

A tomato selection experiment

BY NEIL GILBERT

John Innes Institute, Bayfordbury, Hertford, Herts.

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This paper presents the results of an experiment involving the F_1 , F_2 , F_3 and F_4 of all crosses between eighteen English tomato varieties. Williams & Gilbert (1960) described the behaviour of the F_1 's and F_2 's in previous years. I am now concerned to compare the F_3 's and F_4 's, selected for early yield, with the parents, F_1 's and F_2 's. The purpose is to find out whether, at the beginning of a programme of crossing and selection, the F_1 's and F_2 's tell us any more than do the parents about the relative performance of the inbred lines finally obtained. If (as appears) they do not, the initial choice of parents for such a programme can be made solely on the basis of parental performance; it would be a waste of time to make test crosses merely in order to compare the 'combining abilities' of the possible parents.

1. DESIGN OF THIS AND OTHER SELECTION EXPERIMENTS

Even in the case of a population segregating for a single Mendelian gene, we are unable to predict the (stochastic) behaviour of any particular selected line. We can, however, consider the behaviour of a population of lines, each experiencing the same selection pressure. The average response to selection can then be compared with the theoretical prediction, using the variance between lines as the estimate of error. It seems to me, therefore, that a useful selection experiment must involve replication of distinct, similarly treated lines. Experiments to compare, say, one upwardly selected line with one selected downwards may have some practical interest but are of little use for theory. An ideal selection experiment would therefore start with an F_2 family (or several different F_2 's), select from it a dozen plants to give F_3 's, select (similarly) a dozen F_4 's from each of those F_3 's, and so on. We should also like to backcross each line to each parent in each generation. Clearly, the problem is what to leave out of the experiment. In the present case, I was concerned to compare the responses of crosses from different parents to a uniform selection pressure. The replication was therefore made between parents; each of the 153 crosses (excluding reciprocals) between the eighteen parents was represented by one line in each generation. In each cross, the highest yielding of twenty F_2 plants was chosen to give F_3 seed and, similarly, the best of twenty of these F_3 plants gave F_4 seed. The yields of individual F_3 and F_4 crosses are then of small significance in themselves, since the individual lines are not replicated; it is the average performance of each parent, as represented by that parent's seventeen crosses, that is meaningful. I chose the number 18 to give a reasonable number of degrees of freedom between parents. The actual parents employed, all standard English varieties, are listed by Williams & Gilbert (1960).

They were chosen by Mr L. A. Darby, tomato breeder at the Glasshouse Crops Research Station. They include both common varieties and some less often grown. The 153 F_1 crosses, the derived F_2 , F_3 , F_4 families and the eighteen parents were grown outdoors in 1960 in a 13×13 lattice square design in two replicates, there being two extra plots per block. Each plot consisted of twenty-four plants. Plots carrying the hybrids were split into four for generations. Plots carrying parents were split into two parts A and B, carrying plants of the same variety grown from seed taken in two different years. This was to test the occurrence of maternal effects caused by season, since the seed of the different hybrid generations were taken in different years. Thus each parent was represented by a total of forty-eight plants, and each generation of each cross by twelve plants. The total number of plants, 8208, could not reasonably be exceeded in an experiment wherein each individual plant had to be measured. In addition, a guard row was grown on the perimeter of the whole experiment. There were forty-six missing plants (mostly rogues but also some apparently normal plants which flowered well but set no fruit). They were evenly distributed between generations. The totals of sub-plots containing such plants were adjusted accordingly. For each plant in the experiment, the date of first flowering and the number and weight (oz.) of first three weeks' ripe fruit were recorded. Average fruit weights were determined from the sub-plot totals. All results given here are on a per-plant basis, and are corrected (where necessary) for rows and columns of the lattice square design.

One consequence of taking $k = 18$ parents and $n = 4$ generations is, that $(k - 2)/4 = n$; this means that, with each parent replicated four times as often as each cross, the parental main effects (t) in each generation are estimated as accurately as one-half the means of the parental yields ($p/2$) (ignoring the correlation between the errors of sub-plots within one plot). This is useful, as a large part of the analysis is concerned with comparing t and ($p/2$).

