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Gains from the clonal and the clonal seed-orchard options compared for tree breeding programs

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Summary. Gains expected from clonal propagation of selections for plantation from a breeding population were compared with those expected from seed propagation via clonal seed-orchards of selections from the same breeding population. Assumptions were made about numbers of clones selected, size of the breeding population, relative sizes of additive and dominance genetic variance components and time required for various operations. Even when dominance variance is zero, considerable extra gain is obtained by the clonal option over the seed-orchard option; mostly due to the shorter time between selection in the breeding population and field planting. When dominance variance equals additive variance, the advantage of the clonal option due to time saved is approximately equal to the advantage due to genetics (i.e. use of more of the additive variance, use of non-additive variance and greater precision of selection). This means that there is a substantial gain to be made simply by getting superior genotypes into plantations more quickly via the clonal option. The gains obtainable through the use of clonal forestry may also be obtained through seed orchards, but some decades later. In no case was the seed-orchard option superior to the clonal option in terms of the gains obtained. No clonal propagation program can advance without a strong sexually-based breeding program to supply it with improved genotypes. The opportunity for improvement comes from genetic recombination.

Key words: Tree breeding – Clonal forestry – Seed-orchards – Genetic gains

Introduction

The aim of forest tree breeding is to provide material of high genetic quality for propagation in the short term as well as the long term. There are several ways in which superior material may be propagated for plantations, the most important ones being harvesting seeds from clonal seed-orchards and vegetative propagation of outstanding trees for direct use in plantations. The latter (the clonal option) has an ever increasing number of advocates who argue persuasively for investment in it (McKeand 1981).

This paper attempts to compare in quantitative terms the clonal option and the clonal seed-orchard option as methods of transferring genetic improvements made in a long-term breeding program to forest plantations and to evaluate the reasons for the advantage of one over the other.

Such a comparison cannot be made in general terms because each program, whether clonal or seed-orchard based, will vary in detail. To overcome this problem a model program must be used to allow detailed specifications of the alternatives to be compared.

Methods

Model specification

The basis of the model used in this paper is that at some time, T, in the future it will to desirable to establish a plantation of genetically-improved stock. The model predicts the gain in this plantation. There are two components in the production process. The first component is the long-term breeding population which is undergoing cycles of selection and testing; the second is the process of harvesting the gains made in the breeding population. We wish to compare two options for this process. The first option is the propagation of

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clones for direct use in the plantation at time T. Selections are made in this program at year $T - t_C$ (t_C is defined in Table 1). The second option for harvesting gains is the clonal seed-orchard program where a seed-orchard is established from clonal material which has been selected from the breeding population in year $T - t_S$ (see Table 1). The time when selections are made will depend on the relative rate of growth. We have considered two possible time scales for this, a relatively slow-growing species in Northern Europe, such as *Pinus sylvestris* or *Picea abies*, and a relatively fast-growing species such as *Pinus radiata* in Australia. Seed from the seed-orchard must be germinated and planted out in the plantation at time T. Each of the components and options is explained in detail below, but all are constrained by the same set of basic assumptions.

Basic assumptions

1. No epistasis. All genetic variance may be described in terms of additive (V_A) and dominance (V_D) variances.
2. The genetic variance between individuals ($V_A + V_D$) can be partitioned: within a full-sib family; $0.5\,V_A + 0.75\,V_D$; between full-sib families; $0.5\,V_A + 0.25\,V_D$.
3. The variance does not change from generation to generation.
4. The magnitude of the experimental error in clone/progeny tests depends on the size of the experiment. We assume that the experiments are sufficiently well-replicated to ensure the error is small in relation to the genetic effects and can be ignored.
5. Possible constraints and losses due to inbreeding in the program are ignored.

The model program

We assume that there are two components involved in our comparison:

- a long-term breeding population (B);
- a method of harvesting the gains made in B. There are two options for this:
  - a clonal propagation program for direct use (the clonal option which gives rise to the clonal population – C)
  - a clonal seed-orchard program (the seed-orchard option which gives rise to the seed-orchard population – S).

Continuous breeding (B). Full-sib families are produced by controlled crosses; randomly-selected seeds from each family are cloned and tested until they are sexually mature. This is a very powerful testing procedure which enables use to be made of variation both within and between families. The two best clones within each family are then selected and a new generation of full-sib families are generated in a 'single-pair' mating design. Such a program is similar to one proposed by Cotterill (1984), but with clonal testing instead of progeny testing. The clonal procedure suggested tests clonal replications of the progeny and is thus both a clonal test and a progeny test. Here we assume that selection is entirely within families in order to keep a sufficient genetic base, and that the cycle time between generations of the breeding population is $t_B = 15$ years. Gains made by the continuous long-term breeding program are added to both the gains of the clonal option and the seed-orchard option (the actual method of breeding here is probably not crucial).

