Use of a Controlled-Nutrient Experiment to Test Heterosis Hypotheses

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ABSTRACT

A controlled-nutrient (CN) experiment was conducted to test three heterosis hypotheses with reference to tomato yield, and its components, for a set of two inbred lines and their hybrid that had previously exhibited considerable heterosis under field conditions. The CN treatments consisted of periodic applications of differential doses of nutrient solution to plants reared individually in containers filled with vermiculite. Ripe fruit were harvested, counted and weighed over a period of 340 days. The data permitted the partitioning of yield into a closed system of five component variables. Heterosis was not exhibited by yield, nor yield components, at any of the four nutrient levels. Hence the total heterosis phenomenon was classified as nutrient-dependent: heterosis occurring under field conditions, but not under the nutritional restrictions of the CN experiment. Three heterosis hypotheses were examined for their ability to explain all of the nutrient-dependent aspects of the heterosis phenomenon. Hypothesis 1: Heterosis is a consequence of a more efficient hybrid metabolic system in that it can produce more product with equal input. Hypothesis 2: Heterosis is a consequence of the somatic multiplication of additive component traits. Hypothesis 3: Heterosis is a consequence of a faster hybrid growth rate. Although none of the hypotheses are rejected by the field data, the first two are rejected by the CN experimental results. The third hypothesis fits all aspects of the nutrient-dependent heterosis phenomenon remarkably well. It is speculated that the indeterminate pattern of plant development responsible for yield and its components is due to two major gene systems: genes that determine morphogenetic, and genes that determine growth rate manifestations of growth. Under this hypothesis, the CN technique permits separation of the responses due to these two gene systems.

APPLICATION of heterosis (hybrid vigor) to agricultural production is a multi-billion dollar enterprise. It represents the single greatest applied achievement of the discipline of genetics. Ironically, however, the physiological and genetical bases of heterosis are not entirely understood. Therefore the objective of this study is to shed some light on this subject with regard to yield, and its component parts, in an indeterminate, self-fertilizing plant, the tomato (genus: *Lycopersicon*).

This study utilizes data from two different experiments. These include a previous field experiment (GRIFFING 1948, 1953), and a controlled-nutrient (CN) greenhouse experiment which is now reported for the first time. These experiments are coordinated in the sense that the CN experiment utilizes genetic material which was included in the field study. Thus the detailed analyses of the CN experiment will be used to elucidate the heterotic field performance of the same genetic material.

The field experiment involved a diallel of six tomato inbred lines and all possible F_1's. The variables studied were yield, and yield components, as illustrated in Figure 1. The parents collectively exhibited a wide range of variation for all variables. One aspect of the analysis performed on the field data, which will be used later, was the estimation of the pattern of genotypic relationships among the yield variables as given in Figure 1. In this representation, double-headed arrows indicate simple correlation coefficients, and single-headed arrows represent standard partial regression coefficients (SEWALL WRIGHT's path coefficients). These statistics were estimated by functions of appropriate genotypic variance and covariance components. The pattern of relationships indicates that yield and its components are a highly correlated genetic system of variables.

The genetic material chosen for the CN experiment consisted of two parents and their F_1 which exhibited the greatest yield heterosis in the field experiment. These included: P_1 = Red Currant (*Lycopersicon pimpinellifolium*), P_2 = Devon (*L. esculentum*; a domesticated variety) and the $F_1 = P_1 \times P_2$. The two parental species are very closely related. Complete fertility occurs on crossing, and it is widely accepted that *L. pimpinellifolium* should be regarded, more appropriately, as a variety of *L. esculentum*.

Arithmetic and logarithmic means for the field data of these genotypes, with respect to yield and its components, are given in Table 1. Both arithmetic and logarithmic means are presented because both scales of measurement are used in the CN analyses. In
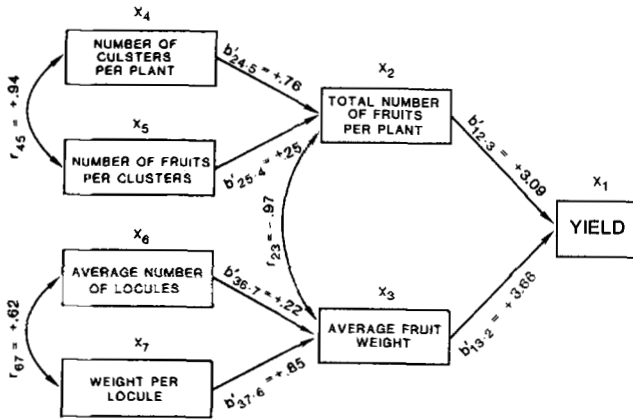
FIGURE 1.—Diagrammatic representation of the partitioning of yield into component variables, showing path and correlation coefficients.

addition to the means, potence values are given. The potence value will be defined and discussed at length in the next section. Suffice it to say at this point, that the potence value is a standardized measure of the deviation of the F_1 mean from the midparental value. A potence value in excess of one indicates that the hybrid performance is greater than either parent and, following SHULL's (1914, 1948) definition, heterosis is expressed.

From the potence values of Table 1, it is clear that heterosis in yield is expressed when measured on either scale. However, the yield heterosis is not accompanied by heterosis in any of the components of yield. In fact, on the arithmetic scale, the first-order components of yield, namely X_2 = number of fruits and X_3 = average fruit weight, exhibit negative potence values. This phenomenon of heterosis in a compound variable and lack of heterosis in its components, has been recognized for some time and is an integral part of a genetic hypothesis for the explanation of heterosis. This hypothesis will be discussed later.

The CN experiment is the primary subject of this study. The experiment is designed to control genotypes and nutritional environments systematically so that genotypic and nutrient response curves can be derived, and inferences from these responses made with respect to the manifestation of heterosis of yield and yield components. The objective of the study is to test various heterosis hypotheses for their ability to explain the total expression of heterosis in both field and CN experiments.

MATERIALS AND METHODS

This section sets out the experimental and analytical procedures for the CN experiment.

Experimental procedures: The parents and F_1 chosen for the CN study are those that exhibited the greatest heterosis in the field experiment. These are: P_1 = Red Currant, P_2 = Devon, and $F_1 = P_1 \times P_2$. This choice of material is useful in that the parents exhibit large differences in all traits of interest. P_1 has many small fruits that are

TABLE 1

Arithmetic and logarithmic means and potence values for the yield variables as expressed by the parents and hybrid grown under field conditions

Variable[a]	Genotypes			Potence
	P_1	F_1	P_2	
Arithmetic means				
X_1	678	2552	1996	1.85
X_2	1287	612	41	−0.08
X_3	0.5	4.2	49.1	−0.85
X_4	133.5	93.5	8.9	0.36
X_5	10.5	8.4	5.2	0.21
Logarithmic means				
$_1X$	2.8069	3.3988	3.2890	1.46
$_2X$	3.0933	2.7789	1.5993	0.58
$_3X$	−0.2864	0.6199	1.6897	−0.08
$_4X$	2.0989	1.9322	0.9414	0.71
$_5X$	0.9944	0.8467	0.6579	0.12

[a] See Figure 1 for variable description. Note $_iX$ is the mean of the logarithmic transformation of variable X_i.

produced in many-fruited clusters. P_2 has relatively few, large fruits in clusters having few fruits per cluster. These large differences facilitate the quantitative analysis of yield and its components. Many of the early studies of heterosis, as expressed in self-fertilizing plants, involved some form of the interspecific cross: Red Currant (*L. pimpinellifolium* alias *L. racemigerum*) × *L. esculentum*. These include; ASHBY (1937), LUCKWILL (1937), WHALEY (1939a,b), ROBBINS (1941) and POWERS (1941, 1944, 1945). Therefore, the present study of heterosis, using this particular genetic material, is in keeping with previous studies.

Because it was desired to evaluate the influence of different nutritional levels on yield and its components, it was necessary to establish nutritional regimes which would ensure that all three genotypes received exactly the same quantity of nutrients for a relatively long period of time (340 days). Therefore, the treatment decided upon was that of periodic applications of differential doses of nutrient solution to plants reared individually in two-gallon crocks. The crocks were filled with plaster-size vermiculite. Nutrients were supplied as a modified Knop's solution, and four nutrient levels were established as follows: N_1: 10 ml of 2 × normal nutrient solution daily; N_2: 20 ml of 2 × normal nutrient solution daily; N_3: 40 ml of 2 × normal nutrient solution daily; N_4: 100 ml of 2 × normal nutrient solution daily.

Two complete replications of all possible combinations of genotypes and nutrient regimes were included in the experimental design. Finally the experiment was conducted in a standard greenhouse and maintained over a period of 340 days.

Ripe fruits were harvested, counted and weighed every 5 days. Numbers of clusters bearing ripe fruit were recorded and summed over the experimental period. Using the three kinds of observations, five different variables were defined as follows: X_1 = yield (total weight of ripe fruit); X_2 = total number of ripe fruit; $X_3 = X_1/X_2$ = average fruit weight; X_4 = total number of clusters; and $X_5 = X_2/X_4$ = average number of fruits per cluster.

