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Some Experimental Results concerning Age Dependency of Different Components of Variance in Testing Norway Spruce (Picea abies (L.) Karst.) Clones

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Summary

A Norway spruce clonal test, established with 5 clones on 5 extremely contrasting sites in 1967 and remeasured for plant-height 10 times until 1981 has been used to estimate the relative importance of the components of variance for "locations", "clones", "locations × clones", "blocks", and "experimental error" dependent on the time. The results show, that in this study "blocks" and "interaction" are of minor importance, accounting to less than 5% of the total variation. Clones account for roughly 10%. These three sources of influence remain more or less constant over time. Considerable changes however occur in the components for "locations" and "experimental error". The first one increases quickly until it reaches a plateau at about 70%, the last one decreases correspondingly and ends up after few years at 15%. All values are quite stable at the end of the time of measurement. These results are discussed on a more general background.

Key words: Norway spruce, clonal test, components of variance, early testing.

Zusammenfassung

Eine Fichten *(Picea abies)*-Klonprüfung, die 1967 mit 5 Klonen auf 5 extrem unterschiedlichen Standorten begründet worden war und seither bis 1981 10 mal für das Merkmal Pflanzenhöhe aufgenommen worden ist, wird verwendet, um den Beitrag der Variationsursachen „Anbauorte", „Klone", „Anbauorte × Klone", „Blöcke" und „Versuchsfehler" in Abhängigkeit von der Zeit zu schätzen.

Die Ergebnisse zeigen, daß in diesem Versuch „Blöcke" und „Interaktion" mit weniger als 5% einen unbedeutenden Beitrag zur Gesamtvariation leisten. „Klone" erklären rd. 10% der Variation. Diese 3 Variationsursachen bleiben über die Zeit mehr oder weniger konstant. Erhebliche Veränderungen treten aber im Laufe der Zeit bei den Varianzkomponenten „Anbauorte" und „Versuchsfehler" ein. Erstere nimmt rasch zu, bis sie nach wenigen Jahren ein Plateau bei rd. 70 % erreicht, letztere nimmt entsprechend ab, bis sie sich bei etwa 15% stabilisiert. Erstaunlich ist die Stabilisierung aller Varianzkomponenten bereits nach wenigen Jahren.

Die Ergebnisse werden vor einem breiteren Hintergrund diskutiert.

Herrn Professor Dr. W. Langner zum 80. Geburtstag gewidmet.

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Introduction

Testing clonal material under different site conditions resulted repeatedly in pronounced differences of variance components depending on time. During the first years after test establishment site influences play a minor role and clonal influences are predominant. These are still strongly under the influence of the nursery site. Only after some years the site influences increase and finally by far the biggest part of variation can be explained by site influences, the clonal component decreases simultaneously.

This rule is not only true for clones but for other plant material as well. Huehn (1974) could show for Norway spruce single tree progenies and controlled crosses, measured from 1959—1971 for tree height, that the variance components for progenies considerably decreased while variance components for planting sites increased correspondingly. The component for interaction did not change much. In this study the different variation components seem to approach fixed values asymptotically.

Finally the plateau-values reached 25% for progenies, 60% for locations, roughly 8% for interaction and 7% for experimental error.

Nichols (1965) already describes a change of variance components for *Pinus radiata* wood characteristics depending on age in 1965.

Lewark (1981) found for the same clonal material used in this study strong annual fluctuations for variance components of annual ring width, basic density and other wood characters. The consequences resulting from these findings for early selection are discussed by Lewark and elsewhere (Kleinschmit and Knigge 1967).

In clonal tests these components of variance can be partly interpreted genetically.

For a judgement on the silvicultural use of clones the time of evaluation plays due to the influences discussed above a considerable role. Valid conclusions can be drawn only after the components of variance have been stabilized.

The following three questions have to be answered:

1. Do the components of variance stabilize sufficiently at all? Theoretically a continuous fluctuation during growth development would be possible too.
2. If the components of variance stabilize, in which age can this be expected?

Table 1. — Climatic and site conditions of the field experiments.

