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Efficiency Changes Due to Use of Doubled-Haploids in Recurrent Selection Methods

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Summary. Efficiency comparisons are made among standard recurrent selection methods and for the same methods modified by the inclusion of haploid and cloning techniques. These comparisons are made with respect to five different gene models representing different levels of heritability and also with respect to unrestricted versus restricted total plant numbers.

When comparisons are made either among the standard diploid or among the modified haploid selection methods, the advantages of clonal and general combining ability selection over individual selection largely disappear when a restriction on total plant numbers is imposed. However, the very considerable advantages of haploid over diploid selection methods, measured on a per cycle basis, do not disappear when total plant numbers are restricted.

When the genetic gains are measured on a yearly basis, it becomes clear that the key to the successful inclusion of the haploid technique, as a device to increase the efficiency of standard recurrent selection methods, is the development of rapid doubled-Haploid extraction procedures.

I. Introduction

The first report identifying a haploid flowering plant was made by Blakeslee et a. (1922). The haploid occurred in experimental studies involving *Datura stramonium* (L). In 1924 Blakeslee and Belling reported the identification of additional haploid *Datura* plants. But more importantly, they also reported the first doubled-haploid plant. These authors, and others since 1924, realized the plant breeding potential inherent in these doubled-haploid plant forms. This recognized potential involves the production of inbred lines. Thus, if a procedure for easily obtaining doubled-haploids could be developed, it would greatly accelerate the extraction of homozygous lines from heterozygous breeding material. Then these homozygous lines could be used directly as pure-line varieties in self-fertilized crops or used as inbred lines in the production of hybrids. A vast literature has developed concerning various ramifications of these concepts (see Kasha 1974).

However, the use of doubled-haploids in less obvious ways to increase the efficiency of selection, rather than to produce a homozygous end-product, has not received sufficient attention. Although, the suggestion that doubled-haploids "may prove useful as an adjunct to recurrent selection" was first made by Chase (1952) and later reiterated by Chase (1974) and Collins and Legg (1974); there has been no critical study of efficiency changes which would result if standard recurrent selection methods were augmented by the use of doubled-haploids. Hence, the objective of this study is to explore some of the consequences of including haploid techniques in otherwise standard selection procedures. Also, since the cell culture technique (which appears to be the most promising technique for the production of doubled-haploids) may prove valuable in the cloning process, the utility of clonal material will also be considered as an adjunct to standard recurrent selection methods.

II. Characterization of the Conceptual Population Undergoing Selection and Description of the Selection Methods

A. Characterization of the Conceptual Population Undergoing Selection

It is assumed that traits undergoing selection are controlled by typically quantitative genetic systems. This implies the involvement of genes at many loci which are scattered at random over the entire chromosome set. It is further assumed that individual gene effects are small relative to the total phenotypic standard deviation. For approximations to be entirely valid, it must be assumed that the genome can be regarded as

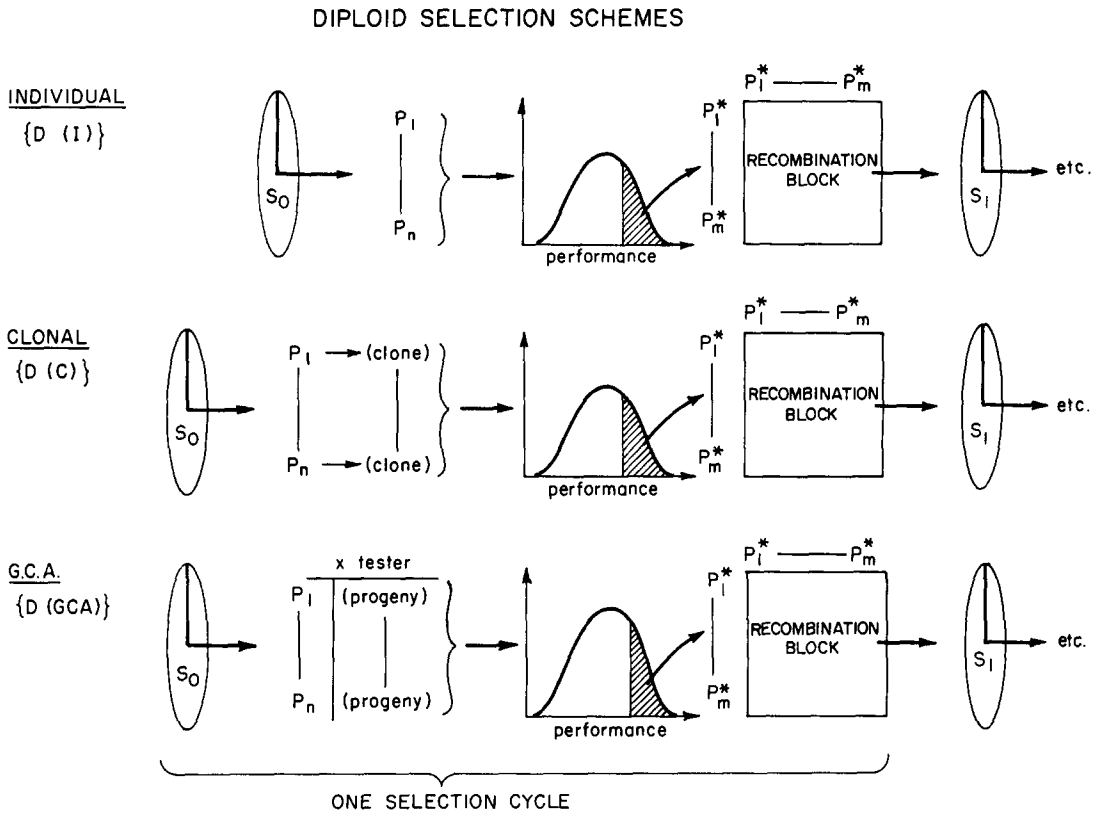

Fig. 1. Diagrammatic representation of the steps required to complete a cycle for the standard diploid recurrent selection schemes: D(I) = diploid individual selection; D(C) = diploid clonal selection; and D(GCA) = diploid general combining ability selection

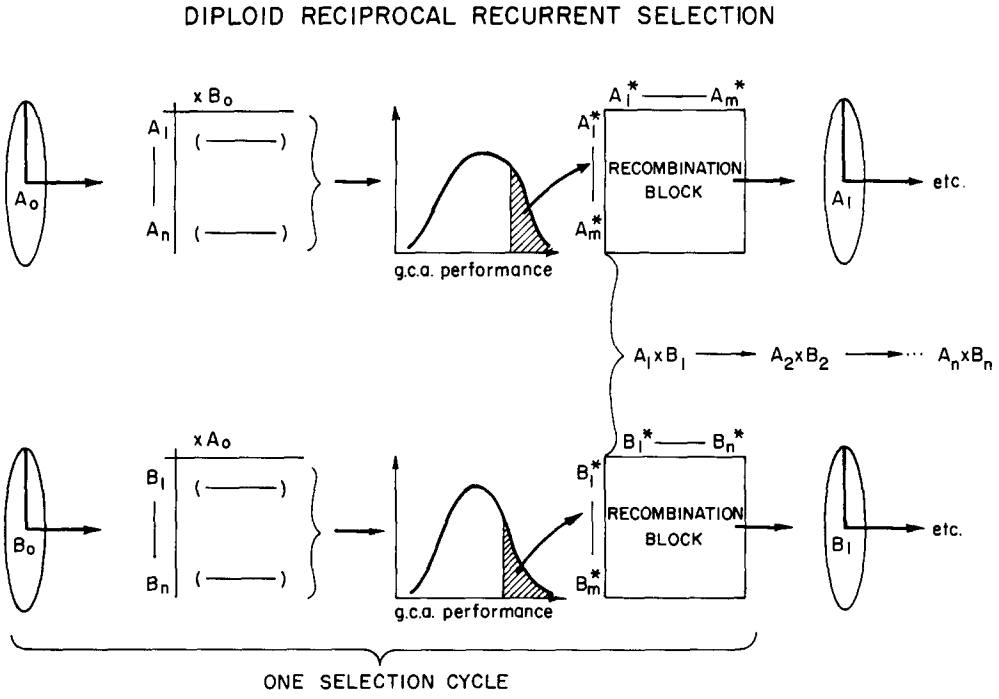

Fig. 2. Diagrammatic representation of the steps required to complete a cycle for D(RRS) = diploid reciprocal recurrent selection

