COMPONENTS OF GENETIC VARIANCE IN THE CULTIVATED STRAWBERRY[1]

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FISHER (1918) subdivided genotypic variance (the variance due to genetic variation) into three components: (1) a part due to the average effects of genes (now called additive genetic variance), (2) a part due to allelic interactions of genes that is called dominance variance, and (3) a part due to nonallelic interactions of genes that is called epistatic variance. A sound plant breeding program will include the use of information on the relative importance of these components. Thus, in strawberries, if it is found that most of the genotypic variance is additive, then a simple breeding program of mating the best with the best over several generations would quite likely be a good approach. In contrast, if it is found that the dominance variance is the most important portion of the genetic variation, then it would be worth considering a procedure such as reciprocal recurrent selection (COMSTOCK, ROBINSON and HARVEY 1949). However, if epistatic variance is the major component, then test crosses with evaluation of small samples of plants followed by testing of large progenies of the best crosses would probably be superior to other methods. The important factor to stress when epistasis is important, and when the material can be vegetatively propagated, is the need to identify superior genotypes immediately and maintain them in the population by asexual reproduction. In all three cases, it would be desirable to provide for testing in several locations and years if the genotype × environment interactions were found to be important. Selection of the best breeding procedure based on a knowledge of the components of genetic variance must logically be expected to give the maximum genetic progress towards the objectives of a breeding program.

Evidence obtained by COMSTOCK, KELLEHER and MORROW (1958) was interpreted to show that epistatic variance may be very important in strawberries. This conforms with the suggestion of WRIGHT (1956) that in a species such as the strawberry where there is "a combination of prevailing uniparental reproduction with occasional crossbreeding," variability is comparable to that under random mating except that the binding of the population to a single adaptive peak is avoided. The resulting peaks of adaptive excellence he interpreted as a consequence of pleiotropy and epistasis, where the effect of pleiotropy on the net worth may be considered statistically as epistasis. He considered the natural breeding system of such a species to be one of violent alternations between the selection of

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favorable genotypes and the breakdown of these resulting from the rise of new types as a result of crossing. Such a system produces adaptive genotypes capable of taking advantage of any temporary set of environmental conditions rather than genotypes which are steps in a progressive evolution. It may be concluded that crossing individuals that belong to different adaptive peaks will frequently give rise to progenies with mean values below that of their parents.

In a breeding program involving such a species, genetic advance expressed as the percentage improvement of selected individuals over the mean of the non-selected population is not as good a standard as one where genetic progress is measured as the percentage improvement of selected individuals over the mean of individuals from the best selectional peaks.

The present paper presents estimates of additive, dominance and epistatic variance for strawberry yield and certain components of yield. Diploid meiotic behavior was assumed. The results are used to estimate the "genetic progress" to be expected using three breeding procedures. Genetic progress is defined as the percentage improvement of selected plants over the average of the best cultivars for the region under consideration.

MATERIALS AND METHODS

Eight clones taken from the population of cultivars used in breeding at Ottawa were used as parents. These were crossed according to diallel mating design (AA) of COCKERHAM (1963) to give a total of 56 progenies (the selfs being excluded). Estimates for two progenies which failed to produce enough plants were obtained from the reciprocals of the two, after it was found that reciprocal and maternal effects were non-significant.

In addition to the 56 progenies, vegetatively propagated plots of 4 standard cultivars (Cavalier, Grenadier, Guardsman and Redcoat) were also included in each block for estimating environmental variation within plots. They also provided a standard for measuring genetic progress. Records were taken on the "individual plant," which was defined as the original plant plus two runner plants for the vegetatively propagated cultivars and a seedling plus two runner plants for the progenies.

The control cultivars were tested and found to be free of known virus diseases and together with the seedlings, which were assumed to be free of virus at germination, were maintained in this state throughout the experiment by rigorous control of insects, especially aphids, which act as vectors for the viruses.

The seedlings were grown in flats in a greenhouse and later in cold frames until they were of a size comparable with the plants of the vegetatively propagated cultivars. Both were then planted in the field in a randomized complete block design with 5 replicates. Each progeny and cultivar was represented in each replicate block by a plot consisting of 10 individual plants. Once each had set two runner plants, all further runners were removed. Flowers were removed from any plant which produced them in the planting year. The planting was established in the spring of 1961 and harvested in the summer of 1962.

