# Multiclonal Mixtures and Number of Clones

## II. Number of Clones and Yield Stability (Deterministic Approach with Competition)

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(Received 3rd June 1988)

### Summary

Theoretical investigations on the number of clones in clonal mixtures have been performed with regard to phenotypic yield stability. These studies are a generalization (inclusion of competitive effects between the clones in the mixture) of a simple, deterministic model, which has been developed in Hühn (1988) for an approach without consideration of competitive effects. For each clone i, i = 1, 2, . . . , n, a parameter $u_i$ with $0 \leq u_i \leq 1$ describes the different survival (in pure stand) of the clones (with respect to the entire rotation time [$\underset{i=1,2,..,n}{\text{Min}}\ u_i = k$ and $\underset{i=1,2,..,n}{\text{Max}}\ u_i = 1$]. The change of $u_i$ caused by competition of clone i with clone j shall be proportional to the frequency of j with a proportionality coefficient $c_{ij}$. Using the two characters 'survival' and 'yielding-ability' and a simple linear, additive competition-model together with several simplifying assumptions [proportionality between 'survival' and 'yielding-ability'; equal proportions of the clones in the mixture; $c_{ij}=c$ for each i and for each j] the yield $\mu$ of a clonal mixture can be calculated and explicitly expressed as a function of n, k and c: $\mu=\mu$ (n, c, k).

For different conditions numerical results on clone numbers can be calculated. For example, such conditions are:

1. For given values of k and c:
$|\mu(n) - \lim_{n\to\infty} \mu(n)|$ lower than $g_1$(%) of this existing limit.
2. For given values of n and c:
| range of $\mu(k)$ — maximal range | lower than $g_2$ (%) of this maximal range.
3. For given values of n and k:
Realization of a certain percentage yield-increase or yield-decrease compared to the situation without an inclusion of competitive effects (c=0).

To give a rough characterization of the numerical magnitude of the resulting clone numbers the results can be summarized as follows: The clone numbers are in the tens rather than just a few clones or in the hundreds.

Finally, the possible limitations and restrictions of the numerical results, which may be caused by the different simplifying assumptions are discussed critically.

*Key words:* Clonal mixtures, number of clones, yield stability, deterministic approach with competition.

### Zusammenfassung

Theoretische Untersuchungen zur Frage der Anzahl von Klonen in Klonmischungen werden hinsichtlich des Aspektes "phänotypische Stabilität" durchgeführt. Diese Untersuchungen stellen eine Verallgemeinerung (Einbeziehung von Konkurrenzeffekten zwischen den Klonen) eines einfachen, deterministischen Ansatzes dar, der in Hühn (1988) für ein Modell ohne Berücksichtigung von Konkurrenzeffekten entwickelt worden ist.

Für jeden Klon i, i=1, 2, . . , n, beschreibt ein Parameter $u_i$ mit $0 \leq u_i \leq 1$ die unterschiedlichen Überlebensfähigkeiten (im Reinbestand) der Klone (bezogen auf die gesamte Umtriebszeit) [$\underset{i=1,2,..,n}{\text{Min}}\ u_i=k$ und $\underset{i=1,2,..,n}{\text{Max}}\ u_i=1$]. Die durch Konkurrenz von Klon i mit Klon j bedingte Veränderung von $u_i$ soll der Häufigkeit von j proportional sein mit einem Proportionalitätskoeffizienten $c_{ij}$. Unter Heranziehung der beiden Merkmale "Überlebensfähigkeit" und "Ertragsfähigkeit" bei Verwendung eines einfachen linearen und additiven Konkurrenzmodells sowie einer Reihe von weiteren vereinfachenden Annahmen (Proportionalität zwischen "Überlebensfähigkeit" und "Ertragsfähigkeit"; gleiche Klonhäufigkeiten in der Mischung; $c_{ij}=c$ für alle i und für alle j) läßt sich die Leistung $\mu$ einer Klonmischung berechnen und als Funktion von n, k und c explizit angeben: $\mu=\mu$ (n, c, k). Für unterschiedliche Bedingungen lassen sich konkrete numerische Angaben über Klonanzahlen ableiten. Solche Bedingungen sind z. B.:

1. Für vorgegebene Werte von k und c:
$|\mu(n) - \lim_{n\to\infty} \mu(n)|$ kleiner als $g_1$ (%) von diesem existierenden Grenzwert.
2. Für vorgegebene Werte von n und c:
| Variationsbreite von $\mu(k)$ — maximale Variationsbreite | kleiner als $g_2$(%) von dieser maximalen Variationsbreite.
3. Für vorgegebene Werte von n und k:
Forderung bestimmter prozentualer Mehr- bzw. Minderleistungen bezüglich der Situation ohne Berücksichtigung von Konkurrenzeffekten (c=0).

Als größenordnungsmäßige Angabe kann man die Resultate dahingehend zusammenfassen, daß die resultierenden Klonanzahlen eher in 10er Größenordnungen, als bei einigen wenigen Klonen oder bei 100er Größenordnungen liegen.

Abschließend werden die durch die vereinfachenden Annahmen bedingten möglichen Einschränkungen der Ergebnisse kritisch diskutiert.

### Introduction and Problem

For many tree species clonal forestry has become an important tool for tree breeding purposes as well as for commercial use. There are many economic and management reasons for employing clones in forestry. Most forest tree breeders agree to the necessity to develop multiclonal varieties to maintain a sufficient genetic diversity in the populations.

High production with minimal risk are the required criteria. An unsolved problem is the evaluation of appropriate numbers of clones in clonal mixtures. Many quite different numerical recommendations have been presented in the literature (see, for example: Hühn, 1984; Libby, 1982).

In a series of publications we want to give some contributions to this problem with regard to different relevant aspects (yield stability; yielding ability; juvenile-mature correlations; risk considerations).

In a first paper (Hühn, 1988) some quantitative, theoretical approaches and numerical results had been presented, which are concerned with the appropriate number of clones in clonal mixtures with regard to phenotypic stability. These results are based upon a simple deterministic model without considering the competitive effects between the clones in the mixture. Phenotypic stability had been measured by the variance concept, that means: maximum stability = constant yield under varying conditions (locations, years, silvicultural practices etc.).