	Aurich	Escherode	Lingen	Schöningen	Andreasberg
Elevation above sea-level	1o m	3oo m	27 m	21o m	8oo m
Precipitation annual	79o mm	8oo mm	759 mm	765 mm	1.5oo mm
during vegetation period	37o mm	36o mm	349 mm	375 mm	61o mm
Mean temperature annual	8,2°C	7,6°C	9,2°C	8,o°C	4,4°C
during vegetation period	14,1°C	14,o°C	15,4°C	14,7°C	1o,4°C
Climatic characterization	sea climate without temperature extremes; high air humidity; high wind velocity	comparatively balanced humid cool climate	high air humidity frequent late frosts, high wind velocity	high summer temperatures, high annual temperature variation; low air humidity	long winters with high snow cover
Exposition	flat	north-west exposition, low inclination	flat	flat	south exposition mean inclination
soil type	Podsol from poor sand	Pseudoclay on red sand stone, mean nutritional level	Podsol on aeolic sand deposits above fluvial sand, low nutritional level	Para-brown-earth, high nutritional level	Podsolic pseudo-clay, high stone percentage, low nutritional level
Earlier stand	Norway spruce, site index class 9	Norway spruce, site index class 12	Farmland after heath vegetation	Norway spruce site index class 11	Norway spruce site index class 4

3. Which numerical values do the different components of variance (clones, locations, interactions, experimental error) finally reach?

These three questions shall be followed in this study using data of a Norway spruce clonal test of the Lower Saxony Forest Research Institute.

Material and Methods

The data analyzed originate from a set of 5 Norway spruce clones grown under extreme variable site and climatic conditions.

Climatic and site conditions for the 5 plantation sites are summarized in *Table 1*. These show, that elevation above sea level ranges from 10 m to 800 m, annual precipitation from 759 mm to 1.500 mm, mean annual temperatures between 9,2° C to 4,4° C. This covers as much variation as available in northern Germany excluding very few extremes.

Soil nutrition varies from very poor to rich and the physical soil conditions from light sands to heavy, claysoils with high water table.

These facts explain, that the plantation sites cover a broad range, reaching from marginal sites to optimal sites for growing Norway spruce. On these sites 5 Norway spruce clones have been planted in 1967, representing some of the clones of the early propagations in Escherode. All clones originate from one population and have been selected for growth vigour and rootability. The variation of the clones is very much restricted as compared to the sites. The ortets had an age of 30 years when the cuttings have been taken. Therefore a higher within clonal variation has to be expected due to topophysis effects as compared to more juvenile clonal material.

The field tests have been established with 7 years old "balled" transplants, spacing 2 × 2 m with 7 × 7 plants per plot. The experiment has been layed out as randomized Block experiment with two replications, only on the field test Escherode one clone is only represented in one block, three others are three times replicated. The very variable climatic and site conditions are especially good for the study of the stabilization of the variance components. The comparatively narrow genetic base of the clones results in an underestimation of the variance components of clones.

Height measurements are available for the years 1967, 1968, 1969, 1971, 1972, 1973, 1974, 1975, 1976 and 1981, except the 1967 measurement for Escherode. All replacements and all plants of which the complete set of measurements was not available have been excluded from the evaluation to prevent additional experimental error.

We have the following situation:

1. factor (i) (A)	sites $i = 1, 2, \ldots, a$	$(a = 5)$
2. factor (j) (B)	clones $j = 1, 2, \ldots, b$	$(b = 5)$
3. factor (k) (C)	blocks $k = 1, 2, \ldots, c$	$(c = 2)$
4. factor (t) (D)	time $t = 1, 2, \ldots, d$	$(d = 10)$

No combined evaluation for all times of measurement have been carried out. Each time of measurement has been evaluated separately.

The following terms have been used:

Y_{ijkl} = value of plant l of block k and clone j on site i.

For each ijk-combination, which means for every plot, there exists n_{ijk} single plants (replications). n_{ijk} can maximally reach 49. These numbers can vary however considerably due to losses, therefore non-orthogonal evaluation was necessary.

The data have been processed according to the following structure:

factor A (sites) and B (clones) crossclassification,

factor C (blocks) hierarchical within A × B combinations.

All three factors are regarded as random. A detailed biometrical treatment of this structure is given by Rasch (1971).

The model has the following form:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + w_{ij} + \gamma_{ijk} + e_{ijkl} \quad (1)$$
$$(i = 1, 2, \ldots, a;\ j = 1, 2, \ldots, b;\ k = 1, 2, \ldots, c;\ l = 1, 2, \ldots, n_{ijk})$$

μ = overall mean
α_i = effect of location i
β_j = effect of clone j
w_{ij} = interaction between site i and clone j
γ_{ijk} = effect of block k for site i and clone j
e_{ijkl} = experimental error.

Since at the site Escherode one clone has only one replication and the 1967 measurement is missing the following two data sets have been processed separately:

I. Without site Escherode; this results in
$a = 4; b = 5; c = 2; d = 10$

II. Without the clone, only once represented in Escherode and without the 1967 measurement.
This results in:
$a = 5; b = 4; c = 2; d = 9$
Both sets have been evaluated non-orthogonal because of the different n_{ijk}values. In addition there has been carried out an orthogonal evaluation according to the following procedure:
The minimal $n_{ijk} = n$ has been located. All the other n_{ijk} have been fixed to the same constant n by selection of the first n values in each ijk-combination. This resulted in $n = 23$. The comparison of the two evaluations is discussed later on.

