

grammes d'amélioration devraient être suffisamment souples afin de pouvoir être modifiés dans l'avenir.

Zusammenfassung

Titel der Arbeit: Probleme einiger Auslesemodelle in der Forstpflanzenzüchtung.

Ein kritischer Überblick über einige Methoden der Forstpflanzenzüchtung führt zu dem Schluß, daß die verlässliche Einschätzung des Züchtungsfortschritts nur in wenigen einfach gelagerten Situationen möglich ist. Beim Vergleich verschiedener Selektionsverfahren müssen die biologischen Eigenschaften der Baumart berücksichtigt werden. Diese Verhältnisse können zu einer völlig anderen Beurteilung einer bestimmten Auslesemethode führen. Ein allgemein „bestes“ Verfahren gibt es nicht.

Schätzungen genetischer Varianzen und Heritabilitäten der wichtigsten Merkmale waren seither ungenügend. Daher ist es in den meisten Fällen zu früh, Erwartungswerte für den Züchtungsfortschritt denkbarer Verfahren zu vergleichen.

Der Wert quantitativ-genetischer Methoden wird gegenwärtig darin gesehen, daß diese Methoden eine rationelle Grundlage für die Planung zukünftiger Experimente bieten. Diese Experimente sollten sowohl Fortschritt bei der Züchtung als auch Informationen theoretischer Art liefern, wie sie für eine erweiterte Anwendung von Methoden der quantitativen Genetik benötigt werden.

Da noch keine Gewißheit über die beste Züchtungsmethode besteht, sollten Züchtungsprogramme flexibel sein und künftige Änderungen erlauben.

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Clonal Selection, and An Alternative Seed Orchard Scheme

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I. Introduction

It seems reasonable that the answer to the question: "What kind of seed orchard shall we have?", will depend in large part on the characteristics of the species in question.

It is the purpose of this paper to discuss mass selection, family selection, family-plus-mass selection, and clonal selection in terms of "clonal seed orchards," "seedling seed orchards," and a third alternative seed orchard scheme. This scheme involves evaluation of candidate trees, clones or families at a site or sites other than the seed orchard site, and combines some of the best features of each of the other two seed orchard systems.

The effects of such species characteristics as: (1) ease and expense of control-pollination; (2) ease and expense of vegetative propagation; (3) sexual precocity of grafts and seedlings; (4) genotype-environment interaction; (5) heritability of the characteristic or index being selected; (6) juvenile-adult correlation of this characteristic or index; (7) demand for seed; (8) inbreeding depression; and (9) cost and value; are discussed in terms of the selection and seed orchard schemes. In addition, factors associated with these schemes which determine variability, selection efficiency, and selection intensity are discussed in general.

Since the term "clonal selection" has been used to mean different things, including selection within a clone for

sports or disease-free individuals (BARCOCK and CLAUSEN, 1927), and since clonal selection has not been given a general theoretical treatment in the literature, this treatment is presented below. The treatment is general, and the experiments utilize herbaceous material. The principles apply, however, to forest trees as well as to other organisms which can be vegetatively propagated (LARSEN 1956, Chap. 7). It will be shown that clonal selection is useful not only for species which are normally vegetatively propagated, but also for species where the progeny of the selected individual will be produced sexually. To use clonal selection with species which normally reproduce by seed: (1) vegetative propagation must be inexpensive and reliable; and (2) the vegetative propagules must rapidly take on characteristics which are realistic for, and comparable to, seedlings.

II. Clonal Selection²⁾

In selection or breeding studies, where a genotype is poorly defined on the basis of the performance of a single organism, it is frequently possible to use supplementary information from relatives of the organism to more accurately identify its genotype. The more genes shared, or closer the relative, the more applicable is the relative's performance to the genotype of the organism in question

²⁾ This section is based on a dissertation submitted to the Graduate Division of the University of California in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Genetics.

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(LUSH, 1945). The closest genetic relationship possible is that developed by cloning.

BURTON and DeVANE (1953) considered selection between clones of tall fescue in some detail. They pointed out that the variance between clones is composed of a clonal component (σ_{cl}^2), and an environmental component which is reduced by cloning (σ_e^2/k), where k is the number of individuals per clone. They expressed broad-sense heritability using clonal averages (h_b^{2*}) as $h_b^2/[h_b^2 + (1.00 - h_b^2)/k] = \sigma_g^2/(\sigma_g^2 + \sigma_e^2/k)$, where h_b^2 is broad-sense heritability of uncloned plants and σ_g^2 is the total genetic variance. Total genetic variance is equivalent to σ_{cl}^2 in the absence of "c" effects (that is, effects due to non-genetic influences common to individuals of a given clone or family but different for different clones or families).

Five levels of cloning, including one individual per clone, and six levels of broad-sense heritability between zero and one, have arbitrarily been chosen to illustrate the principles of clonal selection. For example, assuming an arbitrary total variance of 1,000, where $h_b^2 = 0.10$ (i. e., $\sigma_g^2 = 100$ and $\sigma_e^2 = 900$), then h_b^{2*} for $k = 3$ is $100/(100 + 900/3) = 0.250$. Table 1 presents values of h_b^{2*} for the heritabilities and cloning levels considered.

Table 1. — Broad-sense Heritabilities Based on Clonal Averages (h_b^{2*})

h_b^2	Number of Individuals per Clone (k)				
	1	2	3	6	10
0.00	0.000	0.000	0.000	0.000	0.000
0.10	0.100	0.182	0.250	0.400	0.526
0.20	0.200	0.333	0.428	0.600	0.714
0.30	0.300	0.462	0.563	0.720	0.811
0.50	0.500	0.667	0.750	0.857	0.909
0.75	0.750	0.857	0.900	0.945	0.968
0.90	0.900	0.947	0.964	0.982	0.989
1.00	1.000	1.000	1.000	1.000	1.000

Table 2. — Selection Intensities (v) and Selection Differentials (i) Arbitrary Maximum Number of Plants: 500.

