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1. Preliminary investigations in the development of a schematic model for yield heterosis in maize.

Simple diagrammatic models have served traditionally in discussions of heterosis to illustrate gene action postulated for certain allelic and non-allelic situations. Inasmuch as the total number of genes involved has been very small, no schematic representation of the entire heterotic process has been possible. The value of such expanded diagrammatic treatments will be questioned on the basis of restrictions imposed on number of loci, level of dominance, type of epistasis, etc., and on their general inappropriateness in interpreting experimental data. In spite of these limitations, it would seem that those basic genetic concepts held important in yield heterosis should be expected to function well enough collectively in diagrammatic models to give recognizable facsimiles of known yield patterns. A model which meets these latter considerations should qualify to serve as illustrative material and to stimulate further development of schematic representations, should this be deemed worthwhile. This, rather than the presentation of critical conclusions, is the purpose of this investigation.

In holding to the most widely accepted views, allowance is made for a predominance of action by dominant, favorable genes. Inter-locus effects are predominately additive with certain allowance made for non-additivity. Allelic series are used to gain variability and to force a greater awareness of their presence. Yield is treated as the terminal result of the interplay of gene action on simpler component traits in the belief that this is valid, and that it will gain greater attention in the future.

Description of the model: For purposes of the model it is assumed that (1) a multiple allelic series exists at each locus, (2) within each series, dominance of favorable alleles over less favorable alleles is the general rule, the exception involving an occasional instance of intermediate dominance, (3) gene action among loci conditioning the same trait is additive except for occasional epistasis exhibited between certain non-alleles, (4) unfavorable epistatic combinations will have been minimized under selection, (5) the various component traits are independent, non-compensatory, and show strictly a multiplicative relationship, and (6) no linkage is present.

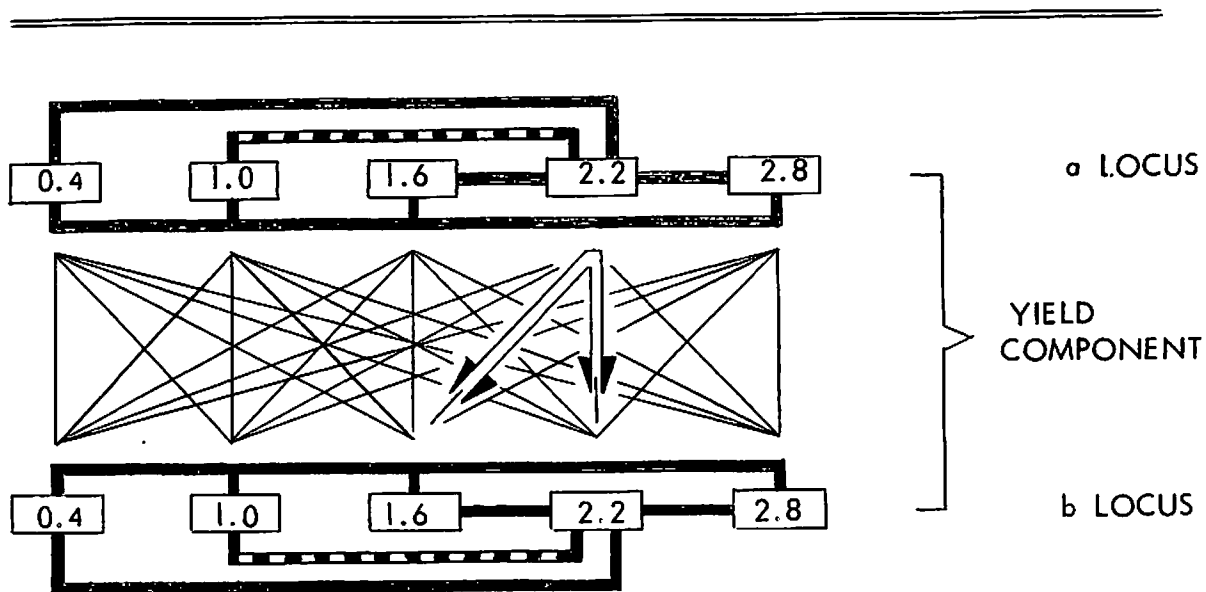
Eight loci are assigned letter designations of a through h. These eight loci are grouped into four pairs (a and b, c and d, e and f, g and h), each pair specific for one of four different yield components. For convenience of calculation, bushel per acre values of 0.4, 1.0, 1.6, 2.2, and 2.8 are assigned to the five alleles which form the allelic series at each locus. These are values found through trial and error to give realistic yields under conditions of the model. Within each series, the alleles 1.0 and 2.2 express a strict intermediate dominance relationship whose combined value is 1.6. Dominance is expressed in all other combinations.

