shoot elongation and flushing of buds as well as the process of bud induction. Differences in the appearance and elongation behaviour of adventitious buds derived from induction steps was influenced by the type of cytokinin used. Additional research is needed to determine the general mechanisms of the dependence of cytokinin concentrations including their interaction with other metabolites influencing formation and development of shoots (e.g. nitrogen, Selby and Harvey, 1980). The positive effect of gelrite used as gelling agent on propagation has also been reported for other tree species (Eucalyptus — MacRae and Van Staden, 1990). The stimulation of the development of small adventitious buds using gelrite could be valuable for juvenile and adult spruce explants.

The formation and propagation of adventitious bud clusters of juvenile spruce explants can serve as a means to multiply seed material from controlled pollination as well as selected somatic embryos (e.g. transgenic plants).

Stimulation of shoot elongation in adventitious buds of juvenile spruce explants via a cytokinin induction might also offer a way to overcome the difficulties in shoot elongation existing with adult plant material of Norway spruce in vitro.

Despite these first encouraging results much more research work is needed to determine the general mechanisms of shoot elongation in spruce and put it to practical use.

Conclusions

1. The type and concentration of cytokinins used for a repeatable process of adventitious bud induction influences the later elongation behaviour of newly formed buds in Norway spruce.

2. Treatments of already formed spherical adventitious buds with 0.5 mg 1\(^{-1}\) zeatin or 0.05 mg 1\(^{-1}\) kinetin or 0.5 mg 1\(^{-1}\) to 1.0 mg 1\(^{-1}\) 2IP allow the propagation of adventitious bud clusters as well as the elongation of newly formed buds.

3. The elongation of preformed terminal meristems in adventitious buds is stimulated by a treatment with 0.1 mg 1\(^{-1}\) to 0.3 mg 1\(^{-1}\) zeatin [4.55 x 10\(^{-7}\) M — 1.36 x 10\(^{-8}\) \pm 0.01 mg 1\(^{-1}\) kinetin [4.64 x 10\(^{-8}\) M].

4. Comparing the influence of gelrite and agar-agar on adventitious bud formation gelrite supported the formation of adventitious buds.

Acknowledgements
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References


Time Trends in Age-Age Covariances and Correlations — Examples from Norway Spruce Clones

By M. Hühn\(^1\) and J. KLEIN-SCHMITZ\(^2\)

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Summary
A Norway spruce clonal test, established with 5 clones on 4 extremely contrasting sites in 1987 and remeasured

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\(^1\) Institut für Pflanzenbau und Pflanzenzüchtung der Universität Kiel, Olaus-Hansenstr. 40, D-24118 Kiel

\(^2\) Niedersächsische Forstliche Versuchsanstalt, Abt. Forstpfanzenzüchtung, D-38382 Stuifenberg

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for height 10 years until 1981 has been used for an investigation of the following 3 topics:

1. Description of juvenile—mature correlations by LAMBERT's formula.

2. Investigation of time trends in age—age covariances, age—age correlations and standard deviations.


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One obtains nearly perfect linear dependency between covariance and age as well as between standard deviation and age. The correlation coefficients show a rapid decrease in the first years, while this decrease diminishes and finally tends asymptotically towards a specific constant level.

The proposed new formula for age-age covariances provides a considerably better fit between observed and expected values than Lambech's formula.

**Key words:** Age-age correlation, Norway spruce, time trends in variances and covariances, Lambech's formula.

**Zusammenfassung**

Elne Fichten (*Picea abies*)-Klonprüfung, die 1967 mit 5 Klonen auf 4 extrem unterschiedlichen Standorten be- gründet worden war und die seither bis 1981 10mal für das Merkmal "Höhe" aufgenommen worden ist, wird zur Unter- suchung der folgenden 3 Punkte herangezogen:


Während Jugend-Alters-Kovarianzen wie auch die Standardabweichungen streng linear vom Alter abhängen, zeigen die Jugend-Alters-Korrelationen einen starken Abfall in den ersten Jahren, um sich dann asymptotisch einem bestimmten Niveau zuzuwenden.

Die vorgeschlagene neue Formel für Jugend-Alters-Korrelationen weist im Vergleich zur Lambech-Formel eine wesentlich verbesserte Anpassung an die experimentelle Ertragswerte auf.

**Introduction and Problem**

Juvenile-mature correlations are of major interest in breeding of forest trees. The efficiency of an early selection will be partly determined by the numerical value of the juvenile-mature correlation. Therefore, many investigations have been carried out to estimate these juvenile-mature correlations and to develop efficient early selection techniques (e.g. Sikkala, 1974; Squillace and Gannel, 1974; Nanson, 1969, 1976; Lambech, 1983; Lambech et al., 1983; Kang, 1985; Jiang, 1987; Riemenschneider, 1988; Bur- don, 1989).