Min. number of Parents		Number of Individuals per Clone (k)				
		1	2	3	6	10
50	v	10%	20%	30%	60%	100%
	i	1.755	1.400	1.159	0.644	0.000
25	v	5%	10%	15%	30%	50%
	i	2.063	1.755	1.554	1.159	0.798
15	v	3%	6%	9%	18%	30%
	i	2.268	1.985	1.804	1.458	1.159
5	v	1%	2%	3%	6%	10%
	i	2.665	2.421	2.268	1.985	1.755

With increasing k , h_b^{2*} increases at all h_b^2 between zero and one, the relative rate of increase being inversely related to h_b^2 . This is to be expected, since cloning reduces only the environmental component of variance, which is a major component of total variance at low h_b^2 , but is a relatively minor component at higher h_b^2 .

Suppose that a maximum is placed on the number of plants which can be raised in a single experiment. Suppose also that due to inbreeding considerations, a minimum is placed on the number of parents required to initiate each

³⁾ In this paper, the * will indicate that the heritability depends on the number and relationship of individuals in a family or clone.

generation. The ratio of this minimum and maximum sets the selection intensity (v). The difference in standard deviations between the mean of the population and mean of the selected parents is the selection differential (i) (LERNER 1958, Box 11). Values of i may be taken directly from $z/\frac{1}{2}(1+a)$ and $z/\frac{1}{2}(1-a)$ in PEARSON'S (1931) Table II. Values of v and i are presented in Table 2 for an arbitrary maximum experiment population of 500 plants, with the minimum number of parents arbitrarily set at 50, 25, 15 and 5. The v 's are the ratio: (number of genotypes selected)/(genotypes available). Thus, if each genotype is cloned 10 times and 50 parents are required, all 50 clones (500 plants) must be used as parents and there is no selection in this extreme case.

As k increases from 1 to 10, i decreases more rapidly (both in absolute and relative values) with 50 parents than with 5 parents. Thus, the more parents required, or less intense the potential selection, the less favorable is the system for clonal selection. This is reasonable, since it is more important to accurately identify genotypes if only a few genotypes are being selected. If a large number of genotypes are being selected, many of the better ones will be selected even if individually they are poorly identified.

The heritabilities in Table 1 and the selection differentials in Table 2 are based on the variances of the clonal averages. These variances decrease both with increasing k (since the variance of clonal averages = $\sigma_g^2 + \sigma_e^2/k$) and decreasing h_b^2 (since σ_e^2 becomes relatively larger with decreasing h_b^2). Standard deviations for combinations of h_b^2 and k are presented in Table 3, based on a variance of 1000 for the uncloned population.

Table 3. — Standard Deviations of Clonal Averages.

h_b^2	Number of Individuals per Clone (k)				
	1	2	3	6	10
0.10	31.6	23.5	20.0	15.8	13.8
0.20	31.6	24.5	21.6	18.2	16.7
0.30	31.6	25.5	23.1	20.4	19.2
0.50	31.6	27.4	25.8	24.1	23.5
0.75	31.6	29.6	28.9	28.1	27.8
0.90	31.6	30.8	30.5	30.3	30.2

Table 4. — Expected Gains Using Clonal Selection

h_b^2	Number of Individuals per Clone (k)				
	1	2	3	6	10
<i>Fifty Parents</i>					
0.10	5.55	5.99	5.80	4.07	0.00
0.20	11.09	11.42	10.71	7.03	0.00
0.30	16.64	16.49	15.07	9.46	0.00
0.50	27.73	25.59	22.43	13.30	0.00
0.75	41.59	35.51	30.15	17.10	0.00
0.90	49.91	40.83	34.08	19.16	0.00
<i>Five Parents</i>					
0.10	8.42	10.35	11.34	12.55	12.74
0.20	16.84	19.75	20.97	21.68	20.93
0.30	25.26	28.52	29.50	29.16	27.33
0.50	42.11	44.25	43.89	41.00	37.49
0.75	63.16	61.41	58.99	52.71	47.23
0.90	75.79	70.61	66.68	59.06	52.42

Most efficient at h_b^2 ; Better than $k = 1$ at h_b^2

Expected gain can be calculated by multiplying the selection differential in standard deviations (\bar{i}) by the appropriate standard deviation from *Table 3*, by the appropriate heritability (h_b^{2*}) from *Table 1*. These calculations have been performed for 50 and 5 parents, and are presented in *Table 4*.

At the relatively low selection intensities developed with a requirement of 50 parents out of 500 plants, selection on the basis of clonal averages proves to be less efficient than single-phenotype selection at h_b^{2*} of 0.30 and above. At lower heritabilities, a slight improvement over single-phenotype selection is possible using averages of two individuals per clone.

The picture is considerably changed at the higher selection intensities developed with only five parents out of 500 plants required. At h_b^{2*} of 0.50 and less, some level of cloning is more efficient than single-phenotype selection. At h_b^{2*} of 0.10, for instance, selection based on averages of ten individuals per clone gives 151% of the gain expected from single-phenotype selection. At h_b^{2*} of 0.75 and 0.90, however, single-phenotype selection is more efficient than clonal selection.

Up to this point, "c" effects, non-additive genetic variance, and differential generation time have not been considered. It is possible that it may take longer to run an experiment population through a clonal generation than a seedling generation. If generations are continuous, for instance not limited by season, then gain per unit time becomes more important than gain per generation. By setting $t = 1.00$ for the seedling, or single-phenotype generation, t for the clonal generation can be expressed on the basis of seedling generation time. The expected gain per unit time then becomes $\bar{i}oh_b^{2*}/t$. Thus, if it takes 12 years for a generation using seedlings, but 15 years for a generation using ten individuals per clone, $t = 1.25$ for clones of ten, and expected gain per unit time (*Table 4*, five parents, h_b^{2*} of 0.10) remains 8.42 for $k = 1$ but is reduced to 10.19 for $k = 10$. The relative efficiency of $k = 10$ is reduced from 151% of $k = 1$ per generation to 121% per unit time. It is possible that clonal generation time may be shorter than seedling generation time. In this case, t is less than 1.00, and the relative efficiency of clonal selection is improved. If selected plants become sick or die before the crosses mature, having clonal replicates may save as much as the time required to regrow the generation.