The clonal option (C). Here, we assume that the best available tested clones from the breeding population are selected without considering relationships among ortets. The selected clones are multiplied vegetatively, grown and planted in the forest. In this case there is only one stage of selection. Clones have an average life span before being discarded from population C and are not used further. The length of time between measurement in the breeding population and this average time in the plantation (t_C) is taken as either 8 years (*P. sylvestris*/*Picea abies*) or 5 years (*P. radiata*).

The seed-orchard option (S). For this option there are two stages of selection. The first stage is to select the best families. The second stage is the selection of only one clone per family, in order to avoid possible inbreeding. This is not a difficult restriction as family size can be manipulated to give the appropriate selection intensities. The selected clones are multiplied vegetatively and placed in a clonal seed-orchard producing seed for a plantation program. Seeds are harvested, germinated and plants grown and planted in the forest. A seed-orchard has a finite life span after which it is no longer used. The length of time between measurement in the breeding population and the average time of usage in plantations by this option (t_S) is taken as 25 years (*P. sylvestris*) or 15 years (*P. radiata*). It might be possible to use an 'advancing front' to reduce the average life span of the seed-orchard by replacing obsolete clones more frequently than under standard orchard management. However, we have taken two representative values of t_S which we believe to be realistic although we acknowledge that others may apply in practice.

Gain formulae. The expected response to selection between families is (Falconer 1981):

$$i_f\, h_f^2\, \sigma_f$$

where i_f is the intensity of selection between families, h_f^2 is the heritability of family means and σ_f is the observed standard deviation of family means.

The expected response to within-family selection is:

$$i_w\, h_w^2\, \sigma_w$$

where i_w is the intensity of selection within families, h_w^2 is the heritability of within family deviations and σ_w is the observed standard deviation within families; in this case the values are clonal means estimated without error.

In the present simplified model, environmental effects are vanishingly small because we have assumed that there are sufficient replications for this to be so. In this case the standard deviations are:

$$\sigma_f = (0.5\,V_A + 0.25\,V_D)^{1/2} \quad \text{and} \quad \sigma_w = (0.5\,V_A + 0.75\,V_D)^{1/2}\,.$$

The heritabilities are:

$$h_f^2 = 0.5\,V_A/(0.5\,V_A + 0.25\,V_D)\,,$$

$$h_w^2 = 0.5\,V_A/(0.5\,V_A + 0.75\,V_D)\,.$$

So the response to family selection is:

$$i_f\, 0.5\,V_A/(0.5\,V_A + 0.25\,V_D)^{1/2}$$

and the response to within-family selection is:

$$i_w\, 0.5\,V_A/(0.5\,V_A + 0.75\,V_D)^{1/2}\,.$$

A factor k is introduced which is interpreted as the correlation between the measured and the desired character. This is partly because experiments are measured and decisions are made before the experiment has fully matured. Sites, experimental techniques and value criteria for decisions may differ from those in the actual forest situation. This factor k is assumed to be the same for all selection situations.

Gain for long-term continuous breeding (B). The best two out of m clones within each family selected. This intensity of selection is $i_B(2/m)$. For a family size of 10, $i_B(2/10) = 1.27$ (intensities of selection from Becker 1968), and for a family

Table 1. Symbols used in the text, their meaning and numerical values assumed

Symbol	Meaning	Numerical values
B	The continuous long-term breeding population	
C	The population selected for the clonal option	
S	The population selected for the seed-orchard option	
t_B	The duration of one cycle in the breeding population	15 years
t_C	The average time between measurements of the clone tests and planting the selected clones	8 and 5 years
t_S	The average time between measurements of the clone tests and planting trees derived from the seed-orchard	25 and 15 years
n	The number of cycles of breeding in the breeding population	
b	The gain from $(n-1)$ cycles of breeding in the breeding population	
V_A, V_{GCA}, V_{SCA}	The additive genetic, General and Specific Combining Ability variances	
V_D	The dominance genetic variance	0 or V_A
i_B	The within-family selection intensity in the breeding population	$i(2/10) = 1.270$ $i(2/100) = 2.328$ $i(2/200) = 2.580$
i_C	The selection intensity for selecting clones in the clonal option	$i(0.05) = 2.063$ $i(0.01) = 2.665$
i_{S1}	The selection intensity when selecting between families for the seed-orchard option	$i(0.5) = 0.798$ $i(0.1) = 1.755$ $i(1/6) = 1.498$ $i(1/15) = 1.937$
i_{S2}	The selection intensity when selecting the best clone in each of the best families for the seed-orchard option	$i(1/10) = 1.539$ $i(1/2) = 0.564$ $i(1/17) = 1.794$ $i(1/7) = 1.352$
k	The correlation between the trait measured in the trial and the desired character at harvest time in the forest	
σ_f	Observed standard deviation of family means	
σ_w	Observed standard deviations within families i.e. clonal means estimated without error	
h_f^2	Heritability of family means	
h_w^2	Heritability of within family deviations	
m	Number of genotypes per family	
T	Arbitrary time at which plantation is established	

