

with propagation time and the variance among cuttings from a single stock plant. In our tests, we observed wide variation among cuttings taken from a single 40 cm-long shoot. On the other hand, it is well documented (HARTMANN and KESTER, 1975; FEGE, 1983) that variation in the physiological quality of stock plants induced by major environmental differences will influence propagation success. It has also been noted (FARMER *et al.*, 1986) that primary ramet effects can account for variance in first year growth (including number of primary roots) of balsam poplar cuttings. However, in the study of FARMER *et al.* (1986) primary ramets (the source of cuttings) were grown in separate pots rather than a nursery, and there were other experimental conditions which differed from this test. Thus work to date on balsam poplar indicates that "C" effects may be highly variable from test to test, depending upon the nature of preconditioning, the characteristics observed and the environmental conditions under which they are observed. While this does not reduce their importance, it does make evaluation of "C" effects complex and generalization inappropriate.

#### Acknowledgement

This study was supported by an Operating Grant from the Natural Sciences and Engineering Research Council of Canada.

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## Genetic Consequences of Combining Selective Cone Harvesting and Genetic Thinning in Clonal Seed Orchards

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(Received 23rd December 1987)

#### Summary

For a clonal seed orchard with progeny-tested clones, there are two options to increase the genetic gain, selective cone harvest and genetic thinning. This paper evaluates the effect of combining these two options. Formulae are given to calculate consequences on genetic gain, effective population size (these two effects are tabulated), selfing, and flexibility. Selective harvesting and genetic thinning regimes that maximize genetic gain at a preset effective population size were calculated. An example was given to demonstrate how to choose a thinning regime, given a certain fraction of clones which must be harvested. In a situation where seed orchards produce surplus seeds, a combination of selective harvesting and genetic thinning may often be more beneficial than a more intensive ge-

netic thinning. Also, optimal clone number when all clones are harvested is calculated.

*Key words:* Genetic gain, genetic diversity, selfing, roguing, cone harvest, clonal number.

#### Zusammenfassung

Die Konsequenzen selektiver Klonbeerntung und genetischer Durchforstung in Klonsamenplantagen

In nachkommenschaftsgeprüften Samenplantagen gibt es zwei Möglichkeiten der Verbesserung: Klonweise Beerntung der besten Klone oder Entfernung der schlechtesten Klone. In diesem Beitrag wird die Möglichkeit untersucht, beide Verfahren zu kombinieren.

Formeln für Genetic Gain, effektive Populationsgröße (Tabellen), Selbstung und Flexibilität werden erläutert. Genetische Verbesserung durch verschiedene Alternativen von Klonbeerntung und Durchforstung, ausgehend von der gegebenen effektiven Klonzahl, werden berechnet. An einem Beispiel wird die Durchforstungsintensität demonstriert für den Fall, daß eine gewisse kleinste Anzahl von Klonsamen beerntet werden soll.

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Bei Überproduktion von Samen kann ein kombiniertes Verfahren vorteilhafter sein als die reine Durchforstungsalternative.

Optimale Klonanzahlen nach genetischer Durchforstung werden berechnet.

### Introduction

For existing clonal seed orchards there are two ways to increase genetic gain by utilizing progeny-test information. These are selective cone harvesting and genetic thinning. In the first case, cones are collected only from clones with high breeding value; thus, only seed parents are improved. In the second alternative pollen parents are improved as well as seed parents by the irreversible removal of clones with low breeding values. Selective cone harvesting has some advantages over genetic thinning, such as a larger genetic diversity, lower level of selfing and the flexibility to make adjustments to the genetic composition of the orchard at a later stage. As seed orchards mature, surplus production of seeds is rather frequent which makes the practice of selective cone harvesting an attractive alternative.

In this paper we present methods and calculations by which the genetic effects of different scenarios of selective harvesting, genetic thinning, and combinations of these two options can be evaluated.

### Model

We assume that there are  $n$  unrelated clones in a productive, genetically-tested seed orchard. The reproductive output (seed and pollen) of the clones is equal, and there is a panmictic situation (with some reduction as for as selfing is concerned). The clones are equally affected by selfing. If selective cone harvesting and/or genetic thinning were performed, based on progeny test information, then  $n_H$  represents the clones harvested for seeds and  $n_R$  represents the clones that contributed to the orchard's pollen. In this situation, the orchard pollen cloud is produced from  $n_R$  clones (Remaining clones), but the seed crop is produced only by the  $n_H$  clones (Harvested clones). When selecting good clones, a genetic gain is obtained. This gain is predicted to be proportional to the selection intensity ( $i$ ).