Analytical procedures; characterization of yield: Yield of a plant exhibiting an indeterminate type of growth is best represented as a cumulative function over time. Such yield functions for the three tomato genotypes over a total period of 340 days are illustrated in Figure 2. Cumulative yield up
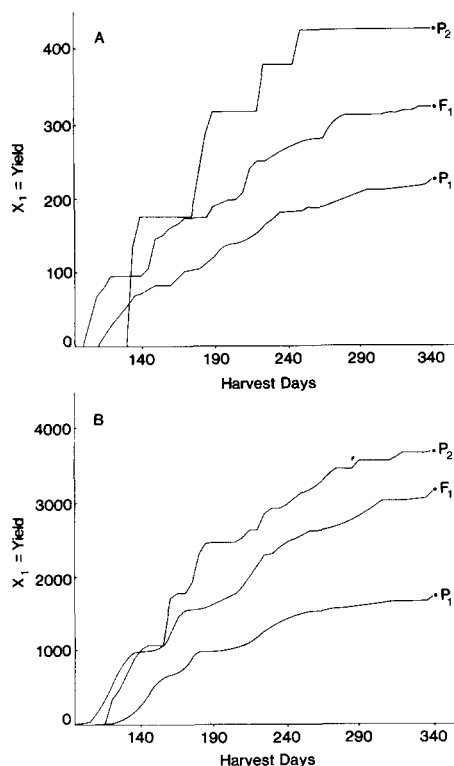
FIGURE 2.—Tomato yield represented as a cumulative function over time. A, yields for N_1, and B, yields for N_4.

TABLE 2

ANOVA structure for analyses of arithmetic and logarithmic CN data with regard to yield and its component variables

Source	d.f.	MS	E(MS)
Genotypes: (G)	2		
Linear: [G(L)]	1	$M_{G(L)}$	$\sigma_E^2 + 8\sigma_{G(L)}^2$
Quadratic: [G(Q)]	1	$M_{G(Q)}$	$\sigma_E^2 + 8\sigma_{G(Q)}^2$
Nutrients: (N)	3	M_N	$\sigma_E^2 + 6\sigma_N^2$
Replications: (R)	1	M_R	$\sigma_E^2 + 12\sigma_R^2$
G × N	6		
G(L)N	3	$M_{G(L)N}$	$\sigma_E^2 + 2\sigma_{G(L)N}^2$
G(Q)N	3	$M_{G(Q)N}$	$\sigma_E^2 + 2\sigma_{G(Q)N}^2$
G × R	2	M_{GR}	$\sigma_E^2 + 4\sigma_{GR}^2$
N × R	3	M_{NR}	$\sigma_E^2 + 3\sigma_{NR}^2$
Residual	6	M_E	σ_E^2

to a given point in time can be regarded as a yield variable. The yield variable used in this study is that for the entire period of 340 days. Such a variable can be partitioned into a closed system of components as illustrated in Figure 1. Note, however, that Figure 1 involves seven variables; this study considers only the first five, $X_1, \ldots, X_5$. On the arithmetic scale, relationships among the components are multiplicative, i.e., $X_1 = (X_2)(X_3)$, $X_2 = (X_4)(X_5)$, and therefore, $X_1 = (X_3)(X_4)(X_5)$. On the logarithmic scale, relationships become additive, i.e., $_1X = {_2}X + {_3}X$, $_2X = {_4}X + {_5}X$, and therefore, $_1X = {_3}X + {_4}X + {_5}X$, where, $_iX = \log(X_i)$. Choice of an appropriate scale is complicated and will be examined for each variable separately.

The experimental design, which includes all possible combinations of three genotypes and four nutrient levels arranged into two randomized blocks, produces a pattern of data which can be analyzed by a factorial analysis of variance (ANOVA). Structure of this ANOVA, including expectations of mean squares, is given in Table 2. The ANOVA is suitable for all variables measured on either scale of measurement. These ANOVAs provide the following kinds of statistical information: (i) tests of significance for various sources of variation, (ii) estimates of the magnitude of variation generated by different sources of variation, and (iii) information which is useful in determining the appropriate scale of measurement.

Analytical procedures; characterization of heterosis: Heterosis was first defined by SHULL (1914) and further clarified by him in 1948, to be a descriptive term for "hybrid vigor," irrespective of the biological mechanism used to explain the phenomenon. A number of operational definitions of heterosis have been suggested. In this study, a standardized operational definition is used which is constructed as follows. Let P_1, P_2 and F_1 represent phenotypic mean values for a quantitative genetic variable for which the parental lines are homozygous. Variability generated by

these three mean values can be characterized by two statistically orthogonal contrasts:

$$\text{Linear: } L = P_1 - P_2$$
$$\text{Quadratic: } Q = 2F_1 - (P_1 + P_2).$$

A standardized measure of genetic non-additivity can be defined as the ratio of these contrasts, i.e.,

$$h_p = Q/L = [2F_1 - (P_1 + P_2)]/(P_1 - P_2) \qquad (1)$$
$$= (F_1 - MP)/(P_1 - MP),$$

where it is assumed that $P_1 > P_2$, and the midparental value is calculated as $MP = (1/2)(P_1 + P_2)$.

In the above representation, L measures the difference between the homozygous parents, and Q measures the deviation of the F_1 from the midparental value. Genetic interpretation of these parameters depends on the complexity of the underlying genetical system. If genotypic differences are due to a single locus, then h_p is strictly a measure of the dominance parameter.

In a quantitative genetic situation in which genotypic differences at many loci are involved, h_p is a function of many dominance parameters, possibly differing in magnitude and even in sign, as well as interactions between alleles at different loci. Hence h_p becomes a generalized measure of nonadditivity of the F_1 relative to the parents. In this case, h_p will be denoted by WIGAN's (1944) term of "Potence." Clearly, $h_p > 1$ is an operational manifestation of SHULL's verbal definition of heterosis.

The above representation is for a single variable. However, when a compound variable is partitioned into a closed system of two component variables, various questions arise: Can the compound potence value be expressed as a function of the component potence values? Is it possible to have heterosis in the compound variable when heterosis does not occur in the components? If so, what are the conditions for such an event to occur? The following presentation answers these questions in terms of a generalized algebraic argument.

To simplify the argument, it is assumed that the compound variable is partitionable into two components whose relationship is additive. (In the present study, the logarithmic transformation provides such a model system, e.g., $_1X = {_2}X + {_3}X$).

Then let,

$$_iP_a = {_j}P_a + {_k}P_a,$$
$$_iP_b = {_j}P_b + {_k}P_b,$$
$$_iF_1 = {_j}F_1 + {_k}F_1,$$

where, i denotes the compound variable, and j and k denote components as measured on the ath or bth parents or the F_1. Assume that $_iP_b < _iP_a$, or $(_jP_b + _kP_b) < (_jP_a + _kP_a)$. Then the compound potence value becomes,

$$h_i = (_iF_1 - _iMP)/(_iP_a - _iMP).$$

There are two possible configurations with regard to relative magnitudes of the component variables as expressed in the parents.

Configuration 1: One parent (P_b) is superior to the other parent (P_a) for both component traits, i.e.,

$$_jP_a < _jP_b \quad \text{and} \quad _kP_a < _kP_b.$$

Note that: $_iP_a = (_jP_a + _kP_a) < _iP_b.$

Configuration 2: Each parent is superior to the other parent for one component trait only, i.e.,

$$_jP_a < _jP_b \quad \text{and} \quad _kP_b < _kP_a.$$

Also assume: $_iP_b < _iP_a.$

These two configurations are now treated separately.

Configuration 1

The potence value for the compound variable with the necessary restrictions is:

$$h_i = (_iF_1 - _iMP)/(_iP_b - _iMP) \tag{2}$$

which can be rearranged as,

$$_iF_1 = _iMP + h_i(_iP_b - _iMP).$$

Similarly, potence values for the components can be given as:

$$_jF_1 = _jMP + h_j(_jP_b - _jMP), \tag{3}$$

and

$$_kF_1 = _kMP + h_k(_kP_b - _kMP). \tag{4}$$

Substitute (3) and (4) into,

$$_iF_1 = _jF_1 + _kF_1,$$

to obtain,

$$_iF_1 = [_jMP + h_j(_jP_b - _jMP)] + [_kMP + h_k(_kP_b - _kMP)]. \tag{5}$$

Then substitute (5) into (2) to arrive at,

$$h_i = [x_j/(x_j + x_k)](h_j) + [x_k/(x_j + x_k)](h_k), \tag{6}$$

where,

$$x_j = (_jP_b - _jP_a) > 0$$
$$= \text{parental difference for the } j\text{th component,}$$
$$x_k = (_kP_b - _kP_a) > 0$$
$$= \text{parental difference for the } k\text{th component,}$$

and note that,

$$x_j + x_k = (_iP_b - _iP_a) > 0$$
$$= \text{parental difference for the compound trait.}$$

The relationship given in (6) answers the first question. For this configuration, it is possible to express the compound potence value as a function of the component potence values.

To determine conditions for the component potence values, which are necessary for expression of heterosis in the compound variable, let $h_j = 1 - \alpha$, and $h_k = 1 - \beta$, where

α and β are constants. Substituting these potence values into (6) produces,

$$h_i = 1 - [x_j/(x_j + x_k)]\alpha - [x_k/(x_j + x_k)]\beta$$
$$= 1 - (\text{weighted average of } \alpha \text{ and } \beta).$$

Then for $h_i > 1$, it is necessary that $(\alpha, \text{ or } \beta, \text{ or } \alpha \text{ and } \beta) < 0$. Hence for this configuration, it is not possible to have heterosis in the compound variable, if heterosis does not occur in at least one of the components.