That the plants were grown at all is due to the painstaking work of the glasshouse and garden staff of this Institute. For the recording I was entirely dependent on the help of Mr W. Williams and members of the Department of Plant Breeding. Mr Williams made the selections from the F_3 . By permission of Dr F. Yates, I was able to use the Rothamsted electronic computer for a large part of the analysis; this depended on the work of the engineering and punch staff of the Department of Statistics. Mere thanks are insufficient, for the experiment could not have been made without this help. I am grateful to Mr N. W. Simmonds, the Editor, and the Referee for their valuable suggestions.

2. REJECTION OF OBSERVATIONS ON FLOWERING DATE

Analysis of flowering date showed that it was significantly affected by various environmental factors. For this character there was an average difference between A and B parents (seed of the same varieties taken in different years); and this difference interacted with parents and with blocks. Blocks also interacted with generations. Consequently, the experimental results obtained depend on the particular blocks used in the experiment and on the particular year in which the

seed was taken. Evidently, flowering date in tomatoes is not a satisfactory character for this kind of experiment since it is at the mercy of such environmental disturbances. These results are therefore omitted from this paper. The other three measurements showed no such effects.

3. APPARENT SELECTION FOR HETEROZYGOSITY OF A MENDELIAN GENE

Two parents ('Exhibition' and 'Moneymaker') are homozygous for the recessive Mendelian gene u (uniform), which prevents 'greenback' discoloration of the fruit. This, incidentally, gives some check that the various crosses are true to label. The genotypes of the plants selected from F_2 and F_3 can be ascertained from their F_3 and F_4 progenies. In selecting for early yield, this allele was ignored. Other things being equal, we should expect a 1:2:1 ratio in the selected plants (as well as in each progeny before selection). In the total of 71 families segregating for u , there were 628 U and 218 u plants. χ^2 (1 d.f.) for a 3:1 ratio is 0.27. The plants selected from the F_2 families to give F_3 seed were in the proportion $4uu:22Uu:6UU$. From the twenty-two F_3 families still segregating for this gene, the selection was $1uu:17Uu:4UU$. There is some possibility of misclassification among the ten UU plants, for with a progeny of twelve the probability of classifying a Uu parent as UU is about 3.2%; but such misclassification would act *against* the observed excess of heterozygotes. The total segregation of $5uu:39Uu:10UU$ may possibly indicate some selection against uu genotypes, but even if we compare the $Uu:UU$ frequencies for a 2:1 ratio there is still a decided excess of heterozygotes. Apparently, the Uu heterozygote has been unconsciously selected. This is rather surprising, as it seems to be a valid generalization (no more) that hybrid vigour in inbreeding organisms is of the dominance type and therefore fixable. Direct measurement of these three genotypes against similar genetic backgrounds would be necessary to establish firmly such a heterozygote advantage, if it exists. The effect might be due to linkage.

4. WITHIN-PLOT VARIANCES

Each generation of each cross was represented by six plants in each of two sub-plots, giving ten degrees of freedom for within-plot variance. The standard deviations were analysed as observations in their own right. It is more usual to analyse log variance, but this square-root transformation gives much the same answer and has the recommendation that it is the S.D. that is used in estimating percentiles. These figures are available for yield and fruit number only, since the fruit weights were estimated from sub-plot totals. Although the parents were grown in sub-plots of twelve plants each, the standard deviations quoted here are calculated within sets of six plants, and so are comparable with the S.D.'s of the other generations. A significant correlation was found between within-plot S.D. and plot mean. Part of the differences between the S.D.'s of different generations may therefore be explained away as a reflection of differences between generation means. The crude standard deviations have therefore been corrected for their

observed within-generations regression on the means (Table 1). Taking these figures at their face value, it appears that a conspicuous increase in variability in F_2 has almost disappeared by F_4 , in which case little further advance under selection can be expected. Now parental 'main effects' can be estimated from the

Table 1. *Average within-plot standard deviations*

	Yield		Fruit Number	
	Crude	Corrected	Crude	Corrected
Parents	8.48	8.86	3.72	3.90
F_1	9.07	8.81	3.70	3.62
F_2	9.73	9.78	4.22	4.26
F_3	9.58	9.55	4.17	4.15
F_4	9.15	9.02	4.07	3.94
		(± 0.18 approx.)		(± 0.08 approx.)

S.D.'s of the 153 crosses. It is found that there is strong parental control of the variability of the crosses. This may be partly explained by the similar effects on the means. The figures in Table 2 are therefore corrected as before for the regression on the mean. (This regression was found to be homogeneous between main effects and interactions; it showed no curvature.)

