (*Pinus sylvestris* L.) 20 and for Lodgepole pine (*Pinus contorta* Dougl.) there are 6.

The zones are based on the results from provenance testing and by considering the fact that there is a climatic gradient from south to north. The selection of Scots pine provenances has been based on the idea of clinal variation and short-distance transfers. The choice of Norway spruce and Lodgepole pine provenances is less dependent on the concept of the cline since one has accepted long-distance transfers. The major emphasis on this zonation has been on the environment and the environmental causes considered are of the type presented in Figure 4, that is, predictable and explained by adaptation to site by growth-rhythm (Fig. 6).

The handling of interaction could be refined by a more appropriate choice of genetic material than that used in the provenance studies. Firstly there are indications that the provenance studies do not include the most promising parts of the natural variation (Krutzsch, 1975*a*; Rosvall & Ericsson, 1982). Secondly there are results showing that some provenances are more widely adapted than others (Eiche & Gustafsson, 1970; Johnsson, 1971; Eiche & Andersson, 1974; Remröd, 1976; Lindgren et al., 1980).

Finally we can use the great local variation for growth-rhythm characters when we establish seed orchards or clonal mixtures (Dietrichson, 1969*a* and *b*; Hagner, 1970*c*; Johnsson, 1973; Eriksson et al., 1976).

A more complete analysis of the environmental causes behind interaction will most probably also give a better handling of genotype × environment interaction. So far we have concentrated on studying the adaptation to the growing season, that is one type of predictable environmental cause, by regression techniques. These studies will be reviewed in the following sections. A couple of studies (Ekberg et al., 1982; Werner, personal communication) have used analyses of variance and found significant effects of interaction not necessarily explained by bad adaptation to the growing season. There are also indications that differences in allocation of resources between genotypes cause interaction. Thus Langlet's (1936) studies on needle dry matter content or management studies, e.g. different spacing and fertilizer regimes, on clonal material (Hattemer et al., 1977) could be interpreted in this way. There are no estimates, however, on the relative importance of unexplainable versus explainable environmental causes or of the importance of predictable versus unpredictable causes within the latter group.

Economic considerations will certainly also cause changes to the present breeding zones. Thus the difference in yearly value production between the smallest and largest zones is nearly tenfold. This comparison, however, overestimates the difference in absolute gains from a breeding effort since one can expect higher relative genetic gains per hectar in the small northern zones. The problem in the region is bad survival, a character that is relatively easily improved. Still one could expect that equivalent effects of genotype × environment interaction will give fewer zones in the north than in the south. Economic considerations on the losses due to bad adaptation within zones speaks in favour of generally bigger zones for Scots pine in northern Sweden (Lindgren, personal communication). Recent studies (Hägglund & Svensson, 1982) on site classification on the other hand show that there is a lot to gain from linking management and site index even more closely than presently done. This speaks in favour of a zonation not only based on macroclimate, but on edaphic factors as well.

Adaptation to site by growth-rhythm in Sweden

As noted above most of the studies on genotype × environment interaction have, directly or indirectly, been based on the hypothesis that interaction occurs due to bad synchronization between the genotype and the environment. This has been an obvious approach since the length of the growing season varies so much within the country. If the genotypes differ in their start and termination of the growth the same group will have different reactions in sites with long and short growing periods.

Studies on interaction in the spring have concentrated on the occurrence of frosts and their immediate impact on the growth. Meteorological studies (Perttu, 1981) show that the occurrence of spring-frosts vary as much on a macro- as on a microgeographical scale.

Interaction caused by late growth cessation has also been studied and its negative effects resulting in plant damage has been specifically analysed. Positive effects of late cessation on growth capacity have also been observed (Ekberg, personal communication).

Finally problems with plant survival and damage have been attributed to bad synchronization despite lack of observations on growth-rhythm.

Norway spruce

Langlet (1960) observed a single spring frost and showed that damage to the year's shoot is closely correlated to the timing of bud-flushing. Dormling and Eriksson (1981) have frozen plants in different stages of bud-flushing and found that the plants are most sensitive during the first phase of shoot elongation but nearly as sensitive several weeks ahead.

Langlet (1960), studying the IUFRO-1938 series at the age of 15–20 years outside Stockholm has observed that time of bud-flushing depends of provenance. Materials from Sweden and Finland as well as provenances coming from the Alps flush early, those coming from east-central Europe flush late. Krutzsch (1975*b*) studying the same experiments some years later showed that the relation between provenances with regard to flushing is relatively independent of the location of the observation site (Stockholm 59° lat, Umeå 64° lat). The provenances from the Alps, however, are comparatively later in Umeå than in Stockholm.

The relation between the timing of bud-flushing and economically important damage cannot easily be explained. Thus Langlet (1960) shows that both early flushing northern types and late flushing east-central European provenances survive and avoid damage much better outside Umeå than the late flushing provenances from the Alps. A similar relation between provenances was shown by Dietrichson (1969*a*) for spring frost damage to the early wood.

Langlet (1960) observed hardly any damage in tests parallell to that in Umeå. These tests are situated outside Stockholm and in Southern-most Sweden. Heavy frost damage due to spring frosts have, however, been observed in severe sites in this region, but they have not been related to timing of bud-flushing. However, my own observations in an experiment outside Stockholm indicate that spring frosts might hit genotypes indiscriminately despite big differences in timing of bud-flushing. This occurs when spring frosts come after all genotypes have started to flush and meteorological observations show that these incidents are quite frequent in some sites.

It is well known that the growing season terminates at different dates in various parts of the country, but its dependence on site conditions does not seem to be appropriately acknowledged.

The timing of growth cessation is primarily controlled by night length (Dormling et al., 1968) and natural populations react to night lengths such that their growth cessation is locally adapted (Dormling, 1973). The genetic control of this mechanism is fairly well established (Eriksson et al., 1978). Temperature also influence this process (Dormling, 1977), and

Dietrichson (1964) has shown that good site index and wet conditions delay cessation. The difference in timing of late wood production between provenances is observed by Dietrichson (l.c.) in the same experiments as studied by Langlet (1960). Provenances from Sweden and Finland start their late wood production early and finish it early. Materials from west-central Europe start and finish late and those from east-central European sources finish earlier than those from west-central Europe (Krutzsch, 1975*a*).