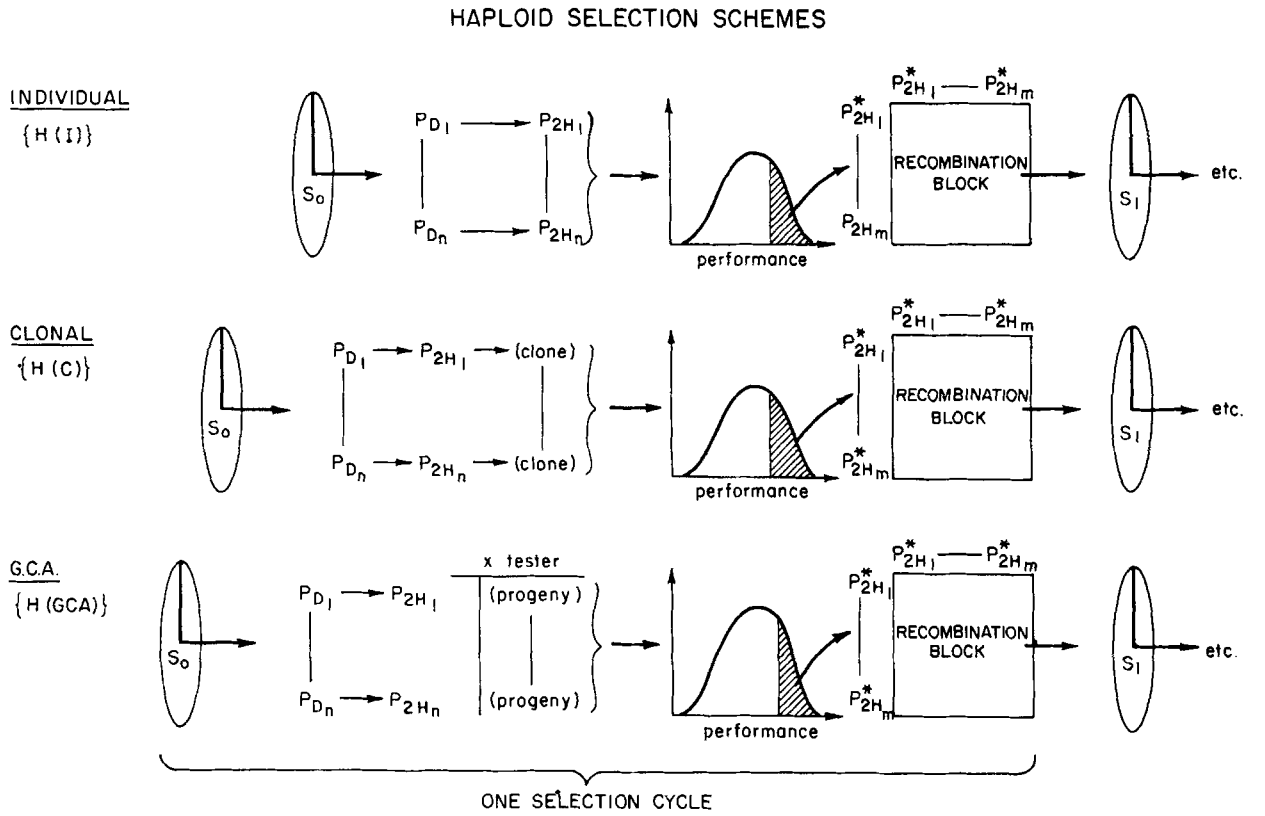

Fig. 3. Diagrammatic representation of the steps required to complete a cycle for recurrent selection schemes that have been augmented by the inclusion of doubled-haploids. These schemes are denoted as: H(I) = haploid individual selection; H(C) = haploid clonal selection; and H(GCA) = haploid general combining ability selection

being composed of numerous independently segregating, non-interacting genotypic blocks of loci. These blocks need not be reduced to the dimensions of individual loci. In general, a fairly large Darlington recombination index suffices.

The basic population undergoing selection is assumed to be a random-mating population in equilibrium. Even if the species under consideration does not normally mate at random, it is assumed that such a mating system can be imposed upon the selected population through controlled crossing in every cycle of the selection procedure.

B. Description of Selection Methods

All selection methods discussed in this study are recurrent in the sense that selection occurs in repeated, consecutive cycles. Each cycle consists of (i) evaluation of a sample of individuals from the breeding population on the basis of some measure of performance, and (ii) random mating of all individuals surviving a truncation of the distribution of performance scores. Progeny from these matings produce the breeding population to be used in the next cycle of selection.

1. Diploid selection methods

The four diploid selection methods considered in this study are given diagrammatically in Figs. 1 and 2. They include: (i) D(I) = diploid individual selection, (ii) D(C) = diploid clonal selection, (iii) D(GCA) = diploid general combining ability selection and (iv) D(RRS) = diploid reciprocal recurrent selection.

With individual selection, the individual's phenotype is the criterion of selection; with clonal selection the individual's genotype is evaluated on the basis of its mean clonal performance, and with general combining ability (hereafter abbreviated to GCA) selection the individual's genotype is evaluated on the basis of the mean performance of its half-sib proge-

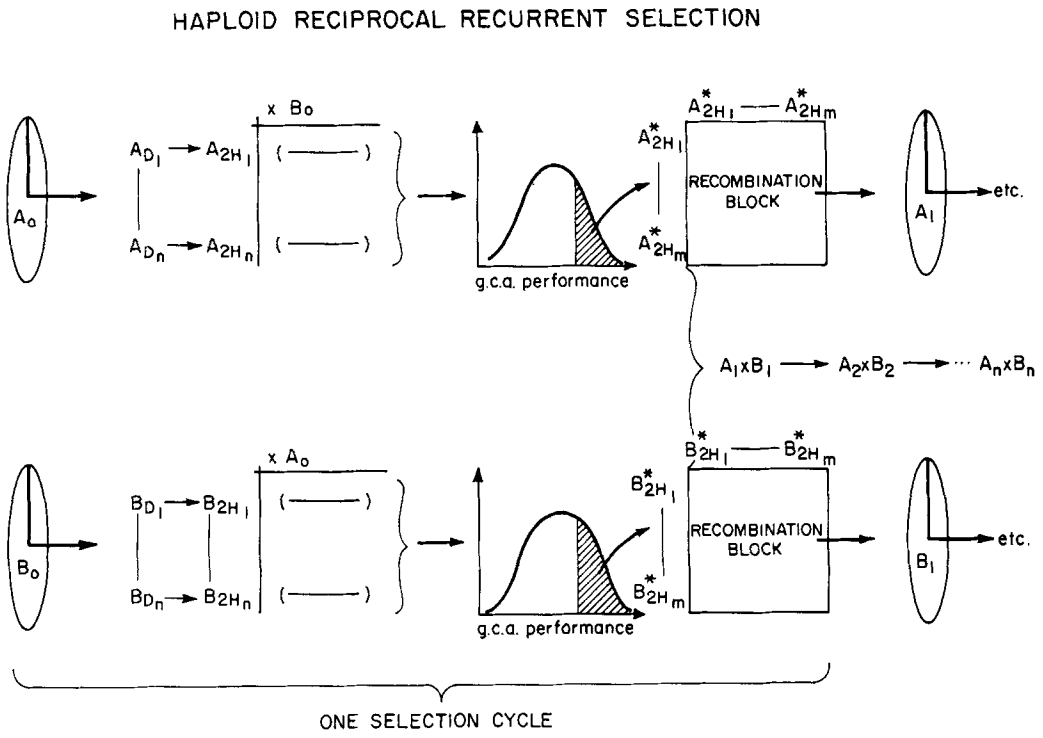

Fig.4. Diagrammatic representation of the steps required to complete a cycle for H(RRS) = haploid reciprocal recurrent selection

ny. Reciprocal recurrent selection is a special procedure in which two populations are simultaneously selected in such a manner that each acts as the GCA tester for the other. Theoretically, in D(RRS) each cycle of selection produces a new improved varietal cross which, over time, asymptotically becomes a single-cross.