Table 2. *Analyses of variance of corrected within-plot S.D.'s*

	d.f.	Mean squares			
		F_1	F_2	F_3	F_4
Yield					
Main effects	17	9.24	8.09	8.73	4.92
Interactions	134	3.74	4.94	4.38	5.67
Fruit number					
Main effects	17	1.79	1.30	1.35	0.85
Interactions	134	0.82	1.09	0.99	1.26

These figures suggest that, even after allowing for the regression on the mean, there is some parental control of variability in yield but not in fruit number. This conclusion is supported by the correlations between these main effects and the S.D.'s of the parents themselves (Table 3).

Table 3. *Correlations (16 d.f.) between S.D. main effects and parental S.D.'s (both corrected for regression on mean)*

Parents \times	Yield	Fruit number
F_1	+0.262	-0.178
F_2	+0.345	+0.190
F_3	+0.264	-0.125
F_4	+0.422	-0.125

Now the parental and F_1 variabilities should be free from genetic segregation; and the average S.D.'s quoted behave accordingly. The parents transmit 'environmental' variability as well as average yield to their offspring. (The smallest parental yield S.D. was 5.8, and the largest, 10.3.) There is, of course, always the possibility that the parents were not completely homozygous.

5. GENERATION MEANS

Although, for each sub-plot, yield = fruit number \times average fruit weight, these generation means naturally do not satisfy the same relation exactly. As mentioned in the previous paper (Williams & Gilbert, 1960), high early yield is associated with high fruit number rather than large fruit size. This has held true during selection, for the response in yield from F_2 to F_4 has been achieved by an increase in fruit

Table 4. *Generation means*

	Yield	Fruit number	Fruit weight
Parents	22.1	10.1	2.32
F_1	27.0	11.4	2.43
F_2	24.6	10.8	2.35
F_3	25.2	11.1	2.36
F_4	26.0	11.7	2.32
Mean top-parent	25.5	12.5	2.58
	(\pm 0.43*)	(\pm 0.19*)	(\pm 0.022*)
	(\pm 0.61†)	(\pm 0.25†)	(\pm 0.033†)

* S.E. of difference between two F means.

† S.E. of difference between parental and one F mean.

The 'top-parent' is the largest of the two parents in each cross.

number, the fruit weight remaining constant. (These responses to selection are of the order of magnitude predicted from the selection pressure—1 in 20 per generation—and the observed within-plot variances.) The F_1 hybrid vigour is relatively greater in yield than in fruit number or weight. This confirms the result of the previous paper, that—to a large extent—heterosis for yield results from the combination of one parent's high fruit number with another parent's high fruit weight.

6. ANALYSES OF VARIANCE

These analyses (Table 5) are made by fitting additive main effects (general combining abilities, g.c.a.) for each parent. The 17 d.f. for main effects are split into 1 d.f. for regression on parental means and the 16 remaining d.f. for deviations of the main effects from this regression. This 1 d.f. for regression of main effects on parental means is also the 1 d.f. for regression of each cross on its mid-parent.

Throughout this paper, the term 'interaction' is used in its statistical sense of a departure from additivity. As expected, the interactions (i.e. specific combining

abilities, s.c.a.) increase in size in F_3 and F_4 , confirming that the individual F_3 and F_4 family means signify very little since they have responded unequally to selection. In other words, the data tell us nothing about the average response to selection of particular crosses (but they can tell us something about the average response of all crosses involving a particular parent). This is equally true of fruit weight, even though that character shows no *systematic* response to selection (section 9).

Table 5. *Analyses of variance*

	d.f.	Mean square			
		F_1	F_2	F_3	F_4
Yield					
Main effects (g.c.a.):					
Regression on parents	1	13393	21400	21409	19262
Remainder	16	703	382	643	624
Interactions (s.c.a.)					
Error	135	274	210	355	488
Error	608	169	169	169	169
Regression on parental differences	1	250	1	402	709
Fruit number					
Main effects:					
Regression on parents	1	7082.9	9979.5	11319.3	13384.8
Remainder	16	129.4	76.6	93.7	147.1
Interactions					
Error	135	59.1	40.8	81.4	120.9
Error	608	31.6	31.6	31.6	31.6
Regression on parental differences	1	304.6	0.1	206.4	234.0
Fruit weight					
Main effects:					
Regression on parents	1	14.4492	19.3526	17.7664	15.9304
Remainder	16	0.2181	0.2039	0.1683	0.2633
Interactions					
Error	135	0.0762	0.0982	0.1729	0.1956
Error	608	0.0751	0.0751	0.0751	0.0751
Regression on parental differences	1	3.5827	3.0830	1.6769	1.7316

The terms for 'regression on parental differences' are discussed in section 10.

