

A NEW APPROACH TO THE STUDY OF HETEROSIS WITH SPECIAL REFERENCE TO
UNIFYING THE CONCEPT OF COMBINING ABILITY WITH HERITABILITY

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SUMMARY

In this paper a new method is presented whereby the variance of F_1 in the cross between two breeds is partitioned into an additive fraction, a non-additive fraction, and an environmental one, just as we do in selection theory. The concept of combining ability is strictly according to the definition given by its first proponents Sprague and Tatum (1942), that is, to a partitioning into general versus special combining ability. The model used is the usual one given in Falconer (1981). Four stocks of *D. melanogaster* of diverse origin involving five different traits, body length, breast width, wing length, body weight, and number of bristles were employed in the crosses, to test the applicability of the theory proposed. The results show that the method is quite general, and with appropriate assumptions, can be applied in a wide range of cases, in both animal and plant breeding.

INTRODUCTION

The problem of heterosis is a long standing one, and just as with pure-breeding in the past, success with exploitation in practice has long preceded and outstripped theory. As late as 1981, Mayo was able to say, 'In view of its very great success (with hybrid maize in the United States), the genetical theory underlying the manifestation of heterosis is not well developed.' In a communication in 1984, the senior author suggested a method of analyzing heterosis that would permit us to treat the problem in the same way as we do for selection in the parental breeds. The only postulates used were the usual definitions for heterosis, for general and special combining ability, and the mathematical model in Falconer's book. A series of experiments were started in 1984 by the junior author, using the classical organism *D. melanogaster* to test the theory. The following is a report of part of this work.

Theory

As originally proposed, the combining abilities, general and special (henceforth designated as GC and SC respectively), were but arithmetical procedures in breeding without relevance to **genetical** theory. Gradually, however, geneticists began to grope and feel for their meaning, and it became clear that GC would be attributable to the additive gene effects, and SC to the non-additive. Starting from **this** fundamental postulate, we have

$$A_{F1} = (A_1 + A_2)/2, \quad 1a$$

$$V_{AF1} = (V_{A1} + V_{A2})/4; \quad 1b$$

where A designates the additive genetic value of the trait in breed 1, and V_{A1} the additive genetic variance of the same. Since the total phenotypic variance of F_1 can always be expressed as

$$V_{F1} = V_{AF1} + V_{NAF1} + V_E, \quad 2a$$

where V_{NA} stands for the non-additive genetic variance, and V_E the environmental component, we have an expression for estimating the non-additive variance component ($= V_D + V_I$, where D means dominance and I interaction respectively):

$$V_{NAF1} + V_E = V_{F1} - \frac{1}{4}(V_{A1} + V_{A2}), \quad 3a$$

or dividing throughout by V_{F1} ,

$$(V_{NAF1} + V_E)/V_{F1} = 1 - (V_{A1} + V_{A2})/4V_{F1} \quad 3b$$

This can be regarded as percentage heterosis as far as practical features are concerned. V_A can of course be estimated from the heritability of the trait, as $h^2 V_P$. In terms of combining ability,

$$V_{F1} = V_{GC1} + V_{GC2} + V_{SC12} + V_E; \quad 2b$$

and since GC varies with the number of crosses made with different breeds, and this has to be taken account of, for each breed there will be $n-1$ crosses if there are n breeds (disregarding reciprocals). Hence

$$\begin{aligned} GC_1 &= \frac{\sum_1^n \text{all crosses made with breed 1}}{(n-1) \text{ breed 1} + \sum_2^n \text{the other breeds}} \\ &= \text{breed 1} + \frac{\sum_2^n \text{the other breeds}}{n-1} \end{aligned} \quad 4a$$

$$V_{GC1} = \frac{1}{4} V_{A1} + \frac{1}{4(n-1)^2} (V_{A2} + V_{A3} + \dots + V_{An}). \quad 4b$$

Similar expressions hold for breed 2 and the other breeds. Then we have for the estimation of V_{SC12} :

$$\begin{aligned} V_{SC12} + V_E &= V_{F1} - V_{GC1} - V_{GC2} \\ &= V_{F1} - \frac{1}{4}(V_{A1} + V_{A2}) - \frac{1}{4(n-1)^2}(V_{A1} + V_{A2}) \\ &\quad - \frac{2}{4(n-1)^2} (V_{A3} + V_{A4} + \dots + V_{An}) \end{aligned} \quad 5a$$

which may be divided throughout by V_{F1} to obtain the corresponding percentage (3b).

On the other hand, since by definition,

$$H_{ij} = F_1(ixj) - MP,$$

where H_{ij} = heterosis of the cross ixj , $F_1(ixj)$ = offspring of the cross ixj , and MP = mean of parents $(P_i + P_j)/2$. Hence

$$V_{F1(ixj)} = V_H + V_{MP} + 2cov(H, MP), \quad 6a$$

where the last term is zero, since by reason of the recombination of gametes, there is no correlation between the non-additive component of the parent generation and the H_{ij} of F_1 , nor between the additive component of parents and H_{ij} provided we remember that heterosis as we have defined it consists entirely of the non-additive component of F_1 . Hence V_H may be estimated from the relation

$$V_H = V_{F1(ixj)} - \frac{1}{4} (V_{P_i} + V_{P_j}). \quad 6b$$

Equating V_H with V_{SC12} and subtracting 6b from 5a, we have V_E , the environmental component, which of course includes the errors of sampling.