Assuming that the selected plants are to be used for sexual reproduction, the amount of additive variance (σ_a^2) in σ_g^2 must be considered. Suppose that "p" is the proportion of additive variance in σ_g^2 . The expected gain is related to the narrow-sense heritability (h_n^2). But $\sigma_a^2 = p\sigma_g^2$, so that $h_b^{2*} = \sigma_a^2/(\sigma_g^2 + \sigma_e^2/k) = p\sigma_g^2/(\sigma_g^2 + \sigma_e^2/k) = ph_b^{2*}$. If $p = 1/2$, all values in *Table 4* would be divided by 2, but the relative efficiencies would remain exactly the same. This is because the effect of cloning is only on σ_e^2 , and the genetic correlation between members of a clone (barring somatic mutation) is 1.00. Therefore, the decision of whether to use single-phenotype or some level of clonal selection is based on broad-sense heritability, and is not affected by the presence of non-additive genetic variance. Of course, if non-additive variance is appreciable, some form of selection based on specific combining ability and performance of the offspring may be preferable to either single-phenotype or clonal selection of the parents.

Vegetative propagules of the same plant may be similar not only due to a common genotype, but also due to en-

vironmental modifications of the physiology and morphology of the parent plant which are more or less shared by the propagules. This is a special case of "c" effects, and is perhaps the most disturbing feature of a clonal selection scheme. This source of variation (σ_c^2) would not appear in a seedling population, nor would it contribute to gain in the long run. It results in non-equivalence of total genetic and clonal variance: $\sigma_{cl}^2 = \sigma_g^2 + \sigma_c^2$. Broad-sense heritability of seedlings is $\sigma_g^2/(\sigma_g^2 + \sigma_e^2)$, while h_b^{2*} for clones is $\sigma_g^2/(\sigma_g^2 + \sigma_c^2 + \sigma_e^2/k)$. The general behavior is illustrated by comparing clonal selection ($k = 3$) at four levels of σ_c^2 for low and medium heritability. Seedling selection ($k = 1$) also serves as a basis for comparison (*Table 5*).

Table 5. — Expected Effect of Variance Associated with Cloning (N = 500; Parents = 5; Variance of Seedling Population = 1000).

	k = 1	k = 3			
		$\sigma_c^2 = 0$	$\sigma_c^2 = 10$	$\sigma_c^2 = 100$	$\sigma_c^2 = 500$
h_b^{2*}	0.100	0.250	0.244	0.200	0.111
v	1%	3%	3%	3%	3%
\bar{i}	2.665	2.268	2.268	2.268	2.268
σ	31.6	20.0	20.2	22.4	30.0
Gain	8.42	11.34	11.18	10.16	7.55
Decrease	—	—	1.4%	10.4%	33.4%
h_b^{2*}	0.500	0.750	0.739	0.652	0.428
σ	31.6	25.8	26.0	27.7	34.2
Gain	42.11	43.89	43.58	40.96	33.20
Decrease	—	—	0.7%	6.7%	24.4%

Increasing σ_c^2 decreases h_b^{2*} , but partially compensates for this by increasing the standard deviation. Selection intensity (v) and selection differential (\bar{i}) are unchanged by σ_c^2 . The total effect of increasing σ_c^2 is to decrease expected gain from clonal selection. Gain ($\bar{i}oh_b^{2*}$) is decreased relatively more at low heritabilities than at higher heritabilities.

Three factors influencing the usefulness of clonal selection, broad-sense heritability, relative importance of non-additive genetic variance, and relative generation time of seedling and clonal populations, may be estimated efficiently by analyzing a cloned parent population and offspring from these clones (LIBBY, 1962).

The magnitude of "c" effects due to cloning may be roughly evaluated by a method used successfully with *Mimulus*. It may be possible, at the expense of longer clonal generation time, to reduce "c" effects variation by a two-stage cloning scheme (LIBBY and JUND, 1962).

Experimental

Two series of selection experiments for internode length in yellow monkey flower (*Mimulus guttatus*, FISCH.) were carried out for three generations. In one, selections were based on the averages of three individuals per clone. In the other, selections were based on the performance of single plants of seedling origin. Long- and short-internode families were developed from all possible crosses among the seven most extreme plants or clones of the previous generation, with an equal number of seedlings grown from each cross (LIBBY, 1962). The number of survivors available for selection, and the selection intensities for each line and generation, are presented in *Table 6*.

Observed values, essentially free of between-generation environmental effects, were obtained for gain and reach

Table 6. — Population Size (N) and Selection Intensity (v).

Lines	Generation					
	1		2		3	
	N	v	N	v	N	v
Un long	319	2.19%	125	5.60%	126	5.56%
Un short	319	2.19%	123	5.69%	95	7.37%
Cl long	105**	6.67%	42	16.67%	42	16.67%
Cl short	105	6.67%	42	16.67%	42	16.67%

Un = Selection based on single phenotypes (k = 1).
 Cl = Selection based on clonal averages (k = 3).
 **105 clones (k = 3) = 315 plants.

Table 7. — Gain and Reach for Selection Experiments.

	Selection Scheme	Generation			Total
		1-2	2-3	3-4	
Predicted Reach	Uncloned	506**	427	405	1338
	Clonal	324	244	244	812
Observed Reach	Uncloned	516	384	354	1254
	Clonal	364	192	237	793
Predicted Gain	Uncloned	157	132	125	414
	Clonal	162	121	121	404
Observed Gain	Uncloned	281	98	59	438
	Clonal	180	164	139	483

** The predicted and observed values are internode lengths, in millimeters transformed to a logarithmic scale to correct skewness and reduce correlation of variance to size.

by taking the difference between the means of the long and short internode lines (gain), and between the means of the selected parents (reach). Predicted values were obtained by assuming: (1) a narrow-sense heritability of 0.31; (2) a broad-sense heritability of 0.43 (these heritabilities were obtained from a clonal analysis and parent-offspring regression of the first two clonal generations (LIBBY, 1962); (3) no "c" effects due to cloning (LIBBY and JUND, 1962); (4) a uniform total variance in all generations of 11,252, which is the value of $\sigma_g^2 + \sigma_e^2$ of the base population; and (5) the selection intensities from Table 6. The predicted and observed values for each line and generation are presented in Table 7. Note that the clonal selection is theoretically superior to single-phenotype selection at the relatively high selection intensities practiced in generation 1-2, but inferior at the lower intensities of generations 2-3 and 3-4.

