

# An Algorithm for Increasing the Genetic Quality of Seed from Seed Orchards by using the Better Clones in Higher Proportions

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## Abstract

Traditional clonal seed orchards are established using clones in equal proportions. When there is information on the genetic value of individual clones there is good reason to use better clones in higher proportions. An algorithm is presented for calculating suitable proportions for each clone, and incidentally for calculating the appropriate number of clones. It is assumed that there is a negative effect of having a clone in a high proportion which is proportional to its representation in the seed orchard. A single factor was used to incorporate certain assumptions about heritabilities, juvenile-mature correlations and the like. The optimal representation of a clone in the orchard was found to be linearly dependent to its genetic value.

Numerical examples in which selections for inclusion in a seed orchard are based on progeny trial results are given and indicate that the genetic gain in plantations derived from orchard seed may be increased by 7–15% using the suggested algorithm compared with the best choice of clones in equal proportions.

*Key words:* Breeding value, clone, genetic gain, *Pinus radiata*, seed orchards.

## Zusammenfassung

In der traditionellen forstlichen Samenplantage sind alle Klone zu gleichen Anteilen vertreten. Falls Zuchtwerte für die Klonkandidaten zur Verfügung stehen, bestehen gute Gründe die besseren Klone mit erhöhten Rametzahlen zu verwenden und damit ungleiche Klonanteile herbeizuführen. Ein Algorithmus macht es möglich, relative Klonanteile (Rametzahlen) für verschiedene Klone und auch eine optimale Klonzahl als solche zu berechnen.

Die optimale relative Frequenz von Klonen in einer Samenplantage ist direkt proportional zum relativen Zuchtwert der Klone.

Einige Beispiele an Hand von Ergebnissen von Nachkommenschaftsprüfungen lassen erkennen, daß der Anbauwert von Plantagenachkommen bei ungleicher, relativer Klonbeteiligung um 7 bis 15% über dem Anbauwert von Nachkommen bei gleichen Klonanteilen liegen kann.

## Introduction

There are disadvantages in having small numbers of clones in a seed orchard such as increased levels of pollination between ramets of the same clone (selfing), leading to inbreeding depression in plantations. Having only a few clones also leads to decreased levels of genetic diversity in plantations which could lead to greater risk in the event of disease. LIBBY (1982) has suggested that the most robust strategy for clonal forestry is to use a mixture of from 7–25 clones. Seed orchards go through genetic recombination

before the seed is produced and so each resultant tree is genetically unique. Thus the risk due to lack of genetic diversity in clonal seed orchards of few clones is probably less than for clonal forestry. A seed orchard could consist of many clones, but with only a few in large proportions. The disadvantages are caused by the high proportion of clones rather than the low numbers as such.

It is becoming more common for progeny test and other information to be available about the genotypes, which are possible candidates for cloning in a seed orchard, and so they can often be ranked according to their genetic value. The usual way of utilizing this information is truncation selection. All genotypes above a certain value are utilized, all below that value are rejected. It is possible to trade-off the advantage of high breeding value against the disadvantage due to high proportion in a seed orchard in a more sophisticated way. For any given level of genetic gain the higher the breeding value, the greater the proportion in the seed orchard that can be sustained. It follows that clones with high breeding value should be used in higher proportions than clones with lower breeding values, as suggested by LINDGREN (1974). In other words, better genotypes should be exploited more, which may actually be seen as the most fundamental rule of breeding. The present paper develops an algorithm for calculating the optimal set of proportions for different clones. The algorithm also calculates or suggests the optimal number of clones to be included in unequal proportions. For comparison, a technique (derived from LINDGREN 1974) to calculate the optimal number of clones in equal proportions is also presented.