7. INTERACTIONS

The correlations between interactions (special combining abilities) in different years and generations are small (Table 6). This confirms the finding (of the previous paper) that the interactions, although genetically significant, are unpredictable.

The 1960 correlations between F_1 and F_2 include an environmental component because the F_1 's and F_2 's occurred together on the same whole-plots. Since a correlation r only refers a fraction r^2 of the variance of one variate to the second variate, a correlation must in most circumstances be about $\frac{1}{2}$ or more before it can

Table 6. *Correlations between interactions (s.c.a.) (134 d.f.)*

Same generation in different years:

	F_1		F_2
	1957	1958	
			Yield
1958	0.069		1958
1960	0.206	0.252	0.273
			Fruit number
1958	0.017		
1960	0.150	0.162	0.256
			Fruit weight
1958	0.179		
1960	0.150	0.009	0.004

Between F_1 and F_2 generations in the same year:

	1958	1960
Yield	0.152	0.484
Fruit number	0.062	0.498
Fruit weight	0.019	0.266

give worth-while prediction. Although these correlations are all positive, therefore, they are not large enough to give useful prediction. For this we must rely entirely on the main effects.

8. REGRESSION RELATIONS BETWEEN MAIN EFFECTS

The yield y of the cross between parents i and j is $y = m + t_i + t_j + t_{ij}$, where t_i, t_j are the parental main effects or general combining abilities. We have just seen that the interaction (specific combining ability) t_{ij} is unpredictable. I shall now consider how the main effects in different generations are related to each other and to the corresponding parental quantity ($p/2$) ($\frac{1}{2}$ parental mean). The regression coefficient of t on ($p/2$) is also the regression of individual cross yields on their mid-parental values. The regressions presented here are phenotypic regressions. It is possible to correct for error (assuming that genetical and environmental effects are additive) and so obtain 'genetic' regressions. The procedure is discussed in the appendix to Williams & Gilbert (1960). The resulting matrices are not positive definite (either because of sampling errors or because the assumption of additivity is wrong) and so the multiple regressions are nonsensical; while the simple genetic regressions (on one variate only) tell the same story as these phenotypic regressions. The S.S. for regression of each generation's main effects on parents have already been given in Table 5.

Table 7 is given *in extenso* to make the point that, for fruit weight (which is not responding consistently to selection), the preceding generation alone gives as good prediction as any, and better than the parents; whereas for fruit number and yield, predictions from the immediately preceding generation and

Table 7. *S.S. for regression of main effects (g.c.a.) on the main effects of previous generations*

Regression	S.S. absorbed by regression		
	Yield	Fruit number	Fruit weight
F_2 on F_1 and $\frac{1}{2}p$	23,000	10,500	20.8
F_1	18,300	9,800	20.0
$\frac{1}{2}p$	21,400	10,000	19.4
F_3 on $F_2, F_1, \frac{1}{2}p$	21,600	11,400	19.2
F_2, F_1	18,500	10,900	19.0
$F_2, \frac{1}{2}p$	21,600	11,400	19.0
$F_1, \frac{1}{2}p$	21,500	11,400	19.0
F_2	18,500	10,900	18.6
F_1	13,000	9,500	18.1
$\frac{1}{2}p$	21,400	11,300	17.8
F_4 on $F_3, F_2, F_1, \frac{1}{2}p$	21,300	14,000	18.7
F_3, F_2, F_1	18,800	13,800	18.7
$F_3, F_2, \frac{1}{2}p$	21,100	13,900	18.3
$F_3, F_1, \frac{1}{2}p$	21,200	14,000	18.7
$F_2, F_1, \frac{1}{2}p$	19,600	13,500	18.5
F_3, F_2	18,800	13,700	18.3
F_3, F_1	18,500	13,600	18.7
F_2, F_1	13,400	12,600	18.5
$F_3, \frac{1}{2}p$	20,700	13,900	18.1
$F_2, \frac{1}{2}p$	19,500	13,400	17.7
$F_1, \frac{1}{2}p$	19,600	13,400	18.4
F_3	18,400	13,600	18.1
F_2	13,400	12,500	17.6
F_1	8,100	10,200	18.2
$\frac{1}{2}p$	19,300	13,400	15.9

from the parental means are equally good (and supplement each other to some extent). Similar conclusions hold for the relations between the individual crosses in different generations (which is hardly surprising since we have seen that the interactions are poorly correlated). There is no sign of curvature in these regressions.