This one series of experiments can hardly be said to test clonal selection. However, the experimental data from the clonal lines conformed reasonably well to predicted values over the three generations. Furthermore, the realized gain in the clonal lines is greater than the realized gain in the single-phenotype lines, totaled over the three generations, indicating at least no serious failure of clonal selection as an alternative to single-phenotype selection.

Experience with this organism may be used to illustrate the time factor in alternative selection schemes. A few vegetative propagules can be started from a seedling about three weeks after the seed germinates. However, shoots from such rooted nodes develop faster than newly-germinated seedlings, so that the propagules complete their development about 1 or 1½ weeks after the seedlings. If a few seedlings develop slowly, the final selection of the parents for the next generation must be delayed until the slow plants can be scored. However, if a few individual plants in a clonal scheme develop slowly, their clones can often be selected or eliminated on the basis of the completed performance of the other members. Finally, in a complex crossing system such as was used in these ex-

periments, it was possible to make all six reciprocal crosses per genotype the same day with clones of three. It typically took a week or more for a single plant to produce the number of flowers necessary to complete six reciprocal crosses. Using a single-phenotype generation time of 1.00, the clonal generation time for k = 3 varied from about 0.90 to about 1.05 under the conditions of these experiments.

III. Relative Efficiencies of Clonal, Family, Family-Plus-Mass, and Mass Selection

The two levels of family relationship most frequently proposed for evaluation in a "seedling seed orchard" are full-sibs and half-sibs. Within each of these levels, two possible alternatives will be considered. The first is family selection (using random members of the best families in the seed orchard). The second is family-plus-mass selection (using information from relatives to supplement information from individuals, and using the individuals which score highest on this combined index in the seed orchard). WRIGHT (1960) explored the advantages and disadvantages of these and related schemes in detail. WRIGHT (1960) and LERNER (1958, Chap. 5) have expressed the efficiency of family selection schemes as a ratio based on single-phenotype (mass) selection. Since clonal selection is a form of family selection, these same formulae are applicable, and the ratios may be directly compared. Comparative efficiencies for a range of heritabilities and family sizes are presented in Table 8.

The relative efficiencies of family-plus-mass selection are greater than one, and greater than the comparable Table 8. — Relative Efficiencies of Clonal, Full-sib and Half-sib Family Selection

h ²	n	$\frac{1 + (n-1)r_G}{\sqrt{n[1 + (n-1)r_P]}}$			$\frac{\sqrt{1 + \frac{(r_G - r_P)^2}{1 - r_P}} \cdot \sqrt{\frac{(n-1)}{1 + (n-1)r_P}}}{\sqrt{n[1 + (n-1)r_P]}}$		
		Genetic gain from family selection			Genetic gain from family-plus-mass selection		
		Genetic gain from mass selection			Genetic gain from mass selection		
		Clones	Full-sibs	Half-sibs	Clones	Full-sibs	Half-sibs
.10	100	3.03	2.07	1.38	3.03	2.13	1.57
	10	2.29	1.44	0.93	2.29	1.52	1.18
	6	2.00	1.28	0.87	2.00	1.36	1.11
	2	1.35	1.04	0.87	1.35	1.10	1.02
.20	100	2.19	1.53	1.06	2.19	1.62	1.30
	10	1.89	1.26	0.85	1.89	1.36	1.12
	6	1.73	1.17	0.82	1.73	1.26	1.08
	2	1.29	1.01	0.86	1.29	1.08	1.02
.30	100	1.80	1.27	0.89	1.80	1.38	1.18
	10	1.64	1.13	0.79	1.64	1.25	1.08
	6	1.55	1.08	0.78	1.55	1.19	1.06
	2	1.24	0.99	0.85	1.24	1.06	1.02
.50	100	1.41	1.00	0.70	1.41	1.15	1.06
	10	1.35	0.96	0.70	1.35	1.11	1.04
	6	1.31	0.95	0.72	1.31	1.09	1.03
	2	1.15	0.95	0.83	1.15	1.03	1.01
.75	100	1.15	0.82	0.58	1.15	1.03	1.012
	10	1.14	0.83	0.63	1.14	1.02	1.008
	6	1.12	0.84	0.66	1.12	1.02	1.006
	2	1.07	0.91	0.81	1.07	1.009	1.002
.90	100	1.05	0.75	0.53	1.05	1.005	1.002
	10	1.05	0.77	0.59	1.05	1.004	1.001
	6	1.04	0.79	0.63	1.04	1.003	1.001
	2	1.03	0.88	0.80	1.03	1.002	1.0003

$r_G = 1.0$ for clones.
 0.5 for full-sibs.
 0.25 for half-sibs.
 $r_P = h^2 r_G$.
 n = plants per family or clone.

relative efficiencies of family selection using full-sibs or half-sibs. Comparable relative efficiencies for clones under the two family selection schemes are identical, since there is no genetic variation within a clone. Family selection may be more or less efficient than mass selection, depending on family size and heritability. A clonal relationship is more efficient than that of full-sibs, which is more efficient than that of half-sibs.

It may be noted that the ratios of clonal/mass selection in Table 8 are not the same as the comparable ratios which can be developed from Table 4. The formulae used in Table 8 make the tacit assumption that selection intensities, and therefore selection differentials, are equal. This assumption will be discussed in greater detail below. The Table 8 ratios can be made equal to ratios from Table 4 by multiplying by the correction factor (\bar{i}_c/\bar{i}_m) , the appropriate selection differentials (Table 2).

IV. Genotype-Environment Interaction

Inherent in most "seedling seed orchard" proposals is the condition that the candidate seedlings or families will be tested in only one environment, that of the seed orchard. Past agricultural experience has indicated that this is inadequate, and it is common procedure to test an improved variety in several locations and for several years before it is released for planting on a large scale.

