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, 1990). 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 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 l^{-1} zeatin + 0.05 mg l^{-1} kinetin or 0.5 mg l^{-1} to 1.0 mg l^{-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 l^{-1} to 0.3 mg l^{-1} zeatin [4.55 x 10^{-7} M— 1.36 x 10^{-6}] ± 0.01 mg l^{-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.

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

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Summary

A Norway spruce clonal test, established with 5 clones on 4 extremely contrasting sites in 1967 and remeasured for height 10 times until 1981 has been used for an investigation of the following 3 topics:

1. Description of juvenile-mature correlations by LAMBETH's formula.
2. Investigation of time trends in age-age covariances, age-age correlations and standard deviations.
3. Proposal of a new formula for juvenile-mature correlations dependent on age.

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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 correlations provides a considerably better fit between observed and expected values than LAMBETH's formula.

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

Zusammenfassung

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

1. Verwendung von LAMBETH's Formel zur Beschreibung von Jugend-Alters-Korrelationen.
2. Untersuchung zeitlicher Trends von Jugend-Alters-Kovarianzen, Jugend-Alters-Korrelationen sowie von Standardabweichungen.
3. Vorschlag einer neuen Formel für Jugend-Alters-Korrelationen in Abhängigkeit vom Alter.

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 zu nähern.

Die vorgeschlagene neue Formel für Jugend-Alters-Korrelationen weist im Vergleich zur LAMBETH-Formel eine wesentlich verbesserte Anpassung an die experimentell erhaltenen Werte 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 (i.e. SZIKLAI, 1974; SQUILLACE and GANSEL, 1974; NANSON, 1969, 1976; LAMBETH, 1983; LAMBETH et al., 1983; KANG, 1985; JIANG, 1987; RIEMENSCHNEIDER, 1988, BURDON, 1989).

Closely connected with juvenile-mature correlations are, of course, aspects of trends in variances dependent on age (NAMKOONG et al., 1972; NAMKOONG and CONKLE, 1976; FRANKLIN, 1979; LAMBETH et al., 1983; FOSTER, 1986; HUEHN et al., 1987; GILL, 1987; BENTZER 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 LAMBETH (1980):

$$r(x) = A + B \cdot \ln x \qquad (1)$$

where $x = t/T$ 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 LAMBETH'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 correlations dependent on age.

The same experimental clonal material which has been analyzed in HUEHN 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 Aurich, Lingen, Schöningen and Andreasberg, all located in northern Germany and a description of the clonal material have been presented in detail in HUEHN 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 "balled" transplants, spacing 2 m x 2 m with 7 x 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 1587 included single plants.

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

$$r(T) = A - B \cdot \ln T \qquad (2)$$

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

$$\hat{A} = \frac{\sum_{i=1}^{N} r(T_i) + \hat{B} \cdot \sum_{i=1}^{N} \ln T_i}{N} \qquad (3)$$

$$\hat{B} = \frac{\left(\sum_{i=1}^{N} \ln T_i\right)\left(\sum_{i=1}^{N} r(T_i)\right) - N \cdot \sum_{i=1}^{N} r(T_i) \cdot \ln T_i}{N \cdot \sum_{i=1}^{N} (\ln T_i)^2 - \left(\sum_{i=1}^{N} \ln T_i\right)^2} \qquad (4)$$

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:

$\hat{A} = 0.843$ and $\hat{B} = 0.263$. 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*).

