

nerally revealed a higher genetic variation (diversity and/or heterozygosity). On the other hand, no relationship between aluminium sensitivity and genetic diversity was obtained in studies where the Al-sensitivity of Norway spruce was tested under controlled hydroculture conditions (GEBUREK *et al.* 1986).

Finally these results, although limited to one montane region, demonstrate that genetic changes shall occur in Norway spruce if the sensitive trees (e.g. subsets S) die prior to reproduction or if the reproduction rate of sensitive trees is decreasing (SCHOLZ 1986). Even though the tolerant trees exhibit a generally higher genetic diversity, particular alleles at some loci (e.g. G-6-PDH-A₁, MDH-C₃) and many rare alleles will decrease in frequency and may ultimately be lost. This is true even if the genetic causes for tolerance/sensitivity are associated with other gene loci closely linked to the enzyme loci analysed in this study (hitch-hiking effect).

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Clonal Mixtures, Juvenile-Mature Correlations and Necessary number of Clones*

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Summary

In all fields of forest tree breeding and, therefore, in clonal forestry too, an utilization of juvenile-mature correlations with regard to an improvement of early testing must be of special interest. Both ages ('juvenile' and 'mature') are related with each other. This relation has been described quantitatively by r_E (= juvenile-mature correlation based upon the means of the single clones) and r_M

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(= juvenile-mature correlation based upon the means of mixtures of different clones). If we have $r_M > r_E$ an improvement of the efficiency of early testing may be realized by using mixtures instead of single clones.

In this paper an explicit expression for r_M has been derived, which depends on 7 parameters: $r_M = r_M(n, b, b^*, t, h^2, (h^*)^2, r_E)$ with n = number of clones in the clonal mixture, h^2 and $(h^*)^2$ = heritability at juvenile and mature age respectively, b and b^* = exponents from FAIRFIELD-SMITH'S empirical law for variances at juvenile and mature ages respectively, t = exponent from FAIRFIELD-SMITH'S empirical law for the covariance between juvenile and mature ages. Numerical results obtained by using this r_M -function are given and discussed.

Finally, a useful approximation is derived and discussed, which gives a simple relation between r_M , r_E and n : $n^k = r_M(1-r_E)/r_E(1-r_M)$ with $k = \text{const.}$ This approximation shows a sufficient accuracy for the major part of the interesting parameter intervals, which are relevant for practical applications.

Proceeding from a given r_E and a required numerical level of r_M the necessary number n of clones can be computed numerically by using this relation, if an estimate of k is available. For example, for $k = 1$ and a required numerical level of $r_M = 0.90$ one obtains: $n = 36$ for $r_E = 0.20$, $n = 21$ for $r_E = 0.30$, $n = 14$ for $r_E = 0.40$, $n = 9$ for $r_E = 0.50$ and $n = 6$ for $r_E = 0.60$.

Application of these theoretical results on experimental data of KLEINSCHMIT (1983) for older Norway spruce clonal tests gives an almost perfect fit between the empirical r_M -values and the theoretically expected values.

Very rough summarized conclusion: The necessary clone numbers for clonal mixtures are in the tens rather than just a few clones and rather than in the hundreds.

Key words: Clonal mixtures; juvenile-mature correlation; early testing; number of clones; juvenile selection; tree breeding.

Zusammenfassung

In allen Bereichen der Forstpflanzenzüchtung und daher natürlich auch beim Arbeiten mit Klonen, kommt der Ausnutzung von Jugend-Alters-Korrelationen eine besondere Bedeutung hinsichtlich einer Verbesserung der Frühselektionsmöglichkeiten zu. Beide Zeitpunkte ('Jugend' und 'Alter') stehen in Beziehung zueinander, und diese Beziehung wird quantitativ beschrieben durch r_E (= Jugend-Alters-Korrelation auf der Basis der Mittelwerte der einzelnen Klone) und r_M (= Jugend-Alters-Korrelation auf der Basis der Mittelwerte von Klonmischungen aus verschiedenen Klone). Falls $r_M > r_E$ ist, kann eine Verbesserung der Effizienz einer Frühselektion durch die Verwendung von Mischungen anstelle von Einzelklonen erreicht werden.

In der vorliegenden Arbeit wird ein expliziter Ausdruck für r_M abgeleitet, der von sieben Parametern abhängt: $r_M = r_M(n, b, b^*, t, h^2, (h^*)^2, r_E)$ mit n = Anzahl Klone in der Klonmischung, h^2 und $(h^*)^2$ = Heritabilität zum Jugend- bzw. Alterszeitpunkt, b und b^* = Exponenten aus „FAIRFIELD-SMITH's empirical law“ für Varianzen zum Jugend- bzw. Alterszeitpunkt, t = Exponent aus „FAIRFIELD-SMITH's empirical law“ für die Kovarianz zwischen Jugend und Alter. Numerische Ergebnisse unter Anwendung dieser r_M -Funktion werden berechnet und diskutiert.

Abschließend wird eine nützliche Approximation abgeleitet und diskutiert, die eine einfache Relation zwischen r_M , r_E und n angibt: $n^k = r_M(1-r_E)/r_E(1-r_M)$ mit $k = \text{const.}$ Diese Approximation weist eine ausreichende Genauigkeit für den größten Teil der interessierenden Parameterintervalle, die für praktische Anwendungen in Frage kommen, auf.

Geht man von einem gegebenen r_E und einer bestimmten, geforderten numerischen Höhe für r_M aus, kann die notwendige Anzahl n von Klone unter Verwendung dieser Relation numerisch berechnet werden, falls ein Schätzwert für k zur Verfügung steht, z. B.: Für $k = 1$ und eine geforderte numerische Höhe von $r_M = 0,90$ erhält man: $n = 36$ für $r_E = 0,20$; $n = 21$ für $r_E = 0,30$; $n = 14$ für $r_E = 0,40$; $n = 9$ für $r_E = 0,50$ und $n = 6$ für $r_E = 0,60$.

Die Anwendung dieser theoretischen Resultate auf experimentelle Daten von KLEINSCHMIT (1983) für ältere Fichten-Klonprüfungen zeigt eine beinahe perfekte Übereinstimmung zwischen den empirischen r_M -Werten und den theoretisch erwarteten Werten.

Sehr grobe, zusammenfassende Schlussfolgerung: Die notwendigen Anzahlen von Klone für Klonmischungen liegen eher in 10er Größenordnungen als bei einigen wenigen Klone oder in 100er Größenordnungen.

Introduction

An increasing interest in clonal forestry and essential improvements of methods of vegetative propagation lead to intensive breeding work of multiclonal varieties.

The aim of this paper is to give some theoretical approaches and numerical results concerning the necessary number of clones in clonal mixtures with regard to juvenile-mature correlations.

Relations between the juvenile-mature correlations of clonal mixtures and their number of clones can be simply described quantitatively and conclusions can be derived.