Individual plant yield in grams and berry number were recorded for each of the eight picks necessary to complete the harvest. From these records, total yield, marketable yield (all picks averaging over 3.5 grams per berry), early yield (the first pick) and late yield (the last pick) were obtained.

The data were analyzed following the primary diallel analysis given by COCKERHAM (1963) but extended by the procedure of MORROW, COMSTOCK and KELLEHER (1958) using vegetatively propagated plants as an aid in calculating environmental variation. Thus the extension of COCKERHAM's procedure in the present paper is identical in principle to the extension of Experi-

ment II (COMSTOCK and ROBINSON 1952) as used by MORROW, COMSTOCK and KELLEHER (1958). However, before using the cultivar values for this purpose, individual values were transformed so that the mean of all cultivars was equal to the mean of all progenies. This transformation involved multiplying each individual value for each character for the cultivars by the following factor:

$$\frac{\text{Mean value for all progenies for a character}}{\text{Mean value for all cultivars for the same character}}$$

This transformation of the cultivar data was a simple procedure to bring the variance values for progenies and cultivars onto the same relative scale without distorting the relative magnitude of measurements within cultivars. Estimates for variance components for general (σ^2_g) and specific (σ^2_s) combining ability using COCKERHAM's method were checked against Method 3 Model 2 of GRIFFING (1956). Variances of the combining ability estimates were calculated following the method outlined by GRIFFING for Method 3 Model 2.

The methods of COMSTOCK and ROBINSON (1952), MORROW, COMSTOCK and KELLEHER (1958), GRIFFING (1956) and COCKERHAM (1963) are based on the assumption of bivalent pairing at meiosis. COMSTOCK, KELLEHER and MORROW (1958) accepted the evidence of DARROW (1937) and POWERS (1944) that the garden strawberry had bivalent chromosome pairing at meiosis in spite of an octoploid chromosome number. Additive, dominance and epistatic variance estimates were calculated in the present paper based on the same assumption. Values of σ^2_w (the genetic variance within progenies) were obtained by subtracting the variance within cultivars (environmental variance) from the variance within progenies (environmental plus within-progeny genetic variance). The total genetic variance (σ^2_G) was obtained by adding to σ^2_w the genetic variance between progenies ($2\sigma^2_g + \sigma^2_s$).

The actual calculation of the additive and dominance values followed the procedure used by COMSTOCK, KELLEHER and MORROW (1958) but unlike their procedure, actual estimates of epistasis were obtained by assuming that all digenic interactions were equally important and that the total of all higher order gene interactions were of small magnitude relative to the total genetic effect. This was achieved by using the following formulae:

$$\sigma^2_A \text{ (additive variance)} = 4\sigma^2_g - \frac{(\sigma^2_w - 2\sigma^2_g - 3\sigma^2_s)}{6}$$

$$\sigma^2_D \text{ (dominance variance)} = 4\sigma^2_s - \frac{(5\ (\sigma^2_w - 2\sigma^2_g - 3\sigma^2_s))}{6}$$

$$\sigma^2_E \text{ (epistatic variance)} = 2\ (\sigma^2_w - 2\sigma^2_g - 3\sigma^2_s)$$

Thus $\sigma^2_A + \sigma^2_D + \sigma^2_E$ was equal to $\sigma^2_w + 2\sigma^2_g + \sigma^2_s$ which was equal to the total genetic variance σ^2_G.

Percentage genetic progress for each character was calculated as follows for each of the three breeding methods which were compared:

$$\frac{100\ ((\text{Mean of progeny population} + \text{Expected response}) - \text{Mean of standard cultivars})}{\text{Mean of standard cultivars}}$$

The calculation of expected response was based on the FALCONER (1961) definition and was equal to $i\sigma_p h^2$, where i was the selection intensity, σ_p was the phenotypic standard deviation and h^2 was the heritability.

The three breeding procedures compared for their relative levels of genetic progress were as follows: (1) exploitation of the additive variance in each of several successive generations, (2) exploitation of all the genetic variation—additive, dominance and epistatic—by a one-step selection among all individuals and (3) exploitation of all the genetic variation by selection of the best progenies, based on small numbers of individuals per progeny, followed by selection of the best individuals in the best progenies, with large numbers of individuals per progeny.