Table 2. Summary of the gain formulae. To make the formulae comparable a common factor $k(V_A)^{1/2}$ is separated from each formula. For the breeding population the formula given for b is the starting point for selection for the two competing options. For the clonal and seed orchard options the formulae relate to gain achieved in the forest plantation and include the gain (b) made in the breeding population

Time at which gain is calculated	Option (population)	Gain formula
$(n-1)\,t_B$	B (Breeding)	$b = k(V_A)^{1/2}(n-1) \cdot i_B[V_A/(2V_A+3V_D)]^{1/2}$
$n\,t_B + t_C$	C (Clonal)	$b + k(V_A)^{1/2}\, i_C(1+V_D/V_A)^{1/2}$
$n\,t_B + t_S$	S (Seed orchard)	$b + k(V_A)^{1/2}[i_{S1}(V_A/(2V_A+V_D))^{1/2} + i_{S2}(V_A/(2V_A+3V_D))^{1/2}]$

size of 200, $i_B(2/200) = 2.58$. Other numerical assumptions are given in Table 1.

Each cycle of this within-family selection yields a gain of:

$$i_B\, k\, 0.5\, V_A/(0.5\, V_A + 0.75\, V_D)^{1/2} = k(V_A)^{1/2}\, i_B[V_A/(2V_A+3V_D)]^{1/2}.$$

It was convenient to express gain in units of the common factor $k(V_A)^{1/2}$. The formula for the predicted gain in the breeding population after $(n-1)$ cycles of breeding (t_B is 15 years from measurement in generation n to measurement in generation $n+1$ – see Table 1), at time $t_B\,(n-1)$ is given in Table 2.

Long-term continuous breeding is, of course, a step-wise discontinuous process. However, there is a correlation between the age of selections and the gains made. The closer the selections are made to rotation age, the greater the gains made. If this correlation is linear, at least for a period around the optimal age for selections, then the gains in the breeding population can be thought of as increasing linearly with time. In addition, crossing and measurement take place at many different times in a real program so the sum of these stepwise procedures may be continuous. They are also partly under the control of the breeder. Thus, the gains can be harvested at any time, and the later the harvest the greater the gain. It seems justified to consider the gains made in the long-term breeding population as continuous for the purpose of this model (see Figs.). It also avoids problems of arbitrary assumptions about timings for crossing and measurement which could affect the results.

Gains for the clonal option (C). It is assumed that the genetic values of the clones are known without error (i.e. no 'C' effects), and in clonal propagation (but not in sexual propagation) all of the gain from these genetic values can be used, i.e. $h^2 = 1$. In this case the gain will be:

$$i_C\, k\,(V_A+V_D)^{1/2} = k(V_A)^{1/2}\, i_C[1+(V_D/V_A)]^{1/2}.$$

This gain will be added to the gain (b) obtained in the previous $(n-1)$ cycles of long-term continuous breeding (B).

Calculations were made on the assumption that either the best 5% or 1% of the tested clones are selected. It is also assumed that the time between measurements of clonal tests and actual field planting can be either $t_C = 8$ years or $t_C = 5$ years (Table 1). The formula for gain in the forest at time $n\,t_B + t_C$ is given in Table 2.

Gains for the seed-orchard option (S). For the purpose of this analysis, we assumed that the best families are selected at an intensity of i_{S1} and then the very best clone is selected from within these families at an intensity of i_{S2}. (A slightly higher gain would have been obtained by selection of one clone per family based on an optimal index of family value and clonal value.) For selection between families the gain is:

$$i_{S1}\, k\, 0.5\, V_A/(0.5\, V_A + 0.25\, V_D)^{1/2}\,.$$

For selection within families the gain is:

$$i_{S2}\, k\, 0.5\, V_A/(0.5\, V_A + 0.75\, V_D)^{1/2}\,.$$

When these are combined together in the manner indicated above, the two gains are added together. Thus, the total gain is:

$$k\, (V_A)^{1/2}\, [i_{S1}\, (V_A/(2\, V_A + V_D))^{1/2} + i_{S2}\, (V_A/(2\, V_A + 3\, V_D))^{1/2}]\,.$$

Each of the multiple comparisons between the clonal option and the seed-orchard option have been made with the same number of ultimately-selected clones. This was a deliberate choice to make the comparisons as relevant as possible. The time between the date of measurement of the clone tests and the average date of establishment of plantations derived from the resulting seed-orchard was assumed to be $t_S =$ either 25 years or 15 years (to allow for the productive period of the seed-orchard). The formula expressing the expected gains from this option at time $n\, t_B + t_S$ is given in Table 2.