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In this second paper of this series "Multiclonal mixtures and number of clones" we apply the same simple deterministic approach from Hühn (1988). But, additionally, here we include an explicit consideration of the competitive effects between the clones in the mixture by a simple linear and additive competition-model. For this generalized model we present the same methodological approaches, which have been discussed in Hühn (1988). For a discussion of the general concept of modelling this very complex problem of calculating numerical estimates of appropriate numbers of clones in clonal mixtures and for a critical discussion of the simplifying assumptions we refer to Hühn (1988). All theoretical investigations of this paper are based on clonal mixtures which are configurated as intimately mixed plantations.

**Theoretical Investigations and Some Numerical Results**

The final production of a clonal mixture can be described quantitatively by applying two clone-specific parameters: 'survival' and 'yielding ability':

$$\text{TOTAL YIELD} = \sum_{i=1}^{n} \left(\frac{f_i \cdot u_i}{\bar{u}} N\right) \cdot L_i \qquad (1)$$

with

$n$ = number of clones in the mixture,
$f_i$ = frequency of clone i, $i=1, 2, \ldots, n$, in the initial composition of the mixture,
$u_i$ = relative survival parameter of clone i (in pure stand),
$\bar{u}$ = mean of the $u_i$'s: $\bar{u} = \sum_{i=1}^{n} f_i u_i$,
$L_i$ = mean yield of clone i (per plant),
$N$ = final number of plants,
$u_{max}$ = maximum of the $u_i$'s, $i=1, 2, \ldots, n$, and
$L_{max}$ = mean yield of the clone i with $u_i = u_{max}$ (per plant).

Applying several simplifying assumptions (proportionality between the two characters 'survival' and 'yielding ability' (see 'Discussion'), equal proportions of the clones in the initial composition of the mixture) formula (1) reduces to (2).

These $u_i$'s are defined in analogy to the relative fitnesses in 'classical' population genetics, that means that these numbers $u_i$ represent the relative magnitudes of the contributions of the clones to the composition of the population at the final production stage on a per individual basis.

Since only the ratio of the $u_i$'s counts, it does not matter if $\lambda \cdot u_i$ were employed instead of $u_i$; we obtain the same normalized or standardized results in either case.

$f_i\, u_i / \bar{u}$ is the frequency of clone i, $i = 1, 2, \ldots, n$, in the population at the final production stage using $\bar{u}$ as a normalizing factor, so that $\sum_{i=1}^{n} \frac{f_i\, u_i}{\bar{u}} = 1$.

Without loss of generality, we may assume: $u_{max} = 1$, since the $u_i$'s are defined as relative measures.

However, after having adopted this definition the $u_i$'s are fixed and now they are absolute measures.

$$\text{TOTAL YIELD} = \frac{NL_{max}}{u_{max}} \cdot \frac{\sum_{i=1}^{n} u_i^2}{\sum_{i=1}^{n} u_i} \qquad (2)$$

This quantitative approach without an explicit inclusion of the competitive effects between the clones in the mixture has been discussed in Hühn (1988). For further explanations we refer to this publication.

The parameters $u_i$ can be generalized in such a way that the competitive effects between the different clones in the clonal mixture are included:

$$u_i^* = u_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} c_{ij} f_j \qquad (3)$$

To motivate this model (3) we may argue: The first term $u_i$ describes the survival of clone i in pure stand. In the clonal mixture, however, this $u_i$ will be changed due to competitive interactions with the other clones in the mixture. The change of $u_i$ caused by competition of clone i with clone j shall be proportional to the frequency of clone j — with a proportionality factor $c_{ij}$. Furthermore, all these effects $c_{ij} f_j$ between clone i and all the remaining clones shall be additive.

For the special case of equal proportions of the clones in the initial composition of the mixture ($f_i = \frac{1}{n}$ for each i) model (3) can be expressed as:

$$u_i^* = u_i + \frac{1}{n} \sum_{\substack{j=1 \\ j \neq i}}^{n} c_{ij} \qquad (4)$$

In the following numerical calculations only the very special situation of equal $c_{ij}$'s will be considered: $c_{ij} = c$ for each i and for each j. For a critical discussion of this assumption, see: 'Discussion'. (4) gives:

$$u_i^* = u_i + \frac{n-1}{n} \cdot c \qquad (5)$$

For the total yield (denoted by $\mu$) we get (by (2) and (5)):

$$\mu = \frac{NL_{max}}{1 + \frac{n-1}{n} \cdot c} \cdot \frac{\sum_{i=1}^{n} \left(u_i + \frac{n-1}{n} c\right)^2}{\sum_{i=1}^{n} \left(u_i + \frac{n-1}{n} c\right)} \qquad (6)$$

Herewith, the maximal value of the $u_i$'s has been assumed to be one.

For $\mu$ (expressed in $NL_{max}$-units) formula (6) leads to:

$$\mu = \frac{n \sum_{i=1}^{n} u_i^2 + 2c(n-1) \sum_{i=1}^{n} u_i + (n-1)^2 c^2}{[n + (n-1)c] \sum_{i=1}^{n} u_i + n(n-1)c + (n-1)^2 c^2} \qquad (7)$$

This $\mu$-expression (7), of course, is a generalization of (2): For $c=0$ formula (2) ensues from (7).

For the parameters $u_i$, $i=1, 2, \ldots, n$, we apply the same simple deterministic approach from Hühn (1988): We denote the minimal $u_i$, $i=1, 2,$ , n, with k and all the

$u_i$ shall be equally spaced between 1 and k. This assumption gives:

$$u_i = 1 - \frac{1-k}{n-1}(i-1) \qquad (8)$$

with $u_1=1$ (for $i=1$) and $u_n=k$ (for $i=n$).