The expected genetic gain from the resultant seed crop will be:

$$G = i_e h^2 \sigma \quad (1)$$

where  $h^2 \sigma = \text{constant}$ , and  $i_e = (\text{"effective selection intensity"})$  the average of a female and a male component

$$i_e = 0.5 i(n_H, n) + 0.5 i(n_R, n) \quad (2)$$

The following measure of "effective population size" ( $N_e$ ) is used

$$N_e = (\sum f_i)^2 / \sum f_i^2 \quad (3)$$

where  $f_i = \text{contribution of the } i\text{th clone to the orchard's seed crop}$ , and  $1/2N_e$  corresponds to the probability that two alleles in the orchard crop are identical by descent (Li, 1974).

By suitable scaling  $\sum f_i = 1$ , but  $\sum f_i^2$  has to be calculated to get  $N_e$ . There are  $n_R$  pollen parents, thus the contribution on the male side is  $0.5/n_R$ , and for the unharvested clones  $f_i = 0.5/n_R$ . There are  $n_H$  harvested seed parents, and for them the contribution on the female side is  $0.5/n_H$ , thus for these clones  $f_i = 0.5(1/n_H + 1/n_R)$ . Forming sums first over the  $n_H$  harvested clones and then over the  $n_R - n_H$  contributing only as fathers, the following expressions were obtained.

$$\sum f_i = 0.5 ((n_H + n_R)/n_R + (n_R - n_H)/n_R) = 1$$

(which is trivial)

and

$$\sum f_i^2 = 0.25 \left( \sum_1^{n_H} ((n_H + n_R)/(n_H n_R))^2 + \sum_{n_H + 1}^{n_R} 1/n_R^2 \right)$$

Substituting the values of  $(\sum f_i)^2$  and  $\sum f_i^2$  in formula 3, a formula for effective population size is obtained:

$$N_e = 4n_H n_R / (n_R + 3n_H) \quad (4)$$

Examples:

(1) All clones are harvested for seeds,  $n_H = n_R$  inserted in (4) makes  $N_e = n_H$ . Thus the "effective" and the "real" numbers are identical.

(2) only very few clones of a very large number of clones are harvested for cones.

$$\lim_{n_R \rightarrow \infty} N_e = 4 n_H$$

Thus, if cones are picked from few clones in a seed orchard containing many clones, the effective number tends to be 4 times the number of clones utilized as seed parents.

Where inbreeding caused by interfertilization among ramets of the same clone (i.e., selfing) occurs, the effect of this will be:

$$d = c/n_R \quad (5)$$

where  $c = \text{constant}$ ,  $c \leq 1$ . ( $c$  depends on the unit in which  $d$  is expressed, e.g. "fraction of selfed seeds", "impact on forest production by selfing").

One reason to keep males in seed orchards with lower rank than the females is that they may improve in rank from later evaluation of progeny trials. E.g. new characters may be measured when progeny trials grow older or the improved juvenile-mature correlation with increasing age may make decisions at a more-advanced age more reliable. Thus, ranking for height growth is probably sufficiently good at 4 m mean height (cf LINDGREN, 1984), while wood density should be measured later. Assuming that we want to cull for a new character at a later stage, but still have a seed need corresponding to  $n_H$  clones, then the possible gain for the new character evaluated later will be proportional to:

$$i(n_H, n_R) \quad (6)$$

The following equation can be used for numeric evaluation of the benefits connected to certain clone numbers, and thus for choosing optimal clone numbers, if proper values can be assigned to the weighting factors ( $w_1 - w_4$ ):

$$B = w_1 g_1(n_H, n_R, n) - w_2 g_2(n_H, n_R) + w_3 g_3(n_H, n_R) + w_4 g_4(n_H, n_R)$$

The chosen expressions for the functions  $g_1 - g_4$ , outlined and motivated below, are inserted in the expression.

$$B = w_1 (i(n_H, n) + i(n_R, n)) - w_2/n_R - w_3/N_e + w_4 i(n_H, n_R) \quad (7)$$