Comparing gains. For gains to be comparable, they should be compared at the same time from the start of the program. An arbitrary time of $T = 60$ years from the beginning of our model program was chosen as the time for comparison. Gains will actually be harvested after the plantation has grown to maturity, but this may be assumed to be the same for both options. The actual value of T makes absolutely no difference to the results obtained. Other parameters with arbitrary values have been described above and are summarized in Table 1.

One major pair of assumptions was that the dominance variance (V_D) was either zero or equal to the additive variance (V_A in Table 1). Lindgren (1977) reviewed 15 comparisons of V_A with V_D and in only 1 of these cases was the estimate of $V_D > V_A$ (actually $V_{SCA} > V_{GCA}$). Thus we conclude that $V_D \leqq V_A$ covers the range of V_D likely to occur in breeding programs.

Results and discussion

As the main alternative, calculations were carried out assuming that the best 2 out of 20 clones per family were chosen to reconstitute the breeding population, that the best 5% of clones were chosen for the clonal option, that the best half of the families and the best individual out of a family of 10 individuals were chosen in the family selection for the seed-orchard option. To check the influence of different factors, other values have been tried for single variables of the main alternatives. The calculations were carried out for *P. sylvestris* (average seed-orchard life 25 years and average period for use of a clone of 8 years) and for *P. radiata* (average seed-orchard life 15 years and average clone use period of 5 years).

For the *P. sylvestris/Picea abies* timetable, the results of these calculations are given in Fig. 1 and Table 3. There are two parts to the gains made. The first is due to selection itself; part of the gain made by the clonal option is unavailable to the seed-orchard option due recombination. The second is due to the timing of the selection process.

The superiority of the clonal option over the seed-orchard option due to selection without recombination is small when V_D is 0. But the gain due to timing of selection is large. In order to yield a plantation at time $T = 60$ years, selections for a seed-orchard program must be made from the breeding population at 35 years. Selection for the clonal option can be left until 52 years. Advances have been made in the breeding population in the 17 years between seed orchard selections and clonal option selections. The gains made in the breeding population in the 17 years make a major contribution to the difference between the two options in this case. When the dominance variance (V_D) equals the additive variance (V_A), there is an additional advantage (shown in Fig. 1 b) due to the reduced precision of selection for the seed-orchard option as well as increased genetic variance between clones. Dominance variance also reduces the gains made by both options because of reduced gains in the breeding population. Thus the presence of non-additive genetic variance is undesirable for long-term breeding.

The difference between the two options is given in Table 3. The advantage of the clonal option due to selection when $V_D = 0$ is 0.41 units of gain compared with a time advantage of 1.02. But when $V_D = V_A$ the selection advantage becomes 1.77, compared with a time advantage of only 0.83.

As selection intensity is increased, the advantage of the clonal option due to time also increases, but the advantage due to selection remains the same (Table 3). This is because the breeding population makes even more progress in the time between the measurement operations (in this case 17 years) of the two options. When the best 2 out of 100 clones are selected in each family for regenerating the breeding population, the advantage of the clonal option is 2.28 units of gain (0.41 for selection and 1.87 for time) when $V_D = 0$ and is 3.29 (1.77 for selection and 1.52 for time) when $V_D = V_A$.

The difference between options due to time remains the same when the selection intensity for both options is increased. For Table 3 line 7 and Fig. 2 only the best 1% of available clones were taken for the clonal option, a change matched in the seed-orchard option by taking the best 10% of families and the best 1 out of 10 clones per family. The slope of the lines in Fig. 2 is determined only by the selection intensity in the breeding population (2/100 corresponds to $i_B = 2.328$). However, what happens to the difference due to precision of selection depends on the value of V_D. When $V_D = 0$ the selective difference drops from $0.41 - 0.34$ (compare lines 2 and 7), but when $V_D = V_A$ it increases sharply from $1.77 - 2.07$. Increasing the effort of family selection at the expense of within-family