If we denote the juvenile-mature correlation based upon the values of the single clones (= clone means at juvenile and mature ages) by r_E , then we may ask whether or not a low r_E can be increased by using mixtures of clones. Introducing r_M = juvenile-mature correlation based upon the means of mixtures of different clones we usually will have $r_M > r_E$. Furthermore, r_M will increase with an increasing number of clones in the clonal mixtures.

If we have $r_M > r_E$, an increase of the juvenile-mature correlation and, therefore, an improvement of the efficiency of early testing can be obtained by using mixtures instead of single clones. But, what are the necessary numbers of clones, so that r_M will be sufficiently high to enable an early selection of such clonal mixtures with a sufficient precision and efficiency? For a given request according to the numerical value of this correlation conclusions on the necessary number of clones in clonal mixtures can be derived. In a previous paper (HUEHN 1986c) the relation between r_M and r_E has been studied theoretically. Additionally, numerical results on the necessary number of clones in clonal mixtures have been obtained by the statistical condition of a significant difference between r_E and r_M for a given numerical value of r_M .

These investigations can be completed and extended in different ways. One such extension shall be discussed in this paper: The main purpose of this contribution is to give an explicit expression for the function $r_M = r_M(n)$ with n = number of clones in the clonal mixture. For any given required numerical value of r_M this equation $r_M = r_M(n)$ can be solved for n .

Additionally, experimental results on clonal tests of Norway spruce shall be reported, which are in complete agreement with these theoretical results.

Experimental results

Experimental results for juvenile-mature correlations of clonal mixtures with regard to the number of clones in the clonal mixture are given by KLEINSCHMIT (1983) for older Norway spruce clonal tests.

To see how the correlations change groups of clones of different size have been formed (1–100 clones). By this procedure the genetic variance slowly increases within the groups and the expected gain between groups decreases. The correlations between ages 3 and 12 of 0.30 using single clones increase very rapidly if the group size increases: 0.80 with groups of 10 clones, 0.90 with groups of 20 clones, 0.95 with groups of 50 clones, 0.99 with 65 clones and 1.00 for groups of 100 clones.

Simultaneously, the differences in height between the group means and therefore the gain decrease. However, this gain can be realized at an early stage if the correlations are sufficiently high. In this experimental study the juvenile-mature correlation reaches an approximate constant value for groups of 20–30 clones. Increasing this number results in no further significant changes of the correlation.

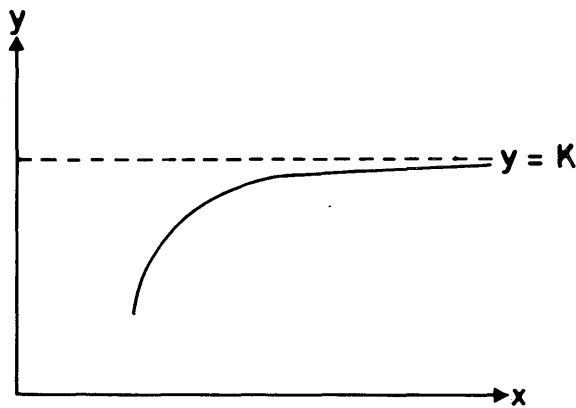


Figure 1. — Graph of a saturation curve $y = y(x)$ with asymptote $y = K$.

For further information concerning the experimental material and the numerical results of the correlation study we refer to KLEINSCHMIT (1983) and HUEHN and KLEINSCHMIT (1986).

Theoretical investigations

For all following theoretical investigations we assume equal proportions of the clones in the clonal mixture.

Additionally, all theoretical studies are based on a certain, given time interval from time T_1 (= defined as 'juvenile age') until time T_2 (= defined as 'mature age'). No discussion shall be performed here concerning the optimal place of these ages T_1 and T_2 . Extended experimental and theoretical studies on the question "What is the optimum selection age?" have been published in the literature: See, for example, the recent paper of KANG (1985). But here, both ages shall be given and they are related with each other, where this relation shall be described quantitatively by r_E and r_M . For increasing n the correlation r_M tends to $r_M = 1$ asymptotically. Therefore, the function $r_M = r_M(n)$ must be of the form sketched in Figure 1.

Many such specific saturation curves are known from the literature. In many biological applications there have been found an extensive experimental evidence which indicates that many factor effects can be described very well by an expression similar in form to the MICHAELIS-MENTEN equation of enzyme chemistry:

$$y = K \cdot \frac{cx}{1+cx}, \quad c = \text{const} \quad (1)$$

If we identify:

$$y \rightarrow r_M$$

$$x \rightarrow n$$

$$K \rightarrow 1$$

$$\text{we obtain: } r_M = \frac{cn}{1+cn} \quad (2)$$

Thus we have a hyperbolic relationship between r_M and n . For $n = 1$ the correlation r_M equals r_E and (2) gives: $c = r_E / (1 - r_E)$. Combining this expression for c with (2) leads to:

$$r_M = \frac{nr_E}{1+(n-1)r_E} \quad (3)$$

For a given, required numerical value of r_M the necessary clone numbers n can be calculated by using (3):

$$n = \frac{r_M(1-r_E)}{r_E(1-r_M)} \quad (4)$$

Application of (3) to the experimental results of KLEINSCHMIT (1983) (see: chapter 'experimental results') gives the results of Table 1.

Thus, we get an almost perfect fit between the empirical r_M -values and the theoretically expected values calculated by (3).

Equation (3) has been obtained by no exact derivations. Heuristic considerations and analogy to saturation-curves from other scientific fields gave rise to (3). Such a poor motivation of an explicit formula used for estimation purposes must be very unsatisfactory. Therefore, we will present some more convincing considerations and plausible reasons leading to (3).

$r_M = r_M(n)$ is, of course, a discontinuous function, where the admissible values of n are only integers. But, for theoretical investigations such terms are usually confined to the continuous case.

We denote:

$x_{ij} + \epsilon_{ij}$ = phenotypic pure stand mean of clone j from mixture i at juvenile age, where x_{ij} = 'true' pure stand value of clone j from mixture i at juvenile age and ϵ_{ij} = random deviation from this 'true' value.

$x_{ij}^* + \epsilon_{ij}^*$ = phenotypic pure stand mean of clone j from mixture i at mature age, where x_{ij}^* = 'true' pure stand value of clone j from mixture i at mature age and ϵ_{ij}^* = random deviation from this 'true' value.

Now, we consider groups of n clones = clonal mixtures. All these clonal mixtures shall be composed with equal proportions of the n clones.

Under the simplifying assumption of no significant mixing effects the means of these clonal mixtures can be expressed as:

$$y_i = \frac{1}{n} \sum_{j=1}^n (x_{ij} + \epsilon_{ij}) = \frac{1}{n} \sum_{j=1}^n x_{ij} + \frac{1}{n} \sum_{j=1}^n \epsilon_{ij} = \bar{x}_i + \bar{\epsilon}_i$$

= phenotypic mean of mixture i at juvenile age, where the summation is over those clones j , which are included in the clonal mixture i .

$$y_i^* = \frac{1}{n} \sum_{j=1}^n (x_{ij}^* + \epsilon_{ij}^*) = \frac{1}{n} \sum_{j=1}^n x_{ij}^* + \frac{1}{n} \sum_{j=1}^n \epsilon_{ij}^* = \bar{x}_i^* + \bar{\epsilon}_i^*$$

= phenotypic mean of mixture i at mature age, where the summation is over those clones j , which are included in the clonal mixture i .