Where:  $B$  is the benefit from different combinations of  $n_H$  and  $n_R$ .  $B$  represents "forest production" (or a similar measure of benefit). The factor  $w_1, w_2, w_3$  and  $w_4$  are relative weights put to different advantages and disadvantages associated to numbers of clones. The chosen designations of the functions  $g_1 - g_4$  are motivated as follows:

$g_1(n_H, n_R, n)$  is likely to be a good predictor of genetic gain,  $g_2(n_H, n_R)$  is likely to be a good predictor of losses due to selfing among different ramets of the same clone (cf LINDGREN, 1974) (selfing within a ramet is considered as a constant of no importance for the calculations carried out in this paper.),  $g_3(n_H, n_R)$  is used as a predictor of the

effect of diversity on benefit. The given formula of  $g_3 = 1/N_c$  assumes that the reduction in benefit is equivalent to the inbreeding in a hypothetical seed crop harvested from a stand established from the seed orchard crop. (Theoretically this is simple and logical, although there is not much empirical information. Actually, it is not even known for certain if diversity is always to the benefit of a seed orchard crop.), and  $g_4(n_H, n_R)$  is used as an evaluator of the advantage of being able to switch genetic composition of the orchard in the future and the option of dividing the harvest in different compartments for different uses. As there may be a lower optimal clone number later, the suggested function may underestimate the advantage.

We have assumed panmixia, which evidently is unrealistic. If the clonal contributions vary somewhat in a way uncorrelated to the genetic value of the clones, the terms  $w_1g_1$  and  $w_4g_4$  are not influenced (even if realized gains are more likely to deviate from estimated in either upward or downward direction). The  $w_2g_2$  and  $w_3g_3$  values are influenced in a more direct way. The influence on  $w_2g_2$  may be treated as a factor to be considered in the estimation of  $w_2$  (see LINDGREN, 1974, who estimated that the actual frequency of selfing in a seed orchard is 35% higher than it would have been in a seed orchard had each clone contributed equally to the fertilizing pollen cloud at each moment). For  $w_3/N_c$ , deviations from panmixia would justify a more complex formula for  $N_c$  than formula 4.

The entries are converted to fractions to make them less dependent on initial clone number ( $n$ ).

Let  $P_H = n_A/n$  and  $P_R = n_R/n$  (thus proportion of initial clones rather than actual clone numbers).

$$i_c = 0.5 i(P_H) + 0.5 i(P_R) \quad (8)$$

$$n_r = N_c/n = 4 P_H P_R / (P_R + 3P_H) \quad (9)$$

$$d_r = d_n/c = 1/P_R \quad (10)$$

where  $n_r$  is "the relative effective clone number" and  $d_r$  is "the relative selfing effect".

The following approximation was made to get formula 8:  $i(x, n) = i(x/n)$ . This way the calculations become independent of  $n$ . In a case where  $n$  is known it is recommended to use the exact values, which may be obtained by the aid of the methods described by LINDGREN and NILSSON (1985).

### Calculations

To calculate "the relative effective clone number" independent of  $n$ ,  $n_r$  was calculated from (9) using  $P_H$  and  $P_R$  as entries. Table 1 shows the "effective selection intensity" ( $i_c$  according to formula 8) and the "relative effective clonal number" under different harvesting/thinning situations.

A situation where inbreeding is constant for different  $P_H$  means that there is a constant number of clones after thinning, thus  $P_R = \text{constant}$ . Evidently, the lower the  $P_H$ , the higher the gain will be at a constant rate of selfing.

For a given  $n$  and  $N_c$ , there is a combination of  $n_H$  and  $n_R$  that maximizes  $i_c$ . To search for the maximum, we express  $n_R$  as a function of  $n_H$  and  $N_c$ . Formula (4) may be transformed to  $N_c(n_R + n_H) - 4n_H n_R = 0$ , from which  $n_R$  is solved:

$$n_R = 3n_H N_c / (4n_H - N_c).$$

Then dividing by  $n$ , the following expression is obtained:

$$P_R = 3P_H n_r / (4P_H - n_r) \quad (11)$$

Note that  $n_r \leq 4P_H$

Table 1. — "Effective selection intensity" ( $i_c$ , formula 8, proportional to genetic gain, upper numbers) and "Relative effective clonal number" ( $n_r$ , formula 9, lower numbers) arranged by the fraction of initial clones harvested for cones ( $P_H$ ) and fraction of initial clones remaining after genetic thinning ( $P_R$ ).