Using the explicit expressions for $\sum_{i=1}^{n} u_i$ and $\sum_{i=1}^{n} u_i^2$:

$$\sum_{i=1}^{n} u_i = \frac{n(1+k)}{2} \text{ and } \sum_{i=1}^{n} u_i^2 = nk + \frac{(1-k)^2 n(2n-1)}{6(n-1)} \qquad (9)$$

the total yield $\mu=\mu$ (n,c,k) can be expressed as:

$$\mu = \frac{\left(c + \frac{n(1+k)}{2(n-1)}\right)^2 + \frac{n^2(n+1)(1-k)^2}{12(n-1)^3}}{\left(c + \frac{n(3+k)}{4(n-1)}\right)^2 - \frac{n^2(1-k)^2}{16(n-1)^2}} \qquad (10)$$

Numerical calculations of $\mu$ can be easily performed by (10). But before, a slight restriction of the possible parameter values must be introduced: The competition factors c may be positive or negative. For negative c-values the $u^*_i$ from (5) can be negative too. This absurd situation, of course, must be excluded. If we assume, that all the $u_i$ shall be equally spaced between k and 1 we require for all subsequent numerical calculations the following restriction of the admissible parameter values:

$$k + c \geq 0 \qquad (11)$$

For $c \geq 0$ such an additional condition, of course, is unnecessary. Some numerical results of $\mu$ (for different clone numbers n, two different k's and two different c's) are presented in *figures 1a* and *1b*.

One obtains the following main results and conclusions: 1. For each given k (that means, for a given variability of the different $u_i$'s, $i=1, 2, \ldots, n$) and each c we investigate $\mu=\mu(n)$:

The yield $\mu$ decreases with increasing clone numbers n. This decrease is most rapid for low numbers n, while for larger n only insignificant small changes of $\mu$ exist. Or mathematically expressed: $\lim_{n\to\infty} \mu(n)$ exists (for each k and for each c).

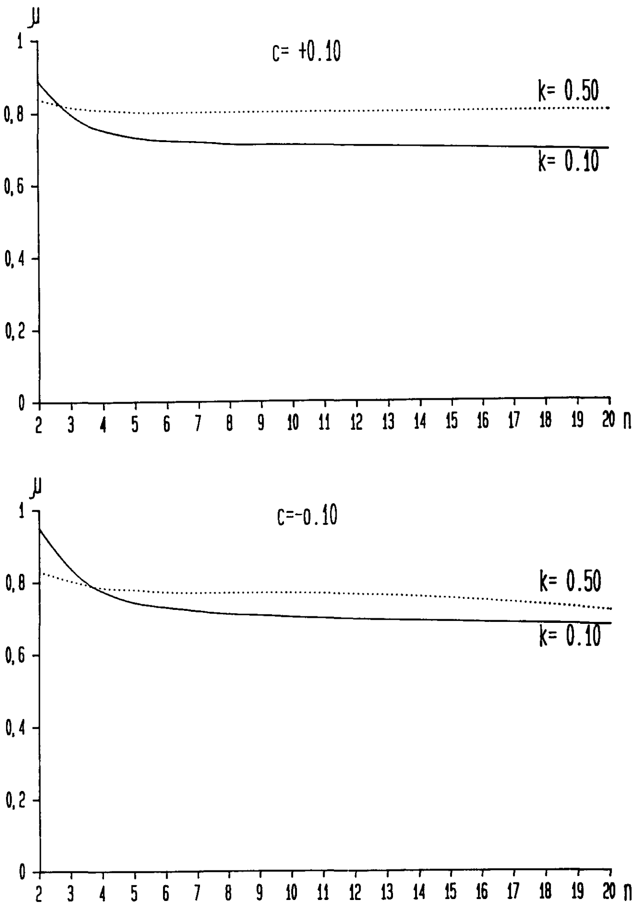
This approach towards the limit seems to be an aspect of yield level rather than an aspect of yield stability. But, insignificant changes of $\mu$ with increasing n, of course, would be also an aspect of yield stability.

Decreasing mean yield $\mu$ with increasing clone number n is, of course, an obvious result since inferior clones must be also included in the mixture if n should be increased.

The limit of $\mu$ can be obtained from (10) directly:

$$\lim_{n\to\infty} \mu = \frac{\left(c+\frac{1+k}{2}\right)^2 + \frac{(1-k)^2}{12}}{\left(c+\frac{3+k}{4}\right)^2 - \frac{(1-k)^2}{16}} \qquad (12)$$

Now we may ask for the clone number n, for which $\mu$ has reached the limit so far that the difference will be



*Figures 1a and 1b.* — Numerical values of the total yield $\mu$ (calculated by (10)) for different clone numbers n, two values of the competition parameter c (c = + 0.10 and c = — 0.10) and two values of the parameter k (k = 0.10 and k = 0.50).

smaller than $g_1$ % of this limit. These numbers n may be considered as appropriate numbers of clones in clonal mixtures under the simplifying assumptions mentioned before with regard to yield stability aspects. Based on the relation

$$\mu = \mu(n,c,k) = \frac{100+g_1}{100} \lim_{n\to\infty} \mu \qquad (13)$$

these numbers n can be calculated by using the numerical values of $\mu$ (n, c, k) (by (10)) and $\lim_{n\to\infty} \mu$ (by 12)).

Some numerical results are given in *table 1*: For the percentage $g_1$ we use the values: 20%, 10%, 5% and 1%. Lower percentages would be quite unrealistic. The resulting clone numbers n are not too much influenced by different c-values (see: *Table 1*) — with some exceptions for very large positive ov very large negative c-coefficients. But, both situations are of little interest for practical applications. Here, most coefficients will be low or medium (positive or negative). In this intermediate interval around c=0 the clone numbers n turn out to be nearly constant (*Table 1*).