Table 1. — Empirical r_M -values (KLEINSCHMIT 1983) and theoretical estimates of r_M for different clone numbers n .

n	empirical r_M -values	estimates of r_M (by (3))
1	0.31	0.31
10	0.81	0.82
20	0.91	0.90
50	0.95	0.96
65	0.99	0.97
100	1.00	0.98

For the juvenile-mature correlation r_M based upon the means of clonal mixtures we obtain:

$$r_M = \frac{\text{Cov}(y_i, y_i^*)}{\sqrt{V(y_i) \cdot V(y_i^*)}} = \frac{\text{Cov}(\bar{x}_i + \bar{\epsilon}_i, \bar{x}_i^* + \bar{\epsilon}_i^*)}{\sqrt{V(\bar{x}_i + \bar{\epsilon}_i) \cdot V(\bar{x}_i^* + \bar{\epsilon}_i^*)}} \quad (5)$$

$$= \frac{\text{Cov}(\bar{x}_i, \bar{x}_i^*) + \text{Cov}(\bar{x}_i, \bar{\epsilon}_i^*) + \text{Cov}(\bar{\epsilon}_i, \bar{x}_i^*) + \text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)}{\sqrt{[V(\bar{x}_i) + V(\bar{\epsilon}_i) + 2\text{Cov}(\bar{x}_i, \bar{\epsilon}_i)] [V(\bar{x}_i^*) + V(\bar{\epsilon}_i^*) + 2\text{Cov}(\bar{x}_i^*, \bar{\epsilon}_i^*)]}} \quad (5)$$

We now assume that the 'true' values and the random deviations are uncorrelated:

$$\text{Cov}(\bar{x}_i, \bar{\epsilon}_i^*) = \text{Cov}(\bar{\epsilon}_i, \bar{x}_i^*) = \text{Cov}(\bar{x}_i, \bar{\epsilon}_i) = \text{Cov}(\bar{x}_i^*, \bar{\epsilon}_i^*) = 0 \quad (6)$$

Combining (5) and (6) gives:

$$r_M = \frac{\text{Cov}(\bar{x}_i, \bar{x}_i^*) + \text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)}{\sqrt{[V(\bar{x}_i) + V(\bar{\epsilon}_i)] [V(\bar{x}_i^*) + V(\bar{\epsilon}_i^*)]}} \quad (7)$$

We introduce parameters λ and λ^* by the definition:

$$\left. \begin{aligned} V(\bar{x}_i) + V(\bar{\epsilon}_i) &= \lambda V(\bar{x}_i) \text{ or } \lambda = 1 + \frac{V(\bar{\epsilon}_i)}{V(\bar{x}_i)} \\ V(\bar{x}_i^*) + V(\bar{\epsilon}_i^*) &= \lambda^* V(\bar{x}_i^*) \text{ or } \lambda^* = 1 + \frac{V(\bar{\epsilon}_i^*)}{V(\bar{x}_i^*)} \end{aligned} \right\} \quad (8)$$

Using λ and λ^* equation (7) can be rewritten as:

$$r_M = \frac{1}{\sqrt{\lambda \lambda^*}} \cdot \frac{\text{Cov}(\bar{x}_i, \bar{x}_i^*) + \text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)}{\sqrt{V(\bar{x}_i) \cdot V(\bar{x}_i^*)}} \quad (9)$$

The 'true' values of the individual clones which are included in the clonal mixtures, of course, must be independent. Furthermore, the values of different clones at juvenile and mature ages are uncorrelated. Thus we have:

$$\left. \begin{aligned} \text{Cov}(\bar{x}_i, \bar{x}_i^*) &= \frac{1}{n} \text{Cov}(x_{ij}, x_{ij}^*) \\ V(\bar{x}_i) &= \frac{1}{n} V(x_{ij}) \text{ and } V(\bar{x}_i^*) = \frac{1}{n} V(x_{ij}^*) \end{aligned} \right\} \quad (10)$$

(9) together with (10) leads to:

$$r_M = \frac{1}{\sqrt{\lambda \lambda^*}} \cdot \frac{\text{Cov}(x_{ij}, x_{ij}^*) + n \text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)}{\sqrt{V(x_{ij}) V(x_{ij}^*)}} \quad (11)$$

A low juvenile value shall imply a low mature value and vice versa. For this relationship we assume linearity. All deviations from this linear relation are defined and interpreted as random deviations. This implies a maximal correlation between the 'true' values x_{ij} and x_{ij}^* . This comment applied to (11) gives:

$$r_M = \frac{1}{\sqrt{\lambda \lambda^*}} + \frac{n \text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)}{\sqrt{\lambda \lambda^*} \cdot \sqrt{V(x_{ij}) V(x_{ij}^*)}} \quad (12)$$

The random deviations ϵ_{ij} of the individual clones, which are included in the same clonal mixture, of course, are *not* independent: The clonal mixture occupies a limited area and the individual clones of this mixture are more or less neighbouring on this area. Thus, we may have many causes of non-independence, for example:

- positive correlation because of a reduced environmental heterogeneity (homogeneity of soil, climate etc.),
- negative correlation caused by competitive effects,
- dependencies by similar exposures to epidemics and diseases,

d. similar effects to the individual clones with regard to many other biotic and abiotic causes like attack of insects, environmental stresses etc.

FAIRFIELD-SMITH (1938) proposed a method, often called 'the Heterogeneity Index Method', for determining optimum plot size from uniformity-trial data. He expressed the empirical relationship of plot size and plot variance as $V_x = V_1/x^b$ where V_x = the variance (calculated on a per unit basis) of the yield per unit area among plots of x units in size, V_1 = the variance among plots of one unit in size, b = an index of soil variability; a measure of the correlation among adjacent basic units, and x = the number of basic units per plot. The index of soil heterogeneity, b , measures these dependencies quantitatively ($b = 1$ indicates the case of independence). This „empirical law of FAIRFIELD-SMITH“ has been developed originally for the consideration of soil heterogeneity. But, this relation has been often applied in very different investigations with very different causes of non-independence (see, for example: GHOSH (1949); WHITTLE (1956); SHRIKHANDE (1957); MATERN (1960); FREEMAN (1963); SAKAI and HATAKEYAMA (1963); LECLERC (1966); HUEHN (1970); NAMKOONG and SQUILLACE (1970); HUEHN (1975); HUEHN (1977)).