2. Haploid selection methods

The haploid selection methods are diagrammed in Fig. 3 and 4. They are similar to their corresponding diploid counterparts except that doubled-haploids are used throughout the testing and crossing procedures.

In the case of haploid individual selection, (H(I)), the phenotypic performances of doubled-haploids are evaluated and subjected to truncation selection. Following evaluation, the selected doubled-haploids are randomly mated to produce the breeding population for the next cycle.

With haploid clonal selection, H(C), clones are produced from each doubled-haploid extracted from the breeding population. Clonal performances are evaluated and random mating is performed among the selected genotypes to produce the breeding population for the next cycle of selection.

Haploid general combining ability selection, H(GCA), implies that the progeny testing procedure is carried out with doubled-haploids produced from the breeding population. Each doubled-haploid is evaluated in terms of the average performance of its half-sib progeny. The breeding population for the next cycle is produced by randomly mating doubled-haploids whose progeny performances exceed the point of truncation.

Haploid reciprocal recurrent selection, H(RRS), represents a program in which two populations are simultaneously selected on the basis of GCA tests. These tests involve appropriate crosses among doubled-haploids. One of the important features of this procedure, in contrast to D(RRS), is that each cycle produces a new group of improved single-crosses, rather than merely an improved varietal cross.

In the following analyses, attention is devoted primarily to those selection procedures involving a single breeding population. The reciprocal recurrent selection methods are mentioned only briefly in the discussion.

Table 1. Increment changes in population mean in terms of covariances among relatives

Selection Method	Diploid	Haploid
Individual	$\Delta\mu_I = (\bar{i})_I(2)[\mathrm{Cov}_D(PO)]\left\{\frac{1}{\sigma^2_{G(D)} + \sigma^2_E}\right\}^{\frac{1}{2}}$	$\Delta\mu_I = (\bar{i})_I(2)[\mathrm{Cov}_H(PO)]\left\{\frac{1}{\sigma^2_{G(H)} + \sigma^2_E}\right\}^{\frac{1}{2}}$
Clonal	$\Delta\mu_C = (\bar{i})_C(2)[\mathrm{Cov}_D(PO)]\left\{\frac{1}{\sigma^2_{G(D)} + (\frac{1}{n})\sigma^2_E}\right\}^{\frac{1}{2}}$	$\Delta\mu_C = (\bar{i})_C(2)[\mathrm{Cov}_H(PO)]\left\{\frac{1}{\sigma^2_{G(H)} + (\frac{1}{n})\sigma^2_E}\right\}^{\frac{1}{2}}$
GCA	$\Delta\mu_{GCA} = (\bar{i})_{GCA}(2)[\mathrm{Cov}_D(HS)] \times \times \left\{\frac{1}{\mathrm{Cov}_D(HS) + (\frac{1}{n})[\sigma^2_{P(D)} - \mathrm{Cov}_D(HS)]}\right\}^{\frac{1}{2}}$	$\Delta\mu_{GCA} = (\bar{i})_{GCA}(2)[\mathrm{Cov}_H(HS)] \times \times \left\{\frac{1}{\mathrm{Cov}_H(HS) + (\frac{1}{n})[\sigma^2_{P(D)} - \mathrm{Cov}_H(HS)]}\right\}^{\frac{1}{2}}$

III. Consequences of Diploid and Haploid Selection

A. General Considerations

Increment changes in the population mean can be determined approximately in very general terms (i.e. in terms of covariances among relatives) for each kind of selection procedure. These changes for individual, clonal and GCA selection are given for both diploid and haploid methods in Table 1. The notation involved is as follows:

$\bar{i}$ = standardized selection differential,
$\mathrm{Cov}_D(PO)$ = diploid parent-offspring covariance,
$\mathrm{Cov}_H(PO)$ = doubled-haploid parent-offspring covariance,
$\mathrm{Cov}_D(HS)$ = diploid half-sib covariance,
$\mathrm{Cov}_H(HS)$ = doubled-haploid half-sib covariance,
$\sigma^2_{G(D)}$ = diploid genotypic variance,
$\sigma^2_{G(H)}$ = doubled-haploid genotypic variance,
σ^2_E = environmental variance,
and n = number of propagules per clone in the case of clonal selection, or number of progeny in the case of GCA selection.

For further details concerning the development of diploid formulae, see Griffing (1960 and 1962). Formulae for haploid selection techniques are derived in a similar manner.

Diploid and haploid formulae for corresponding selection schemes appear similar in that they involve the same kinds of parameters. However, there are important differences which become apparent when the formulae are given as functions of genotypic variance components (Table 2). These components are defined for a random mating population as follows:

$$\sigma^2_{G(D)} = \sigma^2_A + \sigma^2_D$$
= diploid genotypic variance,

where

σ^2_A = additive genetic variance,
and, σ^2_D = dominance variance.

For purposes of making comparisons among selection methods, it is assumed that the genetic model accommodates any level of dominance but is restricted to only two equally frequent alleles. Removal of this restriction is discussed later.

1. Comparisons of different diploid selection methods

It is possible to clarify the advantages of diploid clonal and GCA selection methods relative to individual selection, by the following argument. The $\Delta\mu$ for individual selection is directly proportional to the additive genetic variance, (σ^2_A), and inversely propor-

Table 2. Increment changes in population mean in terms of genotypic variance components

Selection Method	Diploid	Haploid
Individual	$\Delta\mu_I = (\bar{I})_I(\sigma_A^2)\left\{\frac{1}{\sigma_A^2+\sigma_D^2+\sigma_E^2}\right\}^{\frac{1}{2}}$	$\Delta\mu_I = (\bar{I})_I(2)(\sigma_A^2)\left\{\frac{1}{2\sigma_A^2+\sigma_E^2}\right\}^{\frac{1}{2}}$
Clonal	$\Delta\mu_C = (\bar{I})_C(\sigma_A^2)\left\{\frac{1}{\sigma_A^2+\sigma_D^2+(\frac{1}{n})\sigma_E^2}\right\}^{\frac{1}{2}}$	$\Delta\mu_C = (\bar{I})_C(2)(\sigma_A^2)\left\{\frac{1}{2\sigma_A^2+(\frac{1}{n})\sigma_E^2}\right\}^{\frac{1}{2}}$
GCA	$\Delta\mu_{GCA} = (\bar{I})_{GCA}(\frac{1}{2})(\sigma_A^2)\left\{\frac{1}{(\frac{n+3}{4n})\sigma_A^2+(\frac{1}{n})\sigma_D^2+(\frac{1}{n})\sigma_E^2}\right\}^{\frac{1}{2}}$	$\Delta\mu_{GCA} = (\bar{I})_{GCA}(\sigma_A^2)\left\{\frac{1}{(\frac{n+1}{2n})\sigma_A^2+(\frac{1}{n})\sigma_D^2+(\frac{1}{n})\sigma_E^2}\right\}^{\frac{1}{2}}$