$P_H \backslash P_R$	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
.1	1.755 .100	1.577 .160	1.457 .200	1.360 .226	1.276 .250	1.199 .267	1.126 .280	1.052 .291	0.975 .300	0.877 .308
.2		1.400 .200	1.279 .267	1.183 .320	1.099 .364	1.022 .400	0.948 .431	0.875 .457	0.797 .480	0.700 .500
.3			1.159 .300	1.062 .369	0.978 .429	0.901 .480	0.828 .525	0.754 .565	0.677 .600	0.579 .632
.4				0.966 .400	0.882 .471	0.805 .533	0.731 .589	0.658 .640	0.580 .686	0.483 .727
.5					0.798 .500	0.721 .571	0.647 .636	0.574 .696	0.496 .750	0.399 .800
.6						0.644 .600	0.570 .672	0.497 .738	0.419 .800	0.322 .857
.7							0.497 .700	0.423 .772	0.346 .840	0.248 .903
.8								0.350 .800	0.273 .873	0.175 .941
.9									0.195 .900	0.097 .973
1.0										0.000 1.000

The evaluation has to consider the constraints that  $0 \leq P_H \leq P_R \leq 1$ .

Table 2 was calculated by fixing a value of  $n_r$ , "searching" different  $P_H$ -values, calculating the corresponding  $P_R$  (formula 11) and  $i_c$  (formula 8), and identifying the  $P_H$  maximizing  $i_c$ .

The calculations above can be seen as application of formula (7) for a few special cases. The relative weights  $w_2$  and  $w_4$  were put to 0 and proportions of clones instead of numbers were used.

An application of formula 7 in full was done. The following values were used:

$n = 50$ , which may be regarded as a typical value for seed orchards where genetic thinning is applied.

$w_2 = 0.1$  expresses the disadvantage of selfing between and within ramets. This assumes that the disadvantage is one tenth of the share of selfing pollen in a completely-panmictic seed orchard. LINDGREN and MATHESON (1986) (ex-

Table 2. — Values of  $P_H$  and  $P_R$  maximising  $i_c$  (formula 8) for a range of preset  $n_r$  values.

$n_r$	$P_H$	$P_R$	$i_c$
0.1	.055	.137	1.811
0.2	.113	.269	1.462
0.3	.174	.396	1.225
0.4	.238	.517	1.035
0.5	.307	.633	0.870
0.6	.382	.741	0.718
0.7	.467	.839	0.571
0.8	.569	.925	0.422
0.9	.712	.969	0.257

ample 1) used this value, and there is a case made for this particular value by LINDGREN (1987).

$w_3 = 0.1$  was chosen. That means the restricted diversity of a single fullsib family ( $N_e = 2$ ) used for planting a whole site would cause a loss of benefit of 5 percent. There are no reports evaluating the quantitative loss of benefit by using a single full-sib family, but if it was serious it is not likely that this effect would have passed unnoticed.

For  $w_1$  a range of values has been applied: 0.01, 0.02, and 0.05.  $w_1$  expresses the benefit connected to the genetic gain.  $2w_1$  corresponds to the benefit via increasing the selection criterion by one standard deviation. Estimates of  $w_1$  ("yield improvement") have been made by LINDGREN 1974 (p 303,  $r \sigma_A = 0.06$ )  $w_1 = 0.03$ , and by LINDGREN and MATHESON 1986 ("the multiplier" of example 1 = 0.04)  $w_1 = 0.02$ . We feel that  $w_1 = 0.05$  is a high value which can be justified only when there is extremely convincing documentation proving that large genetic gains can be made by selection based on progeny tests.  $w_1 = 0.02$  may correspond to a standard situation, while 0.01 may be a cautious estimate which could be used for young progeny trials with small wind-pollinated progenies.

$w_4$  was assumed either to be 0 or equal to  $w_1/2$ . The latter corresponds to a value of one quarter compared to the improvement in the primary character for the improvement of benefit created by one standard deviation increase for a secondary (uncorrelated) criterion of selection applied as tandem selection.  $w_4$  expresses the flexibility in obtaining improved gain by adjusting the seed orchard after later evaluations, or to use the harvests from different clones for different purposes. We do not feel it is likely that those options would amount to a value exceeding one quarter of the primary genetic gain. As keeping clones only as fathers in seed orchards will be made only when there is surplus seed and this situation is likely only in old seed orchards, where the value of flexibility for the future is limited, low values of  $w_4$  are likely in practical applications.