For different $g_1$'s and different k's the clone numbers from *table 1* have been presented once more in *table 2* — but now, only the resulting n-intervals instead of the explicit dependence on c are given. The clone numbers, of course, decrease with increasing k. If we require an ap-

*Table 1.* — Clone numbers n, for which the difference between yield $\mu$ and $\lim_{n\to\infty} \mu$ is smaller than $g_1$(%) of this limit — for different k's, different c's and different $g_1$'s.

| k | 0 | | | | 0.10 | | | | 0.30 | | | | 0.50 | | | | 0.70 | | | | 0.90 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| c \ $g_1$ | 20 | 10 | 5 | 1 | 20 | 10 | 5 | 1 | 20 | 10 | 5 | 1 | 20 | 10 | 5 | 1 | 20 | 10 | 5 | 1 | 20 | 10 | 5 | 1 |
| -0.20 | | | | | | | | | 3 | 5 | 9 | 40 | 2 | 3 | 5 | 20 | 2 | 2 | 2 | 9 | 2 | 2 | 2 | 3 |
| -0.10 | | | | | 4 | 6 | 10 | 75 | 3 | 4 | 6 | 30 | 2 | 2 | 4 | 15 | 2 | 2 | 2 | 6 | 2 | 2 | 2 | 3 |
| -0.05 | | | | | 4 | 6 | 10 | 50 | 2 | 4 | 6 | 25 | 2 | 2 | 3 | 15 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| -0.01 | | | | | 3 | 5 | 9 | 40 | 2 | 3 | 5 | 25 | 2 | 2 | 3 | 9 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| -0.005 | | | | | 3 | 5 | 9 | 45 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 9 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| -0.001 | | | | | 3 | 5 | 9 | 35 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 9 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| 0 | 4 | 6 | 15 | 75 | 3 | 5 | 9 | 40 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 9 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| 0.001 | 4 | 6 | 15 | 50 | 3 | 5 | 9 | 40 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 9 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| 0.005 | 4 | 6 | 10 | 50 | 3 | 5 | 9 | 45 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 8 | 2 | 2 | 2 | 4 | 2 | 2 | 2 | 2 |
| 0.01 | 4 | 6 | 10 | 50 | 3 | 5 | 9 | 40 | 2 | 3 | 5 | 20 | 2 | 2 | 3 | 8 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 2 |
| 0.05 | 4 | 6 | 9 | 50 | 3 | 5 | 8 | 35 | 2 | 3 | 4 | 20 | 2 | 2 | 3 | 7 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 2 |
| 0.10 | 4 | 5 | 5 | 40 | 3 | 4 | 7 | 35 | 2 | 3 | 4 | 15 | 2 | 2 | 3 | 5 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 2 |
| 0.20 | 3 | 4 | 7 | 30 | 3 | 4 | 5 | 20 | 2 | 3 | 3 | 9 | 2 | 2 | 2 | 5 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |

proach to the limit of at least 1% we have $n \cong 30$ to 75 (for a maximal variability of the $u_i$'s, that means: $k=0$). For an approach of at least 5% only $n \cong 7$ to 15 clones would be sufficient. These numbers decrease to $n \cong 4$ to 6 clones (for $g_1 = 10\%$) or even to $n \cong 3$ to 4 clones (for $g_1 = 20\%$).

2. For each given n and each c we now investigate $\mu=\mu(k)$: Just this aspect will be of special importance for the problem of phenotypic stability. A clonal mixture can be considered as being the more stable the lower it's $\mu$-differences for very different effects of all biotic and abiotic factors (that means, large differences between the possible k's).

For the parameter intervals, which are relevant for practical applications we may conclude from (10) and *figures 1a* and *1b*: The functions $\mu=\mu$ (k) show either decided minima, which are located at very small numerical k-values or the functions $\mu=\mu(k)$ are monotone increasing functions (for each n and for each c). These conclusions can be precised by theoretical considerations proceeding from (10): (10) can be expressed as

$$\mu = \mu(n,c,k) = \frac{Ak^2 + Bk + C}{Dk + E} \qquad (14)$$

with

$$A = \frac{n^2(2n-1)}{6(n-1)},$$

$$B = \frac{n^2(n-2) + 3nc(n-1)^2}{3(n-1)},$$

$$C = \frac{n^2(2n-1) + 6nc(n-1)^2 + 6c^2(n-1)^3}{6(n-1)},$$

$$D = \frac{n^2 + nc(n-1)}{2} \quad \text{and}$$

$$E = \frac{n^2 + 3nc(n-1) + 2c^2(n-1)^2}{2}.$$

A necessary condition of an extreme point is $\frac{\partial \mu(k)}{\partial k} = 0$ which leads to:

$$k = \frac{1}{D}\left[-E \pm \sqrt{\frac{CD^2 + AE^2 - BDE}{A}}\right] \qquad (15)$$

These k-values will be denoted by $k_{min}$.

Because of $D > 0$ and $E > 0$ (in the parameter intervals which are relevant for applications) in (15) the sign — cannot be applied. To clarify the kind of these extrema

*Table 2.* — Resulting intervals for the clone number n dependent on different $g_1$'s and different k's — for the admissible c-values between —0.20 and +0.20.

| $g_1$(%) \ k | 0 | 0.10 | 0.30 | 0.50 | 0.70 | 0.90 |
|---|---|---|---|---|---|---|
| 20 | 3 - 4 | 3 - 4 | 2 - 3 | 2 | 2 | 2 |
| 10 | 4 - 6 | 4 - 6 | 3 - 5 | 2 - 3 | 2 | 2 |
| 5 | 7 - 15 | 5 - 10 | 3 - 9 | 2 - 5 | 2 | 2 |
| 1 | 30 - 75 | 20 - 75 | 9 - 40 | 5 - 20 | 2 - 9 | 2 - 3 |

by (15) we calculate the second derivative at these points — and one obtains:

$$\left(\frac{\partial^2 \mu}{\partial k^2}\right)_{k=k_{min}} = \frac{2A}{Dk_{min} + E} \qquad (16)$$

Because of $A>0$ together with $D>0$ and $E>0$ the second derivative must be positive. Thus, the extreme points by (15) are minima. Some numerical values of $k_{min} = k_{min}$ (n, c) (by (15)) are presented in *table 3*.

Compared to the situation without including competitive effects ($c=0$) one obtains lower $k_{min}$-values (for $c>0$) and larger $k_{min}$-values (for $c<0$) (*Table 3*). But, the general results for $c \neq 0$ are analogous to the results for $c=0$, which have been discussed in HUEHN (1988): The minima are located at very small numerical values of k — with the exception of

a) low clone numbers n and
b) very large negative c-values (see: *Table 3*).

But, both situations are of a very restricted interest for applications.

With increasing n as well as with increasing c the $k_{min}$'s decrease. Additionally, for larger n together with larger positive c-values the function $\mu = \mu(k)$ is monotone increasing. These situations have been indicated tn *table 3* by the sign — —. Thus, for the major part of the range of relevant parameter values we may conclude: $\mu$ increases with increasing k. That means: The total yields of clonal mixtures are the higher the more uniform the $u_i$'s of the included clones.