tional to the phenotypic standard deviation (σ_P). Therefore, the value of $\Delta\mu$ increases as the value of σ_A^2 increases relative to σ_P^2. Since

$$\sigma_P^2 = \sigma_A^2 + \sigma_D^2 + \sigma_E^2 ,$$

it is clear that those selection methods that diminish the contribution of σ_D^2 and/or σ_E^2 tend to make selection more efficient. As can be seen from Table 2, clonal selection diminishes the contribution of the environmental variance, σ_E^2. However, it leaves the contribution from σ_D^2 unchanged. Therefore, clonal selection is particularly useful when most genotypic variance is additive and the environmental variance is relatively large. In the case of GCA selection, the contributions of both dominance and environmental effects are reduced. Hence for any given level of selection intensity and with a sufficiently large number of progeny, the theoretically satisfying result occurs in which $\Delta\mu$ for GCA selection becomes only a function of σ_A^2.

2. Comparisons of different haploid selection methods

Comparisons of different haploid selection methods can also be made from appropriate formulae in Table 2. The advantages of clonal and GCA selection procedures are similar to those of the corresponding diploid procedures. The desirability of clonal selection, due to its ability to reduce the contribution of σ_E^2, and GCA selection, due to its tendency to eliminate both σ_D^2 and σ_E^2, are again clearly demonstrated.

3. Comparisons of diploid and haploid selection methods

For the genetic model involving two equally frequent alleles at a single locus, the phenotypic variances for diploid and doubled-haploid populations are:

$$\text{Diploid: } \sigma_P^2(D) = \sigma_A^2 + \sigma_D^2 + \sigma_E^2$$

$$\text{Doubled-Haploid: } \sigma_P^2(H) = 2\sigma_A^2 + \sigma_E^2$$

There are two important differences between these phenotypic variances: (i) the amount of additive genetic variance generated in the doubled-haploid population is twice that in the random-mated diploid population, and (ii) the dominance component is eliminated from the doubled-haploid phenotypic variance.

With regard to the covariances between relatives, it can be shown that the covariances for the doubled-haploid population are twice the magnitude of their corresponding counterparts in the diploid population, i.e.

$$Cov_H(PO) = (2)Cov_D(PO),$$

and

$$Cov_H(HS) = (2)Cov_D(HS).$$

Therefore, the theoretical advantages of haploid over diploid selection methods are that (i) the variance on which selection operates, σ_A^2, is doubled in all parameters associated with the haploid $\Delta\mu$ in comparison with similar parameters for diploid selection, and (ii) the dominance variance is eliminated from all

Table 3. Increment changes in population mean for diploid selection methods with regard to five genetic models

Model	Selection Methods		
	Individual ($\Delta\mu_I$)	Clonal ($\Delta\mu_C$)	GCA ($\Delta\mu_{GCA}$)
I $\{\sigma_P^2 = \sigma_A^2\}$	$(\bar{i})_I\sigma_A$	$(\bar{i})_C\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{n}{n+3}}\,\sigma_A$
II $\{\sigma_D^2 = \sigma_A^2,\ \sigma_E^2 = 0\}$	$(\bar{i})_I\left(\frac{\sqrt{2}}{2}\right)\sigma_A$	$(\bar{i})_C\left(\frac{\sqrt{2}}{2}\right)\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{n}{n+7}}\,\sigma_A$
III $\{\sigma_E^2 = \sigma_A^2,\ \sigma_D^2 = 0\}$	$(\bar{i})_I\left(\frac{\sqrt{2}}{2}\right)\sigma_A$	$(\bar{i})_C\sqrt{\frac{n}{n+1}}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{n}{n+7}}\,\sigma_A$
IV $\{\sigma_D^2 = 17\sigma_A^2,\ \sigma_E^2 = 0\}$	$(\bar{i})_I\left(\frac{\sqrt{2}}{6}\right)\sigma_A$	$(\bar{i})_C\left(\frac{\sqrt{2}}{6}\right)\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{n}{n+71}}\,\sigma_A$
V $\{\sigma_E^2 = 17\sigma_A^2,\ \sigma_D^2 = 0\}$	$(\bar{i})_I\left(\frac{\sqrt{2}}{6}\right)\sigma_A$	$(\bar{i})_C\sqrt{\frac{n}{n+17}}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{n}{n+71}}\,\sigma_A$

Table 4. Increment changes in population mean for haploid selection methods with regard to five genetic models

Model	Selection Methods		
	Individual ($\Delta\mu_I$)	Clonal ($\Delta\mu_C$)	GCA ($\Delta\mu_{GCA}$)
I $\{\sigma_P^2 = \sigma_A^2\}$	$(\bar{i})_I\sqrt{2}\,\sigma_A$	$(\bar{i})_C\sqrt{2}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{2n}{n+1}}\,\sigma_A$
II $\{\sigma_D^2 = \sigma_A^2,\ \sigma_E^2 = 0\}$	$(\bar{i})_I\sqrt{2}\,\sigma_A$	$(\bar{i})_C\sqrt{2}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{2n}{n+3}}\,\sigma_A$
III $\{\sigma_E^2 = \sigma_A^2,\ \sigma_D^2 = 0\}$	$(\bar{i})_I\left(\frac{2\sqrt{3}}{3}\right)\sigma_A$	$(\bar{i})_C 2\sqrt{\frac{n}{2n+1}}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{2n}{n+3}}\,\sigma_A$
IV $\{\sigma_D^2 = 17\sigma_A^2,\ \sigma_E^2 = 0\}$	$(\bar{i})_I\sqrt{2}\,\sigma_A$	$(\bar{i})_C\sqrt{2}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{2n}{n+35}}\,\sigma_A$
V $\{\sigma_E^2 = 17\sigma_A^2,\ \sigma_D^2 = 0\}$	$(\bar{i})_I\left(\frac{2\sqrt{19}}{19}\right)\sigma_A$	$(\bar{i})_C 2\sqrt{\frac{n}{2n+17}}\,\sigma_A$	$(\bar{i})_{GCA}\sqrt{\frac{2n}{n+35}}\,\sigma_A$

parameters associated with haploid $\Delta\mu$ for individual and clonal selection procedures.

From these considerations it is clear that H(I) is especially powerful in cases of high heritability (i.e. small σ_E^2), and that H(C) has considerable theoretical advantage when the environmental variance becomes relatively large. These and other specific details will now be illustrated with a range of genetic models.

B. Comparisons of Selection Methods with Respect to Five Specific Gene Models

1. Characterization of the responses to selection

In this section comparisons among the selection methods are made with respect to five different gene models chosen to represent different levels of heritability in the narrow sense (i.e. the ratio, $\frac{\sigma_A^2}{\sigma_P^2}$).