The relation between bad synchronization in the autumn and damage is clearly shown by Dietrichson (1964, 1968*a*). The damage in the experimental site outside Umeå in the IUFRO-1938 series is well correlated with late wood production (Dietrichson, 1964). Dietrichson (1969*a*) has also tried to explain Langlet's (1960) data by suggesting that damage by spring frosts delays the growth cessation and that this explains why west-central European provenances become severely damaged in harsh conditions. However, the information behind this statement is weak. Dietrichson (1968*a*) could show however, that frost damage will cause retardation of growth and an increased risk for further frost damage the following years.

Summarizing the evidence about environmental factors causing genotype × environment interaction with Norway spruce in Sweden, it is obvious that synchronization in the autumn is an important factor. There is no clear evidence that the spring causes any genotype × environment interaction of economic importance. This might be due to lack of appropriately designed experiments to study this interaction.

Finally, it is evident that the problems in the most severe sites tested (cf. Rosvall & Ericsson, 1982) hardly will be solved only by selecting for the appropriate genotype. Management methods and change of species must be considered in these situations.

Scots pine

The autumn has been given the greatest attention in studies about the bad synchronization between seasonal rhythm and growth rhythm. However, Eiche's study (1966) indicates that warm periods in the early spring followed by cold periods could be a factor of importance.

The primary factor causing growth cessation is night length (Jonsson et al., 1981). Short nights are required for provenances of northern origin.

Langlet (1936) found that Swedish provenances of southern origin have a lower dry matter content in the needles than the northern ones when grown outside Stockholm. The southern sources develop even less dry matter when grown in Gällivare (67° lat). Dry matter content is closely correlated with survival; high content implies good survival, and the decreased content in southern sources in Gällivare he interprets as an effect of late growth cessation. The differences in Stockholm are not interpreted as an effect on disrupted growth but could be considered a result of differences in allocation of resources.

Dietrichson (1964) observed that central European provenances develop late wood later than Scandinavian sources. Hagner (1970*a* and *c*) has studied several variables developing during July-October, change in bark colour being the most promising for growth cessation studies, and he found differences both between and within provenances. The difference between provenances is largely explained by their latitude of origin.

Dietrichson (1964) shows that poor lignification, resulting from late growth cessation, causes frost damage of economic importance. Time of late wood production is also highly correlated with susceptibility to *Schleroderis lagerbergii* Gremmen (Dietrichson, 1968*b*).

The delineation of breeding zones for Scots pine in northern Sweden has been comprehensively discussed by Campbell (1974*a*). He uses Eiche's (1966) data on survival of provenances in experimental sites covering northern Sweden and shows that the size of the breeding zones should vary drastically because of the differences in site severity observed. Eriksson et al. (1980) have improved the estimate of site severity, and they show that it increases with latitude and altitude. However, adding differences in site productivity to the explanatory model did not improve the fit to the observed data. A variant of Campbell's (1974*a*) approach has been developed for another experimental series by Remröd (1976).All these studies show that survival is improved by moving provenances south and down in altitude. Remröd (l.c.) furthermore claims that there is an optimal transfer distance since the improved survival is countered by a decreased volume production. Thus the provenances show response curves of the type Knight (1970) uses to describe genotype × environment interaction. Eriksson et al. (1976) present similar response curves for volume production when analysing provenance transfer in one experiment at latitude 64°.

There are twenty breeding zones for Scots pine in Sweden. The majority are north of latitude 60° and the delineations here are based on the results obtained by Remröd (1976), and Eriksson et al. (1980). The delineation of the southern zones is based on Johnsson's (1971, 1973) results.

Lodgepole pine

The occurrence of genotype × environment interaction due to bad synchronisation in the autumn has been studied for Lodgepole pine.

Jonsson et al. (1981) have shown that the growth cessation is primarily controlled by night length and provenances of northern origin require shorter nights for initiation of growth cessation than those from the south. They also show that this control causes differential susceptibility to autumn frosts and the clinal pattern they obtain through artificial tests is in good agreement with clines for survival obtained in field tests.

Hagner (1970*b* and 1980), and Dietrichson (1970) observed the timing of several of the autumn characters studied for Lodgepole pine and found av variation largely explained by latitude. The studies by Lindgren et al. (1980), however, indicate that there are certain areas in Canada where the provenances have extremely high stability in Sweden. This implies that the present delineation into 6 zones might be revised.

Conclusions

Swedish forest tree breeding has considered the problems of genotype × environment interaction by subdividing the country into many breeding zones. The zonation is based on provenance studies focusing the attention to the adaptation to the growing period.

There is a convincing evidence that the development in the autumn is important for interaction. Selection with respect to timing of bud flushing for Norway spruce, however, could be questioned. There are indications that sites causing problems to the spruce in spring and early summer give severe damage to the species whole genetic range. Possibly such sites have to be handled with management methods or by change of species.

It is questionable whether the present zonation is suitable to the genetic material that will be used in Swedish forestry. Firstly, many of the tests, especially for Norway spruce, do not include provenances from the areas that have high yielding types. Secondly the zonation is based on the assumption that all provenances have the same stability a fact that could be questioned. Finally there is very limited knowledge about the stability for other genetic units than the provenance.

The practice of exclusively basing the zonation on environmental factors determining the length or timing of the growing period could also be questioned. The provenance studies on which this practice is based cover a very wide range of growing periods and models using these factors will therefore give good explanations to the observed data. The few studies of interaction within parts of this range, however, do not give any simple explanations to the observed interaction.

Finally it must be noted that the zone size at present is determined without relating the cost of interaction to the benefit of having few zones.

References

Burdon, R. D. 1977. Genetic correlation as a concept for studying genotype × environment interaction in forest tree breeding. *Silvae Genet, 26,* 168–175.

Burdon, R. D. 1978. Generalisation of multi-trait selection indices using information from several sites. *N. Z. Journ. For. Sci. 9,* 145–152.

Campbell, R. K. 1974*a*. A provenance-transfer model for boreal regions. *The Norwegian Forest Research Institute. Report 31,* 544–566. Ås.

Campbell, R. K. 1974*b*. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. *Journ. Appl. Ecol. 11,* 1069–1080.

Campbell, R. K. 1974*c*. *Conservation and improvement of genetic resources in Norwegian forests. An evaluation.* 169 pp. Ås: The Norwegian Forest Research Institute.

Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon cascades. *Ecology 60,* 1036–1050.

Dietrichson, J. 1964. Proveniensproblemet belyst ved studier av vekstrytme og klima (The provenance problem illustrated by studies of growth rhythm and climate). *The Norwegian Forest Research Institute, Report 19,* 501–656. Ås.