If we consider the range of the possible $\mu$-values (for any given numerical values of n and c) as an indicator of stability we obtain (because of $\mu$ (for $k=0$) $<$ $\mu$ (for $k=1$) for $n > 2$):

$$\text{range} = \mu \text{ (for } k=1) - \begin{cases} \mu \text{ (for } k=k_{min}), \text{ if } k_{min} \text{ exists} \\ \mu \text{ (for } k=0), \text{ if } k_{min} \text{ doesn't exist} \end{cases} \qquad (17)$$

Application of (10) and (14) gives the range dependent on n and c:

$$\text{range} = 1 - \begin{cases} \dfrac{Ak_{min}^2 + Bk_{min} + C}{Dk_{min} + E}, & \text{if } k_{min} \text{ exists} \\ \dfrac{C}{E}, & \text{if } k_{min} \text{ doesn't exist} \end{cases} \qquad (18)$$

This range tends to a limit for $n \rightarrow \infty$:

$$\lim_{n \to \infty} \text{range} = \begin{cases} \dfrac{1}{3}, & \text{if } c \leq 0 \\ \dfrac{1+3c}{3(1+c)(1+2c)}, & \text{if } c > 0 \end{cases} \qquad (19)$$

Now, we may ask for the clone number n, for which this range has reached the limit so far that the difference will be lower than $g_2$ (%) of this limit. These numbers n may be considered as appropriate numbers of clones in clonal mixtures. That's another definition of 'appropriate clone number' which is based on the range of $\mu$ while the previous approach has been based on $\mu$ itself.

We get the condition

$$100 \text{ range} = (100 - g_2) \cdot \lim_{n \to \infty} \text{range} \qquad (20)$$

This equation (20) can be solved numerically for n (for any given percentage $g_2$ and any given c-value). Some numerical results are summarized in *table 4* with the conclusions:

*Table 3.* — k-values with $\mu = \mu(k)$ = minimum for different clone numbers n and different numerical values of c (for — — no $k_{min}$ —value with $k_{min} \geqq 0$ exists).

| n \ c | -0.20 | -0.10 | -0.05 | -0.01 | -0.005 | -0.001 | 0 | 0.001 | 0.005 | 0.01 | 0.05 | 0.10 | 0.20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 0.363 | 0.314 | 0.289 | 0.270 | 0.267 | 0.265 | 0.265 | 0.264 | 0.262 | 0.260 | 0.240 | 0.216 | 0.167 |
| 4 | 0.316 | 0.256 | 0.225 | 0.201 | 0.198 | 0.196 | 0.195 | 0.195 | 0.192 | 0.189 | 0.165 | 0.135 | 0.075 |
| 5 | 0.290 | 0.222 | 0.189 | 0.161 | 0.158 | 0.155 | 0.155 | 0.154 | 0.151 | 0.148 | 0.121 | 0.087 | 0.019 |
| 6 | 0.273 | 0.201 | 0.164 | 0.135 | 0.132 | 0.129 | 0.128 | 0.127 | 0.125 | 0.121 | 0.092 | 0.055 | -- |
| 7 | 0.262 | 0.186 | 0.148 | 0.117 | 0.113 | 0.110 | 0.109 | 0.109 | 0.106 | 0.102 | 0.071 | 0.033 | -- |
| 8 | 0.254 | 0.175 | 0.135 | 0.103 | 0.099 | 0.096 | 0.095 | 0.095 | 0.091 | 0.088 | 0.056 | 0.016 | -- |
| 9 | 0.247 | 0.166 | 0.125 | 0.093 | 0.089 | 0.085 | 0.085 | 0.084 | 0.081 | 0.077 | 0.044 | 0.003 | -- |
| 10 | 0.242 | 0.159 | 0.118 | 0.084 | 0.080 | 0.077 | 0.076 | 0.075 | 0.072 | 0.068 | 0.034 | -- | -- |
| 15 | 0.228 | 0.139 | 0.095 | 0.059 | 0.055 | 0.051 | 0.050 | 0.050 | 0.046 | 0.042 | 0.006 | -- | -- |
| 20 | 0.221 | 0.129 | 0.083 | 0.047 | 0.042 | 0.039 | 0.038 | 0.037 | 0.033 | 0.029 | -- | -- | -- |
| 25 | 0.216 | 0.123 | 0.077 | 0.039 | 0.035 | 0.031 | 0.030 | 0.029 | 0.025 | 0.021 | -- | -- | -- |
| 30 | 0.214 | 0.119 | 0.072 | 0.035 | 0.030 | 0.026 | 0.025 | 0.024 | 0.020 | 0.016 | -- | -- | -- |
| 35 | 0.212 | 0.117 | 0.069 | 0.031 | 0.026 | 0.022 | 0.022 | 0.021 | 0.017 | 0.012 | -- | -- | -- |
| 40 | 0.210 | 0.114 | 0.067 | 0.028 | 0.024 | 0.020 | 0.019 | 0.018 | 0.014 | 0.009 | -- | -- | -- |
| 45 | 0.209 | 0.113 | 0.065 | 0.026 | 0.022 | 0.018 | 0.017 | 0.016 | 0.012 | 0.007 | -- | -- | -- |
| 50 | 0.208 | 0.112 | 0.063 | 0.025 | 0.020 | 0.016 | 0.015 | 0.014 | 0.010 | 0.005 | -- | -- | -- |
| 75 | 0.205 | 0.108 | 0.059 | 0.020 | 0.015 | 0.011 | 0.010 | 0.009 | 0.005 | 0.000 | -- | -- | -- |
| 100 | 0.204 | 0.106 | 0.057 | 0.017 | 0.012 | 0.008 | 0.008 | 0.007 | 0.003 | -- | -- | -- | -- |
| 200 | 0.202 | 0.103 | 0.053 | 0.014 | 0.009 | 0.005 | 0.004 | 0.003 | -- | -- | -- | -- | -- |
| 500 | 0.201 | 0.101 | 0.051 | 0.011 | 0.006 | 0.002 | 0.001 | 0.000 | -- | -- | -- | -- | -- |

a. The resulting clone numbers n are nearly independent on different c-values. Exception: Low percentages $g_2$ and simultaneously large positive c-values. Here n decreases with increasing positive c-values. This situation is of minor interest for applications.

b. For each competition coefficient c: n decreases with increasing percentage $g_2$.