The concept of the number of clones in seed orchards deserves further attention than is possible here, especially as there are some indications that the optimal number may often be rather small when dealing with clones where information is available on their genetic value (LINDGREN, 1974). Most managers of clonal seed orchards have tended to be conservative in their approach to the numbers of clones to include. There are examples of orchards with more than 50 clones, but most have between 20 and 40. The reason for choosing this number is to keep inbreeding low (often assumed to be proportional to  $1/n$  where  $n$  is the number of clones in the seed orchard) and to keep the genetic base broad (see GIERTYCH, 1975). However, it is possible to retain genetic diversity within a breeding population and yet maximize genetic gain in plantations by keeping breeding populations separate from seed production populations (e.g. LINDGREN and GREGORIUS, 1976). Such an approach would lead to a reduced need for large number of clones in the seed orchard itself. The algorithm suggested here does not present a single solution for all seed orchards. It presents a method for obtaining the appropriate

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solution for any particular planned seed orchard given estimates of breeding values as well as factors (such as heritability) involved in calculations of various multipliers. The algorithm suggests a superior alternative to any solution using a fixed number of clones in equal proportion.

### Model and mathematics

We assume there are  $m$  unrelated (or with the same degree of relationship) candidate clones, from which  $n$  are to be included in a clonal seed orchard. The expected breeding value of the  $i$ th clone is  $g_i$ . The proportions of ramets of different clones selected for the seed orchard is allowed to vary, the proportion of the  $i$ th clone being  $p_i$ ; where

$$0 \leq p_i \leq 1 \text{ and } \sum p_i = 1$$

There is some disadvantage in having a clone in a high proportion, which we assume may be expressed on the gain scale by the term  $cp_i$  where  $c$  is a constant. If the advantage of having clone  $i$  in proportion  $p_i$  is expressed as  $p_i g_i$ , the corresponding disadvantage is assumed to be  $cp_i^2$ . It may be considered that from the genetic value of clone  $i$  ( $g_i$ ), a disadvantage term  $cp_i$  is subtracted, making the net gain  $g_i - cp_i$ . The value of  $g_i$  must be expressed on a scale commensurable with  $cp_i$ , which frequently makes it necessary (but not simple) to introduce a multiplier to scale  $g_i$  suitably. We also assume that the  $g_i$ 's are ordered according to size such that  $g_i$  has the highest value.

The expected genetic value of the seed orchard crop will be:

$$G = \sum G_i = \sum p_i (g_i - cp_i) = \sum p_i g_i - c \sum p_i^2 \quad (1)$$

The arguments why  $\sum cp_i^2$  (or  $cp_i$ , if expressed on the level of individual clones) seems to be a relevant expression of disadvantage are as follows:

1. The disadvantage of increased selfing is approximately proportional to  $p_i$ .
2. The probability that an adjacent tree in the resulting stand will have a common ancestor will be approximately proportional to  $p_i$ .
3. The occurrence of inbreeding other than selfing in the resulting stand will be approximately proportional to  $p_i$ .
4. The value of an individ  $i$  is given by the variable  $X_i$ , there  $\text{Var}(X_i) = \text{Var}(X)$  for all  $i$ .  $\text{Var}(\sum p_i X_i) = \sum p_i^2 \text{Var}(X)$ . This implies that the variation of the expected average performance of the seed orchard crop (in characters not closely correlated to  $g_i$ ) is linearly dependent on  $\sum p_i^2$ . Examples of such characters are (1) characters not selected for, like disease resistance in a diseasefree environment; and (2) interactions like those expressed in the concepts "genotype-environment interaction" or "stability".

The actual value of  $c$  is not the same in all instances, but may be estimated as in the numerical examples (cf LINDGREN, 1974 for discussion and an example of numerical evaluation of  $c$  considering only selfing). A more detailed consideration of the best value of  $c$  is beyond the scope of this paper. Factors we consider may be of relevance for the occurrence of selfing are listed below. For each factor a numerical value may be assigned and their product is " $c$ ". Some, but not all, factors are relevant when considering disadvantages other than selfing for clones in higher proportion.

1. The frequency of self-pollination will differ from  $1/n$ ,

2. shielding effect (selfing reduced by avoiding placing ramets of the same clone together),
3. proportion of inbred seed differs from proportion of inbred pollination,
4. lower germination of inbred seed,
5. lower viability of inbred seedlings before planting,
6. lower yield of inbred plants.
7. correction for compensatory growth of mixtures.