Table 8. *Coefficients of regression of main effects on parents*

Regression	Yield	Fruit number	Fruit weight
F_1 on $p/2$	0.66	0.68	0.73
F_2 on $p/2$	0.83	0.80	0.84
F_3 on $p/2$	0.83	0.86	0.81
F_4 on $p/2$	0.79	0.93	0.77

The values of these regression coefficients are not of great practical importance, in the sense that a breeder can only take the best that offers itself. The coefficients are all less than unity, confirming the result (of the previous paper) that although

the F_1 and F_2 generation means exceed the parental mean, the dispersion of the various crosses within the F_1 and F_2 generations is smaller than that of the parents themselves; and heterosis is rarely observed in crosses involving the best parents. The increase in size of these regressions from F_1 to F_2 is significant; I shall not attempt to interpret it in terms of dominance. The increase from F_2 to F_4 in the fruit-number regression coefficient, implying that the response to selection $F_4 - F_2$ is correlated with parental size, is not significant when tested against the appropriate error derived from $(F_4 - F_2)$ interactions (Table 10).

The 'remainder' terms in the analyses of variance in Table 5 show that the difference between the actual main effect and the value predicted by regression on the parent, is significant. But it is unpredictable (Table 9).

Table 9. *Correlations between deviations of main effects (g.c.a.) from parental regression (15 d.f.)*

Same generation in different years:

	F_1			F_2
	1957	1958		1958
			Yield	
1958	0.421			
1960	0.186	0.371		-0.091
			Fruit number	
1958	0.216			
1960	0.153	0.341		-0.035
			Fruit weight	
1958	0.397			
1960	0.253	0.439		0.225

Different generations in 1960:

		F_1	F_2	F_3
Yield	F_2	0.517		
	F_3	0.088	0.146	
	F_4	-0.182	-0.145	0.383
Fruit number	F_2	0.678		
	F_3	0.212	0.296	
	F_4	-0.039	0.150	0.471
Fruit weight	F_2	0.674		
	F_3	0.685	0.672	
	F_4	0.761	0.653	0.721

For fruit number and yield (which are responding to selection) there is good correlation between successive generations, but it is impossible to predict these 'deviations from regression' from F_1 to F_4 . Fruit weight, which is not responding to selection, shows useful correlations between all generations. In spite of the deviant 1958 x 1960 F_2 figures, there is definite correlation between the same generation in different years.

9. RESPONSE TO SELECTION

From the practical point of view, the breeder must concentrate on the actual yield attained, rather than the increase achieved by selection. But it seems possible that the increase from F_2 to F_4 may lend itself to more sophisticated methods of prediction than can be used on the F_4 alone.

Table 10. *Analysis of variance of ($F_4 - F_2$)*

	d.f.	Mean square		
		Yield	Fruit number	Fruit weight
Mean difference between generations	1	3477	366.3	0.0505
Main effects:				
Regression on parents	1	28	124.7	0.0832
Remainder	16	574	95.9	0.0823
Interactions (= error)	135	315	69.2	0.1320

The interactions (specific combining abilities) M.S. is used as error because, as shown in section 6, individual crosses have responded unequally to selection. The 'regression on parents' M.S. provides a test of the significance of the difference between the F_4 and F_2 regression coefficients in section 8. In yield and fruit number there is some heterogeneity of main effects, i.e. the general combining abilities of different parents have responded differently to selection. Crosses involving one of the poorer parents might be expected to respond, on average, more than those involving one of the better parents; but there is no such effect. Nor are the responses correlated with the 'environmental' variabilities discussed in section 4 (or with the increase from F_1 to F_2 of such variability).