Dietrichson, J. 1968*a*. Klimaskader, vekstrytme og höydeutvickling. Resultater fra et 12 år gammelt granproveniensforsök på Rödser i Aremark (Climatic damage, growth rhythm and height development. Results from a 12 year old Norway Spruce provenance trial at Rödser in Aremark). *The Norwegian Forest Research Institute, Report 21,* 141–158. Ås.

Dietrichson, J. 1968*b*. Provenance and resistance to Scleroderris lagerbergii Gremmen (Crumenula abietina Lagerb.). The international Scots pine provenance experiment of 1938 at Martrand. *The Norwegian Forest Research Institute, Report 25,* 395–410. Ås.

Dietrichson, J. 1969*a*. The geographic variation of spring-frost resistance and growth cessation in Norway spruce (Picea abies (L.) Karst.). *The Norwegian Forest Research Institute, Report 27,* 91–106. Ås.

Dietrichson, J. 1969*b*. Growth rhythm and yield as related to provenance, progeny and environment. *FAO—IUFRO, 2nd World Consultation of Forest Tree Breeding, Washington 7–16/8, 1969. Section II FO-FTB-69-2/3,* 1–15.

Dietrichson, J. 1970. Geografisk variasjon hos Pinus contorta Dougl. En undersökelse med sikte på treslagets bruk i Norge (Geographic variation in Pinus contorta Dougl. A study aiming at the use of the species in Norway). *The Norwegian Forest Research Institute, Report 28,* 111–140. Ås.

Dormling, I. 1973. Photoperiodic control of growth and growth cessation in Norway spruce seedlings. *IUFRO WP S 2.01.4. Symp. on Dormancy in Trees, Kornik, 1973.* 16 pp.

Dormling, I. 1977. Kritisk nattlängd för knoppskjutning hos gran av olika härkomst: inverkan av ljusintensitet och temperatur (Critical night length for bud-set in Picea abies (L.) Karst.: influence of light intensity and temperature). *Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 27,* 18–25. Stockholm.

Dormling, I., Gustafsson, Å. & Wettstein, D. von. 1968. The experimental control of the life cycle in Picea abies (L.) Karst. I. Some basic experiments on the vegetative cycle. *Silvae Genet. 17,* 44–64.

Dormling, I. & Eriksson, G. 1981. Varierar frostkänsligheten under skottskjutningen hos gran av olika ursprung? (Does the resistance to late spring frosts vary between Norway spruce populations?). *Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 31,* 87–94. Uppsala.

Eiche, V. 1966. *Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden* (Studia For. Suec. 36). 219 pp. Stockholm.

Eiche, V. & Gustafsson, Å. 1970. Population research in Scandinavian Scots pine (Pinus sylvestris L.). Recent research. In *Essays in Evolution and Genetics in honor of Theodosius Dobzhanzsky* (ed. M. K. Hecht & W. C. Steere). 209–235. N. Y.: Meredith Corporation.

Eiche, V. & Andersson, E. 1974. Survival and growth in Scots Pine (Pinus sylvestris L.). Provenance experiments in northern Sweden. *Theor. Appl. Genet. 44,* 49–57.

Ekberg, I., Eriksson, G. & Hadders, G. 1982. Growth of intra- and interprovenance families of Picea abies (L.) Karst. *Silvae Genet. 31,* 160–167.

Eriksson, G., Andersson, S., Eiche, V. & Persson, A. 1976. *Variation between and within populations in a provenance trial of P inus sylvestris at Nordanås, Lat. 64° 19', Long, 18°. 09', Alt. 400 m.* (Studia For. Suec. 133). 46 pp. Stockholm.

Eriksson, G., Ekberg, I., Dormling, I., Matérn, B. & Wettstein, D. von. 1978. Inheritance of bud-set and bud-flushing in Picea abies (L.) Karst. *Theor. Appl. Genet. 52,* 3–19.

Eriksson, G., Andersson, S., Eiche, V., Ifver, J. & Persson, A. 1980. *Severity index and transfer effects on survival and volume production of Pinus sylvestris in northern Sweden* (Studia For. Suec. 156). 32 pp. Uppsala.

Grafius, J. E. 1972. Competition for environmental resources by component characters. *Crop Science 12,* 364–367.

Hagner, M. 1970*a*. *A genecological investigation of the annual rhythm of Pinus silvestris L.* (Studia For. Suec. 80). 40 pp. Stockholm.

Hagner, M. 1970*b*. *A genecological investigation of the annual rhythm of Pinus contorta Dougl. and a comparison with Pinus silvestris L.* (Studia For. Suec. 81). 26 pp. Stockholm.

Hagner, M. 1970*c*. *The intra-provenance correlation between annual rhythm and growth of single trees of Pinus silvestris L.* (Studia For. Suec. 82). 40 pp. Stockholm.

Hagner, M. 1980. Geographic variation in Pinus contorta and Picea mariana with respect to cone size, seedling growth rhythm and cotelydons. *Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 30,* 83–101. Uppsala.

Hägglund, B. & Svensson, L. G. 1982. *Site conditions on forest land and wetlands in Sweden. A description and analysis based on data from the National Forest Survey* (Swedish University of Agricultural Sciences, Dept. of Forest Survey, Report 35). 121 pp. Umeå.

Hattemer, H. H., Andersson, E. & Tamm, C. O. 1977. *Effects of spacing and fertilization on four grafted clones of Scots pine* (Studia For. Suec. 141). 31 pp. Stockholm.

Johnsson, H. 1971. Proveniensförsök med tall i Sydsverige (Provenance trials with Scots pine in southern Sweden). *Year book. Inst. for Forest Tree Improvm., Uppsala, Sweden 1970,* 87–128.

Johnsson, H. 1973. Avkommeprövning av en tallfröplantage, baserad på tvååriga avkommor (Progeny test of a Scots pine seed orchard). *Year book, Inst. for Forest Tree Improvm., Uppsala, Sweden 1972,* 140–159.

Jonsson, A., Eriksson, G., Dormling, I. & Ifver, J. 1981. *Studies on frost hardiness of Pinus contorta Dougl. seedlings grown in climate chambers.* (Studia For. Suec. 157). 47 pp. Uppsala.

Knight, R. 1970. The measurement and interpretation of genotype × environment interactions. *Euphytica 19,* 225–235.