The variance components σ^2_e (experimental error), σ^2_{AB} (interaction location $\times$ clones), σ^2_A (locations), σ^2_B (clones) and $\sigma^2_{C\ in\ AB}$ (blocks) are estimated by equating the different mean squares with their theoretical expectations (Rasch 1971).

figure 1a

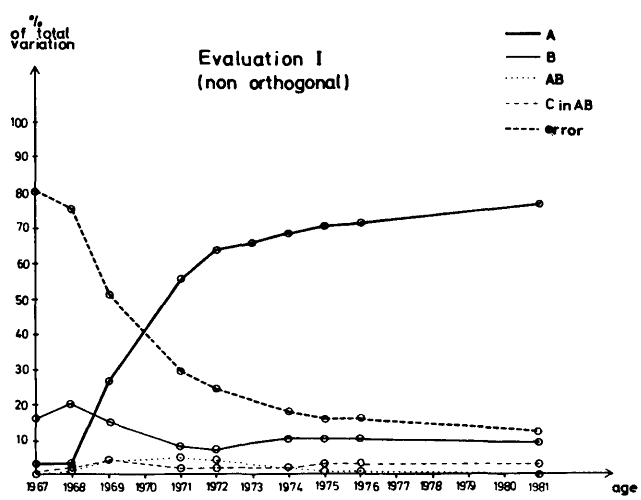
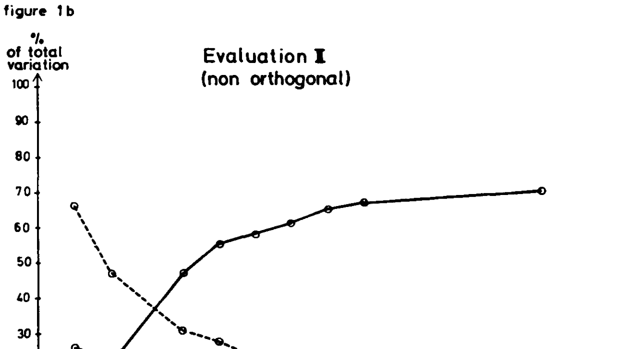


figure 1b



Figures 1a and *1b*. — Proportions of variability for the different sources of variation for the non-orthogonal evaluations I and II dependent on age.

Results

The results of the analyses of variance are not presented here since for the discussion of the questions to be answered only the components of variance are of interest.

In three cases there occur negative components of variance. For σ^2_{AB} in evaluation I for the first measurement and for σ^2_{AB} in evaluation II for the 9th and 10th measurement. This is not unusual in estimating variance components; in addition these estimates have very low numerical values, so it is justified to take these for zero.

To transform the variance components into proportions of variability, the single variance component is divided by the sum of all variance components of the respective time of measurement. The results are presented in *Figures 1a* and *1b*.

In both cases the components of variance of σ^2_{AB} and $\sigma^2_{C\ in\ AB}$ are minor and without practical importance. Their proportions of variability remain more or less constant during the whole time with relative values less than 5%. σ^2_B too has no outstanding importance, remaining nearly constant at about 10%. A significant dependency of age however show σ^2_A and σ^2_e. As shown in *Figures 1a* and *1b* the total variability of the material is dominated by these two sources of variation "locations" and "experimental error". Site influence increases steadily and experimental error decreases continuously. Already after few years about 60% of the total variation can be allocated to site influences. After this time the relative change is minor, indicating that the proportion of variability stabilize quite early. Finally in this study the values for locations reach about 70%, for experimental error about 15%.

This prevailing site influence is not surprising with respect to the quite heterogeneous sites included in this study and the comparative small genetic variation of the clones.

Looking to the first two years of measurement (1967 and 1968) in evaluation I there are obvious irregularities *(Figure 1a)*, which are not to be seen in evaluation II *(Figure 1b)* where the year 1967 is missing. These irregularities are probably caused by the planting-shock.

Discussion and Conclusions

The material, used in this study, is by far too limited to draw general conclusions concerning proportions of variability. 4 respectively 5 sites and 5 respectively 4 clones cannot be regarded as a representative sample of all sites and clones possible. This is especially true for the clones. Having this in mind, the clear trend of the results is even more surprising:

For all components of variance under discussion there is a very evident time-dependent trend (*Fig. 1a, 1b*) with a stabilization of proportions of variability already after few years. The sources of variation AB (interaction) and C in AB (blocks) account together for less than 5% and B (clones) for 10% only; they remain more or less constant in addition. In contrary to these "location" and "experimental error" show an extreme increase respectively decrease until they stabilize after few years on a level of 70% (locations) and 15% (experimental error).