Our estimation of a typical value of the product of all these factors is  $c = 0.1$  when only the inbreeding effects from self-pollination are considered and 0.25 if other disadvantages of large proportions are also considered. As there is no appropriate quantitative genetic model describing the losses due to low genetic diversity, the value of  $c$  is not certain. However it is unlikely to be large as decreased yield in e.g. pure full sib families compared to more diverse materials has not been reported in the literature. A seed orchard crop consists of a large number of full sib families.

The optimum vector ( $p^*$ ) is the one giving the highest possible value of  $G$  which we call  $G_{\max}$ .  $G$  is maximised by

calculating the partial differential,  $\frac{\partial G}{\partial p_i}$ ; and finding the

values of  $p_i$  for which  $\frac{\partial G}{\partial p_i} = 0$ . To meet the constraint

$\sum p_i = 1$ , we introduce the term  $p_k$  (the proportion of the  $k$ th clone) which is expressed in terms of  $p_i$ . Thus

$$p_k = 1 - p_i - S1 \quad (2)$$

where  $S1 = \sum_{j \neq i, k} p_j = 1 - p_i - p_k$  (the use of  $j$  here is arbitrary).

Now (1) may be written as a function of  $p_i$  and the partial derivative evaluated.

$$G = p_i (g_i - cp_i) + S2 + (1 - p_i - S1) (g_k - c(1 - p_i - S1)) \quad (3)$$

where  $S2 = \sum p_j (g_j - cp_j)$

$$\text{Now } \frac{\partial G}{\partial p_i} = g_i - 2cp_i - g_k + 2c(1 - p_i - S1)$$

$$\text{Substituting } 1 - p_i - S1 = p_k; \frac{\partial G}{\partial p_i} = g_i - g_k - 2c(p_i - p_k) \quad (4)$$

$$\text{When } \frac{\partial G}{\partial p_i} = 0 \text{ then } p_i = (g_i - g_k)/2c + p_k \text{ provided } p_k \geq 0 \quad (5)$$

Now the second derivative  $\frac{\partial^2 G}{\partial p_i^2}$  is always negative ( $= -4c$ ) for any value of  $c$  greater than 0. Thus the point where  $\frac{\partial G}{\partial p_i} = 0$  is a maximum. Equation (5) implies that once any  $g_k$  and  $p_k$  are known, the  $g_i$  and  $p_i$  can be calculated.

According to (5)  $p_i$  is linearly dependent on  $g_i$ . Values of  $p_i$  below zero are not acceptable, because proportions cannot be negative. Consequently, there must be a value  $g_0$  corresponding to  $p_0 = 0$ . This value represents the highest genetic value of a clone which is not included (i.e.  $p_0 = 0$ ) in the seed orchard.

$$\text{Thus if } g_i > g_0 \text{ then } p_i = (g_i - g_0)/2c; \text{ or if } g_i \leq g_0 \text{ then } p_i = 0 \quad (6)$$

$$\text{As } \sum p_i = 1; \sum (g_i - g_0)/2c = 1 \quad (7)$$

$$\text{Rearranging (7); } g_0 = \bar{g} - 2c/n \quad (8)$$

where  $\bar{g} = \sum_{i=1}^n g_i/n$

and where  $n$  is the number of clones whose proportions  $p_i > 0$ . The value of  $n$  can be obtained by calculating trial values for  $g_0$  (and also  $\bar{g}$ ) starting with the clone of highest breeding value and working down the ordered list until  $g_0$  is greater than the corresponding value of  $g_j$ . Once the values for  $n$  and  $g_0$  have been calculated, the set of optimal proportions expressed as the vector  $(p^*)$  can be calculated from (6).