If we apply "FAIRFIELD-SMITH's empirical law" to $V(\bar{\epsilon}_i)$ and $V(\bar{\epsilon}_i^*)$ we may write:

$$V(\bar{\epsilon}_i) = \frac{V(\epsilon_{ij})}{n^b} \text{ and } V(\bar{\epsilon}_i^*) = \frac{V(\epsilon_{ij}^*)}{n^{b^*}} \quad (13)$$

For independent ϵ_{ij} 's and ϵ_{ij}^* 's we have: $b = b^* = 1$. Because of the increased similarity of the dependent ϵ_{ij} and ϵ_{ij}^* of the different clones j belonging to the same mixture i we must expect $b > 1$ and $b^* > 1$.

Several theoretical studies and numerical applications are available (HUEHN 1977 and HUEHN 1979) demonstrating that "FAIRFIELD-SMITH's empirical law" can be applied not only to variances, but to covariances too. It is approximately valid for covariances for the most interesting situations occurring in practical applications. Thus we have:

$$\text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*) = \frac{\text{Cov}(\epsilon_{ij}, \epsilon_{ij}^*)}{n^t} \quad (14)$$

For the same reasons as mentioned above for the case of variances, we may assume $t > 1$.

Applying (13) and (14) the r_M -expression (12) can be expressed in a more appropriate form:

$$r_M = \frac{1}{\sqrt{\lambda \lambda^*}} + \frac{n^{1-t}}{\sqrt{\lambda \lambda^*}} \cdot \frac{\text{Cov}(\epsilon_{ij}, \epsilon_{ij}^*)}{\sqrt{V(x_{ij}) V(x_{ij}^*)}} \quad (15)$$

where

$$\left. \begin{aligned} \lambda &= \lambda(n) = \frac{V(x_{ij}) + n^{1-b} \cdot V(\epsilon_{ij})}{V(x_{ij})} \\ \lambda^* &= \lambda^*(n) = \frac{V(x_{ij}^*) + n^{1-b^*} \cdot V(\epsilon_{ij}^*)}{V(x_{ij}^*)} \end{aligned} \right\} \quad (16)$$

For $n = 1$ we have $r_M = r_E$ and (15) together with (16) gives:

$$r_E = \frac{1}{\sqrt{\lambda(1) \lambda^*(1)}} + \frac{1}{\sqrt{\lambda(1) \lambda^*(1)}} \cdot \frac{\text{Cov}(\epsilon_{ij}, \epsilon_{ij}^*)}{\sqrt{V(x_{ij}) V(x_{ij}^*)}} \quad (17)$$

where

$$\left. \begin{aligned} \lambda(1) &= \frac{V(x_{ij}) + V(e_{ij})}{V(x_{ij})} = \frac{1}{h^2} \text{ and} \\ \lambda^*(1) &= \frac{V(x_{ij}^*) + V(e_{ij}^*)}{V(x_{ij}^*)} = \frac{1}{(h^*)^2} \end{aligned} \right\} \quad (18)$$

where

h^2 = heritability at juvenile age,

$(h^*)^2$ = heritability at mature age, since

x_{ij} = clone mean (= estimate of the genotypic value) at juvenile age and x_{ij}^* = clone mean (= estimate of the genotypic value) at mature age.

(17) together with (18):

$$\frac{r_E}{hh^*} - 1 = \frac{\text{Cov}(e_{ij}, e_{ij}^*)}{\sqrt{V(x_{ij})V(x_{ij}^*)}} \quad (19)$$

Combination of (15) and (19) leads to:

$$r_M = \frac{1 + \frac{r_E}{hh^*} (n^{1-t} - 1)}{\sqrt{\lambda\lambda^*}} \quad (20)$$

λ and λ^* can be expressed in the following way:

$$\left. \begin{aligned} \lambda(n) &= 1 + \frac{1-h^2}{h^2} \cdot n^{1-b} \\ \lambda^*(n) &= 1 + \frac{1-(h^*)^2}{(h^*)^2} \cdot n^{1-b^*} \end{aligned} \right\} \quad (21)$$

The correlation r_M , therefore, depends on the seven parameters n , b , b^* , t , h^2 , $(h^*)^2$ and r_E :

$$r_M = \frac{1 + \left(\frac{r_E}{hh^*} - 1\right) \cdot n^{1-t}}{\sqrt{\left(1 + \frac{1-h^2}{h^2} \cdot n^{1-b}\right) \left(1 + \frac{1-(h^*)^2}{(h^*)^2} \cdot n^{1-b^*}\right)}} \quad (22)$$

Because of $t > 1$, $b > 1$ and $b^* > 1$ we obtain the asymptotic property:

$$\lim_{n \rightarrow \infty} r_M = 1.$$

To reduce the computational work of the numerical calculations some simplifications have been assumed:

- The heritability is assumed to be constant for both ages: $h^2 = (h^*)^2$ (see KANG (1985)).
- For r_E we use: $r_E = 0.30$ (see: KLEINSCHMIT (1983) and LAMBETH (1980)).
- Equal exponents from FAIRFIELD-SMITH'S empirical law for variances and covariances: $b = b^* = t$ (see: 'Discussion').

For this numerically restricted situation r_M depends on the three parameters n , b and h^2 (for each given r_E):

$$r_M = \frac{1 + \frac{r_E - h^2}{h^2} \cdot n^{1-b}}{1 + \frac{1-h^2}{h^2} \cdot n^{1-b}} \quad (23)$$

Because of $b > 1$ we have: $\lim_{n \rightarrow \infty} r_M = 1$.

Some numerical results are presented in Table 2.

For each given b and each h^2 the functions $r_M = r_M(n)$ are saturation curves like (2) or (3) — starting with $r_M = 0.30$ for $n = 1$. The asymptotic level for large n increases

- with increasing b (for each given h^2) and
- with increasing h^2 (for each given b).

For further results of these numerical calculations we refer to Table 2

Finally, an interesting approximation of (23) shall be discussed. (23) gives:

Table 2. — Numerical values of r_M (calculated by (23)) for different values of n , h^2 and b for $r_E = 0.30$.