Epistasis involves the allele designated 2.2 at the first locus of a pair. This allele, hereafter designated "suppressor" allele, is specific in its action against either of the two alleles designated 1.6 and 2.2 of the second locus. To be involved these alleles must be the dominant alleles at their respective loci. The effect is that of completely masking the contribution of the second locus. The relationship among non-alleles is otherwise additive.

The diagram on page 31 may help to clarify some of the relationships among alleles and non-alleles within a yield component.

Yield in bushels per acre for an individual genotype is the product of the four component traits, each of these component values being the sum value of the two loci. This is illustrated in Table 1 for three pairs of inbreds and  $F_1$  hybrids. Various combinations of alleles have produced superparental, dominant, partially dominant, intermediate, partially recessive and sub-parental effects at the yield component level. A recessive effect is also possible but does not appear in these illustrations. A deliberate effort was made to include these more extreme component effects for the sake of illustration. Comparable inbred and single cross yields are more easily attained when the dominant and partially dominant component effects alone are used.

Backcross yields: Backcross yields are described in the literature as behaving as if conditioned by additive gene action and answer closely to the formula  $BC = \frac{F_1 + P}{2}$ . Additivity in this reference covers both within and between loci effects, thus, in the case of within locus effects, to a predominance of action by genes showing incomplete dominance. The term additive is used only with reference to between loci effects in this model. Table 2 contains the formula and model values for the backcross populations of the three crosses illustrated in Table 1.



GENE RELATIONSHIPS:




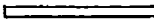
- |   |                        |   |           |
|---|------------------------|---|-----------|
|  | Dominance-Recessive    |  | Additive  |
|  | Intermediate Dominance |  | Epistatic |

Table 1  
Yields of Three Pairs of Inbreds and F<sub>1</sub> Hybrids

Yield Component	Locus	IN 1N			IN 1N			1N 1N			Apparent Gene Action at Component Level
		Inbred A			A x B			Inbred B			
A	a	2.2	2.2	-3.2	2.2	1.0	-1.6	1.0	1.0	-2.6	Subparental
	b	1.0	1.0	x	1.0	1.6	x	1.6	1.6	x	
B	c	0.4	0.4	-3.2	0.4	2.8	-5.6	2.8	2.8	-3.2	Superparental
	d	2.8	2.8	x	2.8	0.4	x	0.4	0.4	x	
C	e	1.0	1.0	-1.4	1.0	1.6	-3.2	1.6	1.6	-3.2	Dominant
	f	0.4	0.4	x	0.4	1.6	x	1.6	1.6	x	
D	g	1.6	1.6	-2.0	1.6	0.4	-3.2	0.4	0.4	-2.0	Superparental
	h	0.4	0.4	x	0.4	1.6	x	1.6	1.6	x	
		28.7 Bu/Acre			91.8 Bu/Acre			53.2 Bu/Acre			
		Inbred C			C x D			Inbred D			
A	a	0.4	0.4	-2.0	0.4	2.2	-2.2	2.2	2.2	-2.6	Partially recessive
	b	1.6	1.6	x	1.6	0.4	x	0.4	0.4	x	
B	c	1.0	1.0	-3.2	1.0	1.6	-3.2	1.6	1.6	-2.6	Dominant
	d	2.2	2.2	x	2.2	1.0	x	1.0	1.0	x	
C	e	0.4	0.4	-3.2	0.4	1.0	-3.8	1.0	1.0	-1.4	Superparental
	f	2.8	2.8	x	2.8	0.4	x	0.4	0.4	x	
D	g	1.0	1.0	-1.4	1.0	0.4	-3.8	0.4	0.4	-3.2	Superparental
	h	0.4	0.4	x	0.4	2.8	x	2.8	2.8	x	
		28.7 Bu/Acre			101.7 Bu/Acre			30.3 Bu/Acre			
		Inbred E			E x F			Inbred F			
A	a	1.6	1.6	-2.0	1.6	0.4	-4.4	0.4	0.4	-3.2	Superparental
	b	0.4	0.4	x	0.4	2.8	x	2.8	2.8	x	
B	c	0.4	0.4	-3.2	0.4	1.0	-3.8	1.0	1.0	-1.4	Superparental
	d	2.8	2.8	x	2.8	0.4	x	0.4	0.4	x	
C	e	1.6	1.6	-3.8	1.6	0.4	-3.2	0.4	0.4	-1.4	Partially dominant
	f	2.2	2.2	x	2.2	1.0	x	1.0	1.0	x	
D	g	1.0	1.0	-2.0	1.0	1.0	-2.6	1.0	1.0	-3.2	Intermediate
	h	1.0	1.0	x	1.0	2.2	x	2.2	2.2	x	
		48.6 Bu/Acre			139.1 Bu/Acre			20.1 Bu/Acre			