At issue is the possibility of a genotype-environment interaction. This may be expressed as follows: $X = G + E + GE$. The individual's (or family's) worth is measured by X , an observed value, which is made up of: G , an average genetic contribution over all reasonable environments; E , a local environmental contribution; and GE , an interaction of the genotype and gross environment of the test site. The local environmental contribution, assumed to be random in nature, may make the individual appear better or worse than its true worth, and thus contributes an error to the judgement of worth. This error may be reduced, as in clonal or family selection, by growing n members of the clone or family. In this case $X = G + E/n + GE$.

If the individual's (or family's) worth is of interest only in one gross environment, the environment of the test, its worth is $G + GE$, the average genetic contribution averaged over all reasonable environments plus its behavior in the specific gross environment of interest. Replication within that environment increases the accuracy with which X estimates $G + GE$ by reducing the error, E . However, if the individual's (or family's) worth is of interest over all reasonable environments, its worth is G , and GE contributes an error to estimating G . No amount of replication within the one test environment will reduce this type of error.

If n is the number of available plants in each clone or family, s is the number of different test sites, and q is the number of plants of each clone or family at each test site, so that $n = sq$, then $X = G + E/sq + GE/s$. Thus, X will most efficiently estimate the worth, G , when $q = 1$, and $s = n$. Operationally, the worth of candidate clones or families is most effectively evaluated for all reasonable environments when the available number of test trees is distributed over the maximum number of test sites which is practical.

Most seed orchard specifications include statements to the effect that the site be suitable for good seed production, and that it should be located where the orchard can be ef-

ficiently and easily managed. For many species, these specifications will not allow a seed orchard site which is typical of the normal sites to be planted to progeny of the orchard. Thus the dilemma: Should we put our "seedling seed orchard" on a typical site to get a reasonable evaluation of the candidate trees, but possibly few and expensive seeds, or should we put it on a good seed orchard site and risk selecting unsuitable parents? For if the genotype-environment interaction is important, and if a good seed orchard site is quite different from the typical normal sites for the species, then GE will contribute more than unreduced error to the candidate evaluations. It will contribute a consistent bias toward selecting generally unsuitable parents.

V. Discussion

The expression $\bar{i}oh^2$ is generally used to predict gain in a selection program. When evaluating alternative plans, it may be worthwhile to consider the effect on each of these factors separately.

The variation of a characteristic or index, which enters the gain expression as the standard deviation, σ , may be considered to be a basic property of the population. This variation changes, however, as its components are manipulated by the breeder. If the breeder selects some subunit of the original population, such as the parents placed in a clonal seed orchard, the genetic component of the total variation is usually reduced within this subpopulation. Similarly, if the environmental component is reduced in a plantation as compared to a wild stand, as suggested by WRIGHT (1960), the total variation is correspondingly reduced. If the environmental component is statistically reduced, by replicating members of a family or clone (for example, see Table 3), the variation of the units selected (clones or families) is correspondingly reduced. The general

formula for this reduction is $\sigma_p = \sigma_p \sqrt{\frac{1 + (n-1)r_p}{n}}$ (LERNER, 1958, Chap. 5). These reductions in total variation may be more than offset by the increased accuracy of genetic identification which results, particularly at lower heritabilities. Whenever argument is based on increased heritability due to such manipulations, however, these reductions cannot be ignored.

The accuracy with which the genetic component of, or contribution to, variation is identified enters the gain expression as the heritability, h^2 . This may be increased by reducing the errors caused by environmental contributions to variation (for example, see Table 1). The effect of increasing heritabilities and, for clonal and family selection, reducing variation is assessed in Table 8. The increase in genetic identification with family-plus-mass selection schemes is accurately assessed by the formula in Table 8 only if the selection index is optimum. Accurate heritability information is needed in order to construct an optimum index. Indexes which are not optimum, due to over- or under-estimates of heritability, will be less efficient than indicated in Table 8. However, in many cases the reduction in actual efficiency will be relatively small.

The selection differential, \bar{i} , is the third factor in the gain expression. It is the difference, in standard deviations, between the average observed value of the selected individuals and the average observed value of the general population. In most artificial selection schemes, it can be related to the selection intensity (see LERNER, 1958, Box 11 and Table 2, above). Selection intensity is the ratio: (the

number selected)/(the number selected from). The smaller this ratio, the larger is the selection differential and the amount of gain possible.

Any one of three considerations may determine the minimum number of genotypes to be chosen in a selection program. The first is the number of individuals required to reproduce the next generation. In organisms such as cattle, this number must be relatively high, as each cow produces only a few calves in her lifetime. With trees, this is much less limiting, as each tree produces thousands, or even millions, of seeds. The second consideration is inbreeding, which may impose a more severe limitation if inbreeding depression is important in the species. Inbreeding is important relative to most "clonal seed orchards" only if: (1) future breeding, limited to progeny of the orchard, is contemplated; or (2) if effective selfing is possible within the seed orchard. It is more of a problem with "seedling seed orchards", as the production orchard could produce a high percentage of inbred seed if this is ignored. The third consideration, narrowing of unselected genetic variability, may also be important with trees. Many foresters would be uncomfortable knowing entire plantations were made up of only one or a few families, even though completely non-inbred.

Other considerations determine the maximum number to be chosen from in a selection program. In a program starting with wild stands, the cost of measuring and evaluating trees determines the maximum number of trees actually considered as candidates for selection. However, it generally works out to be more complex than that. In many programs, not all trees are rated for all characteristics, but they are put through a series of cullings. It would be possible for a tree to have a high enough index value to be selected, but be eliminated on an early culling. Therefore, the selection differential is not as high as the selection intensity would indicate. In schemes involving statistical reduction of environment-caused error, such as clonal, family, or family-plus-mass selection, several additional types of costs are encountered, relating to the maximum number to be selected from. Some of these are: The cost of obtaining related individuals; the cost of the tagging, mapping and record-keeping necessary to maintain the identity of each plant; the cost of the land devoted to the evaluation experiment; and the cost of maintaining the plants until selection is completed.

In most "seedling seed orchard" proposals, the production orchard will be made up of seedlings which have been evaluated on the site. Filling out the orchard by vegetatively reproducing selected seedlings, or planting additional seedlings of selected families, will be of limited importance if practiced at all. Under these conditions, spacing, not cost per tree, dictates a maximum selection intensity. This intensity is identical for all alternative evaluation schemes. This maximum practicable selection intensity seems to be in the neighborhood of about 10% (GODDARD and BROWN, 1961).