Krutzsch, P. 1975*a*. *Die Pflanzenschulenergebnisse eines inventierenden Fichtenherkunftsversuches (Picea abies Karst. und Picea obovata Ledeb.)* (Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 14). 104 pp. Stockholm.

Krutzsch, P. 1975*b*. *Zwei Herkunftsversuche mit Fichte in Schweden (IUFRO 1938)* (Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 16). 93 pp Stockholm.

Langlet, O. 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Ett bidrag till kännedom om tallens ekotyper (Studien über die Physiologische Variabilität der Kiefer und deren zusammenhang mit dem Klima. Beiträge zur Kenntnis der Ökotypen von Pinus sylvestris L.). *Medd. från Statens*

Skogsförsöksanstalt (Sweden) 29, 219–470.

Langlet, O. 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk (Mitteleuropäische Fichte in Schweden, nach den Ergebnissen des internationalen Provenienzversuches von 1938). *Journal of the Royal Swedish Academy of Agriculture and Forestry 99*, 259–329.

Ledig, F. T. & Porterfield, R. L. 1982. Tree improvement in Western Conifers: Economic aspects. *Journal of Forestry, Oct. 1982*, 653–657.

Lindgren, D., Lindgren, K. & Persson, A. 1980. Survival and height increment of Pinus contorta. IUFRO 70/71 series in Sweden. *Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 30*, 103–130.

Namkoong, G. 1969. Nonoptimality of local races. *Proc. 10th Southern Conf. Forest Tree Improvement*, 149–153. Houston, Texas.

Perttu, K. 1981. *Climatic zones regarding the cultivation of Picea abies L. in Sweden. II. Radiation cooling and frost risk* (Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 36). 25 pp Uppsala.

Remröd, J. 1976. *Val av tallprovenienser i Norra Sverige - analys av överlevnad, tillväxt och kvalitet i 1951 års tallproveniensförsök* (Choosing Scots pine (Pinus sylvestris L.) provenances in Northern Sweden—analysis of survival, growth and quality in provenance experiments planted 1951) (Swedish University of Agricultural Sciences, Dept. of Forest Genetics, Res. Notes 19). 32 pp. Stockholm.

Rosvall, O. & Ericsson, T. 1982. Förflyttningseffekter i norrländska granproveniensförsök (Transfer effects of Picea abies in northern Sweden). *Year book, Inst. for Forest Tree Improvement, Uppsala, Sweden 1981*, 85–117.

Shelbourne, C. J. A. 1972. Genotype × environment interaction: its study and its implications in forest tree improvement. *IUFRO Genetics-SABRAO Joint Symposia, Tokyo, October 1972*, 1–27.

Shelbourne, C. J. A. & Campbell, R. K. 1977. The impact of genotype × environment interactions on tree improvement strategy. *IUFRO Joint Meeting on Advanced Generation Breeding, Bordeaux, June 1976*, 73–96.

TESTING METHODS FOR GENERAL AND SPECIFIC ADAPTATION IN CLONAL FORESTRY

KENNETH LUNDKVIST

Department of Forest Genetics
S-750 07 UPPSALA, Sweden

Abstract

Lundkvist, K. 1984. *Testing methods for general and specific adaptation in clonal forestry*. Studia Forestalia Suecica 166. 35–39. ISSN 0039-3150, ISBN 91-576-1847-X.

Inadequate test-site description and the requirement of long-term testing are two limitations of current methods for estimation of genotype × environment interaction in clonal trials. Complementary testing methods in climate chambers are therefore suggested. High emphasis is put on a better understanding of the causal relationship between genotype × environment interaction and environmental factors, particularly when distinction is made between predictable and unpredictable variation. The possibility to utilize a high genotype × environment interaction of clones is pointed out, i.e. by selecting high yielding clones with specific adaptations. Experiments to study the parameters of importance for a high population buffering capacity, mainly the effects of competition, are, however, necessary. Finally, experiments on the genetic and physiological mechanisms of stability are advocated.

Key words: clone, clone test, adaptation, genotype × environment interaction, stability.
ODC 232.12:181

Kenneth Lundkvist, Department of Forest Genetics, Swedish University of Agricultural Sciences, P. O. Box 7027, S-750 07 Uppsala, Sweden.

Introduction

As breeding narrows the genetic diversity in production populations of forest trees, genotype × environment (G × E) interaction will assume an increasing importance and must be considered as well in the prediction of genetic gain (Lindgren, 1983) as in the delineation of breeding zones (Gullberg, 1983).

The interaction is expected to be still more pronounced on the clonal level, and to realize the expected gains in clonal forestry as well as avoiding the risks, extensive clonal trials are required.

When the trial is replicated on many sites, a ranking of the clones is possible with respect to their stability of performance. A regression analysis as suggested by Finlay & Wilkinson (1963) is generally used for the evaluation of such data.

Limitations of current methods for estimation of genotype × environment interaction

Site description

When plants are tested for G × E interaction, the goal should be estimation of *the magnitude* as well as *the cause* of interaction. Regression methods, however, generally only fulfil the first goal, giving little information as to the relationship between interaction and environmental factors. In fact, the site is described in terms of mean production of the plants being tested on that site. The stability of a clone is thus assessed *relative to* the other clones in the trial.

I am, however, inclined to define stability as an inherent character of a clone, associated with its physiological qualities. It is therefore desirable that stability is expressed in some absolute terms where environmental parameters are included. Otherwise, a correct biological interpretation of the data is impeded and conslusions from the trial may be incomplete or misleading, as pointed out by Knight (1970).

Time

In a field test the fluctuations of environmental conditions between years cannot be predicted, so assessments must be made over several years to give a proper estimate of stability. The very harsh conditions, so called "bottle-neck years", may occur only once every second decade.

This requirement of long-term testing is, however, a serious obstacle for an intended program of clonal forestry. The physiological ageing of the clones will reduce the rooting ability and orthotropic growth of the cuttings being produced after the testing period. As long as methods for rejuvenation of mature plants is lacking, this will be a serious problem in clonal testing.

Increase in efficiency and precision of clone testing with complementary methods

The limitations of present methods for clone testing may to some extent be overcome if complementary methods are developed. A better knowledge of the causal relationship between planting site and the performance of different clones will undoubtedly improve our evaluation of field tests. It will, furthermore, help us to improve test site selection and the design of routine clone tests, thus making field testing more efficient. Eventually, some field tests may be substituted for more rapid testing procedures in nurseries and climate chambers.