Closely connected with juvenile-mature correlations are, of course, aspects of trends in variances dependent on age (Namkoong et al., 1972; Namkoong and Conele, 1976; Franklin, 1979; Lambech et al., 1983; Foster, 1988; Huenin et al., 1987; Gill, 1987; Bentzen et al., 1989).

In many applications the phenotypic correlation $r$ for the trait "height" between 2 different ages can be estimated by the formula of Lambech (1980):

$$
\sigma(x) = A + B \cdot \ln x
$$

where $x = t^\prime T$ with

- $t$ = early (= juvenile) age (in years from planting date)
- $T$ = late (= mature) age (in years from planting date)

A and B are constants representing intercept with $x = 1$ and regression coefficient of $r(x)$ on $\ln x$, respectively.

This paper discusses 3 topics:

I) Application of Lambech's formula, based on an experimental data set of 5 Norway spruce clones.

II) Developments in time trends in age-age covariances

age-age correlations

motivated by the height measurement data from the 5 clones.

III) Proposal of a new formula for juvenile-mature correlation dependent on age.

The same experimental clonal material which has been analyzed in Huenin et al. (1987) for variances shall be investigated in this paper with regard to covariances.

**Material and Methods**

The data are height measurements of a set of 5 Norway spruce clones grown under extreme variable site and climatic conditions. These climatic and site conditions for the 4 plantation sites Aurlach, Lingon, Schönningen and Andreasberg, all located in northern Germany and a description of the clonal material have been presented in detail in Huenin et al. (1987). For all these informations we, therefore, refer to this publication.

The field tests on these 4 sites with 5 Norway spruce clones have been planted in 1967, with 7 years old "bailed" transplants, spacing $2 m \times 2 m$ with $7 \times 7$ plants per plot. Layout: Randomized complete block design with 2 replications.

Height measurements are available for the years 1967 to 1969, 1971 to 1976 and 1981. All replacements and all plants with missing measurements in single years have been excluded from the evaluations. Each time of measurement has been analyzed separately (on a per individual tree basis).

For each plot the number of plants varied from 23 to the maximal number 49 due to plant losses. Therefore, non-orthogonal evaluations are necessary with a total number of 1387 included single plants.

Relating all the different later measurements to the measurement one year after planting date (i.e. $t = 1$) it follows:

$$
\sigma(T) = A - B \cdot \ln T
$$

Regressing $r(T)$ on $\ln T$ gives estimates of A and B. These estimates — well-known from linear regression theory — can be expressed as:

$$
A = \frac{\sum_{i=1}^{N} r(T_i) + \hat{B} \cdot \sum_{i=1}^{N} \ln T_i - N \cdot \sum_{i=1}^{N} r(T_i) \cdot \ln T_i}{N}
$$

$$
\hat{B} = \frac{\left(\sum_{i=1}^{N} \ln T_i\right) \left(\sum_{i=1}^{N} r(T_i) - N \cdot \sum_{i=1}^{N} r(T_i) \cdot \ln T_i\right)}{N \cdot \left(\sum_{i=1}^{N} \ln T_i\right)^2 - \left(\sum_{i=1}^{N} \ln T_i\right)^2}
$$

with $N$ = number of included measurements later than the measurement for $t = 1$. In this study we have $N = 8$ (years: 1969, 1971 to 1976 and 1981).

**Results**

The planting date of the test sites is 1967 and all following results on covariances and correlation coefficients are
here related to the measurement one year after planting date (i.e. to the measurements of 1968).

I) Application of Lambeth's formula

To check the goodness-of-fit of the expectations of \( r(T) \) by (2) one needs estimates of \( A \) and \( B \). Regressing \( r(T) \) on \( \ln T \) gives:

\[ A = 0.843 \quad \text{and} \quad \hat{B} = 0.263. \]

Using these estimates in (2) leads to the expectations of \( r(T) \), which are presented in table 1.

The agreement between observed and expected values is reasonably good, but not excellent. We, therefore, may conclude that the age-age correlations of this experimental material can be described with a tolerable accuracy by Lambeth's formula (2).

II) Time trends in age-age covariances and age-age correlations

The experimental results of the age-age covariances, the age-age correlation coefficients and the standard deviations are presented in figure 1.

The main results are:
1. Nearly perfect linear dependency between covariance and age (Fig. 1).