If, however, the plants are evaluated at a site other than the seed orchard site, the picture may change considerably. The maximum number of trees evaluated would depend on the costs involved, rather than on spacing considerations. Suppose, for example, that the cost of obtaining, maintaining, measuring and evaluating an unpedigreed seedling growing in a production plantation is $\frac{1}{2}$ that of these costs for a pedigreed seedling growing in an experimental plantation. Then 10,000 unpedigreed

seedlings could be evaluated for the same cost as 5,000 pedigreed seedlings. More important, the limitation on maximum selection intensity is sharply reduced, relative to "seedling seed orchards". Instead of selecting 500 of 5,000 trees in order to establish a 500-tree seedling seed orchard, the breeder may choose to select the best 50 of the now-available 10,000 unpedigreed trees. Since this germ-plasm requires relocation in the seed orchard anyway, a 1:1 ratio between selected trees and seed orchard trees is no longer so important. The limitation on maximum selection intensity is also reduced for family-plus-mass selection, but not as much as with mass selection. Inbreeding and related considerations probably influenced the breeder to choose 50 unpedigreed seedlings. Since family-plus-mass selection schemes tend to concentrate the individuals selected in a few families, he may decide to require 80 selections with this scheme. For a strict family-selection scheme with 50 families, the maximum selection intensity is 1 of 50, and it is likely the breeder will want the more conservative 5 of 50 intensity. An alternative is to use fewer seedlings of more families. Increased procurement and identification costs may prevent this, or at least increase the number of unpedigreed seedlings which may be evaluated for the same cost. Using this example, family selection remains at an intensity of 10%, family-plus-mass selection increases to 1.6%, and mass selection increases to 0.5%. The selection differentials are, respectively: family $1.755\sigma_f$; family-plus-mass $2.502\sigma_{fm}$; and mass $2.892\sigma_m$; where $\sigma_m = \sigma_{fm} > \sigma_f$. The increased accuracy of genetic identification must more than offset the advantages of greater selection differential and greater variability of the mass selection scheme for an alternative system to be used under the above assumptions.

Factors affecting the comparative costs of rooted cuttings and seedlings will now be considered. (Except for such special cases as blister-rust resistance or resin production, the use of grafted clones for genetic evaluation is questionable, since they are growing on foreign root systems.) For some species, such as *Populus deltoides*, the cost of a rooted cutting is comparable to or less than that of an unpedigreed seedling. For others, such as *Pinus radiata*, the cost of a rooted cutting is probably more than that of an unpedigreed seedling, but less than that of a pedigreed seedling. For other rootable species, the cost of a rooted cutting may be comparable to, or more than, that of a pedigreed seedling. There may still be considerable variation in comparative costs within this general framework, depending on the size of the family or clone developed. In general, it costs about the same to collect, root, and establish one cutting from each of two different trees as it does to root two cuttings from the same tree. Thus, the cost per plant is not much greater for a 2-plant clone than it is for a 100-plant clone, as the main cost is the care required to successfully root the cuttings. Alternatively, it generally costs much more to produce one pedigreed seedling from each of two families than it does to produce two of the same family, and the cost per pedigreed seedling drops markedly as the size of the family increases. The major cost of producing pedigreed seedlings is making, protecting, and harvesting controlled pollinations. Since most tree species produce many seeds per successful cross, large families cost little more than small ones. Thus, the cost advantage may go to clones if it is decided to evaluate many candidate trees with a few individuals per clone, but to some form of pedigreed-seedling scheme if it is decided to evaluate relatively few families, or the indi-

viduals in relatively few families, with many seedlings per family.

VI. General Recommendations

Clonal Seed Orchards. By "clonal seed orchard" is meant phenotypic selection of mature trees, usually from wild stands, and vegetative replication of these trees in seed orchards. There are several circumstances or species characteristics which argue for a clonal seed orchard scheme. It seems to be the most effective short-term approach if early evaluation of juvenile trees has proven to be unacceptable relative to the goals of the selection program. For most species, mature scions grafted onto seedling trees will produce seeds in quantity at least as soon as seedlings, and in some cases may do so much sooner. In addition, clonal seed orchards may be planned with uniform spacing for ease of management, with the clones distributed so as to maximize multiple-outcrossing and minimize selfing. These considerations lead one to the prediction that clonal seed orchards will produce improved seed, in quantity, with minimum inbreeding, in the shortest time of any of the alternatives considered here. The cost of establishing grafts, rooted cuttings, and pedigreed seedlings varies from species to species, and may become limiting for one or the other alternative.

The criticism, occasionally expressed, that clonal seed orchards are a dead-end relative to further genetic improvement, does not seem justified. On the contrary, a clonal seed orchard will significantly reduce the costs of obtaining pedigreed families for second-generation testing. Plantations established from seed from clonal seed orchards will provide material for second-generation mass selection with high selection intensities. In many cases, this second-generation testing can begin soon after establishment of the clonal seed orchard. Furthermore, there is no need for the population to remain closed. Promising families or individuals not included in the original clonal seed orchard may be tested right along with second-generation progeny, increasing the selection intensity in some schemes, and if selected, decreasing the probability of inbreeding.

Progeny testing of members of a clonal seed orchard is frequently practiced for the purpose of roguing the orchard to only "proven clones". In view of the reduced genetic component of variation among the clones in an orchard, and the low selection intensity generally possible, this procedure is questionable as an end in itself. However, if the progeny testing is actually an evaluation for a second-generation seed orchard, then the roguing of a few poor parent clones from the first-generation orchard may be viewed as an added, and interim, benefit of selection among the progeny.

Evaluation and Seed Orchard Combined. This category includes evaluation by families of seedlings ("seedling seed orchard"), evaluation by clonal replication, and mass selection, all in place on the site of the seed orchard. In order to use this scheme, the procurement costs of the plants to be evaluated, the evaluation itself, and the time lag until adequate seed is produced, must be acceptable in comparison to clonal seed orchards. The site of the seed orchard and the care it is to receive during the evaluation phase should be typical of sites and care contemplated for the progeny of the orchard, and the genotype-environment interaction of the species must be at or below an acceptable level. Or, if the seed orchard site is not typical, the genotype-environment interaction must be negligible. The reduction in possible gain due to spacing limitations on the

selection intensity must be more than offset by other considerations.