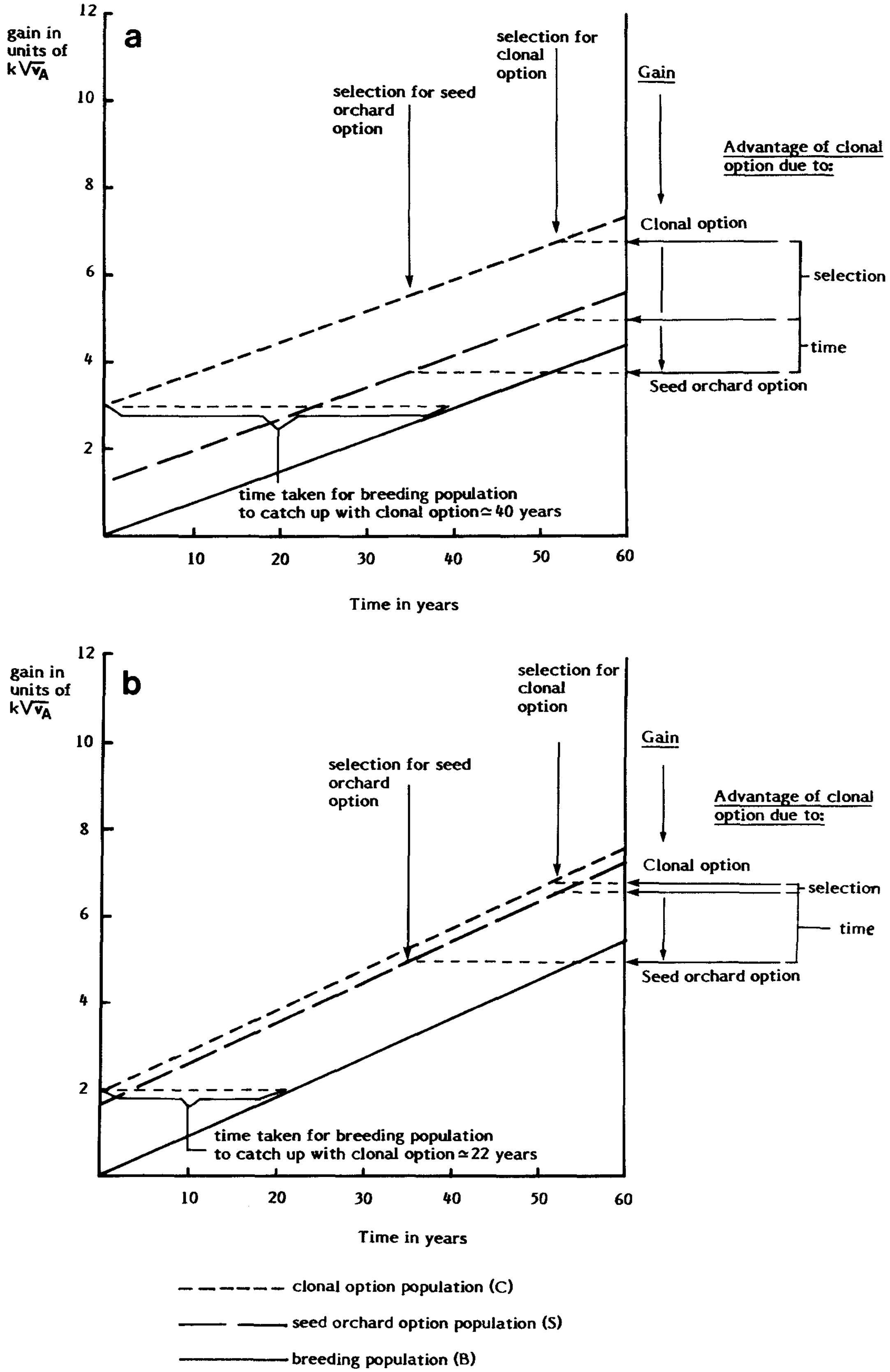

Fig. 1. $i_B(2/10)=1.27$, $i_C(5\%)=2.063$, $i_{S1}(50\%)=0.798$, $i_{S2}(1/10)=1.539$, $t_B=15$, $t_C=8$, $t_S=25$, $V_D=0$ (**a**) or $V_D=V_A$ (**b**). For definition of terms, see text

Table 3. Summary of results of fitting various values for intensities of selection. Tabulated values are the advantage of the clonal option over the seed orchard option in units of standard deviation x k $(V_A)^{1/2}$. Rather than give the selection intensities themselves, we have given the proportions or percentages selected (P_B, P_C, P_{S1} and P_{S2} with subscripts the same as for the selection intensities – see text). The values listed below are for $t_B = 15$, $t_C = 8$, $t_S = 25$