Replicated experiments in climate chambers

If clones are tested in different climates created in climate chambers, the primary gain would be time, since several growing seasons can be run during one year. To ascertain the validity of such early tests on G × E interaction, experiments must be established in the field as well, or the material tested should be taken from existing field trials. Experiments on frost hardiness of pines have shown promising results in this respect (Jonsson et al., 1981).

Climate chamber experiments will also expand our knowledge as to the reasons for ranking shifts of clones tested in different environments. If you delimit the experiment to changes in plant performance following changes in one single environmental factor, each clone will present a response curve in a diagram. Such curves will offer valuable information for the interpretation of observed G × E interaction. The curves in Figure 1 are drawn from arbitrary data but they will demonstrate the use of response curves.

In the top of Figure 1 you find that clones 2–4 have a similar optimum for water supply while clone 1 deviates with respect to its optimum. In a regression analysis, clone 1 will consequently not have a very good fit to the regression line since its yield is plotted against the site mean yield which is strongly influenced by the other three clones. A deviating optimum of one clone will thus be interpreted as a high genotype × environment interaction in a regression analysis.

Secondly, as pointed out by Knight (1970), if a clone test covers a wide range of an environmental factor, suboptimal and superoptimal conditions will be placed adjacent to each other in a yield diagram

	Water supply					
Variety	2	4	6	8	10	12
1	9	14	14	12	10	7
2	5	10	12	13	10	2
3	3	9	14	15	13	8
4	2	8	12	14	11	5

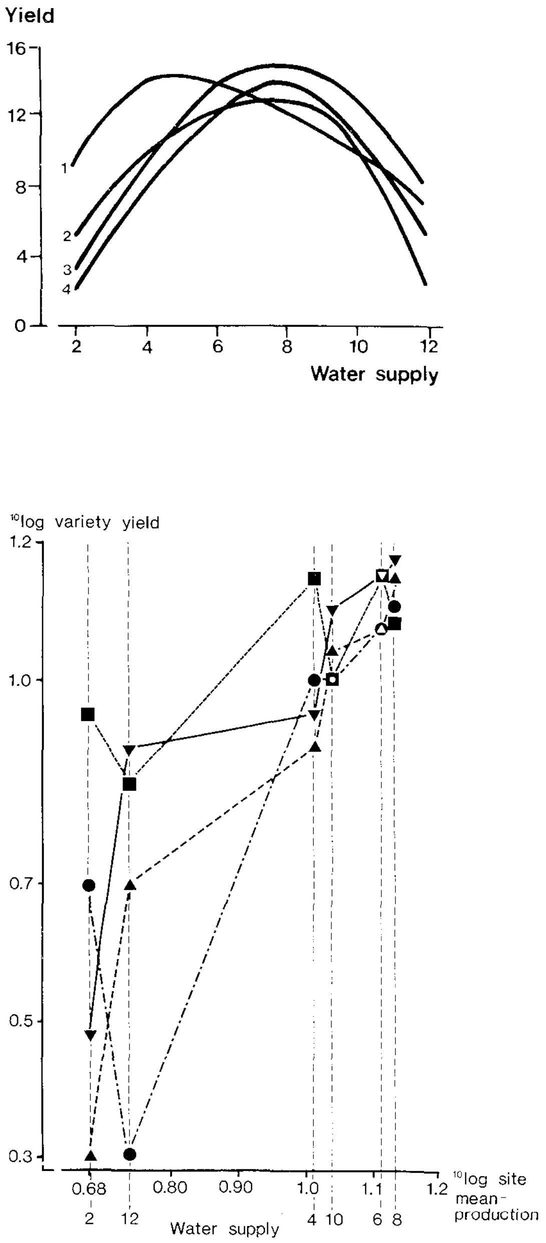

Fig. 1. Top: Response-curves from arbitrary values of plant-yield for different values of water supply.

Bottom: Diagram of individual clone yield on site mean yield, showing G × E interaction of the four clones. Arbitrary data from curves in top of Fig. 1.

(bottom of Fig. 1, water supply level 2 and 12). Consequently, G × E interaction will be significant in the low-yielding part of the diagram. Such an observation in a field test is difficult to interpret correctly if the causal relationship is unknown.

If more than one environmental factor is included, the reaction of each clone will be represented by a response surface of a threedimensional diagram. The shape of the surface will disclose the combined effects of different environmental factors.

Assessment of adaptedness in fitness sets

High stability of clones is very much equivalent to the concept of broad adaptedness in population genetics. The theory of fitness sets presented by Levins (1962, 1968) seems to be very suitable for early testing in climate chambers of forest tree clones and clonal mixtures.

The basis of such experiments is a series of progressively increasing differences between environments. The fitness sets are made from scatter diagrams after pairwise comparisons of yields in the different environments (cf. Fig. 2). As long as the environmental

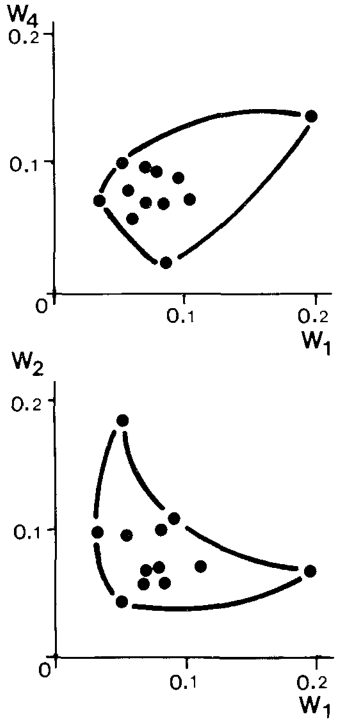

Fig. 2. Fitness form experiments on *Typha* in climate chambers. W_1, W_2 and W_4 signifies biomass produced × area^{-1} × time^{-1} in environments no. 1, 2 and 4, respectively. The difference between environments 1 and 2 is large enough to exceed the phenotypic tolerance of the species tested, so the fitness set becomes concave (from McNaughton, 1970).

differences are small enough, the fitness set as defined by the outer dots is expected to be convex. When the environmental differences are sufficiently increased, the fitness set will assume a more concave shape, indicating that the environmental differences are larger than the individual homeostasis of the clones.

The clones that define the limits of the set will be the ones with a more specific adaptation than those generally adapted clones that remain within the fitness set. McNaughton (1970) have shown in climate chamber experiments that *Typha* species with known specific adaptations define the limits of a fitness set, while species with a broad adaptedness remain within the set.