Experimental Results

A series of experiments to test the above theory were started by the junior author in 1984 using four different stocks of *D. melanogaster* with five traits. The stocks were lines inbred in different localities in China for many generations, and for convenience may be designated 1, 2, 3, 4. The details are given in a paper by Li (1985), now in press. The heritability, parental variance, and additive genetic variance of the various traits are given in Table 1.

Results for the variance of F_1 of the various crosses are given in the first line of each cross in Table 2. Partitioning into components follow in the other lines. The crucial formula is 5a. By equating V_H with V_{SC}

Table 1. h^2 , V_P and V_A of various traits of parental stocks

Stocks	Traits	Body length	Breast width	Wing length	Body weight	No. of bristles
1	h^2	0.3304	0.5693	0.5969	0.3817	0.2048
	V_P	6.5362	0.9384	6.3766	0.0081	4.0024
	V_A	2.1596	0.5342	3.8062	0.0031	0.8197
2	h^2	0.2905	0.5239	0.5944	0.4179	0.0961
	V_P	4.8057	0.3959	3.6596	0.0061	2.9687
	V_A	1.3961	0.2074	2.1752	0.0025	0.2853
3	h^2	0.4638	0.5201	0.6738	0.5442	0.1308
	V_P	7.1792	0.7443	3.4812	0.0158	3.7230
	V_A	3.3297	0.3871	2.3456	0.0086	0.4870
4	h^2	0.5015	0.5639	0.5459	0.5013	0.0498
	V_P	5.1957	0.7667	7.4360	0.0069	3.9006
	V_A	2.6059	0.4323	4.0593	0.0034	0.1942

and subtracting from 5a, we obtain V_E , the environmental component, while $V_{F_1} - (V_{SC} + V_E)$ gives V_{A1j} , the additive component of the cross. All three can then be divided by F_{F_1} to give the % figures in the table, which of course should sum up to unity.

We have thus completed the analysis of F_1 into its additive, non-additive and environmental components. In order to clinch the argument, a test of significance has been made of $cov(H,MP)$ and found not to differ significantly from zero for all traits except number of bristles. Another test, even more convincing, is made of the difference between $cov(H,F_1)$ and V_H , and found to be non-significant in all cases. Thus our original assumption that $cov(H,MP)$ is zero, seems to be justified.

DISCUSSION

In conclusion, by assuming that GC is due to the additive action of the genes concerned in the cross, it is possible to partition the total F_1 variance into an additive portion, a non-additive portion, and an environmental one, and to point out that the non-additive portion, SC, is heterosis per se. We might choose to call the the additive portion general heterosis, but its inclusion is really confusing, and it seems more reasonable to give it some other name, such as heritability of the cross, in analogy

Table 2. V_{F1} , V_{Aij} , V_H , V_E of the various crosses

Cross	Traits	Body	Breast	Wing	Body	No. of
	V_{F1} & % compts	length	width	length	weight	bristles
1 x 2	V_{F1}	3.8484	0.4581	3.0067	0.0070	2.3680
	V_{A12}	0.3423	0.5491	0.6709	0.3179	0.1424
	V_H	0.2632	0.2718	0.1655	0.4921	0.2640
	V_E	0.3945	0.1791	0.1636	0.1900	0.5936
1 x 3	V_{F1}	5.1704	0.4251	2.8772	0.0068	4.2240
	V_{A13}	0.3379	0.6856	0.7143	0.5261	0.0919
	V_H	0.3368	0.0104	0.1435	0.1213	0.5428
	V_E	0.3253	0.3040	0.1422	0.3526	0.3653
1 x 4	V_{F1}	4.4520	0.5171	5.6304	0.0070	3.4471
	V_{A14}	0.3563	0.5831	0.4327	0.3460	0.0937
	V_H	0.3412	0.1756	0.3867	0.4643	0.4268
	V_E	0.3025	0.2413	0.1806	0.1897	0.4795
2 x 3	V_{F1}	5.6118	0.4434	2.6003	0.0055	2.8378
	V_{A23}	0.2811	0.4935	0.6510	0.6263	0.0928
	V_H	0.4661	0.3571	0.3135	0.0050	0.4105
	V_E	0.2528	0.1494	0.0355	0.3687	0.4967
2 x 4	V_{F1}	4.0557	0.4605	4.2420	0.0099	5.3843
	V_{A24}	0.3493	0.4970	0.4888	0.2312	0.0368
	V_H	0.3835	0.3688	0.3461	0.6717	0.6811
	V_E	0.2672	0.1342	0.1651	0.0971	0.2821
3 x 4	V_{F1}	3.5744	0.4291	2.8492	0.0081	3.3723
	V_{A34}	0.5165	0.6265	0.7411	0.4499	0.0739
	V_H	0.1345	0.1197	0.0421	0.2994	0.4348
	V_E	0.3490	0.2538	0.2168	0.2507	0.4913

with what we do for parental breeds. This is not only more economical of thinking, but saves the labor of estimating it again in the analysis of heterosis, which should be concentrated on the SC fraction. Also, from the above demonstration that $\text{cov}(H,MP)$ is zero, V_I , or interaction of the parental generation, does not seem to exist.

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