HOW MUCH GENETIC VARIANCE WILL BE REDUCED THROUGH CLONAL SELECTION?

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Abstract.--Clonal selection is defined here as vegetative propagation of selected clones. Clonal selection offers maximum genetic gain and maintenance of pure lines. Recently narrow genetic base has worried people working with clonal selection. The reduced genetic variance among selected clones can be expressed as $Vg' = Vg(1.0 - i\ h^2(i\ \ c))$ where Vg is the original genetic variance before selection, i is the selection differential in standard deviation, h^2 is heritability and c is the truncation point in standard deviation.

Additional keywords: Phenotypic variance, pure line selection.

My definition of clonal selection is simply selection of clones for vegetative propagation. It should not be confused with producing seedlings from tested clones. The future clonal performance can be predicted from the test record because the genetically pure lines are perpetuated. But the seedling performance cannot be accurately predicted due to gene segregation and recombination.

The usual procedure for clonal selection is asexual reproduction of superior genotypes after a well designed, replicated clonal test. However, in the case of cloning plus-trees from phenotypic selection, or hybrid from hybridization, the original population may be considered as a clonal test with only one replicate per clone. The results from this study are still valid under this condition.

Clonal selection has been popular among horticulturists for years. Most of the fruit trees today belong to a few varieties of clones. In forestry, clonal selection has been successful for poplar (Schreiner 1959) and cottonwood (Mohn, Randall, and McKnight 1970). In the near future when we break thru the barrier for tissue culture; when silage silviculture becomes common practice; clonal selection will become more important.

Greatest genetic gain and uniformity can be obtained by selecting just one best clone. Unfortunately, narrow genetic base is usually associated with seriousness of disease problems and rigidness of adaptation requirements. In order to escape from these disadvantages, planting of clonal mixtures was recommended (Schreiner 1966).

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The question of how much genetic variability will be reduced by clonal selection is not easy to answer unless we have perfect information about the genotypes being selected, or when the number of clones is one. In the first case, we can compute genetic variances among individuals in the selected group as well as in the original population. In the second case the genetic variance is none for a single clone. If we have an estimate of clonal heritability and proportion of selection can we figure out the genetic variance of the selected clones? The answer is positive as indicated in this paper.

Com.utation of the Reduced Genetic Variance

The formula for computing the genetic variance among selected clones is as follows:

$$V = 1 - ih^2(i - c)$$

where V is the fraction of the original genetic variance
i is the selection differential in standard unit
h^2 is the clonal heritability
and c is the truncation point in standard unit

The proof of the formula is shown in the appendix at the end of this paper. However, I would like to illustrate here the procedure of computation and the implication of this formula.

After a clonal test, we can compute the clonal heritability as $h^2 = Vc/(Vc + Ve/n)$ as suggested by Burton and DeVane (1953). An easier way is to compute $h = 1 - (1/F)$; where F is the F-value from analysis of variance table for the clonal test (Kung and Bey 1977). If the F value is non-significant the hypothesis of equal clonal mean should be accepted and no selection should be done. Then we need not be concerned about the reduction in genetic variance. On the other hand when the clonal means are significantly different then selection and heritability become meaningful.

Once we determine the level of culling or proportion of selection, the selection differential and cutoff point in standard deviation can be obtained from a table (Namkoong and Snyder 1969). For example, if we selected 10 percent, the selection differential (i) equals 1.7550 and the cutoff point (C) is 1.28155. Therefore, for $h^2 = .5$ the genetic variance is reduced from 1.0 to

$$1.0 - 1.7550 \times 0.5 \times (1.7550 - 1.28155) = 0.585.$$

Given the original genetic variance as 1.0 and heritability from .1 to 1.0 in steps of 0.1, the reduced genetic variance for various levels of selection proportions are shown in Table 1.

Table 1.--Fraction of genetic variance retained at various levels of heritability and selection proportion. The original genetic variance is 1.0.

Selection Proportion	Heritability									
	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
	Fraction of the Original Genetic Variance									
.90	.971	.942	.914	.885	.856	.827	.798	.770	.741	.712
.80	.958	.917	.875	.833	.791	.750	.708	.666	.625	.583
.70	.949	.899	.848	.797	.746	.696	.645	.594	.544	.493
.60	.942	.885	.824	.769	.711	.653	.596	.538	.480	.422
.50	.936	.873	.809	.745	.682	.618	.554	.491	.427	.363
.40	.931	.862	.794	.725	.656	.587	.518	.449	.381	.312
.30	.926	.853	.779	.706	.632	.559	.485	.412	.338	.265
.20	.922	.844	.766	.687	.609	.531	.453	.375	.297	.219
.10	.917	.834	.751	.668	.585	.501	.418	.335	.252	.169
.05	.914	.828	.741	.655	.570	.483	.397	.310	.224	.138
.01	.910	.819	.729	.639	.549	.458	.368	.277	.187	.097

A Practical Illustrative Example

A black walnut clonal test at Purdue University was reported to this Conference four years ago by Beineke and Masters (1973). Let me extract some of their data to illustrate the problem here.

Character	No. Clones	No. Grafts	Vc	Ve
Foliation date	50	224	24.866	2.310
DBH	17	68	0.062	0.184

Suppose that we would like to select half of the tested clones based on their performance in the nursery. How much genetic variance is there after vegetative propagation of these selected clones?