Table 2  
 Backcross Yields for Crosses in Table 1 as Derived  
 from Formula Based on Additive Gene Action and  
 from the Model

Inbreds Involved	Backcross Values Derived from	P <sub>1</sub>	BC <sub>1</sub>	F <sub>1</sub>	BC <sub>2</sub>	P <sub>2</sub>
A and B	Formula	28.7	60.3	91.8	72.5	53.2
	Model		63.9		76.9	
C and D	Formula	28.7	65.2	101.7	66.0	30.3
	Model		61.2		63.3	
E and F	Formula	48.6	93.9	139.1	79.6	20.1
	Model		90.2		65.9	

Model backcross values in these examples fall above and below those values derived from the formula by amounts ranging from 4.4 bushels to 13.7 bushels respectively. The closest single approach is 2.7 bushels. These are quite typical for this particular model, although closer and more distant approaches to the formula values are possible. Model values in excess of the F<sub>1</sub> appear among segregates of the backcross populations. This is inevitable under the assumptions already made for gene action. It seems reasonable to conclude, however, that such segregates would rarely appear in practice in the face of far greater numbers of loci, and the inevitable restrictions imposed by linkage and population size.

Variety crosses: Yields from variety crosses have ranged from levels below that of the midparent value to levels exceeding that of the better parent. In order to represent wide-based populations for this study, hypothetical frequency distributions had to be established for the alleles at each locus of the model. This has been done in Table 3 for four different populations identified as Alpha, Beta, Kappa, and Sigma. Frequency distributions are symmetrical and confined to three adjacent alleles. These features are necessary in maintaining simplicity

and uniformity. As a compromise, the three-class distribution exploits a portion of the variability of the allelic series, yet allows relatively sharp differences to be drawn between opposing frequency distributions.

Table 3  
Frequency Distributions for Alleles of  
Alpha, Beta, Kappa and Sigma

		Alleles							Alleles				
		0.4	1.0	1.6	2.2	2.8			0.4	1.0	1.6	2.2	2.8
Loci	a			2	11	2	Loci	a	5	5	5		
	b	2	11	2				b		4	7	4	
	c	4	7	4				c	2	11	2		
	d		3	9	3			d			5	5	5
	e	4	7	4				e	5	5	5		
	f			2	11	2		f		1	13	1	
	g		5	5	5			g	2	11	2		
	h	1	13	1				h		1	13	1	
ALPHA						BETA							
		Alleles							Alleles				
		0.4	1.0	1.6	2.2	2.8			0.4	1.0	1.6	2.2	2.8
Loci	a			3	9	3	Loci	a			5	5	5
	b	1	13	1				b	1	13	1		
	c		1	13	1			c	2	11	2		
	d	2	11	2				d		5	5	5	
	e	1	13	1				e	1	13	1		
	f			5	5	5		f			5	5	5
	g	5	5	5				g	4	7	4		
	h	5	5	5				h	2	11	2		
KAPPA						SIGMA							