Configuration 2

The potence value for the compound variable, under the restrictions of configuration 2, is,

$$h_i = (_iF_1 - _iMP)/(_iP_a - _iMP). \tag{7}$$

It can be shown that (7) may be recast as,

$$h_i = [x_j/(x_k - x_j)](h_j) + [x_k/(x_k - x_j)](h_k), \tag{8}$$

where, $x_j = (_jP_b - _jP_a) > 0$, and $x_k = (_kP_a - _kP_b) > 0$, and

$$x_k - x_j = (_iP_a - _iP_b) > 0.$$

Therefore, $[x_j/(x_k - x_j)], [x_k/(x_k - x_j)] > 0$.
Clearly the answer to the first question is, again, yes.

To examine the conditions for values of h_j and h_k necessary for $h_i > 1$, again let, $h_j = 1 - \alpha$ and $h_k = 1 - \beta$. Substitute these potence values into (8) to obtain

$$h_i = [(x_j + x_k)/(x_k - x_j)]$$
$$- \{[x_j/(x_k - x_j)]\alpha + [x_k/(x_k - x_j)]\beta\}.$$

Since $(x_j + x_k)/(x_k - x_j) > 1$, h_i can be greater than one for some values of $\alpha, \beta > 0$. Therefore, the answer to the second question is that it is possible to have heterosis in the compound variable without heterosis in either of the components. This brings the discussion to the third and final question. For heterosis to be expressed in the compound variable, but not in the components, the component variables must conform to configuration 2.

The above argument is a generalization of one made earlier (GRIFFING 1948, 1953). However, theoretical aspects of the problem were briefly discussed by RICHEY (1942). He used the multiplicative, rather than additive, relationship between components and restricted his argument to the case in which the F_1 was strictly intermediate between the parents for both components. He termed the phenomenon of the expression of heterosis in the compound variable when it is not expressed in the components, as "Mock Dominance."

The intriguing fact that it is possible for a compound variable to exhibit heterosis when heterosis is not expressed in the components, has been turned around into a causal explanation of heterosis (WILLIAMS 1959). To set out this hypothesis, it is first necessary to revert to the arithmetic scale on which the relationship between the components is multiplicative. Then the WILLIAMS hypothesis states that when the parents exhibit complementary component expressions, heterosis of the compound variable results from the somatic multiplication of the additively controlled component gene systems. The implication of the hypothesis is that it is the multiplicative action of the genes from the two parents that causes heterosis.

Williams illustrated his hypothesis with a numerical example which is given in Table 3. Note that: (i) the parents are complementary: (ii) the within component genetic differences are additive; and (iii) the compound variable, which results from the multiplication of the component values, exhibits heterosis. Variations of this hypothesis were used extensively in a major review of heterosis (SINHA and

TABLE 3

Numerical example of WILLIAMS' heterosis hypothesis based on the multiplication of additive component traits

Genotypes	Component A	Component B	Variable $(A \times B)$
P_1	3	1	3
F_1	2	2	4
P_2	1	3	3

KHANNA 1975). Finally, the hypothesis will be put to test with experimental data of this study.

RESULTS

Characterization of yield; introductory comments: Cumulative yield functions for the parents and F_1, over the growth period of 340 days, are given in Figure 2. Figure 2A presents cumulative yields for N_1, and Figure 2B for N_4. Yield functions for the other two nutrient levels are similar, but intermediate. Note that the ordinate scales for Figure 2, A and B, are adjusted to provide figures of similar dimension. This transformation of scale is roughly proportional to the level of nutrients applied.

These figures illustrate that the F_1 is strictly intermediate between the parents for most of the growing period. Thus yield heterosis does not occur in the CN experiment. This, of course, is in sharp contrast to the heterosis of yield as expressed under field conditions. Hence the important conclusion from the two experiments is that heterosis in tomato yield is *nutrient-dependent.*

The objective of this study, then, is to use the combined field and CN data to test three heterosis hypotheses. The rejection, or corroboration, of a given hypothesis depends on its ability to explain the total nutrient-dependent phenomenon.

In order to establish reasons for differences in heterotic expression, it is necessary to make a quantitative analysis of yield and its components in the CN experiment. The analysis first involves partitioning yield into a closed system of component variables in a manner similar to that applied to the field data. This partitioning provides the basis for an examination of how genotypic and nutrient responses are reflected among components, and how components fit together to synthesize yield under different nutrient regimes. Analyses are performed on both arithmetic and logarithmic scales of measurement.

Characterization of yield; analysis of data: Five harvest dates (140, 190, 240, 290, 340 days) were chosen from the cumulative yield distributions, and a preliminary examination of the data from the five harvest dates indicated comparable results. Therefore, only the analyses for the final harvest (340 days) were chosen for presentation.

Table 4 lists arithmetic means, and Table 5 lists

TABLE 4

Arithmetic means for the three genotypes grown on the four nutrient levels for each of the five variables (X_1 = yield, X_2 = fruit number, X_3 = fruit weight, X_4 = cluster number, and X_5 = fruit number per cluster)

Trait	Genotype	Nutrient level				Mean
		N_1	N_2	N_3	N_4	
X_1	P_1	107.2	199.1	380.6	831.5	379.6
	F_1	160.5	281.4	594.7	1535.2	643.0
	P_2	213.0	371.4	735.1	1848.7	792.1
	Mean	160.2	283.9	570.2	1405.1	
X_2	P_1	138.5	279.0	553.0	1224.0	548.6
	F_1	36.5	62.0	127.5	361.5	146.9
	P_2	4.5	7.0	13.0	28.5	13.3
	Mean	59.8	116.0	231.2	538.0	
X_3	P_1	0.77	0.71	0.69	0.68	0.71
	F_1	4.40	4.52	4.67	4.26	4.47
	P_2	47.69	53.06	56.88	65.67	55.82
	Mean	17.62	19.43	20.75	23.54	
X_4	P_1	32.5	53.0	90.0	202.5	94.5
	F_1	8.5	13.5	25.0	85.5	33.1
	P_2	2.5	4.5	8.5	15.0	7.6
	Mean	14.5	23.7	41.2	101.0	
X_5	P_1	4.26	5.27	6.15	6.05	5.43
	F_1	4.31	4.70	5.26	4.33	4.65
	P_2	1.83	1.58	1.55	1.98	1.73
	Mean	3.47	3.85	4.32	4.12	

logarithmic means of yield and its components for all possible combinations of genotypes and nutrient levels. As in the field data, P_1 (Red Currant) has a low yield composed of many small fruits, produced in many-fruited clusters, and P_2 (Devon) has a high yield due to a few, large fruits produced in clusters each having few fruits.

Table 6 presents ANOVA results for the five variables as measured on the arithmetic scale. These results are given in terms of relative magnitude and level of statistical significance for each source of variation associated with the ANOVA. Inferences from these ANOVAs are: (i) Genotypes generate highly significant variation in all variables. Both linear and quadratic genotypic components of variation are significant. (ii) Nutrients generate highly significant variation in variables X_1, X_2 and X_4, but not in X_3 and X_5. (iii) Highly significant genotype × nutrient, $(G \times N)$, interaction occurs in variables X_1, X_2 and X_4. The relative amounts of $G \times N$ interaction in these variables is large (X_1: 18.4%, X_2: 36.8% and X_4: 31.0%). The interactions imply that the nutrient responses are different for different genotypes.

Table 7 presents ANOVA results for the five variables measured on the logarithmic scale. As with the arithmetic analyses: (i) Genotypes generate highly sig-

TABLE 5

Logarithmic means for the three genotypes grown on the four nutrient levels for each of the five variables [$_1X$ = log(yield), $_2X$ = log(fruit number), $_3X$ = log(fruit weight), $_4X$ = log(cluster number), and $_5X$ = log(fruit number per cluster)]

Variable	Genotype	N_1	N_2	N_3	N_4	Mean
$_1X$	P_1	2.0298	2.2981	2.5804	2.9199	2.4570
	F_1	2.2055	2.4466	2.7742	3.1862	2.6531
	P_2	2.3279	2.5695	2.8634	3.2667	2.7569
	Mean	2.1878	2.4380	2.7393	3.1243	
$_2X$	P_1	2.1413	2.4449	2.7425	3.0876	2.6041
	F_1	1.5623	1.7915	2.1049	2.5572	2.0040
	P_2	0.6505	0.8451	1.1087	1.4515	1.0140
	Mean	1.4514	1.6938	1.9854	2.3655	
$_3X$	P_1	−0.1115	−0.1468	−0.1621	−0.1678	−0.1471
	F_1	0.6432	0.6551	0.6693	0.6290	0.6491
	P_2	1.6774	1.7244	1.7546	1.8152	1.7429
	Mean	0.7364	0.7442	0.7539	0.7588	
$_4X$	P_1	1.5118	1.7242	1.9543	2.3061	1.8741
	F_1	0.9287	1.1228	1.3891	1.9287	1.3423
	P_2	0.3891	0.6505	0.9287	1.1601	0.7821
	Mean	0.9432	1.1658	1.4240	1.7983	
$_5X$	P_1	0.6295	0.7207	0.7883	0.7815	0.7300
	F_1	0.6336	0.6687	0.7159	0.6285	0.6617
	P_2	0.2614	0.1946	0.1801	0.2915	0.2319
	Mean	0.5082	0.5280	0.5614	0.5672	

TABLE 6

ANOVA results for arithmetic data of variables: X_1 = yield, X_2 = fruit number, X_3 = fruit weight, X_4 = cluster number, and X_5 = number of fruits per cluster