### Examples

#### 1. Hypothetical example

To illustrate the suggested algorithm, calculations are carried out on two examples, the first of which is hypothetical in order to obtain a 'typical' distribution of breeding values. We assume there are 50 progeny tested clones whose estimated breeding values ( $g_i$ ) are proportional to the expectation of ordered values taken at random from a Standard Normal Distribution. These values were obtained from HARTER (1970) and are listed in Table 1 col. 2 ( $\xi(j,50)$ ). If only one clone were selected out of a possible 50, this would correspond to a selection intensity of 2.249 (LINDGREN and NILSSON, 1985). The selection intensities for up to  $n$  clones selected out of the 50 candidates ( $i(n,50)$ ) are presented in Table 1 col. 3 as they represent averages of  $\xi(j,50)$  values for  $j = 1, 2, \dots, n$ . The values of  $\xi(j,50)$  are multiplied by 0.04, a multiplier which reflect the likely heritability, the fact that the measured characters are not the same as those at harvest and the change in variation between measurement and harvest and is intended as a realistic estimate of what may be obtained on a production scale. These values of  $0.04 \times \xi(j,50)$  are presented in Table 1 col. 4. LINDGREN (1974) suggested some possible values for the multiplier  $c$ . Based on more careful considerations we estimate  $c = 0.1$  for this hypothetical example. The value of  $n$  was found to be 10, as  $g_{10}$  is not below the corresponding estimate of  $g_0$  (see Table 1 col. 8) and  $g_n$  cannot be less than  $g_0$  (a condition of (6)). The corresponding value of  $g_0 = 0.0349$  was used and  $(p^*)$  calculated from (6). The results are presented in Table 1 col. 5. Although it would appear that  $n = 9$  would give identical results (Table 1), in

fact  $p_{10}$  is positive but is close to zero and is rounded to 0.0000. The expected genetic value of the seed orchard crop in the optimal mixture ( $G_{\max}$ ) was calculated by summing the individual contributions of clones ( $G_j$ ) according to (1) and is shown in Table 1 col. 6.

In Table 1 col. 7, values of gain for the option of using clones in equal proportions ( $n = j$ ) are given. The number of clones when used in equal proportions giving the maximum gain is  $n = 6$  and yields a  $G$  of 0.0483. Our suggested procedure gives  $G_{\max} = 0.0517$  (Table 1 col. 6) which is 0.0034 or 7% ( $= 100(0.0517-0.0483)/0.0483$ ) greater than the best possible value obtained by using clones in equal proportion.

#### 2. Example using real data

In this example the algorithm is applied to some published data of MATHESON and RAYMOND (1984) on *Pinus radiata* in Australia. The data involved 30 open-pollinated families planted in 11 field trials throughout the country. The families were derived by open-pollination from clones in the Tallaganda seed orchard (see BROWN 1971). For this example we assume that they form 30 candidate clones for a seed orchard.

Because the data were derived from real progeny tests where some specific information was available, we recalculated the value of the multiplier for breeding values. Firstly, the experiments were measured at about 1/4 rotation age. According to LAMBETH (1980) the (age 1): (age 2) regression should be  $1.02 + 0.308 \ln 0.25 = 0.6$  in this case (if applicable — LAMBETH used phenotypic correlations for heights so the regression should only be used with caution). The average diameter at all 11 sites was 14.72 cm. Thus a 'breeding value' of 1 cm corresponds to 0.0679 if expressed as a proportion. If we consider volume rather than diameter then the value per unit gain would be about 2.5 times as much as for diameter. The coefficient of variation of the data when harvested could be expected to be 0.8 of that at measurement. Differences in silvicultural techniques and future use and environmental conditions will introduce a factor of about 0.7. Another factor to be consi-

Table 1. — Results of comparing a hypothetical seed orchard selected from 50 possible candidate clones whose breeding values are assumed to be proportional to those of a Standard Normal Distribution. Col 1 ( $j$ ) is the number of clones, col 2 ( $\xi(j,50)$ ) are the order statistics of the Standard Normal Distribution taken from HARTER (1970). Col 3 ( $i(j,50)$ ) are selection intensities derived from the order statistics and are used in 'the calculation of the equal proportion option (col 7). The selection intensities are the difference between the mean of the selected clones and the overall mean (0 in this case). Col 4 is the breeding values ( $=0.04\xi(j,50)$ ) and col 5 presents the vector  $[p^*]$  of optimal proportions. Col 6 gives the genetic contribution ( $p^*(g_j-0.1p^*_j) = G_j^*$ ). Col 7 presents the genetic value ( $= 0.04i(j,50)-0.1/n$ ) of having  $j$  clones in equal proportion. Col 8 gives the 'trial and error' values of  $g_0 = \bar{g}-2c/n$ , where  $c=0.1$ .