Any use of these populations requires that a reasonably small sample of gametes be selected which can adequately represent the much larger array of possible gametes. Five different symmetrical frequency distributions, each comprising 15 alleles, appear among the populations of Table 3. This establishes a sample size of 15 as the minimum number of gametes needed to satisfy each frequency distribution in a given population. Four symmetrical distributions could have been established with a gamete sample size of 12, or six symmetrical

distributions with a sample size of 18. A choice among five possible symmetrical distributions was felt to be adequate for the construction of the four populations. Two samples of 15 gametes each (designated A and B) are drawn from each population. These are shown in Table 4. Each sample of gametes satisfies the frequency distribution for the alleles at each locus of its respective population. This highly idealistic approach to sampling seemed the only one available at this level of investigation.

The yield for an individual population is the average performance of the 225 combinations involving the gametes of gamete sample A crossed with sample B for that particular population. The yield for the cross of two populations is the average performance of the 225 combinations involving the gametes of gamete samples A of the two populations in question. Yields of individual populations and population crosses involving Alpha crossed to Beta, Kappa and Sigma appear in Table 5. It will be seen that three levels of population hybrid response relative to the midparent value or the higher parent have been obtained.

The construction of a population poses no particular problem other than the choice of eight frequency distributions collectively capable of giving a realistic population yield. Population crosses, however, bring together dissimilar allele frequencies with the possibilities of distinct gains or losses at the yield component level. If epistasis is weak or absent, there is a gain relative to the midparent value where one or both frequency distributions of a component are unlike. If the more favorable allele frequencies come entirely from one parent, the component gain in hybrid combination cannot equal the better parent. If the more favorable allele frequencies enter reciprocally from each parent, gains exceeding the better parent are possible. In the face of increasingly powerful epistasis there is a loss at the component level from the near-midparent level to levels below that of the lesser parent.<sup>1</sup> Increases in the incidence of intermediate dominance act to lessen component gains, mildly in the absence of epistasis, but more strongly in its presence.<sup>2</sup>

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<sup>1</sup>It is because of the need to exploit this effect in population crosses that a minimum of epistasis was assumed within established populations.

<sup>2</sup>The suppressor allele within each yield component is itself reduced by entering into intermediate dominance relationships within its own allelic series.

Table 4  
Gamete Samples Drawn from Varieties Alpha, Beta, Kappa and Sigma

		Gametes														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Loci	a	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.8	1.6	2.2	2.2
	b	1.0	1.6	1.0	1.6	0.4	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0
	c	0.4	1.6	0.4	1.0	1.0	1.6	1.6	1.0	1.0	0.4	1.0	1.0	1.6	1.0	0.4
	d	1.0	1.0	1.0	2.2	1.6	1.6	1.6	1.6	1.6	1.6	1.6	2.2	1.6	1.6	2.2
	e	1.6	1.6	0.4	1.0	1.0	0.4	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.6	0.4
	f	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	2.8	1.6	2.2	2.2	2.2	2.2
	g	2.2	1.6	1.0	1.0	2.2	2.2	1.6	1.0	2.2	1.6	1.6	1.6	1.0	2.2	1.0
	h	1.0	0.4	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Sample A																
Loci	a	2.2	2.2	2.2	2.2	2.8	1.6	2.2	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.2
	b	0.4	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.6	1.0	1.0	1.0
	c	1.0	1.6	0.4	1.0	0.4	1.0	1.6	1.0	1.0	1.6	0.4	1.0	1.0	0.4	1.6
	d	1.6	1.6	1.0	1.6	1.6	2.2	1.0	1.6	1.6	2.2	1.0	1.6	2.2	1.6	1.6
	e	1.0	0.4	1.6	0.4	1.0	1.6	1.0	1.6	0.4	1.6	1.0	1.0	0.4	1.0	1.0
	f	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.2
	g	1.6	1.0	1.0	2.2	2.2	1.0	2.2	2.2	1.0	2.2	1.6	1.6	1.0	1.6	1.6
	h	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.0	1.0
Sample B																
Loci	a	0.4	0.4	1.6	0.4	1.6	1.6	1.0	0.4	1.0	1.0	1.0	1.6	1.0	1.6	0.4
	b	1.6	2.2	1.6	1.0	1.6	2.2	1.0	2.2	1.6	1.6	1.6	2.2	1.0	1.0	1.6
	c	0.4	1.0	1.0	0.4	1.6	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	d	2.2	2.8	2.2	2.2	1.6	1.6	1.6	2.8	2.8	2.8	2.2	1.6	2.8	2.2	1.6
	e	1.6	1.0	0.4	1.0	0.4	1.6	0.4	1.6	1.6	1.0	1.0	0.4	1.0	1.6	0.4
	f	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0
	g	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.6	0.4	1.0	1.0	1.0	1.0	0.4	1.0
	h	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Sample A																
Sample B																