	X_1		X_2		X_3		X_4		X_5	
Variance	A	B	A	B	A	B	A	B	A	B
$\sigma^2_{G(L)}$	17.2	***	45.0	***	78.3	***	47.1	***	80.1	***
$\sigma^2_{G(Q)}$	0.4	*	3.7	***	19.4	***	2.6	***	8.6	***
σ^2_N	63.6	***	14.3	***	0.2	NS	18.8	***	1.2	NS
σ^2_R	0.0	NS	0.0	NS	0.0	NS	0.1	NS	1.0	*
$\sigma^2_{G(L)N}$	17.4	***	34.8	***	1.2	*	30.7	***	3.8	NS
$\sigma^2_{G(Q)N}$	1.0	*	2.0	***	0.2	NS	0.3	NS	0.8	NS
σ^2_{GR}	0.1	NS	0.0	NS	0.0	NS	0.1	NS	2.1	NS
σ^2_{NR}	0.0	NS	0.0	NS	0.0	NS	0.0	NS	0.0	NS
σ^2_E	0.3		0.2		0.7		0.3		2.4	

Results are given in terms of: (i) A = percent of total variation due to each component of variation, and (ii) B = statistical significance of each component. NS = not significant; * = 0.01 < P < 0.05; ** = 0.001 < P < 0.01; *** = P < 0.001.

nificant variation in all variables; and (ii) nutrients generate highly significant variation in $_1X$, $_2X$ and $_4X$, but not in $_3X$ and $_5X$. However the main difference between arithmetic and logarithmic analyses is that the large amounts of $G \times N$ interaction, found in the

## TABLE 7

ANOVA results for logarithmic data of the variables: $_1X$ = log(yield), $_2X$ = log(fruit number), $_3X$ = log(fruit weight), $_4X$ = log(cluster number), $_5X$ = log(number of fruits per cluster)

	$_1X$		$_2X$		$_3X$		$_4X$		$_5X$	
Variance	A	B	A	B	A	B	A	B	A	B
$\sigma^2_{G(L)}$	21.3	***	87.2	***	98.9	***	80.0	***	80.3	***
$\sigma^2_{G(Q)}$	0.6	*	1.7	***	0.8	***	0.0	NS	13.6	***
σ^2_N	77.3	***	10.7	***	0.0	NS	18.0	***	0.0	NS
σ^2_R	0.0	NS	0.0	NS	0.0	NS	0.0	NS	0.3	NS
$\sigma^2_{G(L)N}$	0.0	NS	0.1	NS	0.2	*	0.0	NS	0.6	NS
$\sigma^2_{G(Q)N}$	0.0	NS	0.1	NS	0.0	NS	0.8	NS	0.0	NS
σ^2_{GR}	0.0	NS	0.0	NS	0.0	NS	0.2	NS	0.0	NS
σ^2_{NR}	0.0	NS	0.0	NS	0.0	NS	0.0	NS	0.0	NS
σ^2_E	0.8		0.2		0.1		1.0		5.2	

Results are given in terms of: A = percent of the total variation due to each component of variation, and B = statistical significance of each component. NS = not significant; * = 0.01 < P < 0.05; ** = 0.001 < P < 0.01; *** = P < 0.001.

arithmetic analyses, are removed by logarithmic transformation.

Interpretation of ANOVA results will be made in context of the following examination of each variable. However, to reduce the length of presentation, only "yield" and the primary partition variables, "fruit weight" and "fruit number," are discussed.

Figure 3 presents response curves for X_1 = yield and $_1X$ = log(yield). Figure 3, A and B, shows responses for yield when measured on the arithmetic scale. Figure 3A gives genotypic response curves for each level of nutrients. Response slopes are different for different nutrient levels. Figure 3B gives nutrient response curves for each genotype. At all nutrient levels, P_2 (Devon) has greatest yields, P_1 (Red Currant) has lowest yields, and the F_1 has yields that are intermediate between those of the parents. The most important aspect of Figure 3B is that the response to nutrients, for each genotype, is *linear*. (More detail with regard to the linearity of these responses will be given later). This implies that for each genotype, nutrient responses are *additive* on the arithmetic scale. Slopes of the linear responses are different for different genotypes. Hence for precisely the same amount of nutrients, different genotypes produce different yields; with the F_1 intermediate. Since response slopes are different, a $G \times N$ interaction is generated.

Figure 3, C and D, presents genotypic and nutrient response curves for logarithmic yield data. The most important aspect of the logarithmic representation in Figure 3C is that genotypic responses for each nutrient are essentially linear. Therefore the interesting fact emerges that for the same variable, yield, genotypic stimuli are additive on the logarithmic scale, whereas the nutrient stimuli are additive on the arith-
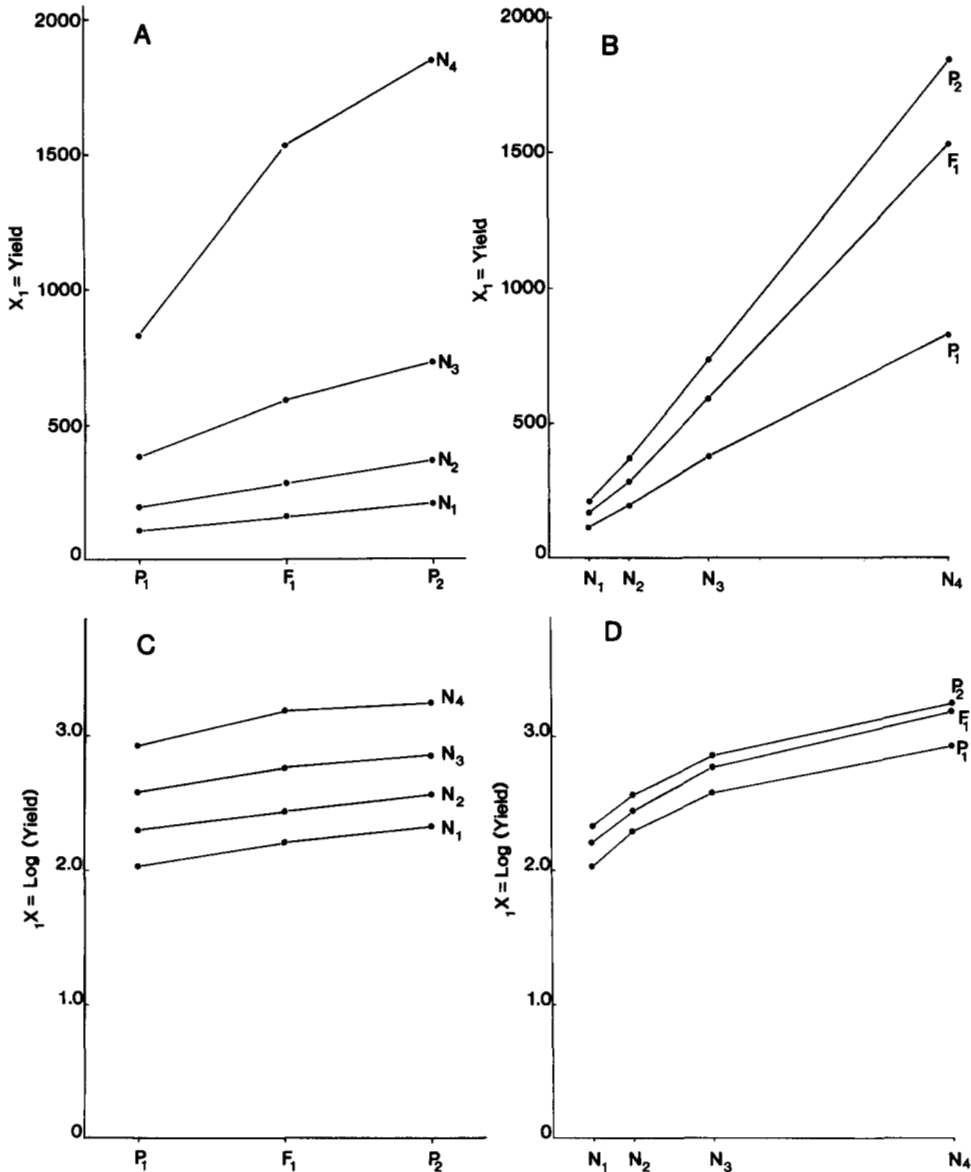
FIGURE 3.—Responses for X_1 = yield, and $_1X$ = log(yield). A = genotypic responses for arithmetic data; B = nutrient responses for arithmetic data; C = genotypic responses for logarithmic data; D = nutrient responses for logarithmic data.

metic scale. Finally, comparison of Figures 3A and 3C, indicates that the logarithmic transformation has removed the $G \times N$ interaction. Thus in Figure 3C all responses are essentially parallel and with the same slope.

Figure 4 presents genotypic and nutrient responses for the variable, "fruit number," when measured on the arithmetic (Figure 4, A and B) and logarithmic (Figure 4, C and D) scales. With regard to the arithmetic data, genotypic responses are apparently curvilinear (Figure 4A), and nutrient responses are linear (Figure 4B). Slopes of the linear responses are different for different genotypes (Figure 4B). This implies that for identical amounts of nutrients, different genotypes produce different numbers of fruit [P_1(greatest), P_2(least), and F_1(intermediate)]. Since slopes are different, a highly significant $G \times N$ inter-

action is generated, as reflected in the ANOVA of Table 6.