The estimation of genetic progress for the first breeding procedure involved using only the additive variance in the calculation of the heritability since only this portion of the total genetic variance could contribute to one step of a breeding procedure extending over several generations. This procedure is the same as the individual selection procedure of FALCONER (1961).

In the second procedure, which is intended to select a new variety in the first generation, the total genetic variance was included in the numerator of the heritability estimate used in the calculation of the genetic progress, since none of this variance would be lost in the vegetative propagation of selected individuals.

Calculations for the last breeding method were based on two distinct steps, the first being designed to select only the best progenies, the second the best individuals from the best progenies. It was assumed that a reserve seed supply was available for all progenies so that a large number of seedlings could be grown for each of the selected progenies. This method differs from the second method only by an increased intensity of selection, achieved without increasing the total number of plants to an impractical high number and without reducing the number of plants selected below a reasonable number. It may be termed a progeny test procedure.

In calculating the relative genetic progress for the first two methods, the percentage of plants selected was assumed to be the best 5%. For the last method it was assumed that the best 5% of the individuals in the best 5% of the progenies were selected.

If the three methods were reapplied to progenies derived from crosses between selected plants, inbreeding would be expected to become an important factor which would tend to limit genetic progress.

RESULTS

Estimates of the variance components for general combining ability (σ^2_g) and specific combining ability (σ^2_s) are given in Table 1 together with estimates of the standard errors of the components. Since both reciprocal and maternal effects were non-significant for all the characters in Table 1, components are not given for these effects. This table also gives values for the relative importance of random errors, obtained by dividing the general and specific combining ability components by their respective standard errors. The smaller the values the more important the random errors.

The random errors involved in the estimation of general combining ability components were relatively larger than those obtained in the North Carolina experiment (COMSTOCK, KELLEHER and MORROW 1958; MORROW, COMSTOCK and KELLEHER 1958). In contrast, the random errors associated with the specific

TABLE 1

Estimates of variance components for general (σ^2_g) and specific (σ^2_s) combining ability and their standard errors (S. E.) together with measures of the magnitude of random errors (σ^2_g/S. E. of σ^2_g and σ^2_s/ S. E. of σ^2_s) in the garden strawberry

Character	σ^2_g	S.E. of σ^2_g	$\frac{\sigma^2_g}{\text{S.E. of } \sigma^2_g}$	σ^2_s	S.E. of σ^2_s	$\frac{\sigma^2_s}{\text{S.E. of } \sigma^2_s}$
Total yield	3508	2273	1.5	3539	1398	2.5
Marketable yield	1814	1350	1.3	3546	1302	2.7
Early yield	349	210	1.7	225	83	2.7
Late yield	488	277	1.8	168	60	2.8

combining ability components were approximately half the magnitude of those in the North Carolina experiment. The average random error control, considering general and specific combining ability together, was approximately the same at North Carolina and Ottawa despite the fact that their experiment consisted of four quarter diallels whilst the Ottawa experiment was a single complete diallel. It is interesting to note that the quarter diallels give better random error control for general than specific combining ability component estimation. In contrast, with the full diallel the reverse was the case with better random error control for specific than for general combining ability component estimation. This difference is reasonable, since the quarter diallels involve a wide range of parents and hence might be expected to give a good general combining ability estimate whilst the full diallel involves all possible crosses for the sample of parents used and hence might be expected to give reliable estimates of specific combining ability.

The within-progeny genetic variance (σ^2_w) given in Table 2 is only correctly estimated if the intraplot variance among samples for cultivars (σ^2_v) can be used to accurately calculate the intraplot environmental variance among the individuals of progenies. Initial attempts to do this, assuming that σ^2_v for cultivars was equal to σ^2_v for progenies (COMSTOCK, KELLEHER and MORROW 1958), gave rise to negative estimates of σ^2_w. Investigation showed that there was a correlation between high yield and high environmental variability. Elimination of this correlation following transformation of the data for the cultivars and reanalysis of these data gave values of σ^2_v which it was assumed were equal to σ^2_v for the progenies. Further support for this decision was evident since before transformation the replicate components for cultivars ranged from twice to nine times the magnitude of their respective progeny replicate components; while after the transformation they ranged from half to twice the replicate component for progenies with two larger and two smaller. Since the transformation eliminated the correlation between yield and environmental variance and equalized the average value for replicate components for progenies and cultivars, it may be concluded that the use of σ^2_v (following transformation) in the calculation of σ^2_w may be expected to give a satisfactory estimate of the latter value.