ALPHA

BETA



Table 4 Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	BETA
Loci a b c d e f g h	1.0	1.6	0.4	0.4	1.6	0.4	1.0	1.6	1.0	1.0	1.6	1.0	0.4	0.4	1.6	Sample B
	2.2	2.2	1.6	2.2	1.6	1.6	1.6	1.0	1.0	1.0	1.6	1.0	1.6	1.6	2.2	
	1.0	1.0	1.0	1.0	1.0	0.4	0.4	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.6	
	2.2	2.2	2.8	2.8	1.6	1.6	1.6	1.6	2.8	2.2	2.8	2.2	2.8	1.6	2.2	
	1.0	0.4	1.6	1.0	1.0	1.6	0.4	0.4	0.4	1.6	1.0	1.6	0.4	1.0	1.6	
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	0.4	1.0	
	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.0	1.6	1.0	1.0	1.0	0.4	1.0	
	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	
Loci a b c d e f g h	2.2	2.8	1.6	2.8	2.2	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	1.6	Sample A
	0.4	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.6	1.0	0.4	1.0	
	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	0.4	1.0	
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	0.4	1.0	
	2.2	1.6	1.6	2.8	2.2	2.8	2.8	2.2	2.2	2.8	1.6	2.2	2.8	1.6	1.6	
	0.4	0.4	0.4	1.0	1.0	1.0	1.0	0.4	1.6	1.6	1.6	1.6	1.0	0.4	1.6	
1.0	0.4	1.6	0.4	1.0	1.0	1.6	0.4	1.6	0.4	0.4	1.6	1.6	1.0	1.6		
Loci a b c d e f g h	1.6	1.6	2.2	2.2	2.8	2.8	2.8	2.2	2.2	1.6	2.2	2.2	2.2	2.2	2.2	Sample B
	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	
	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	0.4	
	1.0	1.6	1.0	1.0	1.0	1.0	1.0	0.4	1.0	0.4	1.0	1.0	1.0	1.0	1.6	
	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	
	2.8	1.6	2.2	2.8	2.2	2.8	2.2	2.6	1.6	2.2	1.6	2.8	1.6	1.6	2.2	
	1.6	1.6	1.0	0.4	0.4	0.4	0.4	0.4	1.0	1.0	1.6	1.6	1.0	1.6	1.0	
1.0	1.6	1.0	1.6	1.6	1.0	1.0	0.4	1.6	0.4	0.4	0.4	1.0	1.0	1.6		