Selection values	Gains ($V_A = 1$, $V_D = 0$)			Gains ($V_A = 1$, $V_D = 1$)		
	Genetic	Time	Total	Genetic	Time	Total
$P_B = 2/10$, $P_C = 5\%$, $P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.02	1.43	1.77	0.83	2.60
Changing values of P_B						
$P_B = 2/100$	0.41	1.87	2.28	1.77	1.52	3.29
$P_B = 2/200$	0.41	2.07	2.48	1.77	1.69	3.46
$P_B = 2/100$, $P_C = 5\%$ $P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.87	2.28	1.77	1.52	3.29
Changing the ratio of P_{S1} to P_{S2}						
$P_{S1} = 10\%$, $P_{S2} = 1/2$	0.42	1.87	2.29	1.65	1.52	3.18
$P_B = 2/100$, $P_C = 5\%$ $P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.87	2.28	1.77	1.52	3.29
Changing P_C to 1%, and P_{S1} values appropriately						
$P_C = 1\%$ $P_{S1} = 10\%$, $P_{S2} = 1/10$	0.34	1.87	2.20	2.07	1.52	3.59
Changing P_{S2} instead						
$P_{S1} = 50\%$ $P_{S2} = 1/50$	0.51	1.87	2.38	2.07	1.52	3.59
Changing the ratios of P_{S1} to P_{S2}						
$P_{S1} = 16.7\%$ (1/6) $P_{S2} = 1/17$	0.34	1.87	2.20	2.10	1.52	3.63
$P_{S1} = 6.7\%$ (1/15) $P_{S2} = 1/7$	0.34	1.87	2.20	2.05	1.52	3.57
$P_B = 2/100$, $P_C = 5\%$ $P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.02	1.43	1.77	0.83	2.60
Changing the value of P_C to 10% and P_{S2} to 1/5						
$P_B = 2/100$, $P_C = 10\%$ $P_{S1} = 50\%$, $P_{S2} = 1/5$	0.37	1.87	2.23	1.50	1.52	3.02
Changing P_{S1} to 100% and P_{S2} to 1/10 instead						
$P_C = 10\%$ $P_{S1} = 100\%$, $P_{S2} = 1/10$	0.67	1.87	2.54	1.79	1.52	3.31

selection makes little difference (in Table 3 compare line 7 with line 10) and no difference at all when $V_D = 0$. Reducing the intensity of selection of clones for the clonal option to $i_C = 1.755$ (i.e. taking the best 10% of clones) decreased the genetic difference between options for both values of V_D (Table 3, line 12) when the adjustment to i_S was within families. Reducing the intensity of selection of clones for the clonal option had the opposite effect when the concomitant adjustment was between families, increasing the genetic difference between options for both values of V_D (Table 3, line 13).

There were values of i_C which minimized the difference between the two options. These were determined by substituting various values of i_C to the equations. The above results show that these values would depend on the value of V_D and also on whether the adjustment to seed-orchard selective values was to i_{S1} or to i_{S2}. The optimum values for i_C were not useful when the adjustments were made to i_{S2}. They were at $i_{S2} = 0$ for both values of V_D. But when the adjustment was to i_{S1}, the optimum values of i_C were 2.655 (selecting the best 1% of clones) for $V_D = 0$ and 1.887 (selecting the best 7.5% of clones) for $V_D = V_A$. There is clearly a multi-dimensional optimal surface with many different solutions for i_C depending on the ratio of selective effort within and between families and the values of V_D.

The model program considered here does not take into account any progeny testing for further selection of seed-orchard clones and may thus underestimate the value of that option. So-called '1.5 generation' seed-orchards are expected to yield more productive seed, but the time required for progeny testing also allows further improvements in the breeding population for clonal option selection. These are separate questions, not easily answered and beyond the scope of this paper. However, this paper has shown the overriding importance of the time advantage of the clonal option and any delay caused by progeny testing may increase this time advantage.

It is possible that some breeding programs may be able to shorten the time between when selections are made and the field plantations, or shorten the average life span of a clone or seed-orchard in use as indicated in our main alternative. Therefore we carried out the

Genetic progress (in units of k $(V_A)^{1/2}$) is presented as a function of time. The lines represent the relationship between the gain obtainable if measurement and selection of clones in the breeding population (B) takes place at the times indicated. Selection is carried out for long-term breeding (B), for a clonal mixture to be used in plantations (C) or for clones to use in a seed-orchard (S). There is a time delay between measurement and field plantation of the material selected on the basis of those measurements. For the purpose of this analysis it is assumed that it is desired to make a plantation at time T (an arbitrary time whose value does not affect the differences between options, but here we assume it is 60 years). The time delay results from evaluation, decision, clonal propagation, plant production, the economic life of a clone in a clonal mixture or seed-orchard and (for seed-orchards) the time taken to attain commercial levels of seed production. There is also a time taken for the breeding population to achieve the gains obtained by the clonal option. The difference between the figures is as follows: **Figs. 1a** and **2a** describe the situation where $V_D = 0$ whereas **Figs. 1b** and **2b** describe the situation when $V_D = V_A$. **Fig. 1** describes the situation when selection in the breeding population is at a level of 2/10 whereas **Fig. 2** describes when selection in the breeding population is 2/100.