Table 5. Increment changes in population mean for diploid selection methods

Selection Method	Model I ($\sigma_P^2=\sigma_A^2$)	Model II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	Model III ($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	Model IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	Model V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)
Individual	2.66 (σ_A)	1.88 (σ_A)	1.88 (σ_A)	.63 (σ_A)	.63 (σ_A)
Clonal					
Restricted 'n'	2.66 (σ_A) (n=1)	1.88 (σ_A) (n=1)	1.98 (σ_A) (n=2)	.63 (σ_A) (n=1)	1.07 (σ_A) (n=12)
Large 'n'	2.66 (σ_A)	1.88 (σ_A)	2.66 (σ_A)	.63 (σ_A)	2.66 (σ_A)
GCA					
Restricted 'n'	1.63 (σ_A) (n=5)	1.36 (σ_A) (n=8)	1.36 (σ_A) (n=8)	.66 (σ_A) (n=19)	.66 (σ_A) (n=19)
Large 'n'	2.66 (σ_A)	2.66 (σ_A)	2.66 (σ_A)	2.66 (σ_A)	2.66 (σ_A)

Model I, ($\sigma_P^2 = \sigma_A^2$), represents the extreme example of high heritability in which all phenotypic variance is additive genetic. Heritability in this case is 1.0. Model II, ($\sigma_D^2 = \sigma_A^2$, $\sigma_E^2 = 0$), and Model III, ($\sigma_E^2 = \sigma_A^2$, $\sigma_D^2 = 0$), represent examples of moderate heritability (0.5). However, a distinction is made between the two models as to whether the lowered heritability is due to non-additive genetic (dominance) or environmental variances. Model IV, ($\sigma_D^2 = 17\sigma_A^2$, $\sigma_E^2 = 0$), and Model V, ($\sigma_E^2 = 17\sigma_A^2$, $\sigma_D^2 = 0$), represent examples having low heritability (.06). Again, in these cases a distinction is made between whether the disturbing influences are due to dominance or environmental effects. The two different models at moderate and low heritabilities are included so that the power of clonal selection will become obvious, and to make clear the differences in response of clonal and GCA selection.

Tables 3 and 4 give the mean changes ($\Delta\mu$'s) for different diploid and haploid selection methods operating within the framework of each of the five gene models. It is clear from these results that most clonal and GCA responses to both diploid and haploid selection are functions of "n" (i.e. the number of propagules in a clone or the number of progeny in a half-sib family). Hence before comparisons can be made among selection methods, values must be assigned to "n".

Two situations which relate to "n" are considered. The first situation is one in which there are no restrictions placed on total plant numbers, so that "n" is taken to be a "large" number. In this essentially infinite case, the proportion saved for breeding is assumed to be the same (P = .01) for all selection methods. This implies a common standardized selection differential, $\bar{i} = 2.67$.

The second situation is that of restricted plant numbers. In this situation, the magnitude of "n" is determined so as to maximize $\Delta\mu$ under the restriction (Robertson, 1957). For this study the following population numbers are chosen:

$T = Nn = 5000$ = total number of plants that can be accommodated in the particular breeding program,

where N = number of different genotypes tested, and

n = number of propagules (or progeny) used for testing each genotype.

Also, $N_e = 50$ = number of different genotypes included in the breeding population.

The value of N_e is held constant in all selection methods and is chosen to be a sufficiently high value

Table 6. Increment changes in population mean for haploid selection methods

Selection Method	Model I ($\sigma_P^2=\sigma_A^2$)	Model II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	Model III ($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	Model IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	Model V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)
Individual	3.77 (σ_A)	3.77 (σ_A)	3.08 (σ_A)	3.77 (σ_A)	1.22 (σ_A)
Clonal					
Restricted 'n'	3.77 (σ_A) (n=1)	3.77 (σ_A) (n=1)	3.08 (σ_A) (n=1)	3.77 (σ_A) (n=1)	1.83 (σ_A) (n=8)
Large 'n'	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)
GCA					
Restricted 'n'	2.80 (σ_A) (n=2)	2.31 (σ_A) (n=5)	2.31 (σ_A) (n=5)	1.20 (σ_A) (n=16)	1.20 (σ_A) (n=16)
Large 'n'	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)	3.77 (σ_A)

so as to reduce the random fixation of genes due to genetic drift to an acceptable level (Robertson 1960).

It is obvious that as the numbers (N,n) change, the proportion (P) of the total number of plants which survive truncation varies. The resulting consequence is that the value of the selection differential changes. Thus an 'n' increases, N decreases, N_e remains constant, P increases and $\bar{i}$ decreases. As an example, consider clonal selection for different values of 'n'.

n	N	N_e	$P = \frac{N_e}{N}$	$\bar{i}$
1	5000	50	.01	2.67
2	2500	50	.02	2.42
5	1000	50	.05	2.06
10	500	50	.10	1.76

The problem, then (with diploid clonal selection, as an example), is to chose 'n' so as to maximize,

$$\Delta\mu_C = (\bar{i})(\sigma_A^2)\left(\frac{1}{\sigma_A^2+\sigma_D^2+(\frac{1}{n})\sigma_E^2}\right)^{1/2}.$$

Results for unrestricted and restricted plant numbers are given in Tables 5 and 6 for diploid and haploid selection methods. It is apparent, especially for GCA selection, that values of 'n' vary considerably with different gene models. In both diploid and haploid situations, the number of progeny required for maximum genetic gain increases as heritability decreases.

2. Relative efficiencies for different selection methods as measured by the ratio of $\Delta\mu$'s

a) Relative efficiencies among diploid selection methods

i. Unrestricted plant numbers

Relative efficiencies for different diploid selection methods as measured by ratios of $\Delta\mu$'s are given in Table 7 for the situation of unrestricted plant numbers. These ratios result in a numerical value which is multiplied by a constant (k). This constant represents the inverse ratio of numbers of years required to complete the cycles for the particular selection methods involved. For example, in comparing D(GCA) and D(C) with the ratio, $\frac{D(GCA)}{D(C)}$,

$$k_3 = \frac{\text{number of years to complete clonal cycle}}{\text{number of years to complete GCA cycle}}.$$

Table 7. Relative efficiencies of different diploid selection schemes. Unrestricted plant numbers

Model	Individual	Clonal	GCA
Individual	D(I)/D(I)	D(C)/D(I)	D(GCA)/D(I)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{2.66}{2.66}=1$	$\frac{2.66}{2.66}(1)k_1$	$\frac{2.66}{2.66}=(1)k_2$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{1.88}{1.88}=1$	$\frac{1.88}{1.88}=(1)k_1$	$\frac{2.66}{1.88}=(1.42)k_2$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.88}{1.88}=1$	$\frac{2.66}{1.88}=(1.42)k_1$	$\frac{2.66}{1.88}=(1.42)k_2$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{.63}{.63}=1$	$\frac{.63}{.63}=(1)k_1$	$\frac{2.66}{.63}=(4.22)k_2$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{.63}{.63}=1$	$\frac{2.66}{.63}=(4.22)k_1$	$\frac{2.66}{.63}=(4.22)k_2$
Clonal		D(C)/D(C)	D(GCA)/D(C)
I		$\frac{2.66}{2.66}=1$	$\frac{2.66}{2.66}=(1)k_3$
II		$\frac{1.88}{1.88}=1$	$\frac{2.66}{1.88}=(1.42)k_3$
III		$\frac{2.66}{2.66}=1$	$\frac{2.66}{2.66}=(1)k_3$
IV		$\frac{.63}{.63}=1$	$\frac{2.66}{.63}=(4.22)k_3$
V		$\frac{2.66}{2.66}=1$	$\frac{2.66}{2.66}=(1)k_3$
GCA			D(GCA)/D(GCA)
I			$\frac{2.66}{2.66}=1$
II			$\frac{2.66}{2.66}=1$
III			$\frac{2.66}{2.66}=1$
IV			$\frac{2.66}{2.66}=1$
V			$\frac{2.66}{2.66}=1$

If, for example, the comparison involves model V, then the ratio $\frac{D(GCA)}{D(C)} = (4.22)k_3$ implies that if both selection methods require the same length of time, GCA would be 4.22 times as efficient as clonal selection.