The level of environmental diffrences where the fitness set turns concave is a breaking-point of particular interest. This is where comparisons between single clones and the same clones in mixtures is beginning to be decisive. If the mixture performs better than the average of single clones, then the homeostasis has been improved and the strategy of adaptation involves a certain amount of genetic variability to assure the highest production and survival in both extremes as well as under intermediary conditions.

Identification of environmental factors

A major advantage with clonal forestry is the potential use of clones with specific adaptation to certain site conditions. High yielding clones with a specific adaptation to *predictable* environmental variation may be selected for if stability for the *unpredictable* factors is taken into account.

However, if the regression technique is to be used for prediction of clonal performance, the choice of test-site must be give some consideration. One should above all pay extra attention to the environmental conditions under which the clones ultimately will be grown. In this context it would be desirable if distinction was to be made between interaction caused by predictable environmental factors and those factors being unpredictable. Candidates for predictable factors would be nutrition, local climate and photoperiod and among the unpredictable factors, drought, frost and temperature during the vegetation period seem to be easy to identify.

When test sites are selected, the predictable variation can be taken into account, while clonal tests involving unpredictable factors require some complementary testing, e.g. in climate chambers. If this was to be realized, the number of clones considered to be safe for forest plantations would be reduced to a level where a substantial genetic gain is possible.

Genetic structure of clonal mixtures

Assessments of stability in clonal tests are made with respect to individual buffering capacity. The selected clones will, however, be grown in mixtures and the significant parameter will then be the *population buffering capacity*. To avoid high yielding clones being discarded because of high genotype × environment interaction in a clonal test, we need to know if its stability is improved in a mixture, i.e. a better knowledge about the factors that are decisive for population buffering capacity.

I believe it is not so much the actual number of clones but rather the specific combinations of genotypes which has influence on the stability. Experimental methods should therefore focus on the effects of interactions between clones, as well. From agricultural species we know that interactions between genotypes have a strong influence on survival and production. In forest trees, however, very little is known about competition and cooperation between genotypes. Should competitive ability differ among genotypes, it will certainly influence selection of clones and decisions on number of clones in clonal mixtures.

Experiments in climate chambers may increase our knowledge on how the stability of mixtures is enhanced compared to single clones (cf. Levins's fitness sets), but information about its mechanisms must be pursued in experiments on interactions between genotypes. With information about interaction-effects at hand, the breeder can more accurately predict the performance of clonal mixtures from selected clones.

Genetic and physiological mechanisms of stability

Whether stability in forest trees is a property of the genotype or one of heterozygosity *per se* is today a matter of conjecture. Basic reasearch is needed to tell us if and how stability is inherited.

Heterozygosity in itself is generally considered a promotor of stability in cross-breeding plants. A multitude of experiments have shown that the coefficient of variation rises after inbreeding, which is interpreted as an effect of a lowered level of heterozygosity. Concurrent results, however, indicate that stability is a property of the genotype itself, as well. Presumedly, both mechanisms are involved also in forest trees. Controlled crosses in the breeding populations with a subsequent selection within ful-sib families would be a profitable option for clonal forestry if the inheritance of buffering capacity was better understood.

A suitable material for experiments with forest trees would be families, pedigrees known for at least two generations, with different inbreeding coefficients. Controlled crosses and cloning of the progeny would tell if improving stability of clones by breeding is a desirable strategy.

The physiological mechanisms of stability is as poorly understood as the genetic ones. The limits of stress that a plant can endure, e.g. by freezing or drought, are set by its physiological processes. Geneticists and physiologists should jointly investigate differences between stable and unstable clones in their developmental processes. Should such differences be detectable by laboratory methods, a screening for clones that are stable unpredictable variation would be possible.

Discussion

Selection of clones for clonal forestry requires a testing procedure, as well for obtaining the potential genetic gains as for a safeguard against calamities caused by climate or pathogens. A broad adaptedness as a guarantee for successful establishment of a stand may be obtained either by selecting clones with high individual homeostasis or by mixing a sufficient number of clones. Both options require some sort of testing to make a selection of stable clones and for the decision of a necessary level of genetic variation.

I have pointed out that field testing has some significant shortcomings acting as obstacles for clonal forestry: the physiological ageing during the testing period and the difficulties to ascertain the causal relationship between the stability of a clone and the environmental factors on the testing site. Furthermore, the causal relationship between stability and the environment is closely interrelated with identification of the parameters that influence the population buffering capacity. Such parameters are difficult to estimate in the heterogenous environment of a field trial.

The potentials of clonal forestry include not only a rapid genetic gain but also a means to adapt the plant material to the specific requirements of the planting site. The selection of clones will then, however, require a better understanding of the causal relationship between stability and environmental factors. In particular, assessment of stability should be made with respect to predictable as well as unpredictable environmental variation. These requirements can not be properly fulfilled in field experiments and I have therefore suggested a strategy of research to be carried out mainly in climate chambers. The purpose of these complementary testing methods is to improve our understanding of the genetic and physiological properties of the selected plant material and to obtain a more accurate prediction of its future performance after planting.

References

Finlay, K. W. & Wilkinson, G. N. 1963. The analysis of adaptation in a plant-breeding programme. *Aust. J. Agric. Res. 14,* 742–754.

Gullberg, U. 1984. Characterizing environments in Swedish forestry in order to minimize the effects of genotype × environment interaction (Studia Forestalia Suecica 166).

Jonsson, A., Eriksson, G., Dormling, I. & Ifver, J. 1981. *Studies on frost hardiness of Pinus contorta Dougl. seedlings grown in climate chambers* (Studia Forestalia Suecica 157). 47 pp. Uppsala.

Knight, R. 1970. The measurement and interpretation of genotype × environment interactions. *Euphytica 19,* 225–235.

Levins, R. 1962. Theory of fitness in a heterogenous environment. 1. The fitness set and adaptive functions. *American Naturalist 91,* 361–373.

Levins, R. 1968. Evolution in changing environments. In *Monographs in population biology 2.* (ed. R. H. Mac Arthur). 120 pp. Princeton, N. J.: Princeton University Press.

Lindgren, D. 1984. Prediction and optimization of genetic gain with regard to genotype × environment interactions (Studia Forestalia Suecica 166).