For the average of the four yield characters, approximately two thirds of the

TABLE 2

Estimates of within-progeny genetic variance (σ^2_w) between progeny genetic variance ($2\sigma^2_g + \sigma^2_s$) and total genetic variance (σ^2_G) for the garden strawberry

Character	σ^2_w (percent)	$2\sigma^2_g+\sigma^2_s$ (percent)	σ^2_G
Total yield	26305 (71.4)	10555 (28.6)	36860
Marketable yield	15686 (68.6)	7174 (31.4)	22860
Early yield	1777 (65.8)	922 (34.2)	2699
Late yield	2079 (64.5)	1144 (35.5)	3223

The figures in brackets represent percentages of the total genetic variance.

total genetic variance (σ^2_G) consisted of within-progeny genetic variance (σ^2_w) compared with a slightly higher value for total yield (the only character directly comparable) for the North Carolina experiment (MORROW, COMSTOCK and KELLEHER 1958).

In Table 3 it is striking to note the high percentages of nonadditive variance ($\sigma^2_D + \sigma^2_E$); 65.8, 69.3, 50.8 and 42.6, respectively, for the four characters. All are equal to or higher than the percentage obtained for total yield in North Carolina (MORROW, COMSTOCK and KELLEHER 1958).

Since σ^2_A, σ^2_D and σ^2_E are calculated on the assumption of insignificant high order gene interactions and equal magnitude of all digenic interactions, it is desirable to consider the effect of deviations from these assumptions. The actual composition of the three genetic components is as shown below for the situation with up to three gene interactions, and will reduce to additive, dominance, and epistatic components when the above assumptions are correct.

$$\sigma^2_A = \sigma^2_a + 5/24\sigma^2_{aa} - 1/12\sigma^2_{ad} - 1/8\sigma^2_{dd} - 1/32\sigma^2_{aaa} - 1/8\sigma^2_{aad} - 7/48\sigma^2_{add} - 5/32\sigma^2_{ddd}$$

$$\sigma^2_D = \sigma^2_d + 7/24\sigma^2_{aa} + 1/12\sigma^2_{ad} - 3/8\sigma^2_{dd} - 3/32\sigma^2_{aaa} - 3/8\sigma^2_{aad} - 29/48\sigma^2_{add} - 23/32\sigma^2_{ddd}$$

$$\sigma^2_E = 1/2\sigma^2_{aa} + \sigma^2_{ad} + 3/2\sigma^2_{dd} + 9/8\sigma^2_{aaa} + 3/2\sigma^2_{aad} + 7/4\sigma^2_{add} + 15/8\sigma^2_{ddd}$$

When high order gene interactions are significant and digenic interactions are equally important, σ^2_A will underestimate the additive variance. When all digenic interactions are not equally important but higher order interactions are negligible, then σ^2_A will over- or underestimate the additive variance depending on the relative magnitudes of σ^2_{aa}, σ^2_{ad} and σ^2_{dd}. When both assumptions are incorrect, they will either tend to cancel each other out to give a good estimate of additive variance, or they will lead to an underestimation of the additive variance. In any event, since the proportion of the digenic and higher order genic interaction involved in the calculation of σ^2_A is small, it is not likely that the additive variance will be very significantly misestimated by violation of either or both assumptions.

Similarly, it is not likely that violations of the assumptions will lead to a very significant misestimation of the dominance variance.

TABLE 3

Estimates of the additive variance (σ^2_A), the dominance variance (σ^2_D), and the epistatic variance (σ^2_E) expressed as percentages of the total genetic variance for the garden strawberry

Character	σ^2_A as percent of σ^2_G	σ^2_D as percent of σ^2_G	σ^2_E as percent of σ^2_G	σ^2_G
Total yield	34.2	18.8	47.0	36,860
Marketable yield	30.7	56.9	12.4	22,860
Early yield	49.2	20.8	30.0	2,699
Late yield	57.4	5.4	37.2	3,223

If all digenic components are equally important and trigenic interactions are significant, then σ^2_E will overestimate epistasis. If, however, trigenic and higher order epistatic interactions are insignificant, epistasis will be underestimated if σ^2_{aa} is more important than σ^2_{dd} but overestimated if the reverse is true.