From the ratios $\frac{D(C)}{D(I)}$ in Table 7, it is clear that clonal selection is more efficient than individual selection for those models (III and V) in which the phenotypic variance is greatly influenced by σ_E^2. Values for the ratio $\frac{D(GCA)}{D(I)}$ for models II, III, IV and V, illustrate that progeny testing tends to eliminate the disturbing effects of both dominance and the environment. Finally values for the ratio, $\frac{D(GCA)}{D(C)}$, for models II and IV illustrate the advantage of progeny testing over clonal selection when dominance is the primary disturbance.

The general conclusions for diploid selection methods with unrestricted plant numbers are as follows. For traits of high heritability, individual selection is superior because it is simplest and takes a minimum amount of time per cycle. For traits of moderate heritability, individual selection is still preferable unless

the length of time per cyle for clonal or progeny testing is not appreciably greater than that for individual selection. Finally, for traits of low heritability, considerable advantage can be realized by use of clonal or progeny testing if the differences between cycle lengths for these methods and individual selection are not too great.

ii. Restricted plant numbers

Table 8 presents relative efficiencies for different diploid selection methods when the total plant number is restricted. The effect of this retriction is clear and drastic. Advantages of clonal and GCA selection over individual selection tend to disappear even if cycle lengths are similar. The only exception might be the use of clonal selection for traits of extremely low heritability when disturbing effects are largely environmental.

b) Relative efficiences among the haploid selection methods

i. Unrestricted plant numbers

Table 9 presents relative efficiencies among haploid selection methods for the situation of unrestricted plant numbers. As with diploid selection procedures, clonal selection exhibits an advantage over individual selection when the environmental variance is an important component of the phenotypic variance. However, the most interesting result is that GCA selection shows no advantage over individual selection for models in which the dominance variance plays a major role. The reason is that the dominance variance component does not influence $\Delta\mu$ with haploid individual selection. This strengthens the position of haploid individual selection even in the situation of unrestricted plant numbers. Clonal selection would be used only for traits that are highly subject to environmental disturbances; GCA selection would not be recommended, except when it is an integral part of a reciprocal recurrent selection program.

ii. Restricted plant numbers

As with diploid selection the relative advantages of haploid clonal and GCA selection methods tend to disappear when restrictions are placed upon the total plant numbers (see Table 10). If haploid clonal and individual selection cycles are similar in lengths of time, clonal selection might be advantageous for traits highly influenced by environmental disturbances.

c. Efficiencies of haploid relative to diploid selection methods

The most important comparisons from the standpoint of this study are those which compare efficiencies of haploid relative to diploid selection methods.

Table 11 presents all possible efficiency ratios involving haploid and diploid selection schemes for the situation of unrestricted plant numbers. It is clear from these results that if cycle lengths are not too different, the advantages of haploid over diploid selection procedures can be enormous (up to approximately six times as efficient).

The question naturally arises as to whether or not these advantages tend to disappear when the more realistic condition of restricted plant numbers is imposed. The very interesting answer to this question appears in Table 12. The advantages of haploid over diploid selection methods are retained in essentially all respects.

Another way to study the advantages of haploid over diploid selection schemes is to determine the situations (or models) in which maximum change in the population mean can be obtained.

The maximum $\Delta\mu$ produced by diploid selection schemes is $\Delta\mu_{max} = (\bar{i})\sigma_A = (2.66)\sigma_A$, and the maximum $\Delta\mu$ that haploid selection schemes can produce is $\Delta\mu_{max} = (\bar{i})(\sqrt{2})\sigma_A = (3.77)\sigma_A$. Genetic models for which these maximum values are obtained are given in Table 13 (unrestricted 'n'), and in Table 14 (restricted 'n').

For unrestricted 'n', haploid individual and clonal selection schemes have the advantage over corresponding diploid methods for those models (II and IV) in which dominance exists. This is due to the fact that the dominance component does not enter into haploid $\Delta\mu$'s but does enter into diploid $\Delta\mu$'s.

For restricted 'n', the advantages of haploid over diploid for individual and clonal selection are maintained. Furthermore, although GCA selection does not yield maximum $\Delta\mu$'s for either haploid or diploid selection schemes, advantages of haploid over diploid GCA are enhanced with restricted 'n' because haploid GCA requires fewer progeny than diploid GCA for every genetic model.

Table 8. Relative efficiencies of different diploid selection schemes. Restricted total plant numbers [T=Nn=5000, $N_e = 50$ (Constant)]

Model	Individual	Clonal	GCA
Individual	D(I)/D(I)	D(C)/D(I)	D(GCA)/D(I)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{2.66}{2.66}=1$	$\frac{2.66}{2.66}=(1)k_1$	$\frac{1.63}{2.66}=(.61)k_2$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{1.88}{1.88}=1$	$\frac{1.88}{1.88}=(1)k_1$	$\frac{1.36}{1.88}=(.72)k_2$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.88}{1.88}=1$	$\frac{1.98}{1.88}=(1.05)k_1$	$\frac{1.36}{1.88}=(.72)k_2$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{.63}{.63}=1$	$\frac{.63}{.63}=(1)k_1$	$\frac{.66}{.63}=(1.05)k_2$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{.63}{.63}=1$	$\frac{1.07}{.63}=(1.70)k_1$	$\frac{.66}{.63}=(1.05)k_2$
Clonal		D(C)/D(C)	D(GCA)/D(C)
I		$\frac{2.66}{2.66}=1$	$\frac{1.63}{2.66}=(.61)k_3$
II		$\frac{1.88}{1.88}=1$	$\frac{1.36}{1.88}=(.72)k_3$
III		$\frac{1.98}{1.98}=1$	$\frac{1.36}{1.98}=(.69)k_3$
IV		$\frac{.63}{.63}=1$	$\frac{.66}{.63}=(1.05)k_3$
V		$\frac{1.07}{1.07}=1$	$\frac{.66}{1.07}=(.62)k_3$
GCA			D(GCA)/D(GCA)
I			$\frac{1.63}{1.63}=1$
II			$\frac{1.36}{1.36}=1$
III			$\frac{1.36}{1.36}=1$
IV			$\frac{.66}{.66}=1$
V			$\frac{.66}{.66}=1$

Table 9. Relative efficiencies of different haploid selection schemes. Unrestricted plant numbers

Model	Individual	Clonal	GCA
Individual	H(I)/H(I)	H(C)/H(I)	H(GCA)/H(I)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{3.77}{3.77}=(1)k_5$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{3.77}{3.77}=(1)k_5$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{3.08}{3.08}=1$	$\frac{3.77}{3.08}=(1.22)k_4$	$\frac{3.77}{3.08}=(1.22)k_5$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{3.77}{3.77}=(1)k_5$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.22}{1.22}=1$	$\frac{3.77}{1.22}=(3.09)k_4$	$\frac{3.77}{1.22}=(3.09)k_5$
Clonal		H(C)/H(C)	H(GCA)/H(C)
I		$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_6$
II		$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_6$
III		$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_6$
IV		$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_6$
V		$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_6$
GCA			H(GCA)/H(GCA)
I			$\frac{3.77}{3.77}=1$
II			$\frac{3.77}{3.77}=1$
III			$\frac{3.77}{3.77}=1$
IV			$\frac{3.77}{3.77}=1$
V			$\frac{3.77}{3.77}=1$

Table 10. Relative efficiencies of different haploid selection schemes. Restricted total plant number [T=Nn=5000, N_e = 50 (Constant)]