With this scheme, it is possible to combine a first-stage gain via the plants or progeny chosen to enter the evaluation, with a second-stage gain by selecting among these candidates at the seed orchard site. Since spacing limitations fix selection intensity at the same value for the alternatives within this scheme, the choice between them will be determined by their relative efficiencies, the values of the predicted gains, and their relative costs. Relative efficiency values for a variety of heritabilities and family sizes are presented in Table 8. Clonal selection is, in all cases, more efficient than family-plus-mass selection (optimum index), which in turn is more efficient than family or mass selection. Under some circumstances, mass selection is more efficient than family selection. Mass selection at the seed orchard site may be thought of as a second-generation seed-production area, and should be the least expensive of the alternatives. Family-plus-mass selection will entail more calculation (both in developing an accurate index and in making selections) than will family selection, but other costs should be equal. Thus, it appears that family-plus-mass selection will be preferred over family selection in most situations. Where rooted cuttings cost the same as (or less than) pedigreed seedlings, clonal selection will be preferred over family-plus-mass selection. Other choices will depend on comparing cost to efficiency of selection, and value of predicted gains.

If inbreeding considerations are important, evaluation of few individuals in each of many families may be preferred over many individuals in each of few families, even though the selection intensity is the same for either case. This can be accomplished with little additional cost with clonal selection, but may require considerable increase in cost with pedigreed seedlings.

Evaluation at a site or sites other than the seed orchard site. This scheme shares many of the requirements, advantages, and disadvantages of evaluation at the seed orchard site. It is to be preferred under two circumstances: (1) Genotype-environment interaction is important; or (2) A higher selection intensity is desired than is possible with evaluation at the seed orchard site. Two added disadvantages are: (1) There is an added cost of establishing the selected plants in the seed orchard; and (2) There will probably be a time-lag until adequate seed is produced.

If genotype-environment interaction is important, the clones or families should be evaluated over a number of representative sites, one of which may be the seed orchard site only if it is representative of sites contemplated for plantation use with progeny from the orchard. Mass selection, or the use of individual-tree information in family-plus-mass selection, becomes a questionable practice. If the seed orchard site is not representative, the time-lag to production may be reduced by growing a few individuals of each clone or family on the seed orchard site. Members of the selected clones or families may start producing some seed shortly after selection. This may be particularly useful in starting third-generation tests. In the case of clonal selection, the remainder of the orchard can be filled in from those individuals already established by approach-grafting to potted seedlings. The ceiling on selection intensity is removed with this scheme, although candidate clones or families must be replicated over several sites.

If genotype-environment interaction is not important, then family-plus-mass selection and mass selection are

admissible alternatives. Furthermore, the seed orchard site may house part of the test. Any trees selected on this site will form an early nucleus of the seed orchard. Since there are no longer any restrictions on selection intensity, the choice of alternative methods becomes more complex. Some of the factors affecting this choice are discussed above.

By selecting on sites other than seed orchard site, early selection and roguing at the seed orchard site remains reversible. Using clonal selection as an example, suppose the orchard is rogued and filled out to the desired spacing using the 25 best-performing clones at age seven. The other clones are not destroyed, nor does their evaluation stop. At age fifteen, it may become apparent that several of the early selections develop poor characteristics, and that several overlooked at age seven have become outstanding at age 15. The poorest clones are removed from the seed orchard, and replaced with the abundant vegetative material available from the outstanding clones in the field tests. This procedure can be repeated as often as new information becomes available from the field tests, and the gains justify the expense.

Clonal Selection. In general, clonal selection seems better suited for obtaining second-generation and later gains, than for making initial selections. It may be used for first-generation evaluation where the genotype-environment interaction is so large, or heritabilities so low, that selection in the wild does not seem justified for clonal seed orchards, or for parents for second-generation testing. However, even in this case it seems unlikely that candidate trees would be chosen for cloning and evaluation completely at random, with no culling.

With many species, cuttings from seedlings and young trees root relatively easily, but cuttings from older trees root with great difficulty. It is also likely that rooted cuttings from seedlings will be more comparable to seedlings than will rooted cuttings from older trees. Thus, the advantage of combining a first-generation gain from field selection of wild trees with a second-generation gain from clonal selection among their progeny is compatible with the advantage of cloning very young plants.

The following is an example of one type of clonal selection which might be feasible:

1. Obtain a set of good seedlings. Many of these may be control-pollinated or open-pollinated seedlings from your first-generation seed orchard. Others may be "super seedlings" from nurseries using wild seed. Others may be the result of control-pollinations or open-pollinations on trees outstanding for characteristics which have recently been considered to be more important than they were when the first-generation seed orchard was established.
2. Plant the seedlings on the seed orchard site. Water, fertilize, etc. to maximize early vegetative growth.
3. Root cuttings from these seedlings. Plant the rooted cuttings in an evaluation design at one or more other sites. The additional sites not only reduce error caused by genotype-environment interaction, but ensure that your population won't be destroyed by a single disaster.
4. Keep the original seedlings at the site clipped in a bush form, to produce abundant scion material.
5. As selections are made based on a clonal evaluation, either use the bushy seedlings whose clones were not selected as stock plants for grafting, or replace them with younger seedlings for grafting.

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Summary

The characteristics of clonal selection are illustrated with a number of theoretical examples. In general, selection based on clonal evaluation may reasonably be considered as an alternative to other selection schemes for characteristics of low heritability, where intense selection is possible, and in the absence of appreciable variance associated with cloning. A selection experiment comparing single-phenotype and clonal selection is briefly described. The results indicate that clonal selection is a workable, as well as theoretical method.

The relative efficiencies of clonal, family family-plus-mass, and mass selection are calculated. At all heritabilities, clonal selection is more efficient than family-plus-mass selection, which in turn is more efficient than family selection or mass selection.

The effect of genotype-environment interaction is discussed. Evaluation of a tree or family at only one site fails to reduce this type of error. Furthermore, evaluations at an atypical site may be biased toward unsuitable selections.