For further results: see *table 4*.

If we require an approach to the limit of at least 1% we have n=100 (or lower n-values for large positive c's, see *table 4*). This number reduces to n = 20 for $g_2$ = 5% (with only slight reductions for large positive c's). This number decreases to n = 10 (for $g_2$ = 10%) or even to n = 5 (for $g_2$ = 20%) (*Table 4*).

For any given clone number n and competition parameter c and numerical values $k_1$ and $k_2$ with $k_1 \neq k_2$ we may investigate the yield-difference Δ:

$$\Delta = \mu(n,c,k_1) - \mu(n,c,k_2) \qquad (21)$$

Using (14) one obtains:

$$\Delta = (k_1-k_2) \cdot \frac{ADk_1k_2 + AE(k_1+k_2) + BE-CD}{(Dk_1+E)(Dk_2+E)} \qquad (22)$$

Situations with Δ = 0 are of special interest: For given n and c different variabilities of the n clones (i.e. different k's) will result in identical yields μ and that's, of course, an aspect of yield stability.

From Δ = 0 together with (22) we get the condition:

$$ADk_1k_2 + AE(k_1+k_2) = CD - BE \qquad (23)$$

(23) can be solved numerically for n (for given numerical values of $k_1$, $k_2$ and c). Some results are presented in *table 5*.

The sign — — indicates: No existing solution n of (23) with n ≥2 *or* condition (11) is not fulfilled.

Such clone numbers don't exist for larger $k_1$'s together with larger $k_2$'s (see: *Table 5*).

Of special interest may be the case: $k_1$=k and $k_2$=0. That means: maximal variability of the $u_i$'s compared to a reduced variability of the $u_i$'s. (23) simplifies to:

$$k = (CD - BE) / AE \qquad (24)$$

Some numerical solutions of (24) are included in *table 5*. That means: For an extension of the range of the $u_i$'s of the n clones from 1-k to the maximal range 1 the yield μ remains unchanged. This increase of the differences between the clones doesn't result in corresponding yield-differences.

3. For each given clone number n and each k we study μ=μ(c): Only some numerical results shall be presented here. No theoretical investigations of μ=μ(c) are given. From (10) and *figures 1a* and 1b we may conclude: μ-differences for different values of the competition coefficient c (for given n and k) are relatively small. Therefore, the competitive effects between the clones of a clonal mixture are of no serious and biasing effect, if they are modelled by (3), (4) and (5) (see: 'Discussion').

To get some information on the amount of these yield-effects caused by competition we used the following procedure: If we relate all the yields to the situation without competition [μ (for c=0) ≌ 100%] we calculate the percentage deviations of the largest negative c-value (we used c = —0.20) and the largest positive c-value (we used c = +0.20). For clone numbers n from n=3 to n=500 the possible yield-increases as well as the possible yield-decreases reach a level of approximately 5% (both compared to the situation c=0). Yield-decreases will be usually obtained for negative competition coefficients c. With regard to varying competition intensities (measured by different numerical values of c) (for given n and k) we, therefore, can establish a pronounced phenotypic yield stability.

For some selected clone numbers n the yield-increases as well as the yield-decreases which can be obtained maximally by applying different k's are:

*Table 4.* — Clone numbers n for different percentages $g_2$ and different c-values satisfying the condition: [$\lim_{n\to\infty}$ range — range] lower than $g_2$% of this limit (for explanations: see text).

| c \ $g_2$(%) | 1 | 2 | 3 | 5 | 8 | 10 | 15 | 20 | 25 |
|---|---|---|---|---|---|---|---|---|---|
| -0.20 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| -0.10 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| -0.05 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| -0.01 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| -0.005 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| -0.001 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| 0 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| 0.001 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| 0.005 | 100 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| 0.01 | 99 | 50 | 34 | 20 | 13 | 10 | 7 | 5 | 4 |
| 0.05 | 88 | 45 | 30 | 19 | 12 | 10 | 7 | 5 | 4 |
| 0.10 | 76 | 39 | 27 | 17 | 11 | 9 | 7 | 5 | 4 |
| 0.20 | 57 | 30 | 20 | 13 | 9 | 8 | 6 | 5 | 4 |

*Table 5.* — Clone numbers n for different values of $k_1$, $k_2$ and c leading to equal yields (for explanations: see text).

| $k_1$ | c \ $k_2$ | 0 | 0.20 | 0.40 | 0.60 | 0.80 |
|---|---|---|---|---|---|---|
| 0.10 | -0.10 | — | 13 | 5 | 3 | 3 |
|  | -0.05 | — | 7 | 4 | 3 | 3 |
|  | -0.01 | — | 6 | 4 | 3 | 3 |
|  | 0 | 16 | 6 | 4 | 3 | 3 |
|  | +0.01 | 14 | 5 | 4 | 3 | 3 |
|  | +0.05 | 9 | 5 | 3 | 3 | — |
|  | +0.10 | 7 | 4 | 3 | 3 | — |
| 0.30 | -0.10 | — | 5 | 3 | 3 | — |
|  | -0.05 | — | 4 | 3 | — | — |
|  | -0.01 | — | 4 | 3 | — | — |
|  | 0 | 6 | 4 | 3 | — | — |
|  | +0.01 | 6 | 4 | 3 | — | — |
|  | +0.05 | 5 | 3 | 3 | — | — |
|  | +0.10 | 4 | 3 | 3 | — | — |

| n | 5 | 8 | 10 | 20 | 30 | 40 | 50 | 100 |
|---|---|---|---|---|---|---|---|---|
| increase | 2.8 | 3.4 | 3.7 | 4.4 | 4.6 | 4.7 | 4.7 | 4.9 |
| decrease | 3.4 | 4.2 | 4.3 | 5.0 | 5.1 | 5.3 | 5.3 | 5.5 |

These 'decreases' are larger than the 'increases' — and both reach approximately 5% with increasing clone numbers n.