Searching for  $n_H$  and  $n_R$  values maximizing B,  $n_H = 1$  was found best. Thus, the fewer clones harvested, the higher the benefit. This extreme solution reflects the fact that seed requirements or seed price has not been considered. Instead, the problem was solved where the seed yield of  $n_H$  clones is sufficient for the coming years, and only  $n_H$  clones should be harvested. How many clones ( $n_R$ ) should remain in the orchard to maximize B? The answers obtained are listed in Table 3.

To get an impression of the optimal clone number in a thinned seed orchard over a wider range of genetic parameters, a special case studied by LINDGREN (1974) was extended. LINDGREN (1974) assumed  $n_H = n_R$ ,  $w_4 = 0$ ,  $w_3 = 0$ ,

Table 3. — Calculation of number of remaining clones ( $n_R$ ) which maximizes the benefit of a seed orchard (according to B, formula 7), provided a certain number of clones are harvested ( $n_H$ ). Fixed entries:  $n = 50$  (number of initial clones in seed orchard),  $w_2 = 0.1$  (importance of selfing),  $w_3 = 0.1$  (importance of effective clone number). Entries allowed to vary:  $n_H$ ,  $w_1$  (importance of genetic gain),  $w_4$  (importance of flexibility).

	$w_1$	.05	.05	.02	.02	.01	.01
	$w_4$	.025	0	.01	0	.005	0
$n_H$							
5		13	6	20	13	28	22
10		16	10	22	17	30	22
20		24	20	27	21	32	22

Table 4. — Optimal number of clones ( $n_{optimal}$ ) remaining of 50 initial clones after thinning of a seed orchard where all clones are harvested ( $n_H = n_R$ ). "Optimal" means maximizing benefit.

$(w_2+w_3)/w_1$	$n_{optimal}$
2	3
3	4
4	5
5	6
6	6
7	7
8	8
9	9
10	10
12	11
14	12
16	14
18	15
20	16
30	21
40	25

$n = 200$ ,  $w_1 = 0.03$ ,  $w_2 =$  different values to find the optimal number of clones in a seed orchard established with progeny-tested clones. Here we study genetic thinning of a seed orchard with  $n = 50$  initial clones as a function of  $(w_2 + w_3)/w_1$ . The number of remaining clones (assuming all are harvested) to maximize benefit are presented in Table 4.

### Discussion

Values of effective selection intensity ( $i_e$ ) and relative effective clonal number ( $n_r$ ) were obtained (Table 1). If genetic information of the orchard's clones to be utilized and a 90% genetic thinning is applied, the genetic gain will be high (1.755) and the genetic diversity will be low (0.1). On the other hand, if the orchard will be managed without the utilization of the genetic information and clones will be harvested from all clones, the genetic gain is nullified (0.0) and diversity is maximized (1.0).

Interpretation and discussion is easiest when one of the parameters concerned ( $i_e$  or  $n_r$ ) is constant and the other is variable. Table 1 provides an example when  $n_r$  is constant (0.8) under three different management options: firstly, when 80 % of the clones were harvested after the removal of 20% ( $P_H = P_R = 0.8$ ); secondly, when 60 % of the clones were harvested after the removal of 10% of the orchard ( $P_H = 0.6$  and  $P_R = 0.9$ ) clones and leaving 30% to participate in pollination only; thirdly, when 50% of the clones were harvested and the remaining were left to participate in the pollination. It is seen that the second option (i.e., combination between selective harvesting from the best clones and removal of the low-ranked clones) provided the highest genetic gain (0.419) compared to the removal of the low-ranking clones (0.350) or the selective harvesting without any removal (0.399).

Table 2 represent the maximal effective selection intensities (i.e., genetic gain) under a constant value of relative effective number of clones (i.e., diversity). Under any  $n_r$  value used, the maximal genetic gain was achieved only when a combination of genetic thinning and selective harvesting was used.