McNaughton, S. J. 1970. Fitness sets for *Typha. American Naturalist 104,* 337–341.

GENOTYPE × ENVIRONMENT INTERACTION OF PROVENANCES OF *PINUS CONTORTA* (DOUGL.).

KATARINA LINDGREN

Department of Forest Genetics and Plant Physiology
S-901 83 UMEÅ, Sweden

Abstract

Lindgren, K. 1983. *Genotype × environment interaction of provenances of Pinus contorta (Dougl.).* Studia Forestalia Suecica 166, 41–44. ISSN 0039-3150, ISBN 91-576-1847-X.

The paper suggests a method for finding groups of good provenances of *Pinus contorta* for use in Sweden, based on the pattern of performance of provenances over a wide range of environmental conditions. When the relative height sums of each provenance group (originating from latitude 52°–63°N in interior British Columbia and the Yukon) were regressed against the equivalent latitude of experimental sites (on latitudes 60°–68°N in Sweden) an indication was obtained that the groups of provenances may be classified. The groups of provenances of southerly origins seem to perform relatively well on mild southerly sites, while the groups of northerly origins perform relatively well on severe northerly sites. The group of provenances of intermediate origin did not show superior performance at any site.

The analyses indicate that:

- the geographic area of origin of provenances may be more important than the latitude of origin itself.
- the number of zones of seed source (breeding zones) to fullfil the present need in northern part of Sweden may be rather small.

Key words: Provenance, *Pinus contorta*, performance, genotype × environment interaction.
ODC 232.12: 174.7 *Pinus contorta:* 181.2

Katarina Lindgren, Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden.

Introduction

In earlier studies on provenance transfer of *Pinus sylvestris, Picea abies* and *Pinus contorta* for use in northern Sweden it has been assumed, that there is a clinal variation related to the latitude and altitude of the origin of the transferred material. This paper suggests another method of finding groups of good provenances, based on the pattern of performance of provenances over a rather wide range of sites. The aim of the analyses is to find provenances, able to perform well over a wide range of environmental conditions.

Material and methods

The experiment, which is a part of the international *Pinus contorta* IUFRO-trial, and the data used are described by Lindgren et al. (1976 and 1980). Height and survival of fifteen provenances originating from the Yukon and British Columbia after 9 years in the field on 12 experimental sites in northern Sweden (Fig. 1) were used. Provenances were pooled in five groups and denoted by their average latitude of origin (Figs. 1 and 2). The range in altitude between provenances varied between 670 and 1,175 metres.

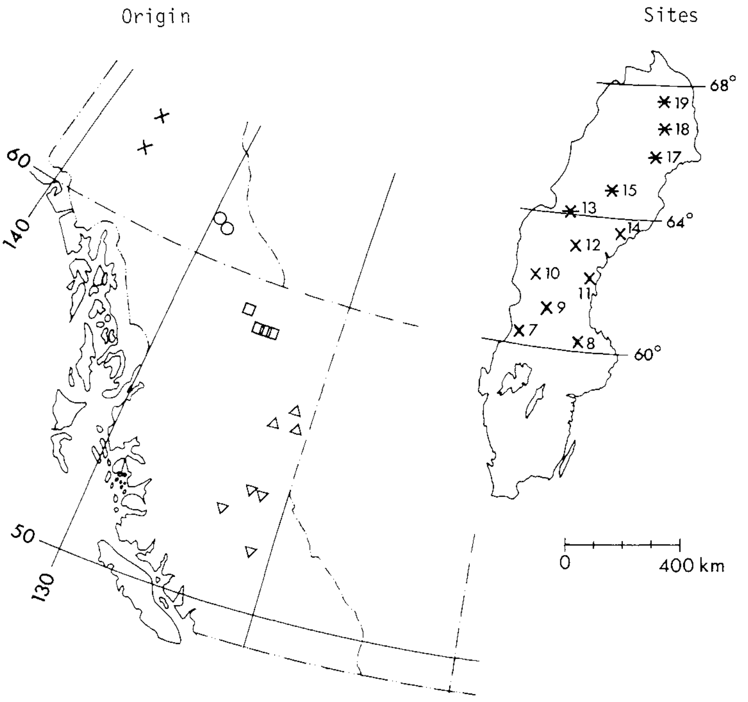

Fig. 1. Origin of five groups of provenances in western Canada and location of experimental sites in Sweden. × denotes sites with equivalent latitude up to 64° and * denotes sites with higher equivalent latitude than 64°.

The reasons for choosing these provenances are:

- They originate from relatively homogeneous areas including several provenances
- They represent the area from which seed is imported to Sweden
- They performed well on several experimental sites (cf. Lindgren et al., 1980, Figs. 9–12).

The reasons for pooling provenances into groups are:

- Individual provenances comprise so few individuals that the statistical errors become large
- As the original stand is probably not available any more we are more interested in provenance areas than in individual stands.

The experimental sites are characterized by "Equivalent latitude" (cf. Lindgren, 1983):

$$\text{Equivalent latitude} = \text{latitude} + \frac{\text{altitude - 300}}{\text{200 or 140}}$$

200 is used, when altitude (m) of site is lower than 300 and 140 is used when altitude is higher than 300 m. The description of the site using the term of equivalent latitude was suggested by Dag Lindgren (personal communication) and is an attempt to combine the relationship between the latitude and altitude of the plantation site. This is almost identical with the transfer scheme used for the official provenance recommendations in the Swedish Silvicultural Act.

As a measure of the performance of a provenance the height sum was used. The height sum is the survival rate multiplied by height of survivors. For Scots pine provenances it was demonstrated that juvenile height sum (at the age of 13 years) gives a good prediction of ranking for mature volume yield (Marklund, 1981).

Results and discussion

The height sum was expressed in per cent of the average of the five groups on each site. The regression line was calculated for the relative height sum of each provenance group as a function of equivalent latitude of site. The sites with equivalent latitude up to 64° and those with equivalent latitude higher than 64° were treated independently as there seems to be a different pattern of relative height sum in those two groups. The results are demonstrated in Fig. 2.