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
$j$	$\xi(j,50)$	$i(j,50)$	$g_j=0.04\xi(j,50)$	$[p^*]$	$G_j^*$	Genetic value for equal proportions	$g_0$
1	2.249	2.249	0.0900	0.275	0.0172	0.0100	
2	1.855	2.052	0.0742	0.197	0.0107	0.0321	
3	1.629	1.911	0.0652	0.151	0.0076	0.0431	
4	1.464	1.799	0.0585	0.118	0.0055	0.0470	
5	1.331	1.705	0.0532	0.092	0.0040	0.0482	
6	1.218	1.624	0.0490	0.069	0.0029	<u>0.0483</u>	
7	1.119	1.552	0.0448	0.050	0.0020	0.0478	
8	1.030	1.487	0.0412	0.032	0.0012	0.0470	0.0345
9	0.949	1.427	0.0380	0.015	0.0006	0.0460	0.0349
10	<u>0.873</u>	<u>1.372</u>	<u>0.0349</u>	<u>0.000</u>	<u>0.0000</u>	<u>0.0449</u>	<u>0.0349</u>

$\sum p_j^* = 1.000$   
 $G_{\max} = 0.0517$

dered is the standard deviation of breeding values scaled to the total phenotypic variation. An expression for this is the square root of the heritability which was estimated to be 0.88, thus the correction factor here will be  $(\sqrt{0.88} = 0.94)$ . All these factors multiplied together are:

$$0.6 \times 0.0679 \times 2.5 \times 0.8 \times 0.7 \times 0.94 = 0.054.$$

The other calculations were carried out as before, except that the mean values were multiplied by 0.054 rather than by 0.04. We used a value of 0.25 for  $c$  this time because we wished to take all disadvantages of large proportions into account, not just self-pollination. The results are presented in Table 2 where column 1 gives the clone name. The other columns are the same as for Table 1 except that columns 3 and 4 are derived from real data instead of being taken from tables of the Standard Normal Distribution. In this case 13 clones were included before the estimate of  $g_0$  fell below  $g_j$ . The expected maximum gain for the equal proportion option occurred at  $j = 10$  (i.e. for 10 clones in equal proportions) and was 0.03685 compared with gain made by using  $(p^*)$  which summed to 0.04255. Thus the suggested procedure yielded an expected gain 14.9% higher than the best equal proportion option.

### 3. Application for a real seed orchard

During the spring 1985 the algorithm was utilized for calculating the number of grafts for a Scots pine seed orchard ( $T_{10}$ ) intended to serve low altitudes at around latitude  $64^\circ$  in Sweden.

There were 208 progeny tested clones available in six different trial series. "Conventionally" the 20 top ranking of these would have been selected. Ranks were converted to standardised values using  $\xi(j, 0.8m)$ , where  $m$  is the number of clones tested in the particular series (six different  $m$ -values). The factor 0.8 was introduced as it was predicted that 20% of the clones would be discarded because of their orchard characters (like graft incompatibility, no flowers etc). The assigned ordered values are denoted  $x_i$ . Formula (1) is applied in the following modified way:

$$G = \sum p_i(x_i - Cp) \quad (9)$$

where  $C = c$  divided by the multiplier required for proper scaling, so that the standard deviation of the adjusted breeding values equals 1.