Seed demand, genetic gain, diversity, rate of selfing, level of contaminating pollen and the reliability of the progeny test information are among the factors a seed orchard manager should consider before a decision is made concerning genetic thinning and selective cone harvest. If there is a shortage of seed, obviously diversity will be favoured due to the inclusion of every clone in harvesting, or at least all clones whose progeny are expected to perform better than alternative seed sources. The lowest-ranking clones, based on progeny-test information, that perform worse than available, unimproved, seed sources could be removed even in a situation of insufficient seed orchard seeds. On the other hand, if there is a surplus of seed orchard seeds, then other factors could be considered. In that situation, selective harvesting and/or genetic thinning could be used. Results obtained from *Table 2* support the combination of both methods. If progeny test information were based on early assessment and the breeder wants to keep the option of adjusting the clonal composition following evaluation of the progeny tests at a more mature stage, then the option of selective harvesting without genetic thinning will be favourable and the entire genetic base of the orchard is maintained. If this decision is made, it is assumed that maintaining low-ranked clones is less harmful than eliminating intermediary ranking ones based on early assessment. Also, if low-ranking clones were consistent among all progeny test sites, then genetic thinning of those clones in combination with selective harvesting among the remaining clones will yield a highly favourable diversity. The removal of some clones, based on genetic thinning, will reduce the management costs and could also increase the outcrossing rate (EL-KASSABY *et al.*, 1986). Drastic removal of trees, on the other hand, will increase the impact of contamination due to reduced pollen production in the seed orchard. The situation is analogous to the higher contamination estimates in low cone years found by EL-KASSABY and RITLAND (1986) or in young orchards (EL-KASSABY *et al.*, 1987). A situation where maintenance of pollen production is important will favour selective cone harvest for improving genetic gain. It is also worthwhile remembering that a drastic reduction in the number of trees could increase the rate of selfing within ramets, with attendant losses in filled seeds and reduced vigour of progeny.

If a seed orchard serves a wide range of planting sites (e.g. harsher and milder sites) or possible uses, then selective harvesting could be conducted to provide seeds for specific planting locations or specific purposes, while the other clones contribute to diversity and reduction of selfing (i.e., pollen clones only), a situation proposed by VAN BUIJTENEN (1971). Thus, a large fraction of the clones may be harvested, but divided into different categories for different uses.

It has been demonstrated that if selective cone harvesting is practised to retain a large number of pollen donors, the effective clonal number tends to be 4 times the number of clones utilized as seed parents. Therefore, the practice of cone harvesting on a clonal basis and the establishment of plantations that consist of a mosaic of several clonal progenies is not as drastic as initially thought. Also, the utilization of a pollen mix derived from a few high-ranking clones for supplemental mass pollination applied to many females also shall not lead to an extreme depletion of genetic diversity.

The effect of the number of clones remaining after thinning ( $n_{11}$ ) on maximizing benefit, given that only a certain number will be harvested, is studied in *Table 3*. In situations where genetic gain obtained by utilizing the progeny test information is low, it seems to be reasonable to leave a large fraction of the clones, even if it is foreseen that only a few clones will be harvested and the flexibility is not regarded as valuable. For many situations, where the number of clones to harvest from can be reduced and still meet seed targets, it seems to be beneficial to leave clones for pollination only. It is not worthwhile to leave clones for pollination when there is no value in flexibility combined with either a high number of clones which have to be harvested or high expected genetic gain. If the expected genetic gain is low, the beneficial number of clones to leave is not strongly dependent on the number to be harvested, provided that number is low.

The optimal number of clones remaining after thinning, if the used values of genetic gain, selfing and effective population size are considered, is rather low (*Table 4*), and thus there are genetic arguments to cull intensively in seed orchards with many clones, if that can be done in an economic way.

In this paper we have assumed that all clones are present in equal proportions in the seed orchard and are represented equally in "flowering". LINDGREN and MATHESON (1986) have pointed out that, in seed orchards comprising clones with known breeding values, it is optimal to deploy clones in proportions linearly related to their breeding values. For thinning of seed orchards, the optimal strategy is certainly not to either cull or leave, but rather, for a number of intermediate ranking clones, to let the percentage of thinning be dependent on their breeding values. Such a strategy is compatible with the desire of a manager to allow for some factors other than clone ranking in thinning, such as tree spacing. Actually, one reason that it is optimal to have some clones contributing both as males and females, while others contribute only as males, is a utilization of the principle introduced by LINDGREN and MATHESON (1986) to allow the better genotypes to contribute more to the progeny of seed orchards.