n	b = 1.3			b = 1.5			b = 1.7			b = 1.9		
	h ² = 0.4	h ² = 0.6	h ² = 0.8	h ² = 0.4	h ² = 0.6	h ² = 0.8	h ² = 0.4	h ² = 0.6	h ² = 0.8	h ² = 0.4	h ² = 0.6	h ² = 0.8
1	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30
3	0.39	0.43	0.47	0.46	0.51	0.56	0.52	0.59	0.64	0.58	0.65	0.70
5	0.44	0.49	0.53	0.53	0.60	0.65	0.62	0.69	0.74	0.70	0.76	0.81
7	0.47	0.53	0.57	0.58	0.65	0.70	0.68	0.74	0.79	0.76	0.82	0.85
9	0.49	0.55	0.60	0.61	0.68	0.73	0.72	0.78	0.82	0.80	0.85	0.88
11	0.51	0.57	0.62	0.64	0.71	0.75	0.74	0.81	0.84	0.83	0.87	0.90
13	0.52	0.59	0.64	0.66	0.73	0.77	0.77	0.83	0.86	0.85	0.89	0.92
15	0.53	0.60	0.65	0.67	0.74	0.79	0.79	0.84	0.87	0.86	0.90	0.93
20	0.56	0.63	0.68	0.71	0.77	0.81	0.82	0.87	0.90	0.89	0.92	0.94
30	0.59	0.66	0.71	0.75	0.81	0.85	0.86	0.90	0.92	0.92	0.95	0.96
40	0.61	0.68	0.73	0.78	0.83	0.87	0.88	0.92	0.93	0.94	0.96	0.97
50	0.63	0.70	0.75	0.80	0.85	0.88	0.90	0.93	0.94	0.95	0.97	0.97
75	0.66	0.73	0.78	0.83	0.87	0.90	0.92	0.94	0.96	0.97	0.98	0.98
100	0.68	0.75	0.79	0.85	0.89	0.91	0.93	0.95	0.97	0.97	0.98	0.99
125	0.70	0.76	0.81	0.86	0.90	0.92	0.94	0.96	0.97	0.98	0.98	0.99
150	0.71	0.77	0.82	0.87	0.91	0.93	0.95	0.97	0.97	0.98	0.99	0.99
175	0.72	0.78	0.82	0.88	0.92	0.94	0.95	0.97	0.98	0.98	0.99	0.99
200	0.73	0.79	0.83	0.89	0.92	0.94	0.96	0.97	0.98	0.99	0.99	0.99

Table 3. — Numerical values of the remainder Δ (from (24)) for different values of n , h^2 and b for $r_E = 0.30$.

n	h^2	b = 1.3			b = 1.5			b = 1.7			b = 1.9		
		0.4	0.6	0.8	0.4	0.6	0.8	0.4	0.6	0.8	0.4	0.6	0.8
1		0.10	0.30	0.50	0.10	0.30	0.50	0.10	0.30	0.50	0.10	0.30	0.50
3		0.09	0.24	0.38	0.08	0.21	0.32	0.07	0.18	0.26	0.06	0.15	0.21
5		0.08	0.22	0.33	0.07	0.17	0.25	0.05	0.13	0.19	0.04	0.10	0.14
7		0.08	0.20	0.31	0.06	0.15	0.22	0.05	0.11	0.15	0.03	0.08	0.10
9		0.07	0.19	0.29	0.06	0.14	0.19	0.04	0.09	0.13	0.03	0.06	0.08
11		0.07	0.18	0.27	0.05	0.13	0.18	0.04	0.08	0.11	0.02	0.05	0.07
13		0.07	0.18	0.26	0.05	0.12	0.16	0.03	0.07	0.10	0.02	0.05	0.06
15		0.07	0.17	0.25	0.05	0.11	0.15	0.03	0.07	0.09	0.02	0.04	0.05
20		0.06	0.16	0.23	0.04	0.10	0.13	0.03	0.06	0.07	0.02	0.03	0.04
30		0.06	0.15	0.21	0.04	0.08	0.11	0.02	0.04	0.06	0.01	0.02	0.03
40		0.06	0.14	0.19	0.03	0.07	0.09	0.02	0.04	0.05	0.01	0.02	0.02
50		0.05	0.13	0.18	0.03	0.06	0.09	0.01	0.03	0.04	0.01	0.01	0.02
75		0.05	0.12	0.16	0.02	0.05	0.07	0.01	0.02	0.03	0.00	0.01	0.01
100		0.05	0.11	0.15	0.02	0.05	0.06	0.01	0.02	0.02	0.00	0.01	0.01
125		0.04	0.10	0.14	0.02	0.04	0.05	0.01	0.02	0.02	0.00	0.01	0.01
150		0.04	0.10	0.13	0.02	0.04	0.05	0.01	0.01	0.02	0.00	0.01	0.01
175		0.04	0.09	0.13	0.02	0.04	0.05	0.01	0.01	0.02	0.00	0.00	0.01
200		0.04	0.09	0.12	0.02	0.03	0.04	0.01	0.01	0.02	0.00	0.00	0.01

$$r_M = \frac{1}{1 + \frac{1-h^2}{h^2} \cdot n^{1-b}} - \frac{\frac{-r_E+h^2}{h^2} \cdot n^{1-b}}{1 + \frac{1-h^2}{h^2} \cdot n^{1-b}} \quad (24)$$

$= \Delta$

Δ has been calculated numerically and some results are presented in Table 3.

For $n > 1$ the term Δ decreases

1. with decreasing h^2 (for each given b and each n),
 2. with increasing b (for each given h^2 and each n) and
 3. with increasing n (for each given b and each h^2).
- In common practical applications the heritability estimates will be medium or low and the clone numbers shall be not too small. Therefore, $10 < n \leq 200$ and $h^2 = 0.4$ will indicate realistic situations. From Table 3 we obtain:

$$\left. \begin{array}{l} 0.04 \leq \Delta \leq 0.07 \text{ for } b = 1.3 \\ 0.02 \leq \Delta \leq 0.05 \text{ for } b = 1.5 \\ 0.01 \leq \Delta \leq 0.04 \text{ for } b = 1.7 \\ 0.00 \leq \Delta \leq 0.02 \text{ for } b = 1.9 \end{array} \right\} \text{ for } h^2 = 0.4$$

But, even for $h^2 = 0.6$ the terms Δ are relatively small:

$$\left. \begin{array}{l} 0.09 \leq \Delta \leq 0.18 \text{ for } b = 1.3 \\ 0.03 \leq \Delta \leq 0.13 \text{ for } b = 1.5 \\ 0.01 \leq \Delta \leq 0.08 \text{ for } b = 1.7 \\ 0.00 \leq \Delta \leq 0.05 \text{ for } b = 1.9 \end{array} \right\} \text{ for } h^2 = 0.6$$

Thus we may conclude:

In a wide range of parameter values relevant for practical applications the term Δ in (24) is sufficiently small (see: Table 3). Therefore, in these situations Δ can be neglected and r_M can be approximated by

$$r_M = \frac{1}{1 + \frac{1-h^2}{h^2} \cdot n^{1-b}} \quad (25)$$

From (25) we obtain:

$$\frac{1-r_M}{r_M} = \frac{1-h^2}{h^2} \cdot n^{1-b} = \frac{1-h^2}{h^2} \cdot \left(\frac{1}{n}\right)^{b-1} \quad (26)$$

If we denote $k = b - 1$ relation (26) can be expressed as:

Table 4. — Necessary numbers n of clones in clonal mixtures (estimated by (29)) for different numerical values of r_E and r_M and different k 's.