Figures 4C and 4D give genotypic and nutrient response curves for "fruit number," as measured on the logarithmic scale. Genotypic responses (Figure 4C) are essentially linear and parallel. Thus genotypic effects are additive on the logarithmic scale. This transformation completely eliminates the large ($\cong 37\%$) $G \times N$ interaction generated on the arithmetic scale. Nutrient response curves depicted in Figure 4D are curvilinear.

Figure 5 presents genotypic and nutrient response curves for "fruit weight" when measured on the arithmetic (Figure 5, A and B) and logarithmic (Figure 5, C and D) scales. Genotypic responses are curvilinear on the arithmetic scale (Figure 5A). This curvilinearity is almost completely removed by the logarithmic transformation (Figure 5C). Hence genotypic effects
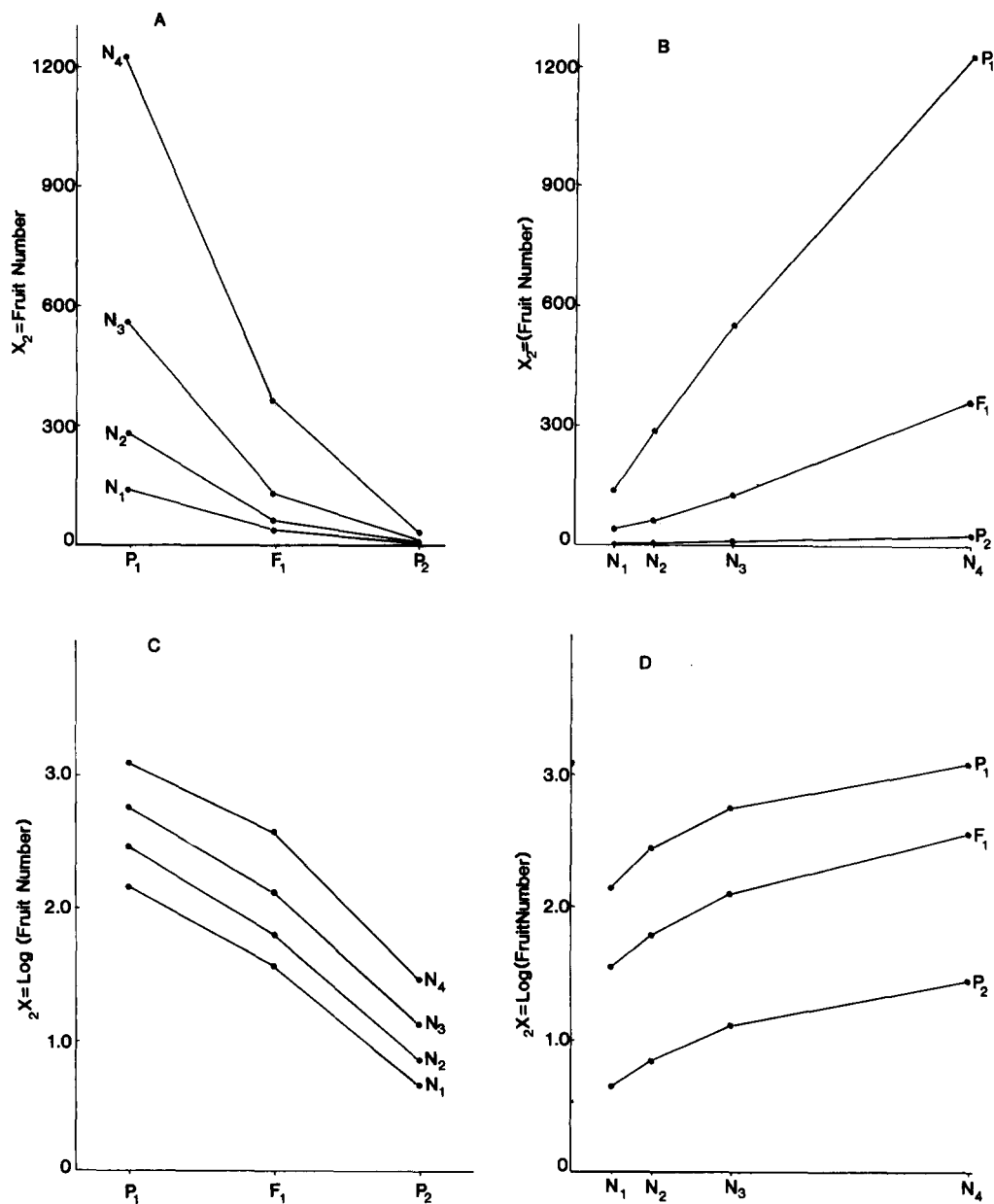
FIGURE 4.—Responses for X_2 = fruit number, and $_2X$ = log(fruit number). A = genotypic responses for arithmetic data; B = nutrient responses for arithmetic data; C = genotypic responses for logarithmic data; D = nutrient responses for logarithmic data.

are additive when measured logarithmically. Different nutrient levels have essentially no effect on P_1 and F_1 fruit size. However, increased nutrients cause some increase in the average fruit size of the large fruited parent P_2. This indicates that lower nutrient levels are insufficient for complete growth of fruit. However, lack of significant variation due to nutrient levels (Tables 6 and 7), demonstrates that this variable exhibits almost complete homeostasis.

Figure 6 illustrates the joint relationships for yield components "fruit weight" and "fruit number," when measured on the arithmetic (Figure 6A) and logarithmic (Figure 6B) scales. Extreme curvilinear relationships exhibited on the arithmetic scale are transformed to linear relationships on the logarithmic

scale. This is consistent with the view that genes responsible for *both* of these variables are operating exponentially. Finally, it is clear from Figure 6B that $_3X$ = log(fruit weight) is invariant (homeostatic) to changes in nutrient levels, whereas $_2X$ = log(fruit number) is responsive (nonhomeostatic) to increased nutrients.

The final aspect of the yield analysis is the demonstration of how yield is synthesized by its components, and how additional nutrients increase yield through particular yield components. Figure 7 provides a diagrammatic representation of yield syntheses for nutrient levels N_1 and N_4. Nutrient levels, N_2 and N_3, produce similar, but intermediate, figures. Since the scale of measurement used in Figure 7 is logarithmic,
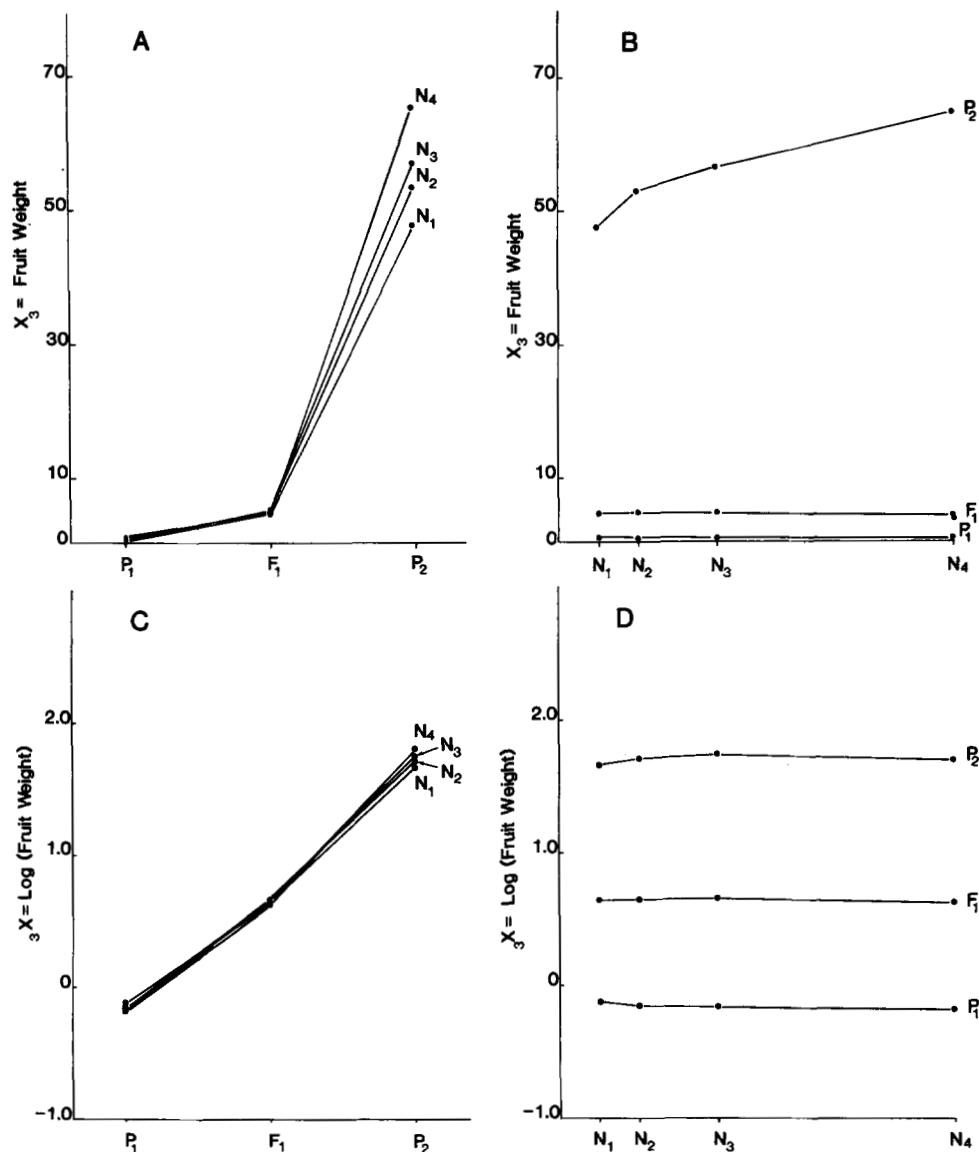
FIGURE 5.—Responses for X_3 = fruit weight, and $_3X$ = log(fruit weight). A = genotypic responses for arithmetic data; B = nutrient responses for arithmetic data; C = genotypic responses for logarithmic data; D = nutrient responses for logarithmic data.

the synthesis of yield by component traits is additive (*i.e.*, $_1X = {_2}X + {_3}X$, $_2X = {_4}X + {_5}X$, and $_1X = {_3}X + {_4}X + {_5}X$). Hence the synthesis is reflected in the length of the vertical graph associated with each genotype.