KAPPA

Table 4 Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Loci	a	2.2	2.8	1.6	1.6	2.2	2.2	2.8	2.8	2.2	2.8	1.6	2.2	1.6	2.8	1.6
	b	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0
	c	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	0.4	1.0	0.4	1.0	1.6	1.0
	d	1.6	2.2	2.2	1.0	1.0	1.6	2.2	1.6	1.6	2.2	1.0	1.0	1.6	2.2	1.0
	e	1.6	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	f	2.2	2.2	1.6	1.6	1.6	2.8	1.6	1.6	2.2	2.8	2.8	2.8	2.2	2.2	2.8
	g	0.4	0.4	1.6	1.6	1.0	0.4	1.0	1.6	1.0	1.6	0.4	1.0	1.0	1.0	1.0
	h	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.6	0.4	1.0
Sample A																
SIGMA																
Loci	a	2.8	1.6	2.2	2.2	2.2	1.6	1.6	2.8	2.2	2.8	2.8	2.2	1.6	2.8	
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	0.4	1.0	1.0	1.0	
	c	1.0	1.0	1.0	0.4	1.0	1.0	1.0	0.4	1.0	1.0	1.6	1.6	1.0	1.0	1.0
	d	2.2	1.0	1.6	2.2	2.2	1.0	1.6	1.0	2.2	1.6	1.0	2.2	1.6	1.6	1.0
	e	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4
	f	2.2	2.2	1.6	1.6	2.8	2.2	1.6	2.8	2.2	1.6	2.8	1.6	2.8	2.8	2.2
	g	0.4	1.6	1.0	1.0	1.0	1.0	1.6	0.4	1.0	1.6	0.4	1.0	0.4	1.6	1.0
	h	1.0	1.0	0.4	1.0	1.0	1.6	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4
Sample B																

Table 5  
 Yields of Individual Populations and of Population  
 Crosses Alpha x Beta, Alpha x Kappa  
 and Alpha x Sigma.

Population	Yield		
	Parental	F <sub>1</sub>	Midparental Value
Alpha	91.3		
Beta	55.9		
Kappa	66.6		
Sigma	83.9		
Alpha x Beta		68.2	(73.6)
x Kappa		84.0	(79.0)
x Sigma		92.4	(87.6)

Component gains and losses are present in each population cross in the strengths necessary to give the level of population hybrid yield sought. In jockeying these effects to obtain the ascending order of population hybrid performance shown in Table 5, a strong association of population with population hybrid becomes evident. This is in accord with actual field results. The attempt to align the internal structure of population Alpha with those of the three other populations to give three specific levels of hybrid response was especially difficult. This was not possible until a detailed study was made of individual component contributions under many combinations of opposing allele frequencies. The construction of populations could then proceed in a stepwise manner. The results indicate what would be required of the internal arrangement of opposing varieties or composites under conditions imposed by the model.

Association of inbred and topcross yields: In general, the literature reports a significant positive association between the yields in inbred and topcross condition. For purposes of the model the gametes from gamete sample A of Alpha are considered as a group of inbreds from a common source population crossed in common to three broad-based testers, Beta, Kappa and Sigma. The topcross yield for each inbred is the average performance of the 15 combinations involving the respective Alpha gamete crossed with the 15 gametes representing each of the other three populations. The yield of each inbred, the topcross yields on each tester and average topcross yield on the three testers appear in Table 6. The

association of inbred yield with average topcross yield is significant beyond the 1% level.

Table 6  
Inbred and Topcross Performance for Inbreds  
(gametes) from Alpha

Inbred Designation	Yield	Topcross Yields			
		Beta	Kappa	Sigma	Average
A1	54.5	59.3	73.9	90.4	74.5
A2	50.3	80.8	79.3	101.1	87.1
A3	23.3	35.4	56.4	60.2	50.7
A4	58.6	53.6	69.9	87.1	70.2
A5	69.2	58.3	79.9	92.9	77.0
A6	85.2	65.6	97.6	109.4	90.9
A7	69.2	63.4	97.1	98.0	86.2
A8	43.3	42.5	72.1	73.0	62.5
A9	69.2	80.6	78.3	90.8	83.2
A10	63.2	76.0	94.0	95.9	88.6
A11	66.8	102.0	91.6	95.9	96.7
A12	85.2	116.1	102.1	107.8	108.7
A13	63.2	79.7	98.4	98.5	92.2
A14	101.2	65.8	94.0	109.5	89.8
A15	43.3	43.5	74.8	75.3	64.5