How far the last measurements (1981) really represent constant plateaus can be only judged after further measurements. However, considering the minor changes during the figure 2a

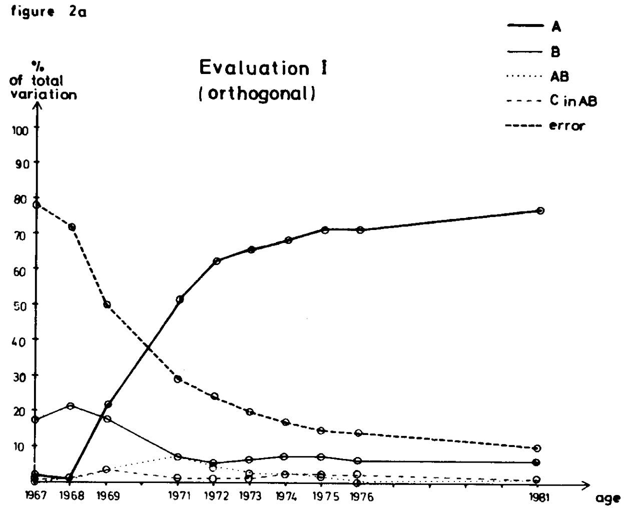
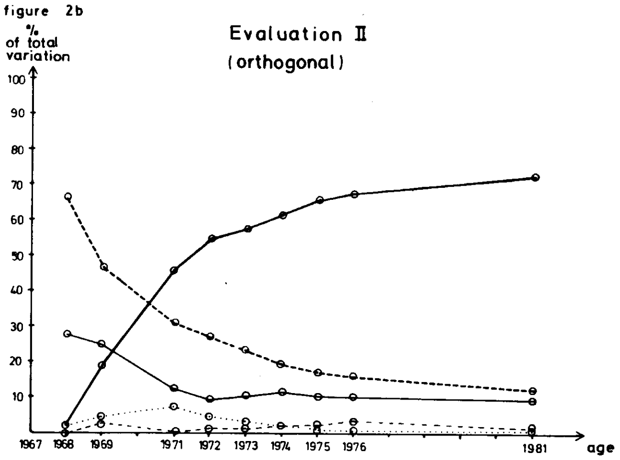


figure 2b



Figures 2a and *2b*. — Proportions of variability for the differen sources of variation for the orthogonal evaluations I and II dependent on age.

recent years, this question may be more of academic interest.

A comparison with the study of HUEHN (1974) the numerical values of the plateaus reached are quite different. This underlines the importance of the material used in the study (restricted genetic variation between the clones) as well as the influence of the actual plantation sites.

A good agreement of both studies however is the fact, that for all sources of variation after few years certain plateau values are reached which do not change considerably further on.

The results obtained for the non-orthogonal evaluations I and II do not show any significant differences (*Figures 1a* and *1b*). Therefore, the addition or deletion of single locations or single clones is of no considerable influence on the variability proportions of the material.

The corresponding orthogonal evaluations, which have been carried out with strongly reduced plant numbers, show the same results (*Figures 2a* and *2b*).

This allows the conclusion, that already much more limited numbers of plants (in this case 23 per plot) are sufficient to get a good estimate for the proportions of variability and the final numerical values of the plateaus. This result is important for future planning of experiments.

The results can be well explained by biological reasons: The plants of all field tests have been grown initially in the same nursery. The differences in growth at the time of plantation establishment can be explained by clonal influences and experimental error mainly. This corresponds to the first measurement of the field tests (1967). From this time onwards the influences of the location (climate and soil conditions) on the further growth of the clones can act. These are initially only disturbed by the planting shock. The clones now start to collect the site information, which is variable in time as well, over the years and reflect this information in health and growth. The annual influences can act annually quite different on the different clones, as to be seen e.g. from the variance components for annual ring width, estimated by LEWARK (1981) for these experiments, ranging from 7% to 53% for clones depending of the year. During further growth development the annual variation however levels out to the location mean. Since the volume (height and diameter) of the trees increases steadily, the relative contribution of the annual environmental variation to the growth is finally so small, that this has nearly no implications on the proportion of variability. The main result of the present study: the fast stabilization of the components of variance in the material, also has implications on the problem of juvenile-mature-correlations. This has been discussed elsewhere (HUEHN and KLEINSCHMIT 1986).

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