With the logarithmic scale, the $G \times N$ interaction is negligible for all variables (see ANOVA's in Table 7), and, therefore, generalized statements as to the effects of nutrient levels hold true for all genotypes. Although $_3X$ = log(fruit weight) and $_5X$ = log(fruits per cluster) are each vastly different for the three genotypes, it is clear from Figure 7, A and B, that they do not change significantly with different N. On the other hand, $_1X$ = log(yield), $_2X$ = log(fruit number) and $_4X$ = log(cluster number) increase significantly with increased nutrients. Therefore, in the first partitioning of yield, $_1X = {_2}X + {_3}X$, added nutrients increase $_1X$ by increasing $_2X$. Then in the next level of partitioning, $_2X = {_4}X + {_5}X$, added nutrients increase $_2X$ by increasing $_4X$. Hence, ultimately, nutrients in-

crease yield by stimulating plant growth which increases the number of clusters. This, in turn, increases the total number of fruits and, thereby, increases yield. In this interpretation, fruit size and number of fruits per cluster are essentially invariant to increased nutrients.

Heterosis analysis: The total heterosis picture, with regard to this study, can be summarized as follows. The genotypes included in both field and CN experiments were: P_1 (Red Currant), P_2 (Devon) and the F_1 ($P_1 \times P_2$). In both experiments the parents were complementary in the sense that each parent had a greater value for one of the two primary components. In the field experiment, heterosis occurred in "yield," but was not expressed in "fruit number" and "fruit weight." However, in the CN experiment, heterosis was not expressed in yield, nor in the components, for any of the four nutrient levels. (See potence values in Table 8.)
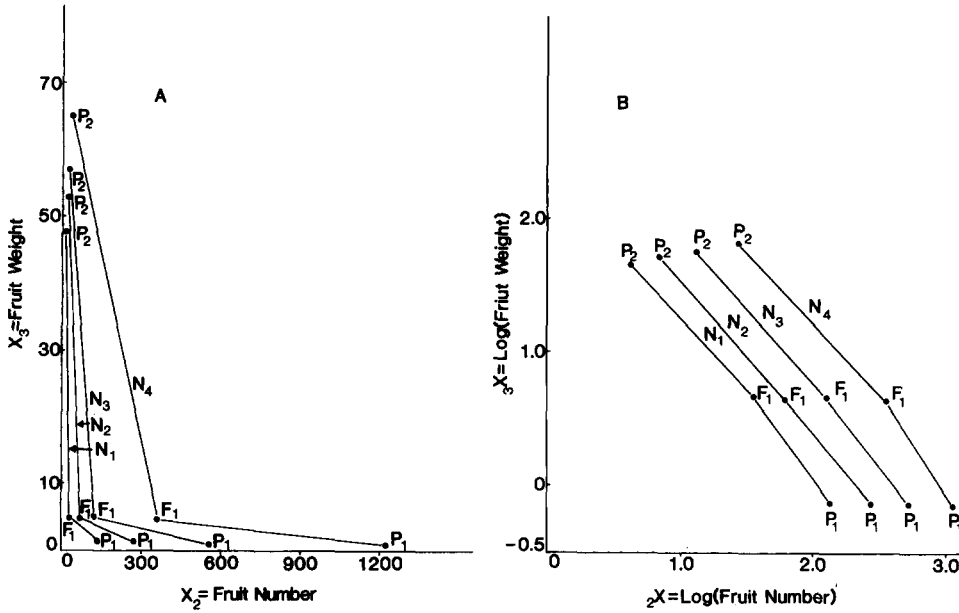
FIGURE 6.—Joint responses for variables fruit number and fruit weight. A = arithmetic data; B = logarithmic data.
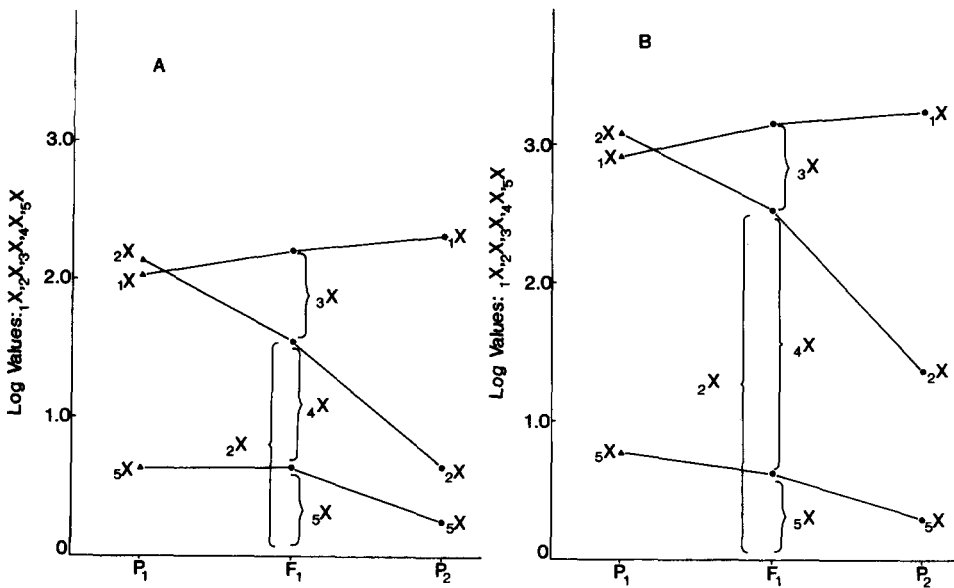

FIGURE 7.—Synthesis of $_1X$ = log(yield) in terms of yield components: $_2X$ = log(fruit number) and $_3X$ = log(fruit weight), $_4X$ = log(cluster number), and $_5X$ = log(fruits per cluster) for each genotype. A = N_1 and B = N_4.

The objective of this section is to utilize the quantitative yield analyses of the previous section to explore the adequacies of three different heterosis hypotheses for the explanation of the above heterosis results. Key to the explanation lies in the ability of a given hypothesis to explain the *total*, apparently inconsistent, results for yield potence values, namely, h_{field} > 1, but $(h_{N1}, h_{N2}, h_{N3}, h_{N4})$ < 1.

Heterosis hypothesis 1: (Heterosis is caused by the fact that the F_1 metabolic system is more efficient than that of either parent in the sense that it can produce more product with the same input of nutrients). This hypothesis could explain the field results, but is rejected by the CN data in which the F_1 means are consistently intermediate with respect to those of the

parents when all three genotypes are provided with exactly the same amount of nutrients.

Heterosis hypothesis 2: [For the case of complementary parents, yield heterosis (as measured on the arithmetic scale) is caused by the somatic multiplication of non-heterotic components.] Results of the field experiment exactly fit the requirements and expectations of this hypothesis. Parents are complementary, components do not exhibit heterosis, but, nevertheless, yield is heterotic. However, this hypothesis does not provide a satisfactory explanation for the *total* heterosis phenomenon. Thus in the CN experiment, although results from each nutrient level also fit the requirements of the hypothesis, it is clear from Table 8 that heterosis in yield does not occur. This is true even though the same genotypes and the same system

TABLE 8

Potence values associated with the variables: $_1X$ = log(yield), $_2X$ = log(fruit number), and $_3X$ = log(fruit weight) for data from different nutrient levels, combinations of levels, and field conditions

			Potence values				
	N_1	N_2	N_3	N_4	A^a	B^b	Field^c
$_1h$	0.18	0.09	0.37	0.54	3.28	2.51	1.46
$_2h$	0.22	0.18	0.22	0.35	0.77	0.58	0.58
$_3h$	−0.16	−0.14	−0.13	−0.20	−0.18	−0.13	−0.08

^{a} A: Parents evaluated at N_3 = four nutrient equivalents; F_1 evaluated at N_4 = ten nutrient equivalents.

^{b} B: Parents evaluated at N_2 = two nutrient equivalents; F_1 evaluated at N_3 = four nutrient equivalents.

^{c} Field: see Table 1.

of yield partitioning is used. In summary, the field result, ($h_{field} > 1$), corroborates the hypothesis, but the CN results, [(h_{N1}, h_{N2}, h_{N3}, h_{N4}) < 1], reject the hypothesis.