*Figure 1.* Age-age covariances, age-age correlations and standard deviations dependent on age.
Linear regression equation: \( w(T^*) = k_1 \cdot T^* + k_2 \) with \( T^* = \text{age (in years)} \) from 1968 until the later measurements, \( w(T^*) = \text{covariance between the two ages} 1968 \text{ and } T^* \), \( k_1 = 47.64 \), \( k_2 = 182.94 \) and a coefficient of determination of 0.996%

2. The correlation coefficients show a rapid decrease in the first years, while this decrease diminishes and finally tends asymptotically towards a specific constant level (\( \approx 0.20 \) (Fig. 1).

3. Nearly perfect linear dependency between standard deviation and age (Fig. 1).

Linear regression equation: \( \sigma_2^* = k_1 \cdot T^* + k_2 \) with \( \sigma_2^* = \text{standard deviation at age} T^* \), \( k_1 = 18.49 \), \( k_2 = 4.56 \) and a coefficient of determination of 0.966%

III) Formula for age-age correlations

Combination of the 2 linear dependencies between covariance and age and between standard deviation and age lead (by definition of the correlation coefficient) to an explicit formula for age-age correlations of the following form:

\[
 r = \frac{c_1 \cdot \text{age} + c_2}{c_3 \cdot \text{age} + c_4} = c_5 \cdot \frac{1 + c_6 \cdot \text{age}}{1 + c_7 \cdot \text{age}}
\]

with constants \( c_i, i = 1, 2, \ldots, 7 \), where \( c_5 = c_6/c_7 \), \( c_4 = c_1/c_3 \) and \( c_7 = c_6/c_4 \) and \( \text{age} = \text{difference between late (= mature) age minus early (= juvenile) age (in years).} \)

Using estimates of these constants obtained from the experimental material of this study leads to the expectations of \( r \), which are presented in Table I.

The agreement between observed and expected values is extraordinary good. We, therefore, can conclude that the age-age correlations of this experimental material can be described with an excellent accuracy by the proposed formula (5). This expression (5) provides a substantially better fit between observed and expected values than formula (2).

Discussion

1. First of all, we want to point to the fact that the experimental data and their numerical results can only serve as examples as they are based on only 5 clones. No general validity can be assumed. Whether or not these results on time trends in variances and covariances and age-age correlations can be generalized to other experimental situations (clones, sites) of Norway spruce or even to other tree species must be investigated in further studies.

2. The proposed formula (5) for age-age correlations provides a clear explanation and description of the asymptotic property indicated by the empirical results (≈ stabilizing correlations): With increasing age the correlation tends to \( c_i/c_5 \). Its numerical value for the present experimental material is 0.19. The correlation coefficient for the last measurement in this study (1981) is 0.24 (Fig. 1).

For the years following 1981, some further decline of the age-age correlation must be expected.

3. The observed and the expected values of \( r \) in Table I are calculated from the same set of data. The expected values are therefore not an independent prediction.

The aim of this study is to check and to compare the goodness-of-fit for the two different functional relationships (2) and (5). By these reasons, in this paper the word "predicted" has been replaced by "expected".

4. The efficiency of early selection strongly depends on the genetic age-age correlation. But, all correlations presented in this paper are phenotypic. Common environmental effects, of course, could bias the covariances and correlations. A refined analysis of age-age correlations, therefore, must include a decomposition of the phenotypic age-age correlation into a genetic and an environmental component. Such an analysis of genetic age-age correlations can be easily carried out by proceeding from clonal means. The experimental material of this study, however, consists of only 5 clones. For such a narrow experimental basis a more sophisticated analysis (decomposition) of the phenotypic age-age correlations seems to be inappropriate.

Table I. — Experimental values of the age-age correlations and the theoretically expected values.

<table>
<thead>
<tr>
<th>age-age correlation</th>
<th>( r )</th>
<th>exper.</th>
<th>expected</th>
<th>value</th>
<th>value</th>
<th>value</th>
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<tr>
<td>1968 - 1969</td>
<td>2</td>
<td>0.74</td>
<td>0.66</td>
<td>0.74</td>
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<td></td>
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<tr>
<td>1968 - 1971</td>
<td>4</td>
<td>0.45</td>
<td>0.48</td>
<td>0.40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968 - 1972</td>
<td>5</td>
<td>0.36</td>
<td>0.42</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968 - 1973</td>
<td>6</td>
<td>0.33</td>
<td>0.37</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968 - 1974</td>
<td>7</td>
<td>0.30</td>
<td>0.33</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968 - 1975</td>
<td>8</td>
<td>0.28</td>
<td>0.30</td>
<td>0.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968 - 1976</td>
<td>9</td>
<td>0.27</td>
<td>0.27</td>
<td>0.27</td>
<td></td>
<td></td>
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<tr>
<td>1968 - 1981</td>
<td>14</td>
<td>0.24</td>
<td>0.15</td>
<td>0.24</td>
<td></td>
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</tr>
</tbody>
</table>

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Susceptibility of P. deltoides Bartr. to Melampsora larici-populina and M. allii-populina
I. Qualitative Analysis of a 6x6 Factorial Mating Design

By Ch. Pichot1) and E. Teissier du Cros2)

(Received 15th September 1992)

Summary

Qualitative susceptibility to Melampsora spp. was observed in a 6x6 F. deltoides factorial mating.