Inbred yield vs. average topcross yield  $r = 0.79^{**}$

Yield performance in diallel of high and low general combiners: Among inbreds classified as high and low general combiners on common testers, the single crosses among high combiners have distinctly outyielded the single crosses among low combiners. The average performance of single crosses between high and low combiners has, in general, exceeded the midpoint between high and low groups, but has not equalled the average of the high group. For the model two diallel series of crosses were made involving the two highest and the two lowest performing inbreds based upon two evaluation schemes, average topcross performance and inbred performance per se. One inbred was common to the two high groups and the same two inbreds were involved in the two low groups. The group averages for high x high, high x low and low x low combinations appear in Table 7. In each case the average yield for the H x H and L x L groups are distinctly different. Where the initial selection

of inbreds was based upon topcross performance, the average for H x L clearly exceeds the mid-group value and, where selection was based upon inbred performance per se, the average for H x L is close to the mid-group value. This is in line with recent findings which suggest that inbred performance per se is based primarily upon additive effects whereas performance in topcross combination involves heterotic effects as well.

Table 7  
Average Yields for Groups of Inbreds within Two Diallel Series Involving Two High and Two Low Performing Inbreds Selected on the Basis of Topcross and Inbred Performance. (Mid-group values in parenthesis.)

Basis of Inbred Selection	Mean Yields of Indicated Groups			Inbreds Involved Under Individual Classifications			
	H x H	H x L	L x L	High	Low		
Topcross Performance	101.2	86.9 (72.3)	43.3	A11	A12	A3	A8
Inbred Performance per se	147.9	91.7 (95.6)	43.3	A12	A14	A3	A8

Summary statements: By assigning values to the alleles of an eight-locus model, it was possible to simulate rather closely the type of yield responses encountered in a typical maize breeding effort. Simulated yields were obtained for inbreds, single crosses, first back-cross generations, varieties, F<sub>1</sub> varietal crosses, topcrosses, and diallels among inbreds of high and low general combining ability. Salient features of the model are the use of yield components within which the members of allelic series, in non-allelic combinations, exhibit additive and non-additive relationships. Dominance, strict intermediate dominance and recessiveness are expressed among the alleles within each multiple allelic series. Yield components themselves exhibit a multiplicative relationship.

The obvious oversimplification in some features, the over-frequency in the use of other features and the uniformity of action in all features throughout the model are conditions imposed by the very limited size

of the model, and the need for simplicity and ease of manipulation. No suggestion is intended that allelic series are in fact present at all loci, or that such series are consistent in any attribute other than having more than two alleles. Furthermore, not every locus can be expected to be involved in epistasis, nor would every instance of epistasis necessarily involve only two loci. Certainly, too, one would expect to find few component traits conditioned by as few as two loci. The writer believes, however, that most features of the model, aside from those which exclude linkage and the possibilities of relationships among component traits, reflect genetic views favored by a majority of maize breeders. Even were this opinion incorrect, it would still appear that enough agreement was found between simulated and known yield behavior patterns to warrant further consideration of this approach, if only for illustrative purposes. Such schematic representations as may result can, in the writer's opinion, aid in a better understanding of the dynamics of yield heterosis.

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1. Restoration of  $A_1$  gene action by crossing over.

Neuffer has undertaken an extensive study of  $a_1^{m-3}$  and  $a_1^{m-4}$ , two independent inceptions of control of  $A_1$  gene action by the Ac system, to determine whether a controlling element, presumed to be associated with the  $A_1$  gene in each case, could be removed by crossing over, thereby restoring  $A_1$  gene action. His results were negative as are those that I have obtained during the course of studies of  $a_1^{m-3}$  and  $a_1^{m-4}$ . My data, however, are limited. My studies of  $a_1^{m-2}$ , on the other hand, have given quite different results. Restoration of  $A_1$  gene action appears to arise from a crossover event which occurs relatively frequently with some states of  $a_1^{m-2}$  but infrequently, if at all, with others.

Nelson (personal communication) has shown that by means of a crossover, Wx gene action may be restored in tests conducted with  $wx^{m-1}$  and  $wx^{m-6}$ , two independent inceptions of control of action of the Wx gene by the Ac system, and also with  $wx^{m-8}$ , controlled by the Spm system. His method of analysis is precise in that it