Heterosis hypothesis 3: (The metabolic system of the hybrid is more efficient in the sense that it produces a higher growth rate. Hence heterosis is caused by differential growth rates such that the hybrid growth rate exceeds those of either parent.) Under this hypothesis, lack of heterosis at all four levels of the CN experiment was due to the CN procedure which forced all three genotypes to have the same growth rate. This experimental procedure provided each plant with a fixed, limited amount of nutrients at periodic intervals. Under the differential growth rate hypothesis, the F_1 would utilize nutrients from a given allocation most quickly while the parents would utilize the nutrients more slowly. Nevertheless, all genotypes would exhaust the supply of nutrients during the interval between allocations. Hence the outcome of such an experimental procedure would be to equalize growth rates so that the response, as measured by yield, would be a reflection of the genotype's assignment of a given amount of nutrient to the variable, yield. In this context, the hybrid is intermediate in relation to the two parents. With regard to the field data, it is clear that the soil represents a potentially unlimited source of nutrients which is constantly available. Therefore differential growth rates would translate into differential nutrient uptakes. The hybrid with its faster growth rate would tap the soil's unlimited nutrient supply for a greater total amount of nutrients over a given period of time. This would explain the manifestation of yield heterosis under field conditions.

This hypothesis can be put to test using the CN experimental data. If the hypothesis is true, the field results can be simulated by assuming that the parents grow at a particular nutrient equivalent regime and the hybrid grows at a higher level regime. For example, potence values calculated under the assumption

that the parents grow at the N_3 level, and the F_1 at the N_4 level, are recorded in Table 8 under the column headed by A^a. Comparisons of potence values for the $N_1, \ldots, N_4$ levels and the field data with those of A^a, indicate that growth responses at the various N-levels can be manipulated to give the field data pattern, namely: $_1h > 1$, and ($_2h$, $_3h$) < 1. Thus the growth rate hypothesis provides an explanation for the transition from the non-heterotic pattern of the CN data to the heterotic field data. Although the potence values, $_2h$ and $_3h$, as given under "A^a" and "Field Data" are quite similar, the yield potence value for A^a ($_1h$ = 3.28) is much larger than that for the field data ($_1h$ = 1.46). Apparently this is due to the fact that the A^a example demands too great a differential nutrient uptake for the hybrid. A little less expectation for the hybrid is considered in B^b. All "h" values become much more closely aligned with those from the field data. This is true especially for $_2h$ and $_3h$. However, the $_1h$ value is still greater for B^b.

The question naturally arises: Is there not a better way in which CN data can be used to provide independent predictions of field nutrient uptake with regard to each parent and hybrid? Assuming that a little extrapolation of CN results is justified, the answer is yes. This is due to the linear yield response (as measured on the arithmetic scale) for each genotype with respect to the different nutrient levels.

For the yield data of Figure 3B, nutrient response regression equations can be determined for each genotype, i.e.

$$P_1: X_1 = 40.50 + 79.79N$$
$$F_1: X_1 = -12.99 + 154.34N \qquad (9)$$
$$P_2: X_1 = 14.55 + 182.94N$$

The linear regression equations fit the data remarkably well, as indicated by the fact that for each of the genotypes, over 99 percent of the variation in yield is attributable to the linear regression.

Assuming that: (i) conversion of nutrients to yield remains constant for the CN and field responses, and (ii) extrapolation of the CN linear responses is justified, relative nutrient-equivalents can be estimated for the three genotypes when grown under field conditions. This is accomplished by substituting the yield datum for a particular genotype in the appropriate equation of (9) and solving for N. Results of this procedure are summarized as follows:

$$P_1: N = 8.0, \quad F_1: N = 16.6, \quad P_2: N = 12.2.$$

The above procedure can be visualized in Figure 8. From this figure it becomes clear how the F_1 field heterosis is produced. As the CN results demonstrate, comparisons of parents and F_1 *for any given nutrient level* indicate that the F_1 yield is invariable intermediate between the parents. However, because of the F_1's faster growth rate, it extracts and utilizes a greater
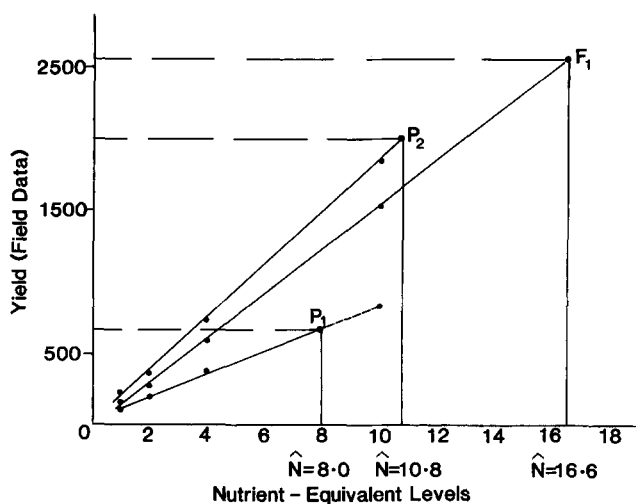
FIGURE 8.—Estimation of nutrient-equivalent levels for P_1, F_1 and P_2 from field yield data utilizing laboratory nutrient response regression relationships.

amount of nutrients from the soil than either parent, during the growing season. Projection of yield responses resulting from differential nutrient uptake levels produces the field heterosis phenomenon.

It is obvious from Figures 4B and 5B that similar projections from regression lines *will not produce heterosis in the component variables.* Thus the field data, in which yield heterosis is accompanied by the absence of heterosis in the component traits, can be explained in terms of the CN results. The incongruous results from the two experiments are totally consistent under the hypothesis of differential growth rates.

The conclusion, then, is that for the particular genotypes used in this study, the hypothesis of differential growth rates, with the hybrid exhibiting the fastest rate, provides a satisfactory explanation of heterosis in tomato yield.

DISCUSSION

Restatement of objectives: The basic objectives of this study were to: (i) characterize the compound variable "yield" in terms of its component variables, (ii) examine the manifestation of heterosis for yield and its components for plants grown under exactly controlled nutritional conditions, and (iii) test various heterosis hypotheses for their ability to explain the total heterosis phenomenon.

Review of experimental results; characterization of yield: The compound variable "yield" was defined to be the cumulative harvest of ripe fruit over a 340 day growth period. This variable was then partitioned into a closed system of component variables as depicted in Figure 1.

A genotype × nutrient factorial ANOVA was performed on all variables for both arithmetic and logarithmic scales of measurement. These ANOVAs provided the following major points of interest: (i) All

variables exhibited highly significant *genotypic* variability on both arithmetic and logarithmic scales of measurement. (ii) Although different nutrient levels generated statistically significant variation in X_1 (and $_1X$), X_2 (and $_2X$), and X_4 (and $_4X$), they did not cause significant variation in X_3 (and $_3X$) and X_5 (and $_5X$). (iii) In all variables, the genotypic variation was more adequately expressed in a linear, or additive-genetic, basis on the logarithmic scale. (iv) The significant nutrient responses for X_1, X_2, and X_4 were completely additive on the arithmetic scale. (v) The $G \times N$ interaction with regard to X_1, X_2 and X_4, as exhibited on the arithmetic scale, was entirely removed by the logarithmic transformation.

Inferences that can be drawn from these ANOVA results are as follows: (i) large, real genotypic differences were expressed in all variables and (ii) different nutrient levels elicited large, real differences for variables X_1, X_2 and X_4. However, variables "fruit weight" and "number of fruit per cluster" were invariant regardless of the nutrient level applied to the plant. Therefore, these two variables exhibited highly controlled homeostasis.

Points (iii) and (iv) illustrate an interesting phenomenon. The two primary factors, genotypes and nutrients, of the factorial experiment operate on different scales of measurement. This is true with regard to each variable. The fact that the genotypic variation is additive on the logarithmic scale is consistent with the assumption that the genes act exponentially. On the other hand, nutrients are the basic inputs for the metabolism of the plant, and assuming that the overall composition of the plant does not change, growth responses would be related to nutrient levels in such a way that they would be additive on the arithmetic scale of measurement. Although these nutrient responses are linear on the arithmetic scale, response slopes are different for the three genotypes, and thus a $G \times N$ interaction is generated as indicated in point (v). However, for any given nutrient level, the genotypic relationships are converted into additive relationships by the logarithmic transformation, with the consequence that the $G \times N$ interaction disappears. Thus the ANOVA results can be interpreted consistently on the basis that the major factors of the factorial experiment are operating on different scales of measurement and act independently when measured on their appropriate scales.

Characterization of yield in terms of the components "fruit number" and "fruit weight," can be examined by their joint responses as illustrated in Figure 6. The extreme curvilinear relationships exhibited on the arithmetic scale, are transformed into linear relationships on the logarithmic scale. This reinforces the argument that genes for both components are operating exponentially. Also of particular interest is the

fact that the linear negative relationships among the genotypes, for each nutrient level, implies that gene action increasing "fruit weight" is associated with a decrease in "total number of fruits." Admittedly there are only three genotypes involved in this relationship, but it illustrates the more general result found in the field data, involving a diallel of 21 genotypes, in which the genotypic correlation for variables $_2X$ and $_3X$ was estimated to be $r_{g23} = -0.97$ (see Figure 1).

The final item of interest in the characterization of yield is that of the synthesis of yield, which on the logarithmic scale, is reflected as the sum of its component parts, i.e., $_1X = _3X + _2X = _3X + _4X + _5X$ (see Figure 7). Because $_3X$ and $_5X$ are homeostatic, it appears that added nutrients increase yield by stimulation plant growth which increases the number of clusters. This, in turn, increases the total number of fruits and, thereby, increases yield.

Review of experimental results; heterosis analysis: In an analysis of heterosis, the first problem is to construct an operational definition of heterosis. For a single variable, the potence value, as given by Equation 1, satisfies this role. However, when a compound variable is partitioned into a closed system of component variables, the potence value concept can be generalized. In the result section, the case of an additive, two-component system was considered and a generalized potence ratio was developed. It was demonstrated that for only the complementary configuration (i.e., each parent is superior to the other parent for one component variable) was it possible for heterosis to be manifest in the compound variable without heterosis in either component.