Model	Individual	Clonal	GCA
Individual	H(I)/H(I)	H(C)/H(I)	H(GCA)/H(I)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{2.80}{3.77}=(.74)k_5$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{2.31}{3.77}=(.61)k_5$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{3.08}{3.08}=1$	$\frac{3.08}{3.08}=(1)k_4$	$\frac{2.31}{3.08}=(.75)k_5$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{3.77}=1$	$\frac{3.77}{3.77}=(1)k_4$	$\frac{1.20}{3.77}=(.32)k_5$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.22}{1.22}=1$	$\frac{1.83}{1.22}=(1.54)k_4$	$\frac{1.20}{1.22}=(.98)k_5$
Clonal		H(C)/H(C)	H(GCA)/H(C)
I		$\frac{3.77}{3.77}=1$	$\frac{2.80}{3.77}=(.74)k_6$
II		$\frac{3.77}{3.77}=1$	$\frac{2.31}{3.77}=(.61)k_6$
III		$\frac{3.08}{3.08}=1$	$\frac{2.31}{3.08}=(.75)k_6$
IV		$\frac{3.77}{3.77}=1$	$\frac{1.20}{3.77}=(.32)k_6$
V		$\frac{1.83}{1.83}=1$	$\frac{1.20}{1.83}=(.66)k_6$
GCA			H(GCA)/H(GCA)
I			$\frac{2.80}{2.80}=1$
II			$\frac{2.31}{2.31}=1$
III			$\frac{2.31}{2.31}=1$
IV			$\frac{1.20}{1.20}=1$
V			$\frac{1.20}{1.20}=1$

Table 11. Efficiencies of haploid relative to diploid selection schemes. Unrestricted plant numbers

Model	Individual	Clonal	GCA
Individual	H(I)/D(I)	H(I)/D(C)	H(I)/D(GCA)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{3.77}{2.66}=(1.42)k_7$	$\frac{3.77}{2.66}=(1.42)k_8$	$\frac{3.77}{2.66}=(1.42)k_9$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{1.88}=(2.01)k_7$	$\frac{3.77}{1.88}=(2.01)k_8$	$\frac{3.77}{2.66}=(1.42)k_9$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{3.08}{1.88}=(1.64)k_7$	$\frac{3.08}{2.66}=(1.16)k_8$	$\frac{3.08}{2.66}=(1.16)k_9$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{.63}=(5.98)k_7$	$\frac{3.77}{.63}=(5.98)k_8$	$\frac{3.77}{2.66}=(1.42)k_9$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.22}{.63}=(1.94)k_7$	$\frac{1.22}{2.66}=(.46)k_8$	$\frac{1.22}{2.66}=(.46)k_9$
Clonal	H(C)/D(I)	H(C)/D(C)	H(C)/D(GCA)
I	$\frac{3.77}{2.66}=(1.42)k_{10}$	$\frac{3.77}{2.66}=(1.42)k_{11}$	$\frac{3.77}{2.66}=(1.42)k_{12}$
II	$\frac{3.77}{1.88}=(2.01)k_{10}$	$\frac{3.77}{1.88}=(2.01)k_{11}$	$\frac{3.77}{2.66}=(1.42)k_{12}$
III	$\frac{3.77}{1.88}=(2.01)k_{10}$	$\frac{3.77}{2.66}=(1.42)k_{11}$	$\frac{3.77}{2.66}=(1.42)k_{12}$
IV	$\frac{3.77}{.63}=(5.98)k_{10}$	$\frac{3.77}{.63}=(5.98)k_{11}$	$\frac{3.77}{2.66}=(1.42)k_{12}$
V	$\frac{3.77}{.63}=(5.98)k_{10}$	$\frac{3.77}{2.66}=(1.42)k_{11}$	$\frac{3.77}{2.66}=(1.42)k_{12}$
GCA	H(GCA)/D(I)	H(GCA)/D(C)	H(GCA)/D(GCA)
I	$\frac{3.77}{2.66}=(1.42)k_{13}$	$\frac{3.77}{2.66}=(1.42)k_{14}$	$\frac{3.77}{2.66}=(1.42)k_{15}$
II	$\frac{3.77}{1.88}=(2.01)k_{13}$	$\frac{3.77}{1.88}=(2.01)k_{14}$	$\frac{3.77}{2.66}=(1.42)k_{15}$
III	$\frac{3.77}{1.88}=(2.01)k_{13}$	$\frac{3.77}{2.66}=(1.42)k_{14}$	$\frac{3.77}{2.66}=(1.42)k_{15}$
IV	$\frac{3.77}{.63}=(5.98)k_{13}$	$\frac{3.77}{.63}=(5.98)k_{14}$	$\frac{3.77}{2.66}=(1.42)k_{15}$
V	$\frac{3.77}{.63}=(5.98)k_{13}$	$\frac{3.77}{2.66}=(1.42)k_{14}$	$\frac{3.77}{2.66}=(1.42)k_{15}$

Table 12. Efficiencies of haploid relative to diploid selection schemes. Restricted total plant number [T=Nn=5000, $N_e = 50$ (Constant)]

Model	Individual	Clonal	GCA
Individual	H(I)/D(I)	H(I)/D(C)	H(I)/D(GCA)
I ($\sigma_P^2=\sigma_A^2$)	$\frac{3.77}{2.66}=(1.42)k_7$	$\frac{3.77}{2.66}=(1.42)k_8$	$\frac{3.77}{1.63}=(2.31)k_9$
II ($\sigma_D^2=\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{1.88}=(2.01)k_7$	$\frac{3.77}{1.88}=(2.01)k_8$	$\frac{3.77}{1.36}=(2.77)k_9$
III($\sigma_E^2=\sigma_A^2$, $\sigma_D^2=0$)	$\frac{3.08}{1.88}=(1.64)k_7$	$\frac{3.08}{1.98}=(1.56)k_8$	$\frac{3.08}{1.36}=(2.26)k_9$
IV ($\sigma_D^2=17\sigma_A^2$, $\sigma_E^2=0$)	$\frac{3.77}{.63}=(5.98)k_7$	$\frac{3.77}{.63}=(5.98)k_8$	$\frac{3.77}{.66}=(5.71)k_9$
V ($\sigma_E^2=17\sigma_A^2$, $\sigma_D^2=0$)	$\frac{1.22}{.63}=(1.94)k_7$	$\frac{1.22}{1.07}=(1.14)k_8$	$\frac{1.22}{.66}=(1.85)k_9$
Clonal	H(C)/D(I)	H(C)/D(C)	H(C)/D(GCA)
I	$\frac{3.77}{2.66}=(1.42)k_{10}$	$\frac{3.77}{2.66}=(1.42)k_{11}$	$\frac{3.77}{1.63}=(2.31)k_{12}$
II	$\frac{3.77}{1.88}=(2.01)k_{10}$	$\frac{3.77}{1.88}=(2.01)k_{11}$	$\frac{3.77}{1.36}=(2.77)k_{12}$
III	$\frac{3.08}{1.88}=(1.64)k_{10}$	$\frac{3.08}{1.98}=(1.56)k_{11}$	$\frac{3.08}{1.36}=(2.26)k_{12}$
IV	$\frac{3.77}{.63}=(5.98)k_{10}$	$\frac{3.77}{.63}=(5.98)k_{11}$	$\frac{3.77}{.66}=(5.71)k_{12}$
V	$\frac{1.83}{.63}=(2.90)k_{10}$	$\frac{1.83}{1.07}=(1.71)k_{11}$	$\frac{1.83}{.66}=(2.77)k_{12}$
GCA	H(GCA)/D(I)	H(GCA)/D(C)	H(GCA)/D(GCA)
I	$\frac{2.80}{2.66}=(1.05)k_{13}$	$\frac{2.80}{2.66}=(1.05)k_{14}$	$\frac{2.80}{1.63}=(1.72)k_{15}$
II	$\frac{2.31}{1.88}=(1.23)k_{13}$	$\frac{2.31}{1.88}=(1.23)k_{14}$	$\frac{2.31}{1.36}=(1.70)k_{15}$
III	$\frac{2.31}{1.88}=(1.23)k_{13}$	$\frac{2.31}{1.98}=(1.17)k_{14}$	$\frac{2.31}{1.36}=(1.70)k_{15}$
IV	$\frac{1.20}{.63}=(1.90)k_{13}$	$\frac{1.20}{.63}=(1.90)k_{14}$	$\frac{1.20}{.66}=(1.82)k_{15}$
V	$\frac{1.20}{.63}=(1.90)k_{13}$	$\frac{1.20}{1.07}=(1.12)k_{14}$	$\frac{1.20}{.66}=(1.82)k_{15}$