4. Finally, we are interested in $\mu$-differences for different clone numbers n.

This aspect shall be only discussed numerically, no theoretical results are given. From (10) and *figures 1a* and *1b we may conclude:* $\mu$-differences for different clone numbers (for given k and given c) decrease with increasing k's (for the same c), while they turn out to be nearly constant with increasing c's (for the same k).
For example:

$$\left.\begin{array}{l} k = 0.10 \\ c = 0.01 \end{array}\right\} \begin{array}{lcccr} 0.674 & \le & \mu & \le & 0.915 \\ (\text{for } n=500) & & & & (\text{for } n=2) \end{array}$$

$$\left.\begin{array}{l} k = 0.90 \\ c = 0.01 \end{array}\right\} \begin{array}{lcccr} 0.951 & \le & \mu & \le & 0.953 \\ (\text{for } n=500) & & & & (\text{for } n=2) \end{array}$$

$$\left.\begin{array}{l} k = 0.10 \\ c = -0.10 \end{array}\right\} \begin{array}{lcccr} 0.667 & \le & \mu & \le & 0.953 \\ (\text{for } n=500) & & & & (\text{for } n=2) \end{array}$$

$$\left.\begin{array}{l} k = 0.10 \\ c = 0.10 \end{array}\right\} \begin{array}{lcccr} 0.686 & \le & \mu & \le & 0.893 \\ (\text{for } n=500) & & & & (\text{for } n=2) \end{array}$$

This aspect can be simply described by using the range v of the $\mu$-values (for a given k and a given c). From (10) and (12) it follows:

*Table 6.* — Ranges of the yield $\mu$ for different c's and different k's.

| c \ k | 0 | 0.10 | 0.30 | 0.50 | 0.70 |
|---|---|---|---|---|---|
| -0.20 | — | — | 0.183 | 0.094 | 0.040 |
| -0.10 | — | 0.286 | 0.153 | 0.073 | 0.028 |
| -0.05 | — | 0.266 | 0.139 | 0.064 | 0.022 |
| -0.01 | — | 0.249 | 0.128 | 0.057 | 0.018 |
| -0.005 | — | 0.248 | 0.127 | 0.056 | 0.018 |
| 0 | 0.333 | 0.245 | 0.126 | 0.055 | 0.018 |
| +0.005 | 0.331 | 0.244 | 0.124 | 0.055 | 0.018 |
| +0.01 | 0.328 | 0.241 | 0.123 | 0.054 | 0.017 |
| +0.05 | 0.309 | 0.226 | 0.114 | 0.048 | 0.014 |
| +0.10 | 0.285 | 0.208 | 0.102 | 0.041 | 0.010 |
| +0.20 | 0.241 | 0.174 | 0.082 | 0.030 | 0.004 |

$$v = \mu \text{ (for } n=2) - \lim_{n\to\infty} \mu \qquad (25)$$

For some selected numerical values of k and c the resulting ranges v have been summarized in *table 6*. One obtains: The range v decreases very rapidly with increasing k's (for any given c). That means: v decreases rapidly with an increasing uniformity of the $u_i$'s of the included clones. For any given k and increasing competition coefficients c the range v changes only slightly (see: *Table 6)*.

The relevance of these results on ranges for the aspect of yield stability is evident: A decreasing range describes an increasing similarity of the possible yields, i.e. increasing stability. The general theoretical expression for these $\mu$-differences can be simply derived: For any given k and any admissible c and clone numbers $n_1$ and $n_2$ with $n_1 \neq n_2$ we may investigate the yield-difference R:

$$R = \mu(n_1,c,k) - \mu(n_2,c,k) \qquad (26)$$

Application of (10) gives R dependent on c, k, $n_1$ and $n_2$. But, this explicit expression shall not be given and discussed in this paper. The same procedures as in HÜHN (1988) can be applied to obtain estimates of appropriate clone numbers for clonal mixtures:

A certain yield difference $R=R_0$ is assumed to be given which may be considered to be sufficiently small to guarantee yield stability when increasing the clone number from $n_1$ to $n_2$. Several possibilities may be investigated:

a) $n_2 = n_1 + 1$, i.e. increasing the clone number by only one additional clone,

b) $n_2 = 2n_1$, i.e. doubling the clone number or

c) $n_2 = tn_1$, i.e. using a multiple of the initial clone number.

For a), b) and c) equation (26) can be solved for $n_1$. This number $n_1$ depends on $R_0$, c and k. $n_1$ can be considered as an appropriate clone number for clonal mixtures under the specified conditions [see, also: HÜHN (1988) for extensive numerical results in the special case c=0]. The resulting clone numbers for $c \neq 0$ are not too much different from those for c=0.

## Discussion

The preceding theoretical investigations are based on many simplifying assumptions. A critical discussion of the numerical results on clone numbers in clonal mixtures primarily must be concerned with the possible limitations and restrictions of these results imposed by the different assumptions.

Some of these assumptions have been critically discussed in HÜHN (1988):

1. Introduction of two characters ('survival' and 'yielding ability') with a presumed proportionality between them.
2. Equal proportions of the clones in the initial composition of the clonal mixture.
3. The total yield has been expressed in $NL_{max}$—units (by (7)), which implies the assumption of constant values for $NL_{max}$ in spite of varying other parameters.
4. Extremely simplified deterministic approach of equally spaced $u_i$-values in the interval from k to 1.

The critical discussion of these assumptions for the special case c=0 in HÜHN (1988) remains valid too for the generalized situation in this paper with $c \neq 0$. Therefore, these considerations shall not be repeated here and we refer to HÜHN (1988). But, only the main conclusion may be mentioned: NONE of these assumptions will impose any serious restrictions of the numerical results on clone numbers, if we are only interested in an approximate and rough numerical level of appropriate clone numbers for clonal mixtures.