r_E	k	$r_M = 0.70$							$r_M = 0.80$							$r_M = 0.90$						
		0.6	1.0	1.4	1.8	2.2	2.6	3.0	0.6	1.0	1.4	1.8	2.2	2.6	3.0	0.6	1.0	1.4	1.8	2.2	2.6	3.0
0.10		160	21	9	6	4	4	3	393	36	13	8	6	4	4	1517	81	24	12	8	6	5
0.20		42	10	5	4	3	3	3	102	16	8	5	4	3	3	393	36	13	8	6	4	4
0.30		17	6	4	3	3	2	2	42	10	5	4	3	3	3	160	21	9	6	4	4	3
0.40		9	4	3	3	2	2	2	20	6	4	3	3	2	2	77	14	7	5	4	3	3
0.50		5	3	2	2	2	2	2	11	4	3	3	2	2	2	39	9	5	4	3	3	3
0.60		3	2	2	2	2	2	2	6	3	3	2	2	2	2	20	6	4	3	3	2	2

$$n^k \sim \frac{r_M}{1-r_M} \quad (27)$$

where the sign \sim means 'is proportional to'. (27) gives:

$$n^k = w \cdot \frac{r_M}{1-r_M}, w = \text{const} \quad (28)$$

Compared to the approximation (25) this constant w must be equal to $1-h^2/h^2$. But here, another estimate for w should be used: The condition " $r_M = r_E$ for $n = 1$ " is valid for the general r_M -formula (22) and, of course, for its specialization (23) too. But, this condition is not valid for the approximation (25). But here, the approximation (25) will be used as an explicit formula for $r_M = r_M(n)$. Therefore, w should be chosen to fit the condition: $r_M = r_E$ for $n = 1$. This leads to $w = 1-r_E/r_E$. Combining this w -value with (28) gives:

$$n^k = \frac{r_M(1-r_E)}{r_E(1-r_M)} \text{ or } n = \sqrt[k]{\frac{r_M(1-r_E)}{r_E(1-r_M)}} \quad (29)$$

For $k = 1$ these expressions (29) reduce to the previous formula (4), which have been introduced there by means of analogy.

If we proceed from experimental data of r_M and n the parameter k may be estimated by least squares principle:

$$\hat{k} = \frac{\sum_n (\log \frac{r_M(1-r_E)}{r_E(1-r_M)}) (\log n)}{\sum_n (\log n)^2} \quad (30)$$

Application of (30) to the data of KLEINSCHMIT (1983) from Table 1 gives $\hat{k} = 1.1$. Therefore, the simplification $k = 1$ seems to be a sufficient approximation.

Numerical calculations shall be given using the general formula (29).

Numerical results

Some selected numerical results for the necessary number n of clones in clonal mixtures (estimated by (29)) are presented in Table 4 — for different numerical values of r_E and r_M and for different k 's. These numerical results of Table 4 demonstrate the strong influence of the parameter k on the resulting clone numbers. There is some experimental evidence that k will be numerically nearby 1. For $0.6 \leq k \leq 1.4$ and a required numerical level of $r_M = 0.90$ we obtain:

$$\begin{aligned} 13 \leq n \leq 393 & \text{ for } r_E = 0.20 \\ 9 \leq n \leq 160 & \text{ for } r_E = 0.30 \\ 7 \leq n \leq 77 & \text{ for } r_E = 0.40 \\ 5 \leq n \leq 39 & \text{ for } r_E = 0.50 \\ 4 \leq n \leq 20 & \text{ for } r_E = 0.60 \end{aligned}$$

In spite of this very strong restriction ($0.6 \leq k \leq 1.4$) of the admissible k -values the range of n for varying k turns out to be very enlarged. For practical applications, therefore, the unknown k will be a considerable disadvantage. k , of course, can be easily determined in different ways, for example:

1. By giving r_M for an arbitrary n with $n \neq 1$. Here, the use of binary mixtures with $n = 2$ will be of special interest.
2. By assuming an additional condition on n , r_E and r_M . But, no further discussion on the estimation of k shall be given in this paper.

To characterize the approximate numerical magnitude of necessary clone numbers in clonal mixtures, which may be relevant for practical applications, we assume $k = 1$ and a

required numerical level of $r_M = 0.90$. From Table 4 we obtain:

$$\begin{aligned} n &= 36 \text{ for } r_E = 0.20 \\ n &= 21 \text{ for } r_E = 0.30 \\ n &= 14 \text{ for } r_E = 0.40 \\ n &= 9 \text{ for } r_E = 0.50 \\ n &= 6 \text{ for } r_E = 0.60 \end{aligned}$$

Thus, for the data of KLEINSCHMIT (1983) with $r_E = 0.30$ we may conclude a theoretically expected necessary number of 21 clones.

Discussion

Only one rotation time from the initial composition of the mixture until the final harvest has been considered.

All theoretical studies are based on a certain, given time interval from time T_1 (= defined as 'juvenile age') (for example, time of the initial composition of the mixture or a given number of years later) until time T_2 (= defined as 'mature age') (for example, time of final harvest or a given number of years earlier). No discussion shall be performed in this paper concerning the optimal times T_1 and T_2 . But, of course, that's one of the main problems in dealing with juvenile-mature correlations and procedures of early testing. "Since much of the material can only be propagated in the juvenile state, test material must be evaluated early enough so that the donors can still be propagated with a degree of success and good future development. But, the earlier the evaluations are made, the greater the risk that these selections will not maintain their superiority at the end of their rotation" (RAUTER 1982). In a recent paper on this topic (KANG 1985) detailed theoretical investigations have been published. It was concluded that extremely early selection time such as earlier than 1/3 of rotation age should be used with caution.

But here, the interval from T_1 to T_2 shall be assumed to be given and fixed. Both ages are related with each other. This relation has been described quantitatively by r_E (= juvenile-mature correlation based upon the means of the single clones) and r_M (= juvenile-mature correlation based upon the means of mixtures of different clones). If we have $r_M > r_E$ an improvement of the efficiency of early testing can be realized by using mixtures instead of single clones. Therefore, relations between r_M and r_E and the explicit expression of $r_M = r_M(n)$ must be of special interest.

In this paper $r_M = r_M(n)$ has been derived explicitly by using several simplifying assumptions — for example FAIRFIELD-SMITH'S empirical law for variances and covariances. This lengthy proof can be abbreviated markedly by proceeding from some plausible assumptions of proportionality:

Approach I

r_M increases with increasing n . This increase $\frac{dr_M}{dn}$ expressed as a fraction of r_M leads to $\frac{1}{r_M} \frac{dr_M}{dn}$ which, therefore, is the rate of increase of r_M . For this rate of increase we assume:

a) rate $\sim 1 - r_M$.

This relation states: The rate of increase of r_M shall be the larger, the more r_M deviates from its limiting value $r_M = 1$.

b) rate $\sim \frac{1}{n}$.

That means: The rate of increase of r_M shall be the lower, the larger the clone number n .