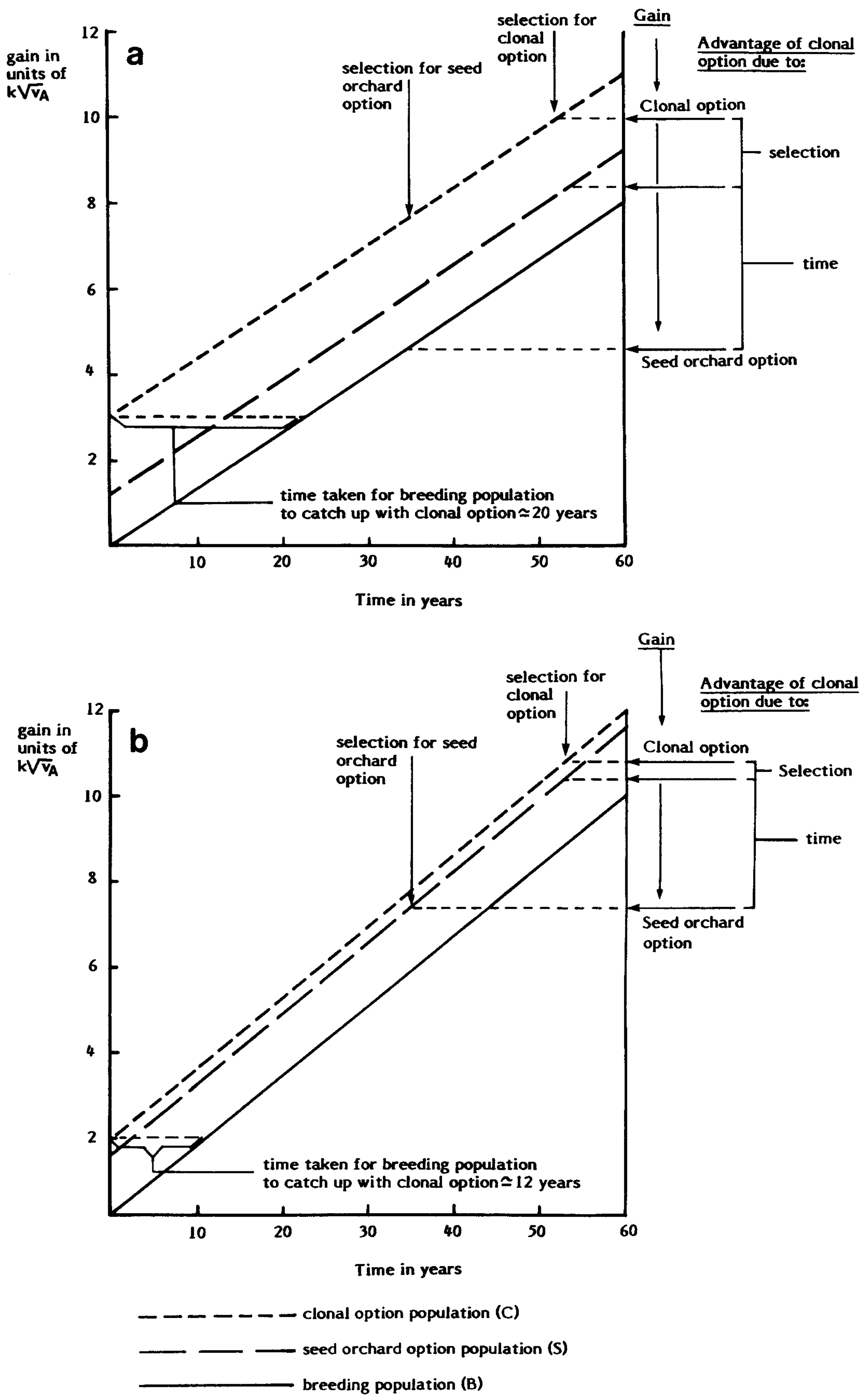

Fig. 2. $i_B(2/100)=2.328$, $i_C(5\%)=2.063$, $i_{S1}(50\%)=0.798$, $i_{S2}(1/10)=1.539$, $t_B=15$, $t_C=8$, $t_S=25$, $V_D=0$ (**a**) or $V_D=V_A$ (**b**). For definition of terms, see text