A combination of significant trigenic and higher components with σ^2_{aa} more important than σ^2_{dd} will give errors in opposite directions which will tend to cancel. The most serious misestimation of epistasis is likely to occur if trigenic and higher order components are significant and σ^2_{dd} is more important than σ^2_{aa} since both will lead to overestimation of epistasis. Even this type of error is not likely to be too serious since it was shown earlier that σ^2_A and σ^2_D are likely to be at most only slightly misestimated and hence, since σ^2_E is obtained by subtraction of σ^2_A and σ^2_D from the total genetic variance, it is not likely to be much in error.

Table 4 shows the relative order of magnitude of genetic progress to be expected following the use of the three breeding procedures outlined in the MATERIALS AND METHODS. Thus, the percentage genetic progress shown under Method 1 represents that expected in the first generation (step) of a breeding procedure (where the best phenotypes are intercrossed) that normally extends over several generations. Method 2 is a one-step breeding procedure designed to exploit all the additive, dominance and epistatic variance in a single step. Method 3 exploits all the genetic variance between progenies (first step) before exploiting it within progenies (second step). In all cases, genetic progress is achieved when the mean of selected plants exceeds the mean of the control cultivars. At each step the 5 percent of the plants with the best phenotypes are saved.

Table 5 shows the raw data from which the values in Tables 1–4 were calculated. The values shown are the average of 100 plants (50 for a cross and 50 for its reciprocal).

DISCUSSION

The very large dominance and epistatic variance which make up 65.8%, 69.3%, 50.8% and 42.6% of the total genetic variance (Table 3) for total, marketable, early and late yields, respectively, is an important genetic characteristic of the population of garden strawberries sampled. The relatively high estimates of epistasis, particularly for total, early and late yield, substantiates the theory

TABLE 4

Genetic progress in one generation under three breeding methods expressed as percent of the mean of four control cultivars. Unselected progeny mean also included

Character	*Method 1* Selection based on additive variance only	*Method 2* Selection based on all the genetic variance	*Method 3* Progeny selection followed by individual selection	Mean of control cultivars (gm per plant)	Unselected progeny mean (gm per plant)
Total yield	—30	— 5	+12	829	474
Marketable yield	—34	—11	+ 5	681	375
Early yield	—13	+37	+79	100	39
Late yield	—18	+17	+57	119	41

TABLE 5

Progeny mean values in grams per plant for a diallel cross involving eight parents in the garden strawberry
TY = total yield, MY = marketable yield, EY = early yield, LY = late yield.

Parent number	Character	Parent number						
		2	3	4	5	6	7	8
1	TY	389	264	364	435	513	275	360
	MY	292	214	305	330	391	213	276
	EY	63	43	36	8	32	17	19
	LY	16	7	16	48	26	15	28
2	TY	..	490	546	525	487	493	423
	MY	..	421	434	384	362	386	309
	EY	..	130	59	28	69	66	31
	LY	..	14	34	50	27	25	41
3	TY	..	..	454	602	624	291	458
	MY	..	..	395	504	536	250	406
	EY	..	..	66	28	98	34	28
	LY	..	..	12	52	28	12	33
4	TY	..	..	..	587	549	510	385
	MY	..	..	..	447	442	430	293
	EY	..	..	..	7	41	42	12
	LY	..	..	..	80	40	33	37
5	TY	..	..	..	..	579	562	478
	MY	..	..	..	..	417	434	350
	EY	..	..	..	..	11	17	14
	LY	..	..	..	..	100	78	146
6	TY	..	..	..	..	..	571	535
	MY	..	..	..	..	..	474	393
	EY	..	..	..	..	..	36	15
	LY	..	..	..	..	..	37	71
7	TY	..	..	..	..	..	..	528
	MY	..	..	..	..	..	..	432
	EY	..	..	..	..	..	..	31
	LY	..	..	..	..	..	..	52

of WRIGHT (1956) regarding the importance of epistasis in a species which is mostly vegetatively propagated. In addition, for a virus free population, different plant sample and northern environment, the results of this experiment were similar to those obtained in North Carolina (COMSTOCK, KELLEHER and MORROW 1958).