Manipulations of the variation and heritability of a characteristic are discussed. The third variable affecting gain, selection intensity, may be determined by spacing considerations alone in a "seedling seed orchard". In other schemes, inbreeding, cost, and value of the predicted gain will determine the selection intensity practiced.

"Clonal" and "seedling seed orchards" are discussed relative to their usefulness and limitations. A third alternative, second-generation evaluation at sites other than exclusively the seed orchard site, offers advantages relative to genotype-environment interaction and selection intensity. It is, however, the most costly in terms of time and money.

The usefulness of clonal, family, family-plus-mass, and mass selection is explored given various conditions, and as variations of "clonal seed orchards", "seedling seed orchards", and "the third alternative". For species which can be realistically propagated by rooted cuttings, clonal selection seems to offer important advantages over alternative selection schemes.

Résumé

Titre de l'article: *Sélection clonale et un autre projet de verger à graines.*

Les caractéristiques de la sélection de clones sont illustrées par un certain nombre d'exemples théoriques. En général, la sélection basée sur la comparaison des clones peut être raisonnablement mise en balance avec d'autres projets de sélection concernant: des caractères à héritabilité faible, une sélection intense possible et l'absence d'une variation appréciable due à la multiplication végétative. Un essai de sélection comparant la sélection de phénotypes

et de clones est décrit brièvement. Les résultats indiquent que la sélection de clones est une méthode valable des points de vue pratique aussi bien que théorique.

On calcule les efficacités relatives de la sélection de clones, de familles, de la sélection massale plus sélection de familles et de la sélection massale. Pour toutes les hérédibilités, la sélection de clones est plus efficace que la sélection massale combinée avec la sélection de familles, qui à son tour est plus efficace que la sélection de familles ou la sélection massale.

L'effet de l'interaction entre le génotype et le milieu est étudié. L'évaluation d'un arbre ou d'une famille dans un seul endroit ne permet pas de réduire ce type d'erreur. Bien plus, des évaluations dans une station non typique peuvent mener à des sélections défectueuses.

Les manipulations de la variation et de l'hérédibilité d'un caractère sont étudiées. La troisième variable affectant le gain génétique, l'intensité de la sélection, peut être déterminée uniquement par des considérations d'espacement dans un «verger à graines de semis». Dans d'autres projets, la consanguinité, le coût et la valeur du gain prévu, détermineront l'intensité de la sélection à pratiquer.

Les vergers à graines «de clones» et «de semis» sont étudiés en rapport avec leur utilité et leurs limitations. Une troisième méthode, l'évaluation de la seconde génération en des emplacements autres que celui du verger à graines, présente des avantages concernant l'interaction entre génotype et milieu et l'intensité de la sélection. Cependant, c'est la méthode la plus coûteuse en temps et en argent.

L'utilité de la sélection de clones, de celle de familles, de la sélection massale plus familles et de la sélection massale est examinée pour diverses conditions données et en tant que variations «des vergers à graines de clones», «des vergers à graines issus de semis» et «de la troisième solution». Pour les espèces qu'il est rentable de multiplier par boutures, la sélection de clones semble présenter de nets avantages par rapport aux autres méthodes de sélection.

Zusammenfassung

Titel der Arbeit: *Klonauslese und eine Alternative im Schema der Samenplantagen.*

An Hand einer Reihe theoretischer Beispiele werden die Kennzeichen der Klonauslese dargestellt. Ganz allgemein dürfte die Auslese auf Grund des Klonverhaltens als eine Alternative zu anderen Selektionsverfahren durchaus in Erwägung gezogen werden für Merkmale mit geringer Hereditabilität, wenn intensive Auslese möglich ist, und bei Nichtvorliegen nennenswerter Varianz in Verbindung mit der Verklonung. Ein Selektionsversuch zum Vergleich der Auslese einzelner Phänotypen und der Klonauslese wird kurz beschrieben. Die Ergebnisse zeigen, daß Klonauslese ein sowohl theoretisch als auch praktisch brauchbares Verfahren ist.

Die relativen Effizienzen der Klon- und der Familienauslese, der Familienauslese in Kombination mit Massenauslese und der Massenauslese werden berechnet. Für Hereditabilitäten jeder Größe ist Klonauslese wirksamer als die Kombination von Familien- und Massenauslese, welche ihrerseits wieder wirksamer ist als Familienauslese oder Massenauslese.

Der Effekt der Genotyp-Umwelt-Interaktion wird diskutiert. Durch Bewertung eines Klons oder einer Familie an nur einem Standort kann diese Art von Fehler nicht vermindert werden. Darüber hinaus können Bewertungen auf einem atypischen Standort verzerrt sein und zu unbrauchbaren Auslesen führen.

Die Behandlung der Variation und der Hereditabilität eines Merkmals werden diskutiert. Die dritte Variable, die von Einfluß auf den Züchtungsfortschritt ist, die Ausleseintensität, dürfte in einer „Sämlings-Samenplantage“ allein durch Überlegungen über den Pflanzverband bestimmt werden. Bei anderen Systemen werden Aspekte der Inzucht, der Kosten und die Höhe des Schätzwertes für den Züchtungsfortschritt die anzuwendende Ausleseintensität bestimmen.

„Klon“- und „Sämlings-Samenplantagen“ werden hinsichtlich ihrer Brauchbarkeit und ihrer Grenzen diskutiert. Eine dritte Alternative, die Bewertung der zweiten Generation an einem anderen Standort als dem der Samenplantage, bietet Vorteile mit Rücksicht auf die Einschätzung der Genotyp-Umwelt-Interaktion und die Selektionsintensität. Sie ist allerdings das aufwendigste Verfahren in terminis von Zeit und Geld.

Die Brauchbarkeit der Klonauslese, der Familienauslese, der Kombination von Familien- und Massenauslese sowie der Massenauslese werden ermittelt für verschiedene Bedingungen und Varianten der „Klonsamenplantagen“, die „Sämlings-Samenplantagen“ und die „dritte Alternative“. Für Species, bei denen die realistische Bewertung von bewurzelten Stecklingen möglich ist, scheint die Klonauslese bedeutende Vorteile gegenüber anderen Verfahren zu haben.

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