In the present paper some further simplifying assumptions concerning the modeling of competitive effects between the clones in the clonal mixture must be considered: The change of pure stand survival $u_i$ by competition between clone i and clone j shall be proportional to the frequency $f_j$ of clone j with a proportionality coefficient $c_{ij}$. Furthermore, all these effects $c_{ij}f_j$ are assumed to be additive. This linear and additive model, of course, describes a very simplified situation. But, a formal justification of (3) or (4) can be obtained backwards: The coefficients $c_{ij}$ shall be defined in such a manner that (3) or (4) are valid. That means, definition of $c_{ij}$ so that the survival in the mixture will be described with sufficient accuracy by (3) or (4). Thus we may conclude: The main and decisive simplification will be not the modeling (3) or (4), but the assumption of equal $c_{ij}$-coefficients: $c_{ij}=c$ for each i and for each j. That's, of course, very unrealistic. In competition situations of clonal mixures some clones will profit by these interactions while others will result in disadvantages. These effects, therefore, will be extremely clone-specific.

The $c_{ij}$'s can be positive and negative and, therefore, in the sums $\sum_j c_{ij}f_j$ or $\sum_j c_{ij}$ from (3) or (4) these terms and effects may be partially cancelled out. The resulting approximations $\sum_j c_{ij}f_j = 0$ or $\sum_j c_{ij} = 0$ imply $u^*_i = u_i$ by (3) or (4) and, therefore, reduce to the situation which has been investigated in the first paper of this series (HÜHN, 1988). Thus, the very simplified model in HÜHN (1988) without an inclusion of competitive effects, nevertheless, is of considerable interest for applications.

Both cases: ($c_{ij}=0$ for each i and each j) and ($c_{ij}=c \neq 0$ for each i and each j) are the extremes. Most realistic situations will be located between them.

This simplified modeling of the competitive effects, of course, can be stepwise improved. For example, we may apply the more realistic assumption : $c_{ij}=c_i$ for each j. But these improvements and generalizations shall not be further discussed in this paper. All the theoretical and numerical investigations of this paper are based on the restriction (11) of the parameters k and c: $k + c \geq 0$. For $c \geq 0$ this condition, of course, is of no relevance. In applications only very small numerical c-values will be of any practical relevance. Therefore, the additional assumption (11) implies no serious restriction of the preceding deterministic approach.

Finally, another simplification must be mentioned: Almost all of the results of this paper have been derived by studying the function $\mu=\mu(n,c,k)$ from (10). These investigations have been performed in the following way: Two of the variables n, c and k are considered as being given and fixed and $\mu$ has been studied dependent on the remaining one variable. For example, for each given k and each c we investigate $\mu=\mu(n)$. An improved procedure, of course, would be the simultaneous variation of all three variables n, c and k. This approach would result in a deeper insight into the functional dependencies and, furthermore, many interesting numerical results may be obtained. But, in this paper we don't present these generalizations.

Some final comments shall be devoted to one of the strongest assumptions of the previous theoretical investigations: the required proportionality between 'survival' and 'yielding ability'. This assumption may be due to vehement criticism.

All results and conclusions which have been obtained in this paper are only valid for populations where this assumption holds.

The survival-parameter describes the shifts of the initial composition of the clonal mixture and the yielding ability-parameter characterizes the different yielding potential of the clones (independent on the selective effects).

In our opinion, a proportionality between these two characters will be a very common situation in the field of practical applications. Many natural selection processes and the different non-systematic artificial thinning procedures too are in accordance with this simplifying assumption: In intimately mixed clonal mixtures lower-yielding individuals will be predominantly rejected if one applies non-systematic artificial thinning procedures. If this larger or lower yielding-capacity reflects a non-environmentally induced clone-specific genetic property, such a thinning approach will result in an increased frequency of the individuals of the higher-yielding clones in the final composition of the clonal mixture compared to the initial composition of the clonal mix. Correspondingly, a decrease of the proportions of the lower-yielding clones will be observed.

Summarizing these facts, we may confirm and justify the required assumption of a proportionality between 'survival' and 'yielding ability'. Under the circumstances described above, this proportionality will be a common situation rather than a quite particular case. The results and conclusions of this paper, therefore, may be considered to be of significant practical relevance and interest.

But, nevertheless, there may be also situations where this assumption doesn't hold. For such cases the previous results and conclusions cannot be applied.

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# Changes in Genetic Parameters and Ranks of Tree Height over Six Growth Years in Tecomella undulata (Sm.) Seem

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(Received 5th December 1990)

### Abstract

Eleven half-sib plant progenies of *Tecomella undulata* (Sm ) Seem were established during 1984. Tree height for six growth years was recorded. Progenies showing good growth in the initial stages were not necessarily performing the same in subsequent years. There were significant differences among the progenies over all the six growth years. Estimates of family heritability, single tree heritability and genetic gains from family and mass selection indicated that the gains were low with both the methods. As components of variance tend to stabilize after fourth year of growth, selection done in the earlier years may not be rewarding. Low values of heritability and genetic gains from family and single tree selection suggested that there is need for other selection procedures for higher genetic gains for tree height.

*Key words: Tecomella undulata*, height growth, half sib progeny trial, heritabilities, family vs. mass selection.

### Introduction

*Tecomella undulata* (Sm.) Seem, an important multipurpose tree of Indian arid zone has been widely exploited for carving, furniture and agricultural implements. As a result population of *T. undulata*, particularly the trees with desirable attributes is going down drastically. Till 1983, however, no effort had been made to understand the variability *in situ* to collect the desirable types and use them in genetic improvement programme. Surveys were undertaken to assess the variability *in situ* for various morphological traits and foliage quality characters (Jindal *et al.*, 1987a and b). Exploitation of germplasm collected during the surveys necessitated the study of between and within family variability and changes in genetic parameters over growth years. Hence eleven half-sib plant progenies trial was established in 1984 to predict the genetic gains from single trees and family selections.

### Material and Methods

During May 1983 survey of *T. undulata* was conducted and 24 plus trees were identified from different parts of Rajasthan. Seeds from these trees were collected and the progenies were evaluated in nursery for many seedling characters. Eleven progenies were transplanted in the field in July 1984 in a randomised complete block design with three replications. Plot size was of two rows, each row accommodating 7 plants. Tree to tree distance within and between rows was 3 m x 3 m. Tree height on all the surviving plants was recorded every December from 1984 to 1989. Some plants which were apparently dead in first or second year showed regeneration. Data of such trees was not included in statistical analysis. Data were