The parameter  $C$  of formula (9) was calculated as the value giving  $n = 20$  the optimal solution of  $G = \sum(x_i - C/n)/n$  (For equal proportions,  $p_i$  of (9) may be replaced by  $1/n$ ). An optimal solution using (6) was found comprising 32 clones. Some bad cone producers were discarded, as was a single extremely early flowerer. The proportion of grafts was increased for a few genetically good clones with a low cone producing capacity with intention of raising their genetic contribution to the calculated  $p_i$ s. The resulting seed orchard comprised 28 clones. The 8 best were estimated to contribute 52.2% of the genes. The proportion of the best clone was 7.8%. Compared to the conventional alternative, with the 20 top ranking clones in equal proportions, the following estimations were done:

Genetic gross gain ( $\sum p_i g_i$ ) increased	4.5%
"Disadvantage" (inbreeding etc) decreased	7%
Genetic net gain increased	8.8%
Cone production increased	2%.

### Discussion and Conclusion

This paper presents a possible way of increasing the gains to be made from seed orchards by increasing the propor-

Table 2. — Numerical example taken from real data (diameters measured at 1.3 m height — originally published by MATHESON and RAYMOND 1984). Here there were 30 possible candidate clones which had been progeny tested on 11 sites in Australia. The disadvantage of having a clone in proportion  $p_i$  is  $cp_i$  where we assume  $c$  is a single factor for all clones and in this case is assumed to be 0.25. Col 1 is the name of the clone (as in the Australian Register of plus trees). Col 2 is the number of clones — as in Table 1. Col 3 is the estimated breeding value (= twice the deviation of the family mean diameter from the overall mean in cm; from MATHESON and RAYMOND 1984) and col 4 is the average breeding values of  $j$  selected clones ( $i(j)$ ) as in Table 1). Col 5 is 0.054 times the breeding values  $g_j$  as in Table 1), Col 6 is the optimum proportions  $[p^*]$ , Col 7 is the genetic contribution of each clone  $G_i$  to the maximum  $G_{max}$ . Col 8 is the value of the seed crop given  $j$  clones in equal proportions (cf col. 7 Table 1). Col 9 is the estimate of  $g_0$  for  $j$  clones.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Clone	j	standardised $\xi(j)$	$i(j)$	$g_j$	$[p^*]$	$G_i$	$.054(i_j) - c/j$	$g_0$
		fam mean						
12038	1	1.819	1.819	.0983	0.164	.00939		
12423	2	1.796	1.806	.0970	0.162	.00915		
80055	3	1.416	1.678	.0766	0.121	.00560	0.0073	
12351	4	1.276	1.578	.0690	0.106	.00450	0.0227	
12236	5	1.128	1.488	.0610	0.090	.00346	0.0304	
12412	6	1.064	1.418	.0576	0.083	.00305	0.0349	
12447	7	0.780	1.327	.0422	0.052	.00152	0.0360	.00019
12315	8	0.750	1.255	.0406	0.049	.00139	0.0365	.00524
12408	9	0.725	1.195	.0392	0.046	.00128	0.0368	.00900
10954	10	0.696	1.146	.0377	0.043	.00116	0.0369	.01187
12378	11	0.611	1.098	.0330	0.034	.00083	0.0366	.01379
12349	12	0.551	1.052	.0299	0.027	.00063	0.0360	.01512
12294	13	0.539	1.013	.0292	0.026	.00059	0.0354	.01620
10957	14	0.297	0.962	.0161	0.000	.00000	0.0341	.01619

$G_{max} = 0.04255$

tions of the most desirable clones. It has been shown from both hypothetical and real data the gains to be made are appreciable. Gain has been expressed in production terms in our examples — the value of  $G_{max} = 0.0517$  in Table 1 represents a gain of 5.17% in "productive value". For the example involving clones from the Tallaganda Seed orchard the best clone (12038) should have a proportion of over 16% because its superior performance enables it to make up for the disadvantages of having it in such a high proportion. The gain estimated for this example was 4.255% as opposed to 3.685% for the best equal proportion option. The actual estimates for gain are dependent on the values chosen for  $c$  and for the multiplier (.04 in the first example and .054 in the second). For simplicity we considered  $c$  to be a constant, but in some circumstances it may be a function or a vector with different values for each clone under consideration. These possibilities do not affect the general thrust of the arguments, or the assumption that there is a disadvantage roughly proportional to  $p_i$ . However there should be an added gain by using variable proportions whatever values are chosen because they are included in the calculations of the equal proportion gain as well as the variable proportion gain. By using our algorithm instead of using equal proportions, whatever gain may be made by selection of clones on the basis of their progeny test, gain can be increased by up to around 15%.