Table 4. Summary of results of fitting various values for intensities of selection. Tabulated values are the advantage of the clonal option over the seed orchard option in units of standard deviation x k $(V_A)^{1/2}$. Rather than give the selection intensities themselves, we have given the proportions or percentages selected (P_B, P_C, P_{S1} and P_{S2} with subscripts the same as for the selection intensities – see text). The values listed below are for $t_B = 15$, $t_C = 5$, $t_S = 15$

Selection values	Gains ($V_A = 1$, $V_D = 0$)			Gains ($V_A = 1$, $V_D = 1$)		
	Genetic	Time	Total	Genetic	Time	Total
$P_B = 2/10$, $P_C = 5\%$						
$P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	0.60	1.01	1.77	0.49	2.26
Changing the values of P_B						
$P_B = 2/100$	0.41	1.10	1.51	1.77	0.90	2.66
$P_B = 2/200$	0.41	1.22	1.63	1.77	0.99	2.76
$P_B = 2/100$, $P_C = 5\%$						
$P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.10	1.51	1.77	0.90	2.66
Changing the ratio of P_{S1} to P_{S2}						
$P_B = 2/100$, $P_C = 5\%$						
$P_{S1} = 10\%$, $P_{S2} = 1/2$	0.42	1.10	1.52	1.65	0.90	2.55
Changing P_C to 1% and P_{S1} to 10%						
$P_B = 2/100$, $P_C = 1\%$						
$P_{S1} = 10\%$, $P_{S2} = 1/10$	0.34	1.10	1.43	2.07	0.90	2.96
Changing P_{S2} to 1/50 instead						
$P_{S1} = 50\%$, $P_{S2} = 1/50$	0.51	1.10	1.61	2.30	0.90	3.20
Changing the ratio of P_{S1} to P_{S2}						
$P_B = 2/100$, $P_C = 1\%$						
$P_{S1} = 16.7\%$ (1/6),						
$P_{S2} = 1/17$	0.34	1.10	1.43	2.10	0.90	3.00
Changing the ratio of P_{S1} to P_{S2}						
$P_B = 2/100$, $P_C = 1\%$						
$P_{S1} = 6.7\%$ (1/15)						
$P_{S2} = 1/7$	0.34	1.10	1.44	2.05	0.90	2.94
$P_B = 2/100$, $P_C = 5\%$						
$P_{S1} = 50\%$, $P_{S2} = 1/10$	0.41	1.10	1.51	1.77	0.90	2.66
Changing the value of P_C to 10% and P_{S2} to 1/5						
$P_B = 2/100$, $P_C = 10\%$						
$P_{S1} = 50\%$, $P_{S2} = 1/5$	0.37	1.10	1.47	1.50	0.90	2.40
Changing P_{S1} to 100% and P_{S2} to 1/10 instead						
$P_{S1} = 100\%$, $P_{S2} = 1/10$	0.67	1.10	1.76	1.79	0.90	2.69

same calculations as before, but with values for t_C and t_S more suited to a *P. radiata* program. The results are presented in Table 4 and show that although the advantage due to time for the clonal option is smaller, our conclusions remain the same as for *P. sylvestris.*

Conclusions

1. The clonal option is considerably superior to the seed-orchard option for any value of V_D (dominance variance). Thus clonal propagation may be highly desirable even in the absence of any dominance effects (corresponding to specific combining ability effects). Any dominance effects will enhance the advantage of the clonal option.
2. The main reason for superiority of the clonal option in the absence of dominance effects is that the time between measurements (selection) and field planting is considerably smaller for the clonal option. The breeding population is achieving genetic improvement constantly so the clonal option can take advantage of advances made after selections for the seed-orchard option have been made.
3. The higher the dominance effects, the greater is the relative advantage of the clonal option. Where the dominance effects are as large as the additive effects, the advantage of the clonal option due to dominance can be twice as large as the time advantage.
4. An additional reason for the superiority of the clonal option is that selection is usually not constrained by relationships between candidates for selection.
5. The more efficient the long-term breeding, the greater is the advantage of the clonal option. Thus, the more we invest in long-term breeding, the more important it is to consider the clonal option. Or, the more we believe in the clonal option, the more we should invest in a sexually-based long-term breeding program.
6. The time taken for the breeding population to make up the gain made by the clonal option varied with the intensity of selection in the breeding population and also the amount of dominance. The larger i_B was the shorter was this catch up time, but the greater V_D was, the longer the catch-up time. When $V_D = V_A$ and $i_B = 1.27$ the catch-up time was about 2.5 generations whereas when $V_D = 0$ and $i_B = 2.328$ the catch up time was less than one generation. It is also only a matter of decades rather than centuries for the seed-orchard option to catch up with the clonal option.

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