Both assumptions can be combined by the condition: rate $\sim \frac{1-r_M}{n}$. This leads to:

$$\frac{1}{r_M} \frac{dr_M}{dn} = k \cdot \frac{1-r_M}{n}, \quad k = \text{const} \quad (31)$$

(31) can be rewritten in the following form:

$$\frac{dr_M}{r_M(1-r_M)} = \left(\frac{1}{r_M} + \frac{1}{1-r_M} \right) dr_M = k \cdot \frac{dn}{n} \quad (32)$$

This expression (32) can be integrated directly:

$$\ln \frac{r_M}{1-r_M} = \ln n^k + C \quad (33)$$

This arbitrary integration constant C can be chosen to fit the condition: $r_M = r_E$ for $n = 1$. This leads to: $C =$

$$\ln \frac{r_E}{1-r_E}. \text{ From (33) we obtain:}$$

$$n = \sqrt[k]{\frac{r_M(1-r_E)}{r_E(1-r_M)}} \quad (34)$$

For $k = 1$ this expression (34) reduces to the previous formula (4), which have been introduced there by means of analogy. This derivation of the n -formula proceeds from assumptions on the rate of increase of r_M . Another, very simple derivation of (4) may be obtained, if we start from a plausible assumption on r_M itself:

Approach II

The deviation of a certain r_M from its limiting value $r_M = 1$ expressed as a fraction of r_M must be the lower the larger the clone number n . If we assume

$$\frac{1-r_M}{r_M} \sim \frac{1}{n} \quad (35)$$

this relation (35) can be expressed as:

$$\frac{1-r_M}{r_M} = f \cdot \frac{1}{n}, \quad f = \text{const} \quad (36)$$

f can be chosen to fit the condition: $r_M = r_E$ for $n = 1$. This leads to $f = 1-r_E/r_E$. Combining this f -value with (36) gives:

$$n = \frac{r_M(1-r_E)}{r_E(1-r_M)} \quad (37)$$

(37) is a special case of (34).

Both approaches of estimating n

- I. using the rate of increase of r_M and
- II. using r_M itself

are based upon assumptions of proportionality:

$$\left. \begin{array}{l} \text{rate} \sim 1-r_M \text{ and } \text{rate} \sim \frac{1}{n} \\ \text{or combined to: } \text{rate} \sim \frac{1-r_M}{n} \\ 1-r_M/r_M \sim \frac{1}{n} \end{array} \right\} \begin{array}{l} \text{for approach I} \\ \\ \text{for approach II} \end{array}$$

Although these assumptions of proportionality seem to be plausible, they have not been proven and derived. Therefore, the underlying linear relationships are plausible, indeed, but nevertheless they are arbitrary and unproven assumptions.

Furthermore, there exists another difficulty connected with the previous approaches I and II: In quantitative biological studies on dynamical processes rates and models using rates are widely used and well-known. But, the parameters whose rates are considered are real physical entities like total dry matter or plant height. But, here the 'rate of increase of r_M ' has been considered. r_M is no real phy-

sical entity, but an abstract theoretical statistical parameter indicating the strength of a linear relationship. The rate of such a parameter, therefore, must be of a quite different meaning compared to the rate of a parameter with a real physical background. Summarizing these critical comments we may conclude that these approaches I and II are no exact and satisfactory proofs of formulae (34) and (37).

A critical discussion of the numerical results on necessary numbers of clones primarily should be deal with an investigation of the numerous simplifying assumptions and their possible importance and resulting restrictions.

For example, the simplification of equal proportions of the clones in the mixtures: This assumption has not been used explicitly in the previous theoretical investigations. But, of course, this assumption very often has been used implicitly. For example,

- 1) the derivation of $y_i = \bar{x}_i + \bar{\varepsilon}_i$ and $y_i^* = \bar{x}_i^* + \bar{\varepsilon}_i^*$ from chapter 'Theoretical investigations' uses the assumption of equal proportions or
- 2) the assumptions (10):

$$\text{Cov}(\bar{x}_i, \bar{x}_i^*) = \frac{1}{n} \text{Cov}(x_{ij}, x_{ij}^*), \quad v(\bar{x}_i) = \frac{1}{n} v(x_{ij})$$

$$\text{and } v(\bar{x}_i^*) = \frac{1}{n} v(x_{ij}^*)$$

are based on equal proportions and

- 3) the assumption: rate $\sim \frac{1}{n}$ implies an equivalence of the different clones according to the rate of increase.

Thus, equal proportions of the clones are implicitly presumed. Unequal proportions will lead to different weights of the single clones and all the theoretical investigations would be complicated extremely. But, there are many arguments indicating that equal proportions of the clones in the mixtures will be an almost necessary condition under the point of view of practical applications (for example: silvicultural practices). Therefore, the simplifying assumption of equal proportions of the clones will be no strong restriction of the previous studies.

Another strong simplifying assumption will be "no significant mixing effects in the clonal mixtures". This assumption has been used several times, for example in deriving $y_i = \bar{x}_i + \bar{\varepsilon}_i$ and $y_i^* = \bar{x}_i^* + \bar{\varepsilon}_i^*$ and in all following theoretical considerations using y_i and y_i^* . But, in this paper no explicit quantitative discussion of mixing effects and competitive relations shall be given. Two reasons may be sufficient to legitimate the approximation caused by the non-consideration of these effects:

1. Competitive effects are usually relatively small. Only in very special, single situations levels of mixing effects of 0.10 or 0.15 can be obtained.

2. A consideration of mixing effects is included in the previous theoretical investigations by an appropriate re-definition of the parameters $\bar{\varepsilon}_i$ and $\bar{\varepsilon}_i^*$.

Therefore, a consideration of existing mixing effects would be realized, if the assumptions on $\bar{\varepsilon}_i$ and $\bar{\varepsilon}_i^*$ (for example, validity of (6), (13) and (14)) are also valid for this situation of redefined parameters $\bar{\varepsilon}_i$ and $\bar{\varepsilon}_i^*$.

An explicit generalization of the previous theoretical investigations including mixing effects provides no difficulty: For mixture i appropriate mixing effects c_i and c_i^* at juvenile and mature ages can be simply introduced by $y_i = \bar{x}_i + \bar{\varepsilon}_i + c_i$ and $y_i^* = \bar{x}_i^* + \bar{\varepsilon}_i^* + c_i^*$. Hence several additional variances and covariances occur in the formulae:

$$V(c_i), V(c_i^*), \text{Cov}(\bar{x}_i, c_i^*), \text{Cov}(\bar{x}_i, c_i), \text{Cov}(\bar{x}_i^*, c_i),$$

$$\text{Cov}(\bar{x}_i^*, c_i^*), \text{Cov}(\bar{\epsilon}_i, c_i), \text{Cov}(\bar{\epsilon}_i^*, c_i), \text{Cov}(\bar{\epsilon}_i, c_i^*),$$

$$\text{Cov}(\bar{\epsilon}_i^*, c_i^*) \text{ and } \text{Cov}(c_i, c_i^*).$$

Additional assumptions on these terms are needed and the mathematical and statistical complexity increases markedly. These generalizations shall not be further discussed in this paper.

Another simplifying assumption in this publication is the assumption of the validity of FAIRFIELD-SMITH'S empirical law for variances $V(\epsilon_i)$ and $V(\epsilon_i^*)$ and for the covariance $\text{Cov}(\bar{\epsilon}_i, \bar{\epsilon}_i^*)$. These assumptions, of course, must be justified by further theoretical and empirical investigations. But, in this paper such studies have not been performed.