It may be argued that to decide an optimal number of clones for a seed orchard in a certain situation is equivalent to assigning a particular relation between the value of  $c$  and the multiplier. Often, the decision on the number of clones in a seed orchard is based on subjective values or on legislative constraints. Assuming these numbers are optimal, it will always be possible to find a better solution by using the clones in different proportions, as was done in

example 3. As the number of clones actually increases, the solution ought to be emotionally acceptable.

The term  $\sum cp_i^2$  may be regarded as a "risk" factor or "disadvantage" factor. It is also closely related to the importance of genotype  $\times$  environment interaction. Preliminary calculations suggest that  $\sum cp_i^2$  is not higher for the optimal unequal proportion solution compared to the equal proportion solution for the same  $c$ . Actually it may sometimes be a little lower. The algorithm suggest making greater use of the best clones, but also using more clones, than the conventional solution. The algorithm may be claimed to produce solutions with a higher net gain with no significant drop in safety, diversity or stability.

There are many factors not taken into account in this paper. We have assumed that the disadvantage of a clone due to its being more frequent is proportional to  $p_i$  with a constant proportionality factor  $c$ . But the relative disadvantage of clones may well vary. Data from *P. radiata* in Australia (MATHESON and GRIFFIN 1984 unpublished) suggests that inbreeding depression varies significantly between the same families as used in the example in this paper. This means that  $c$  is not a constant but a vector ( $c_i$ ) instead. However the values of ( $c_i$ ) are rarely known and it might be just as well to use some average figure. If the values are known with satisfactory accuracy, ( $c_i$ ) may be used instead of  $c$ .

The contribution from different clones can be affected by phenological variation and could be modified by a factor to take this into account. The algorithm yields the optimum proportions of gametes of the clones and the actual clonal proportions should reflect variations in gamete production to achieve the desired proportions of gametes. In example 3 it is exemplified that some modification was done based on cone production.

The suggested algorithm depends on the proportion ( $p^*$ ) being linearly dependent on the genetic values obtained experimentally. The estimates of genetic values are frequently not very reliable and this would certainly affect the values obtained for ( $p^*$ ). However, given the data available, the formula proposed here probably still suggests the best proportions in the mix of clones in the seed orchard. If the information changes as time goes on, the orchard could be thinned towards a new "best" mix calculated from the new information. The algorithm suggested may be of great assistance when practising genetic thinning of existing seed orchards. The multiplier 0.04 is only an esti-

mate for a "typical" situation but if additional information is available another multiplier could be calculated, as shown in example 2.

In an advanced-generation breeding program there will be related candidates for seed orchards which would cause complications to our model. The question also arises for combined selection based on phenotype, progeny test plus information from other types of relatives. However, we would still recommend that the better clones be used in higher proportions even in this more complex situation. A particularly satisfactory feature of this algorithm is that it can be made to apply to multiple characters. Scores from any kind of selection index (expressed on a production scale) may be used instead of breeding values without loss of validity.

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## Genotype-Environment Interaction and Stability in Ten-Year Height Growth of Norway Spruce Clones (*Picea abies* Karst.)

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#### Abstract

Norway spruce cuttings of 40 clones were tested on seven contrasting sites in northern Germany. Analysis of variance for ten-year height growth indicate a highly significant clone  $\times$  site interaction. This interaction may be reduced

by selection of stable clones. Several measures of stability were calculated and discussed. Characterization of sites by the method of genetic correlation indicate that most of the interaction is being generated between sites of high and low elevation. Stratification of the area into two planting