10. TOP-PARENT REGRESSIONS

The analysis by main effects (general combining abilities) is based on the assumption that the genetic contributions from the two parents are equally important to the determination of the yield of the cross. However, it is possible that the better parent will be more important in the event of upwards dominance or of upwards selection. Regression of the yields of crosses on the respective top- and bottom-parents is equivalent to regression on mid-parents and on the absolute difference between the two parents. As mentioned in section 6, the regression on mid-parent is part of the 'main effects' S.S., but regression on the parental difference is orthogonal neither to main effects nor to interactions. The M.S. for 'regression on parental difference' in section 6 represent the *additional* variance due to this source, i.e. they equal the S.S. for regression on top- and bottom-parents (2 d.f.) minus the S.S. for regression on mid-parents (1 d.f.). Now, in the appendix to the previous paper I found that, in the F_1 and F_2 , the regression on parental difference was negligible in all cases except F_1 fruit number and yield. The present

results show that I was wrong to discount this exception; the F_1 yields and fruit numbers show general phenotypic dominance of the top-parent, the regression equation being

$$F_1 \text{ fruit number} = 0.41 (\text{top-parent}) + 0.15 (\text{bottom-parent}).$$

This effect disappears in the F_2 . A similar effect, ascribable to the upwards selection, appears in the F_3 and F_4 : e.g.

$$\begin{aligned} F_4 \text{ yield} &= 0.48 (\text{top-parent}) + 0.22 (\text{bottom-parent}), \\ F_4 \text{ fruit number} &= 0.53 (\text{top-parent}) + 0.30 (\text{bottom-parent}). \end{aligned}$$

Fruit weight, which alters little from generation to generation, shows phenotypic dominance of small fruit size. There was a similar, but non-significant, tendency in 1957 and 1958. An obvious objection is that, since such asymmetry occurs, the analysis by main effects (g.c.a.) is no longer the best way of looking at the situation. This is true, but the analyses of variance of yield and fruit number in section 6 show that it is only just true, for the 'regression on parents' M.S. is far larger than the 'regression on parental differences' M.S., even though the latter may be significantly large on occasion. For fruit weight, on the other hand, the analysis could be improved by weighting the parental main effects. I have not done so here because this character showed no consistent response to selection anyway. It is interesting to note that, although the F_1 crosses have on average a greater fruit weight than their parents, their distribution about that average tends to follow the smaller parent. At the moment we cannot predict *how much* more important the top-parent will be; until we can, these general combining abilities (main effects) are the best that we can do.

11. CONCLUSIONS AND SUMMARY

All 153 crosses between 18 tomato varieties were grown in F_1 , F_2 , F_3 and F_4 . The F_2 , F_3 and F_4 were derived by selfing one plant of the previous generation. The F_2 plant chosen to give the F_3 was selected (1 in 20) for early yield; and the F_3 plant chosen to give the F_4 was similarly selected. Flowering date was an unsatisfactory character. In crosses segregating for the Mendelian gene 'uniform', a significant excess of heterozygotes was selected. The parents transmitted variability of yield (as well as average yield) to their offspring. The division of yield into its components fruit number and fruit size is useful because (1) much of the heterosis in yield can be viewed as a combination effect between these components, (2) the components responded differently to selection, (3) different components showed phenotypic dominance in different directions. The average yield and fruit number responded as expected to selection; fruit size did not. The F_1 generation means for all three characters exceeded the parental means; but the crosses were grouped more compactly about their generation mean than were the parents, so that heterosis rarely occurred in crosses involving the best parents. The yields of each cross were analysed into parental main effects (general combining abilities)

and interactions (specific combining abilities). No useful prediction of interactions could be made in any generation, either from the same generation in different years or from different generations in the same year. The main effects (general c.a.) were analysed into a part due to regression on parental yield, and a deviation from that regression. No useful prediction of the deviations from parental regression could be made in generations which had responded to selection. The actual advance under selection of different crosses, although not uniform, was unpredictable. During advance under selection, the parental means gave predictions of the (relative) performance of each generation's crosses which were as good as predictions based on the previous generation. This may, of course, be connected with the fact that the parents were inbred and that the amount of heterozygosity decreases in each successive generation. These results indicate, therefore, that in an inbreeding species propagated by seed, the early hybrid generations tell us nothing more than do the parental yields about the relative performance of the inbred lines that can be selected from those hybrids. (This generalization from *Lycopersicon esculentum* to inbreeders as a whole may, of course, be false.) The relative performance of F_1 hybrids, on the other hand, is better predicted from other F_1 crosses involving the parents concerned than from the yields of those parents. There was phenotypic dominance of high yield, large fruit number and low fruit weight. The extent of this dominance was not enough to invalidate the analysis by general combining abilities; and since it varied from year to year and from generation to generation, the emphasis that should be given to the top-parent (in contrast to the bottom-parent) in predicting the yields of crosses after selection, is as yet unpredictable.

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