Table 13. Models for which maximum $\Delta\mu$ is obtained for unrestricted total plant numbers

Selection Method	Diploid ($\Delta\mu_{max} = (2.66)\sigma_A$)	Haploid ($\Delta\mu_{max} = (3.77)\sigma_A$)
Individual	I	I, II, IV
Clonal	I, III, V	I, II, III, IV, V
GCA	I, II, III, IV, V	I, II, III, IV, V

Table 14. Models for which maximum $\Delta\mu$ is obtained for restricted total plant numbers

Selection Method	Diploid ($\Delta\mu_{max} = (2.66)\sigma_A$)	Haploid ($\Delta\mu_{max} = (3.77)\sigma_A$)
Individual	I	I, II, IV
Clonal	I	I, II, IV
GCA	None	None

C. Considerations of More General Models

It should be emphasized that comparisons made in this study are completely valid for gene models in which there exists at each locus either (a) an arbitrary number of additive alleles, or (b) two equally frequent alleles exhibiting any degree of dominance. When more complex models are considered, problems of non-orthogonality make algebraic analysis difficult. This section extends somewhat the two-allele dominance gene model to accommodate arbitrary gene frequencies, and in so doing illustrates some of the difficulties involved. However, before making comparisons, some general results can be stated regarding the composition of various genetic parameters.

The haploid parameters of interest for a single-locus gene model which includes any number of alleles having arbitrary frequencies and arbitrary dominance values are:

$$\sigma^2_{G(H)} = 2\sigma^2_A + 4\sum_i p_i\alpha_i\delta_{ii} + \sum_i p_i(1-p_i)\delta^2_{ii} - \sum_{i\neq j} p_ip_j\delta_{ii}\delta_{jj},$$

$$Cov_H(PO) = \sigma^2_A + \sum_i p_i\alpha_i\delta_{ii},$$

and, $Cov_H(HS) = (\frac{1}{2})\sigma^2_A$,

where the additive and dominance gene effects and the additive genetic variance are defined for a random-mating population in equilibrium with the same gene frequencies.

For the case of two alleles, these parameters can be formulated as:

$$\sigma^2_{G(H)} = 2[2p_1p_2(\alpha_1-\alpha_2)^2] + 4p_1p_2(\alpha_1-\alpha_2)(\delta_{11}-\delta_{22}) + \\ + p_1p_2(\delta_{11}-\delta_{22})^2,$$

$$Cov_H(PO) = 2p_1p_2(\alpha_1-\alpha_2)^2 + p_1p_2(\alpha_1-\alpha_2)(\delta_{11}-\delta_{22}),$$

and, $Cov_H(HS) = p_1p_2(\alpha_1-\alpha_2)^2$.

Parenthetically, it should be noted that when the two alleles are equally frequent (or, of course, if there is no dominance) the parameters reduce to $\sigma^2_{G(H)} = 2\sigma^2_A$, $Cov_H(PO) = \sigma^2_A$, and $Cov_H(HS) = (1/2)\sigma^2_A$. These are the values used for comparisons among selection methods in this study.

The mean change for haploid individual selection, is

$$\Delta\mu = (\bar{i})\frac{(2)Cov_H(PO)}{\sqrt{\sigma^2_{G(H)} + \sigma^2_E}},$$

which, for the two-allele model, becomes

$$\Delta\mu = (\bar{i})\frac{(2)\{\sigma^2_A + p_1p_2(\alpha_1-\alpha_2)(\delta_{11}-\delta_{22})\}}{\{[2\sigma^2_A + 4p_1p_2(\alpha_1-\alpha_2)(\delta_{11}-\delta_{22}) + p_1p_2(\delta_{11}-\delta_{22})^2] + \sigma^2_E\}^{\frac{1}{2}}}$$

Cases in which (i) the desirable gene is dominant and (ii) the desirable gene is recessive, need to be considered separately. In both cases the sign associated with the crossproduct term, $p_1p_2(\alpha_1-\alpha_2)(\delta_{11}-\delta_{22})$, and the magnitude of this term, as well as the magnitude of σ^2_A, may change as the frequency of the desirable gene changes.

When the frequency of a dominant desirable gene is less than one-half, the additive genetic variance is greater than the same variance generated by gene frequencies of one-half. However, the cross-product term is negative. The opposite is true when the desirable gene frequency is greater than one-half. The end result is that the efficiency of haploid individual selection is increased when the frequency of the dominant gene is less than one-half. Conversely, the relative efficiency of haploid selection is reduced for a dominant desirable gene whose frequency is greater than one-half.

When the gene model involves a recessive desirable gene, the results are reversed. The relative efficiency of haploid selection is decreased when the desirable gene frequency is less than one-half, and increased when the frequency is greater than one-half.

It is clear that computer simulation studies need to be conducted for a more thorough investigation of this and other more complex models.

IV. Discussion

In this study efficiency comparisons are made within and between haploid and diploid individual, clonal and GCA selection methods using five different gene models for situations of unrestricted and restricted total plant numbers. In comparisons made among diploid selection methods, the advantages of clonal and GCA selection over individual selection, operating with unrestricted plant numbers, largely disappear when the total plant number is restricted. However, the very considerable advantages of haploid over diploid selection schemes, measured on a per cycle basis, do not disappear when total plant numbers are restricted.

The results also show that efficiency comparisons between haploid and diploid selection schemes critically depend on the relative lengths of time (k values) required to complete a selection cycle. Hence, the key to successful inclusion of the haploid technique, as a means of increasing the efficiencies of recurrent selection methods, is the development of rapid doubled-haploid extraction procedures. In this respect the most promising doubled-haploid extraction method appears to be the pollen culturing technique which leads directly to doubled-haploid plants. Nitsch (1974) states that for *Datura innoxia* (Mill.) and *Nicotiana tabacum* (L.) only five months are required to produce an array of doubled-haploids from a genetically heterozygous source. It is hoped that this method can be extended widely to other plant species.

In augmenting diploid selection methods by use of doubled-haploids, it must be realized that the basis for selection is shifted from that of operating on a heterozygous population to that of operating on a population of completely homozygous genotypes. Thus, although heterozygotes are generated every cycle,

they do not enter into the selection process. This implies that selection ultimately results in the production of a single elite genetically homogeneous variety.

If there is considerable heterosis exhibited when doubled-haploids are crossed, then use of hybrids as an end-product rather than an elite variety may be desirable. In this case, reciprocal recurrent selection should be considered. The incorporation of doubled-haploids (as illustrated in Fig.4) not only may make the selection procedure more efficient, but also provides the additional advantage that the products of every cycle are directly usable as single-crosses. In fact, theoretically, each succeeding cycle produces a new wave of improved single-crosses which can be immediately evaluated and used for commercial purposes. In diploid reciprocal recurrent selection (as illustrated in Fig.2), this is not the case. Consecutive cycles merely produce improved varietal crosses which asymptotically result in one, and only one single-cross.

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