Sometimes the main approach of this paper 'Increase of the juvenile-mature correlation by using mixtures instead of single clones' may be useless. For example, if already r_E shows such an extreme numerical level that a further increase of this correlation would be unnecessary for the purpose of improving an early selection. Just this situation of large r_E may be often realized in practical applications, for example in breeding work with fast-growing tree species like poplars and aspen. These applications are characterized by

1. Relatively short time interval between juvenile and mature ages.
2. Small disconnected production areas.
3. Short rotation time.
4. Homogeneous environments.
5. Use of tested clones and mixtures.
6. Reduced effects of genotype-environment interactions.

All these factors 1—6 lead to enlarged r_E -values. But, in many other situations the correlations r_E will be much lower. Here, the efficiency of an early selection can be improved by using mixtures instead of single clones.

In practical applications the numerical value of r_E will be mainly determined by the time T between juvenile and mature ages. If we use a prediction formula $r_E = r_E(T)$ for the estimation of this r_E [for example LAMBETH'S formula, which has been developed for height growth in pines (LAMBETH 1980)], then the necessary clone number n can be expressed dependent on time T and on the required numerical level of r_M . But, these applications shall not be discussed in this paper (see: HUEHN 1986c).

Another disadvantage of the proposed estimation of necessary clone numbers n by (29) must be the unknown parameter k . Theoretically, k cannot be given or determined without postulating further assumptions. Therefore, k should be estimated empirically by using experimental data like those of KLEINSCHMIT (1983). Possibly k may be characteristic for different tree species.

The correlations introduced in the preceding chapters have been considered as phenotypic juvenile-mature correlations. But, the clone means are estimates for the genotypic values of the clones. Thus, the correlation r_E can be interpreted as a genetic correlation and the well-known quantitative genetic theory on indirect selection can be applied (see, for example: NANSON 1976). Therefore, we think that further improvements of the previous results on necessary numbers of clones in clonal mixtures may be obtained by using quantitative genetic models and procedures.

The most general r_M -expression, of course, is formula (22), which depends on the seven parameters n , b , b^* , t , h^2 , $(h^*)^2$ and r_E . But, numerical calculations have been performed only for a simplified situation with

1. $h^2 = (h^*)^2$
2. $r_E = 0.30$
3. $b = b^* = t$

As a critical comment one could suspect a restricted relevance and applicability of these results. But there are several arguments indicating that this will not be true: Referring to experiences from numerous practical applications, we think, that these simplifications are realistic assumptions. The main numerical results which have been obtained from these calculations and the rough numerical magnitude of the necessary number of clones in clonal mixtures will not be altered too much, if we generalize these assumptions 1—3. But, these theoretical studies shall not be presented here in this paper.

Furthermore, in some previous papers (HUEHN 1977; HUEHN 1979) it has been shown: For many relevant applications t can be approximated very well by the arithmetic mean of

$$b \text{ and } b^*. \text{ Because of } t = \frac{b + b^*}{2} \text{ the assumption 3 from}$$

above can be weakened to the assumption $b = b^*$.

Summarizing these comments we may conclude that the simplifications 1—3 cause no strong restriction of the validity of the numerical results.

The main result of the previous theoretical investigations will be the approximate estimation of the necessary number n of clones in clonal mixtures by $n^k = r_M(1-r_E)/r_E(1-r_M)$ with $k = \text{const}$. For example, for $k = 1$ and $r_M = 0.90$ we obtain: $n = 36$ for $r_E = 0.20$, $n = 21$ for $r_E = 0.30$, $n = 14$ for $r_E = 0.40$, $n = 9$ for $r_E = 0.50$ and $n = 6$ for $r_E = 0.60$. These results are in complete agreement to the findings of quite different former studies on the problem of necessary number of clones in clonal mixtures. These investigations have been performed with regard to the different aspects 1) phenotypic yield stability (HUEHN 1985), 2) yielding ability (HUEHN 1986a), 3) risk considerations (HUEHN 1986b) and 4) juvenile-mature correlations (HUEHN 1986c). As a very rough summarizing statement according to the problem of necessary number of clones in clonal mixtures all these former results and the present new results of this paper too may be summarized to the following conclusion: The necessary clone numbers for clonal mixtures are in the tens rather than just a few clones and rather than in the hundreds.

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Influence of the Value Function on Genotype-by-Environment Relations¹⁾

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Summary

In provenance trials of tree species over several sites where tree value is a composite function of several traits, it is generally supposed that the lack of a change in provenance rank in any trait is sufficient reason to select a single best provenance for all sampled sites. In this paper, we show that provenance values may change rank in the absence of rank changes in any component trait. When the value function is affected by the environment, ranking of provenance values may change in the absence of changes in ranking of composite traits.

Key words: Selection index, Genotype-by-environment, Provenance trials, Selection.

Zusammenfassung

Hierbei wird allgemein angenommen, daß das Ausbleiben von Rangverschiebungen bei irgendeinem Merkmal Grund genug ist, um für alle Standorte eine einzige, am besten geeignete Provenienz zu selektieren. In dieser Arbeit zeigen wir, daß die Rangfolge der Provenienzwerte insgesamt sich ändern kann, obwohl bei den einzelnen Merkmalen keine Rangverschiebungen vorkommen. Dies ist der Fall, wenn die Funktion, die den Provenienzwert bestimmt, durch Umweltfaktoren beeinflusst wird.

Introduction

In provenance trials of tree species over several test sites, where tree value is a composite function of several traits, it is generally supposed that the lack of a change in provenance rank in any trait is sufficient reason to select a single best provenance for all sampled sites. For example,

a set of provenances may exhibit no shifts in ranking for either growth or fire resistance, and it may then be assumed that a single best provenance exists for all sites. Alternatively, if rank changes occur over sites in only one trait, it is generally assumed that subdividing planting environments into appropriate genotypic sets according to that one trait, will maximize value (ABOU-EL-FITTOUH *et al.*, 1969). Such conclusions, however, are valid only if two underlying assumptions are satisfied:

- 1) All genetic and environmental effects are linear and independent in their contribution to the phenotype in all traits, and
- 2) The composite value function is constant.

It has been shown that departures from the first assumption can result in changes in provenance ranks in their composite value function over environments (NAMKOONG, 1985). That is, a provenance by environment interaction can exist for composite value even if no rank changing interaction exists in any component trait.

In this paper, we indicate that failures of the second assumption may also occur and results in changes in rank of provenance values in the absence of rank changes in any component trait. Using data from a provenance trial of *Pinus caribaea* (GIBSON, 1982), we demonstrate that the possibility is neither remote nor trivial. In this trial, and in other situations that can easily be imagined, the value function is dependent on the environment. As a result, the choice of best provenance varies with environment even without failure of the first assumption.

The Model

Consider a simple case of linear and independent genetic (g_i) and environmental (e_j) effects for a trait, k . Since genotype-by-environment interactions and departure from linearity are absent, the model can be written as:

$$(1) \quad Y_{ik} = \mu_k + g_{i,k} + e_{j,k}$$

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