The interpretation of the experimental results should be considered in the context of their limitations with respect to the population of parameters to which these estimates apply. First, they are limited since the estimates were only obtained in one season in one location and hence may be considered lacking in generality. In answer to this it may be pointed out that the North Carolina experi-

ment gave essentially similar results for a very different set of environmental conditions. Thus it would appear that although individuals may respond very differently to different environments, progeny populations as a whole appear to have essentially similar genetic architecture. Secondly they are limited since the estimates were obtained using only eight parents out of the population of Canadian and United States cultivated strawberry plants. However, they did include early, main and late cropping types and had as ancestors varieties which have been grown throughout the United States and Canada and hence may be expected to encompass a representative gene pool. Since, however, they did not have as recent ancestors many individuals which could be readily linked with varieties currently being grown in Continental Europe, that portion of the world population of cultivated strawberry plants should not be considered as part of the population to which the results of this paper specifically apply. Nevertheless, in view of the relatively recent (in terms of generations) origin of the cultivated strawberry, from a relatively small group of ancestral types (MANGELSDORF 1927; STAUDT 1961), it would not be surprising if it was ultimately found that all cultivated strawberries had many common genetical attributes.

Since the present experiment, together with the North Carolina experiment, agrees with the genetical theory of WRIGHT, it is logical to examine the effectiveness of various breeding procedures in achieving genetic progress.

Method 3 (progeny selection followed by individual selection) gives good prospects for genetic progress in all four characters (Table 4). With Method 2 (selection of the best phenotypes) progress may only be expected for early and late yields. No progress is indicated for a single generation for any character using Method 1. However, the magnitude of negative genetic progress with this method might decrease in successive generations. Hence, genetic progress might be achieved ultimately by using Method 1. However, the effort expended on it, relative to the possibly nonexistent advantages to be gained and relative to the proven gains by Method 2 or 3, would probably not warrant the time and cost involved.

The advantages of Method 3 over Method 2 depend on the large proportion of the total genetic variance that is within-progeny variance. This constituted 71.4%, 68.6%, 65.8% and 64.5%, respectively, for the four characters (Table 2). It is interesting to note that the first step of Method 3—selection of the best progenies—if accompanied by selection of the best individuals within these progenies, does not result in plants having a better first test average than those selected by Method 2. However, the second step of Method 3, involving large samples from the best progenies rather than further small samples from all progenies (Method 2), results in a superior group (Table 4) due to an increase in the intensity of selection (a smaller proportion of plants selected). A further factor to consider when comparing Methods 2 and 3 is that a phenotypically "good" individual in an otherwise poor cross (a possible selection following Method 2) is more likely to be a genotypically poor result than a "good" individual in a good progeny. Hence, further testing in different environments would likely increase the proportion of poor individuals revealed by Method 2.

The genetic progress estimates obtained following the use of the three methods discussed in this paper are similar in order of importance to the actual genetic progress obtained at Ottawa in experiments designed to evaluate the merits of different breeding procedures. It is not intended that the reader should infer from this that genetic component and genetic progress estimates obtained from different samples of parents should be expected to be the same, but rather that the general order of importance of genetic components and hence the relative merits of different breeding procedures will be similar. Exceptions to this generalization may be expected where special procedures such as intensive inbreeding may have been accompanied by a disruption of the natural genetic structure.

This paper has confined attention mostly to short-term gains which have been shown to be best achieved by Method 3. However, once most of the possible genetic progress has been exploited using this method (following a survey of all potentially useful gene sources) it would be necessary to devise a new procedure. One possibility would be to use Method 1 to exploit characters controlled by a few major genes and to use the resulting selections as one source of parents to be used in Method 3.

SUMMARY

The additive, dominance and epistatic components were estimated for the garden strawberry for total, marketable, early and late yields from an analysis of an 8×8 diallel. All progenies and control cultivars were maintained in a virus-free state.—It was found that epistatic variance made up 47.0%, 12.4%, 30.0% and 37.2% of the total genetic variance for the four characters, respectively. The corresponding figures for dominance variance were 18.8%, 56.9%, 20.8% and 5.4%. The magnitude of the epistatic variance is such as might be expected in a species which is usually asexually propagated.—The sign and size of genetic progress, with such high nonadditive variance (epistatic and dominance), depended on the breeding method. When this exploited only the additive variance, genetic progress was negative for total, marketable, early and late yields. In contrast, genetic progress was positive for the same four characters when the method exploited all the genetic variance.

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