For each of the 3 inocula tested, Melampsora larici-populina races E1 and E2 and M. allii-populina, segregations that occurred in qualitative tests cannot be explained with less than 3 genes for susceptibility-resistance. Comparison with E. Karkov's results (1991) suggest that race E1 would have a recessive resistance gene which is not present in E2. However, the observed segregation pattern cannot be explained without another gene common to E1 and E2.

Within 3 full sib families, qualitative resistance to both M. allii-populina and M. larici-populina may be genetically linked. Obviously, several unidentified races of M. allii-populina were present in the nursery trial.

Keywords: Populus deltoides, Melampsora larici-populina, Melampsora allii-populina, qualitative resistance, segregation, factorial mating.

Introduction

The Populus genus is one of the most widespread and economically important wood resources in the world. But many pests and diseases are encountered on poplars, especially in monoclonal plantations. Among diseases, "Melampsora leaf rust is probably the most widely distributed and serious foliar disease of the Algeiros and Tacamahaca poplars and their hybrids" (Théloen, 1985).

At least 8 Melampsora species can attack poplars, but 3 of them are of major importance: M. allii-populina Klra., M. larici-populina Kles. and M. medusae Thum. Severe damage has been attributed to these pathogens, including growth reduction or even death of plants (Windl and Schiefer, 1981; Stenackes, 1982; in: Pinon, 1984). During the last 10 years, a number of studies has focused on the Populus-Melampsora system, revealing great variability within both host and pathogen, and frequently reporting race-specific interactions.

This report relates qualitative tests of the susceptibility of P. deltoides Bartr. to Melampsora larici-populina and M. allii-populina, which were conducted in the laboratory and nursery at the INRA station near Orleans. Genetic determination of total resistance to rust is approached through our analyses of a 6x6 factorial mating system.

Materials and Methods

A) Origin of the plants

Thirty-three full-sib families from an intraspecific P. deltoides factorial mating involving 6 males and 6 females were tested. Parents came from very distinct sites within the natural range of P. deltoides (Figure 1). Details on the crosses and origin of the parents were provided in Pichot and Teissier du Cros (1989). Table 1 gives the exact number of clones used, maximum 20 per family. A total of 591 clones were included in the study. Ten of the 12 parents were also vegetatively propagated for testing.

Note that clone number 2415 (for example) refers to clone number 15 in the full sib family 24, involving male 2 and female 4.

B) Origin of the rust and culture of inoculum

Urediospores of Melampsora larici-populina (race E1 and E2) and M. allii-populina were sent by J. Pinon from the INRA laboratory of Nancy. Inocula were multiplied by culturing directly on leaves of race-specific clone: Grammont3 (=Ogy) for M. larici-populina race E2; Beaupre for M. allii-populina; and finally, Robusta (non specific) for M. larici-populina race E1.

The spores were cultured at 15h00 photoperiod at 10°C to 25°C, and stored according to the techniques developed by Pinon (personal communication).

Rust susceptibility of progenies was scored both in the nursery and in the artificial environment of controlled environment chambers. Experimental designs varied in each case.

C) Nursery experiments

In spring, 1990 a nursery trial was established with stem cuttings at the INRA station near Orleans. The experimental design utilized 3 complete blocks with plots of 2 ramets per clone. Additionally, 10 clones were chosen as controls. The plots were randomly distributed within blocks. Cuttings were all taken from a first generation stool bed, thus reducing the C effect. Cuttings were planted under a black polythene film to reduce evaporation and to control weeds. Planting distance was 1.2 m x 0.5 m. In winter, 1990 the trial was cut back. In spring, only one stem per stump was retained.

On July 19th 1990 and again on June 18th 1991, a suspension of 7000 spores per ml of M. larici-populina race E1 was sprayed on the lower surface of one leaf per tree.

1) INRA, Centre de Recherches d'Orléans, Station d'Amélioration des arbres forestiers, F-45180 Ardon, France
2) INRA, Laboratoire de Recherches Forestières Méditerranéennes, F-84000 Avignon, France

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