To use the formula or the table, we need to enter the value for clonal heritability. But first we have to know the average no. of grafts per clone. It can be seen that for foliation date the average no. of grafts per clone is n = 224/50 = 4.5; and for DBH it is n = 68/17 = 4. Then we can substitute needed data into the heritability formula as follows:

$$h^2 \text{ (foliation date)} = 24.866/(24.866 + (2.310/4.5)) = 0.98$$

$$h^2 \text{ (DBH)} = 0.062/(0.062 + (0.184/4)) = 0.57$$

When we select 50% of the population, the selection differential is .7979 and the cutoff point is at 0.0000 standard deviation. Given the original genetic variance as 1.0, the genetic variance for foliation date among selected clones is

$$1 - i\,h^2\,(i - c) = 1 - .7979 \times .98\,(.7979 - 0.0) = .38$$

Because the original clonal variance is 24.866, therefore, the actual genetic variance of foliation data among selected clones becomes 24.866 x .38 = 9.45.

By the same procedure, the actual genetic variance for DBH among selected clones is

$$0.062\,(1 - .7979 \times .57\,(.7979 - 0.0)) = .040$$

Discussion

Table 1 shows that small selection proportion and/or high heritability will cause greater reduction in genetic variance. When heritability equals 0.0, or when a trait is not genetically controlled, selection would cause no change in genetic variance. On the other hand, when heritability equals 1.0, or when a trait is controlled completely through genetics, the reduction in genetic variance equals the reduction of phenotypic variance. Therefore, the fraction of phenotypic variance maintained in the selection at various levels can be represented by the last column of Table 1. For example, if we want to know how much of the original phenotypic variance remains in the selection when 10% of the population is selected for a trait with $h^2 = .1$, we can see from Table 1 that the answer is .169, or about 17%.

Because the figures in the last column are the smallest ones among all columns, the reduction rate for phenotypic variance is greater than that for genetic variance. For example, when $h^2 = 0.1$ and selection proportion = Al, 91 percent of the original genetic variance is still retained in the selection while only 9.7 percent of the original phenotypic variance is represented among selected clones.

It comes to my surprise that the actual genetic variance may even become greater than the phenotypic variance in the selection. This happens when the proportion of selection is small and heritability is high. For example, assuming that the phenotypic variance of date of leaf fall as 100 and heritability as .90 then the original genetic variance would be 90. If we select 20% of clones, the phenotypic variance would be reduced to 100 x .219 = 21.9 while the genetic variance would be reduced to 90 x .297 = 26.7. However, it is true only in the selection and not in the next clonal propagation. As we can see in this example: the environmental variance is 100 - 90 = 10, the genetic variance of the 20% selection is 26.7, Assuming the environmental variance is the same for the next propagation, the phenotypic variance among the propagated, selected clones would become 26.7 + 10 = 30.7. Thus, the selected clones in the test plantation may seem to be

uniform. There may be more genetic variance in them than we can see on the surface. Certainly, if we propagate the selection again, they would become more different than they were at the time of selection.

As indicated earlier the formula can be used for vegetative propagation of phenotypic selection. The only change needed to be made here is the use of heritability for phenotypic selection rather than clonal heritability. Let us use data from Beineke and Masters again for illustration. The heritability for DBH given Vc = 0.062 and Ve = 0.184 is .062/(.0624 + .184) = .25. If we go out, select and draft 10% of black walnuts using diameter growth as our guide, the genetic variance for the four-year DBH would be 0.062 x .792 = 0.049. The value of .792 is interpolated between .834 nd .751 which are the value at selection proportion = .10 and h = .2 and .3 respectively in Table 1.

The narrow genetic base has worried many tree improvement workers. It is true that selection changes the variances and their relationship. The reduction in phenotypic variance can be easily seen. The reduction in genetic variance through clonal selection now can be computed. We can balance genetic variability with genetic gain to obtain an optimal selection level when we are working with vegetative reproduction. On the other hand, worry of narrow genetic base may be unfounded for sexual reproduction of truncated selection. During sexual reproduction the genetic variance depends on such things as gene frequencies, dominance, epistasis, linkage and the mating system. The genetic variance is changed by selection only slowly. The population is not likely to exhaust its genetic variance unless it is small, the number of loci is small, the selection is very intense and the mating scheme is very restrictive. None of above warnings can be applied to the present situation of seed orchard management. So we should just concentrate on maximizing genetic gain and not to worry about genetic variance among planted seedlings.

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Appendix

Given a normal distribution with mean (μ), standard deviation (σ), truncation point (x), height of the ordinate at the point of truncation (z) and the proportion selected (p), we have standardized cut off point c and selection differential i as

$$c = (x - \mu)/\sigma$$

$$i = z/p \qquad \text{(Falconer 1972, p. 194)}$$

The variance among selected individuals after truncation, S^2, can be expressed as

$$S^2 = \sigma^2(1 - i(i - c)) \qquad \text{(Cohen 1959)}$$

Furthermore, let (X,Y) have a bivariate normal N (μx, μy, σx^2, σy^2, ρ) distribution, and let S^2 represent the variance in X after truncation. Then the variance Y after truncation can be expressed as

$$\text{Var } (y) = (1 - \rho^2)\ \sigma y^2 + \rho^2\ \sigma y^2 \sigma r{:}n^2 \qquad \text{(Watterson 1959)}$$

Replacing $\sigma r{:}n^2$ by $(1 - i(i - c))$ we have

$$\text{Var } (y) = (1 - \rho^2)\ \sigma y^2 + \rho^2 \sigma y^2\ (1 - i(i - c))$$

$$= \sigma y^2 - \rho^2 \sigma y^2\ (i(i - c))$$

Now, let us consider X as clonal phenotypic value and Y as clonal genetic value, and let us standardize the bivariate distribution as N (0, 0, 1, 1,ρ). Then we can see that ρ^2 is the heritability h^2. So we have

$$\text{Var } (y) = 1 - h^2(i(i - c))$$

$$= 1 - ih^2(i - c)$$