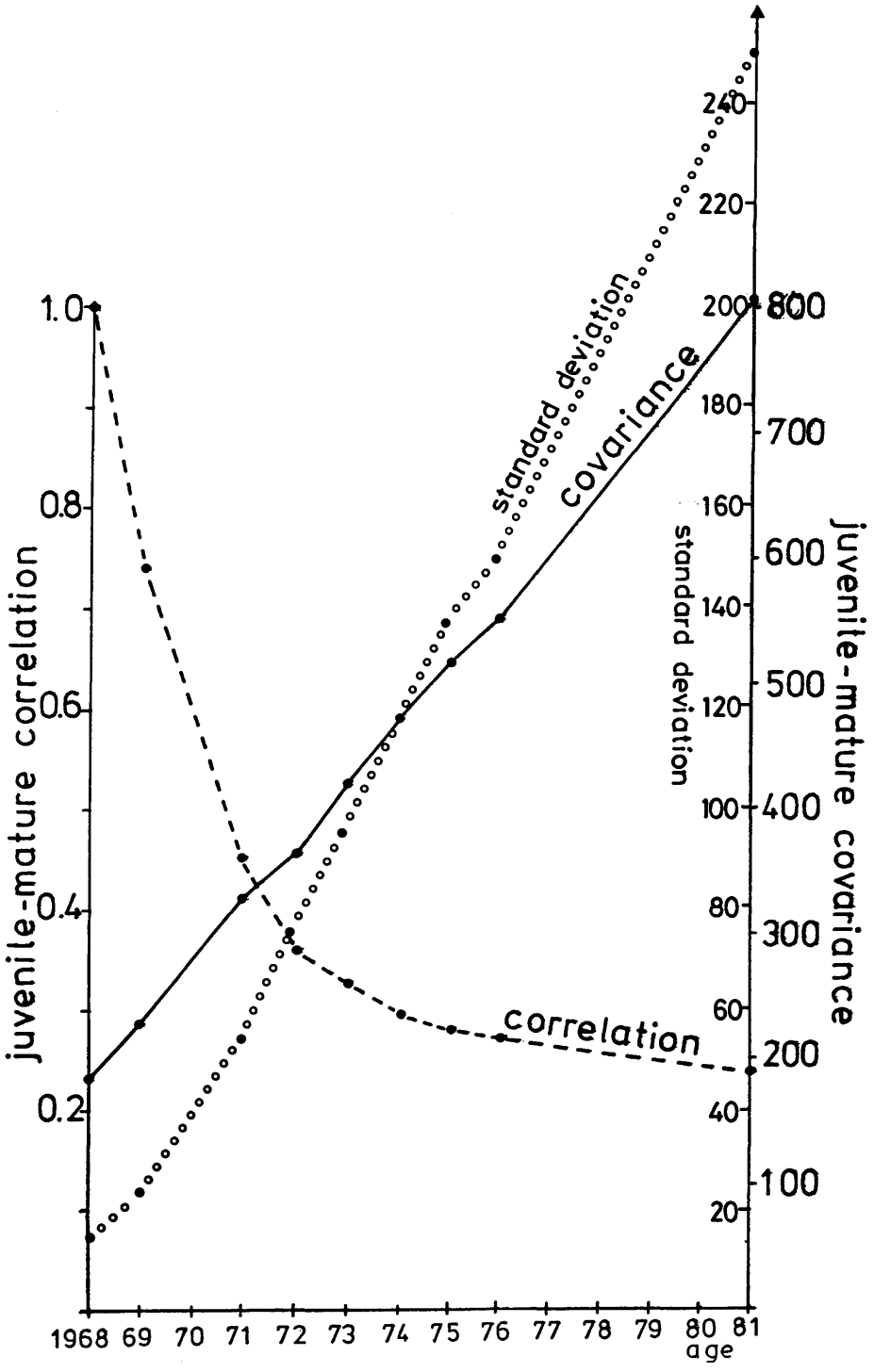

Figure 1. — Age-age covariances, age-age correlations and standard deviations dependent on age.

[Linear regression equation: $w(T^*) = k_1 \cdot T^* + k_2$ with T^* = age (in years) from 1968 until the later measurements, $w(T^*)$ = covariance between the two ages 1968 and T^*, k_1 = 47.64, k_2 = 182.94 and a coefficient of determination of 99.9%].

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: $\sigma_T^* = k_3 \cdot T^* + k_4$ with σ_T^* = standard deviation at age T^*, k_3 = 18.49, k_4 = 4.56 and a coefficient of determination of 99.6%].

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:

(5)

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

with constants c_i, i = 1, 2, . . . , 7, where $c5 = c_2/c_4$, $c_6 = c_1/c_2$ and $c_7 = c_3/c_4$ and age = 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 1.*

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_1/c_3. 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 1* 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 1. — Experimental values of the age-age correlations and the theoretically expected values.

age-age correlation	T	exper. value of r	expected value by (2)	expected value by (5)
1968 - 1969	2	0.74	0.66	0.74
1968 - 1971	4	0.45	0.48	0.40
1968 - 1972	5	0.36	0.42	0.35
1968 - 1973	6	0.33	0.37	0.32
1968 - 1974	7	0.30	0.33	0.30
1968 - 1975	8	0.28	0.30	0.28
1968 - 1976	9	0.27	0.27	0.27
1968 - 1981	14	0.24	0.15	0.24

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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

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(Received 15th September 1992)

Summary

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

For each of the 3 inocula tested, *Melampsora larici-populina* races E1 and E2 and *M. allii-populina*, segregations that occured in qualitative tests cannot be explained with less than 3 genes for susceptibility-resistance. Comparison with EL KARKOURY's results (1991) suggest that race E1 would have another virulence 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.

Key words: 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 Aigeiros and Tacamahaca poplars and their hybrids" (THIELGES, 1985). At least 8 *Melampsora* species can attack poplars, but 3 of them are of major importance: *M. allii-populina* KLEB., *M. larici-populina* KLEB. and *M. medusae* THUM.. Severe damage has been attributed to these pathogens, including growth reduction or even death of plants (WIDIN and SCHIPPER, 1981; STEENACKERS, 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.

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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 17° C to 20° 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.