We have assumed that all clones show an identical reaction to selfing. This is certainly not the case, and it is possible to extend the model to consider different reactions to selfing. One of the consequences is that a clone producing much selfed progeny should, preferably, be used as pollen donor only, while a clone which produces very little selfed progeny is more attractive for cone-harvesting than if judged from the breeding value alone.

In this paper, we have presented the two conventional approaches to seed orchard management (i.e., genetic thinning and selective harvesting) and also a new and novel approach involving their combination. (The approach may have been used in practice in some advanced programs the recent last years but without theoretical background.) We feel that information will be of value to seed orchard managers and tree breeders since it permits them to attain the desired genetic gain without unnecessarily sacrificing diversity and also provides them with the option of keeping the clones in the orchard for longer periods until later progeny-test evaluation which is most needed for traits like wood density.

#### Acknowledgements

This work was conducted while YUSRY A. EL-KASSABY was a Visiting Scientist at the Department of Forest Genetics and Plant

Physiology, Swedish University of Agricultural Sciences, Umeå, Sweden. The visit was supported by Bröderna Edlunds donationsfond kindly provided by the Committee for Planning and Budgeting of the Faculty of Forestry. We gratefully acknowledge the careful reading and helpful suggestions of M. D. MEAGHER, as well as for corrections suggested by R. D. BARNES. PETER KRUTZSCH formulated the German summary.

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## Genetic Variation Among Five Giant Sequoia Populations

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(Received 22nd March 1988)

### Summary

Rooted cuttings from five giant sequoia populations from the southern part of the species' range were planted in four blocks at a nursery in Moscow, Idaho. Significant genetic variation was found between populations in growth, crown form, patterns of cold acclimation, and cold hardiness, but not in phenology. Block effects were also strong. Six individuals were identified as potentially adapted to the planting site. Additional testing of these genotypes should be conducted on a broad range of sites in the future.

*Key words:* Giant sequoia, populations, cold hardiness, genetic variation, adaptation.

### Introduction

Giant sequoia (*Sequoiadendron giganteum* [LINDL.] BUCHHOLZ) is a popular ornamental in the United States, Europe, and Asia (MURI, 1978; LIBBY, 1981), although its current native range is restricted to a narrow strip (418 km long and no more than 24 km wide) on the west slopes of Sierra Nevada Mountains in California. Despite its broad popularity, few studies of population variation in this species have been reported in the literature.

Genetic variation among trees from different origins can be an especially important consideration when introducing a species as an exotic, particularly for characteristics that influence early survival. The few provenance studies that have been established with giant sequoia have demonstrated the existence of genetic variation among its populations. GUINON *et al.* (1982) found significant variation in frost resistance, winter damage and early height among two-year-old giant sequoia seedlings, which were sampled from 22 provenances grown in Escherode, West Germany. FINS (1979) and FINS and LIBBY (1982) found genetic variation in seeds and seedling characteristics among giant sequoias sampled from 34 native populations. MAHA-

LOVICH (1985) found small but significant differences between populations in early growth, and larger differences in crown shape and basal taper in young trees planted at Foresthill, California. And MELCHIOR and HERRMANN (1987) found significant differences in height, diameter at breast height and diameter at half height between four provenances of 14-year-old giant sequoias planted on three sites in West Germany. At the Rengsdorf site, height growth was slightly negatively correlated with elevation of the source.

The purpose of this study was to identify populations and/or individuals of giant sequoia that are potentially well-adapted to environments in northern Idaho. The early winter of 1983–84 provided an excellent opportunity to assess the response of young giant sequoias to early cold temperatures, as well as their ability to recover from cold damage. We measured genetic variation among five provenances in growth, phenology, cold-hardiness and crown characteristics.

### Materials and Methods

Study materials consisted of 174 rooted cuttings of giant sequoia from the Mountain Home, Garfield, Cedar Flat, Giant Forest and Whitaker populations, all in the southern part of the species' range. Cuttings were collected from one-year-old seedlings in October 1980, rooted during the winter of 1980–81, and planted in four blocks at a nursery site in Moscow, Idaho on June 31, 1981. A total of 200 cuttings were originally planted. All were in good to excellent condition at the time of planting. The plantation was watered during the first, second, and fourth summers. Survival was greater than 95% during the initial years of establishment, and dropped to 87% (174 trees) after the winter of 1983–84.

#### 1. Phenological and growth traits

This phase of the study began in July 1984, and continued through spring 1985. Total height and fourth year elongation were measured weekly, and diameter was

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