The provenance group originating from latitude

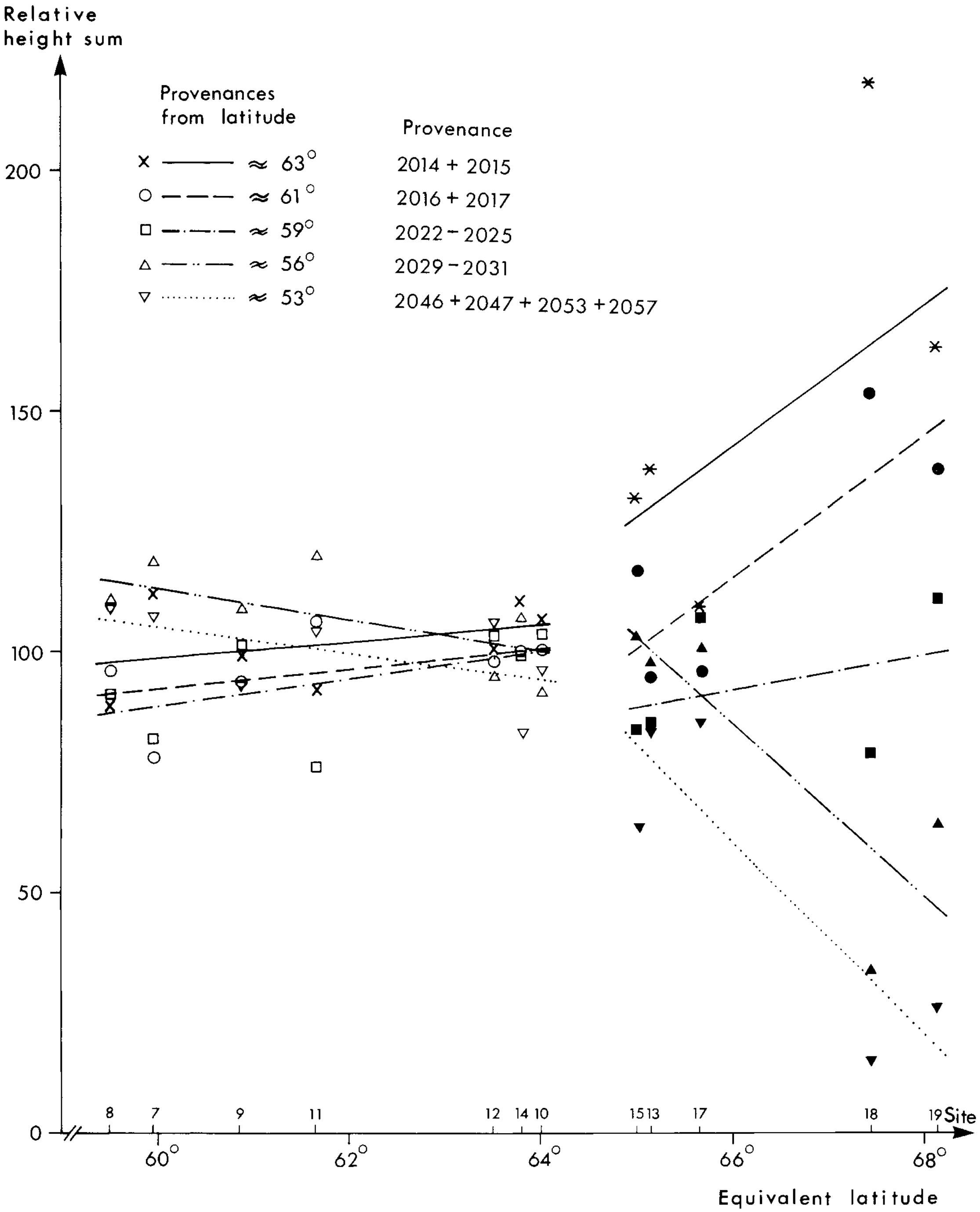

Fig. 2. The relationship between relative height sum of five groups of provenances originating from latitude 52°–63° N and the equivalent latitude of experimental sites. The empty signs denote the sites with equivalent latitude up to 64° and the filled ones denote sites with higher equivalent latitude than 64°. Each symbol in this figure is based on between 31 to 97 planted trees, with an average of 56 trees per point.

56°N seems to perform best on the sites with equivalent latitude up to 63°N. Around and above equivalent latitude 64°N the most northern provenance group was always best, and its superiority increased with increasing equivalent latitude. The intermediate provenance groups from latitudes 59° and 61°N were never superior. Provenances from latitude around 53°N performed rather well on the mildest sites but they were the poorest performers on sites with severe environmental conditions (Fig. 2).

Based on an analysis of variance explained by the regression of the data for the sites up to equivalent latitude 64°N, the hypothesis that the individual regression lines do not differ from the average line (= 100) could not be rejected ($F_{8;20} = 2.37$) i.e. no genotype × environment interaction could be proven. However, the differences approached significance (if, $F_{8;20} = 2.45$, then $p = 0.05$). The ranking of the slopes of the lines is close to expectation of a higher positive regression coefficient the more northern the origin. A more detailed analysis supporting this result may be found in Lindgren (1983).

A model including the assumption of more or less clinal variation with latitude of origin of *Pinus contorta* provenances will probably not result in recommendation of optimal provenances. The group of provenances originating from latitude around 59°N will be predicted to be best on some sites by such a model (cf. Lindgren, 1983).

It seems probable that two—three zones of breeding materials of *Pinus contorta* may be sufficient for the present need in northern Sweden, one for northern Norrland and another for southern Norrland and northern Svealand. The inferiority of the most northern material in southern Norrland is so small that it is justified to include it as a part of the breeding programme.

References

Lindgren, D., Krutzsch, P., Twetman, J. & Kiellander, C. L. 1976. *Survival and early growth of Pinus contorta provenances in northern Sweden* (Royal College of Forestry. Department of Forest Genetics. Res. Notes 20). 42 pp. Stockholm.

Lindgren, D., Lindgren, K. & Persson, A. 1980. Survival and height increment of *Pinus contorta* IUFRO 70/71 series in Sweden. In *Pinus contorta as an exotic species* (Swedish University of Agricultural Sciences, Department of Forest Genetics. Res. Notes 30), 103–133. Garpenberg.

Lindgren, K. 1983. *Provenances of Pinus contorta in northern Sweden.* Doctoral thesis at the Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology. 91 pp. ISBN 91-576-1601-9. Umeå.

Marklund, E. 1981. Äldre tallproveniensförsök ger underlag för produktionsprognoser. *Sveriges Skogsvårdsförbunds Tidskrift 5*, 9–14.

Acknowledgements. This investigation was financed by a grant from the Swedish Council for Forestry and Agricultural Research, and a scholarship from the Swedish University of Agricultural Sciences.