Having developed an operational definition of heterosis and clarified conditions under which heterosis can occur in an additive closed system, attention was turned to an examination of the pattern of yield heterosis in both field and CN experiments. This pattern was one in which heterosis of yield occurred in the field but not in the CN data, i.e., a nutrient-dependent pattern. The objective, then, was to use the CN results to explore the adequacies of various heterosis hypotheses in explaining this nutrient-dependent phenomenon.

Heterosis hypothesis 1: (The F_1 metabolic system is more efficient than that of either parent in the sense that it can produce more product with equal input.) This hypothesis of heterosis, if true, would be of tremendous importance for agriculture, especially if it is to become less dependent on chemical fertilizers in the future. However, with the genetic material in this study, the hypothesis must be rejected because in the CN experiment, in which parents and hybrid receive precisely the same nutrient supply, the hybrid yield is strictly intermediate to those of the parents.

Heterosis hypothesis 2: (Heterosis is a consequence of the somatic multiplication of additive component traits.) This hypothesis is not useful because it will not explain the total nutrient-dependent phenomenon. That is, for the same set of genotypes and the same set of variables, which are associated in the appropriate configuration, the hypothesis does not account for both a strong field heterosis, and a complete lack of heterosis in the CN experiment.

Heterosis hypothesis 3: (Heterosis is a consequence of a faster hybrid growth rate.) This hypothesis is the only one of the three that can explain the total nutrient-dependent heterosis phenomenon. More explicitly, Hypothesis 3 can explain the lack of heterosis in the CN data because the experimental procedure forces the growth rates of the three genotypes to be equal. By relaxing the restriction of equal growth rates, the field heterotic results are explained. Thus under the field conditions, the F_1 would extract a greater amount of nutrients from the soil than that of either parent, and heterosis would be expressed. In the result section, it was shown how the field heterosis could be simulated by assuming that the parents grew under a particular nutrient-equivalent level and the hybrid at a higher level. Potence values for such a simulation were given in Table 8. This was followed by a more exact calculation of relative nutrient-equivalents as predicted from the linear nutrient responses of the CN experiment.

It is obvious that the hypothesis of differential growth rates is the most adequate of those considered in this study for explaining the nutrient-dependent heterosis of tomato yield. This hypothesis has been used in our laboratory to explain other results involving temperature-, nutrient-, and group-dependent forms of heterosis (GRIFFING and LANGRIDGE 1963; MCWILLIAM and GRIFFING 1965; GRIFFING and ZIROS 1971; GRIFFING 1989). The hypothesis is not new and goes back to the earliest days of the heterosis concept [see WRIGHT (1977) for an excellent review]. ROBBINS (1941) used the concept to explain the differential growth of excised tomato roots. The connection of his work to the present studies is that the same kind of cross was used, i.e. (Red Currant) × (domesticated variety). Thus the hypothesis is one of the oldest, but still most valuable, hypotheses in characterizing the phenomenon of heterosis.

Extension and speculation; separation of morphogenetic and growth rate genetic systems: In early discussions of the genetic basis of heterosis, EAST (1936) stated that there are two categories of genes determining characters that express heterosis.

"The evidence indicates that genes may be divided into two main groups functioning differently . . . The first type is concerned with reaction character, and the second with reaction speed. Heterosis is largely a matter of reaction speed."

In modern terms these two aspects of plant development are referred to as "morphogenesis" and "growth rate" (STREET and OPIK 1984). Therefore, in the following discussion, it is speculated that the indeterminate plant growth pattern responsible for tomato yield and its components is due to two major genetic systems which may be characterized as follows:

Morphogenetic gene system: This gene system determines the basic architecture of the plant by controlling the initiation of various organs in the developing structure. Thus the process results in the branching pattern, the positioning of fruit clusters on the main stem and branches, the potential number of fruits per cluster, the potential fruit size, etc. Morphogenetic genes, then, control the patterns by which development unfolds.

Growth rate gene system: This gene system determines, through physiological processes, the rate at which the morphogenetic structure develops. These genes control the rate of total plant development.

Probably the most important aspect of the present study is the opportunity to separate the action of these two proposed gene systems through the CN experimental procedure. With this experimental device, the growth rate system is held constant while the morphogenetic system is allowed to vary. Genetic analysis of this situation with regard to yield and its components, indicates that the morphogenetic genes do not express heterosis. On the contrary, they are essentially additive on the biologically appropriate scale of measurement. This holds true for the entire yield complex. Also the nutritional effects are strictly additive on their appropriate scale of measurement.

Under field conditions, the restriction of uniform growth rates is removed, and the differential growth rate gene systems are superimposed on the morphogenetic systems. Non-additive gene action for yield is expressed and heterosis results.

With the characterization of growth as indicated above, the primary difficulty with the hypothesis that heterosis results from the multiplication of component gene systems (Hypothesis 2), is that it is formulated in terms of relationships determined by the morphogenetic system, but is used to make inferences about the heterosis phenomenon which, for most quantitative genetic variables, would be a function of the growth rate gene system.

The real difficulty of Hypothesis 2, however, arises when the hypothesis is extended as in the following argument: (i) Heterosis of the compound variable is caused by the multiplication of the gene action of one component with that of the other. (ii) Since the components are determined primarily by additive gene action, selection directed at the component level will be effective in fixing a high performance of expression in each component. (iii) Therefore the heterosis

expression of the compound variable can be fixed easily.

The possible errors in this argument could be that either or both statements (i) and (ii) may not be true. Also the argument ignores the possibility of a large negative genotypic correlation between the component variables which could nullify the effects of selection.

It is of interest to note that the above argument was first given by RICHEY (1942), although his paper was overlooked by later authors. However, the argument has been given in various forms by numerous authors including among others: WILLIAMS (1959, 1960), GRAFIUS (1959), DUARTE and ADAMS (1963), and SINHA and KHANNA (1975), whose extensive heterosis review centers around the partitioning of compound variables into component parts. The most extreme positions taken with regard to the partitioning method are those of GRAFIUS (1959) who stated that ". . . genes for yield per se do not exist in barley. Hence yield is an artifact," and SINHA and KHANNA (1975) who declared that heterosis is a mirage, and that "directed heterosis and its fixation appear to be distinct possibilities."

Finally, assume for the moment that a project is established whose goal is to fix the heterosis of tomato yield within a single genotype by selection for the two primary components, "fruit number" and "fruit weight," in an appropriate breeding population derived from the two parental lines of this study. A major difficulty would arise immediately because of the large *negative* genotypic correlation exhibited by these components. This correlation implies that a selection gain in one component automatically causes a negatively correlated response in the other component. (Parenthetically, this correlational phenomenon is interpreted as follows: the two traits are determined by different meristematic growth systems that directly compete for the same internal, limited supply of nutrients and metabolic products that are necessary for growth.) Finally, because the selection procedure has been misdirected, the growth rate genetic system would be dispersed and the heterotic aspect of yield lost. Under these conditions, it would be difficult to achieve the selection goals.

A practical solution to this problem is to direct attention to the increase in the production of the pool of nutrients and metabolic products that limit the expression of both yield components. If this can be accomplished then both yield components can increase, even if they are negatively correlated.

This is the solution provided by the heterosis plant breeding procedure, which involves identifying parents whose hybrid exhibits a faster growth rate and, hence, greater nutrient uptake and higher metabolic activity. In this way, the heterosis plant breeding

procedure provides a solution to the objective of obtaining a greater yield potential in a single genotype.

It is assumed that eventually the search and testing methods of the present heterosis plant breeding procedure may be replaced by molecular biology techniques with which growth rate genes will be identified, manipulated, and combined at will. The beginnings of this activity are discussed, briefly, in the next section.

Extension and speculation; physiological bases of heterosis: The physiological bases of heterosis, in the last analyses, must be rooted in the major metabolic pathways determining growth. The method of attack pioneered by HAGEMAN, LENG and DUDLEY (1967) was focused on the role of metabolic enzyme systems in the production of heterosis. However, the authors found essentially no heterosis expressed in the three major systems studied: (i) energy transfer in seedling growth, (ii) nitrate reductase and nitrogen metabolism, and (iii) energy generation by chloroplasts. Nevertheless, as shown earlier in this study, if these major systems are regarded as components of an overall growth potential, then heterosis can be expressed in the total potential without manifestation of heterosis in the component parts. Thus the suggestion by the authors that heterosis results from a better balanced growth potential, rather than heterosis of individual component parts, is reasonable.

Another method of attack centers on the study of plant growth regulators. In this regard, the work of ROOD et al. (1988) with gibberellins, shows considerable promise. More generally, it appears that several plant growth regulators (e.g., auxins, gibberellins and cytokinins) have similar effects and that interactions among these phytohormones may occur in any developmental process (STREET and OPIK 1984). It may be speculated that for various aspects of growth, each of the two genetically diverse parents used in this study had evolved its own integrated phytohormonal system. On crossing, a unique system was created in the hybrid which resulted in heterosis of growth rate.

In any case, it would appear that the enzymatic and phytohormonal approaches offer promising methods of attacking the heterosis problem at the molecular level. The molecular genetic analyses of these systems, now being initiated, eventually may provide detailed insights into the genetic control of heterosis.

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