schen Genetik in der Pflanzenzüchtung. 1. Teil: Die verschiedenen Formen der genetischen Variabilität und ihre Bedeutung in der Pflanzenzüchtung. Züchter **35**, 156 bis 174 (1965). — 2. COMSTOCK, R. E., and H. F. ROBINSON: The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics **4**, 254—266 (1948). — 3. COMSTOCK, R. E., and H. F. ROBINSON: Estimation of average dominance of genes. In: J. W. GOWEN, Heterosis, p. 494—516. Ames: Iowa State Coll. Press 1952. — 4. CROW, J. F.: Notes on Population Genetics. Mskr. Madison (1962) unveröff. — 5. JINKS, J. L., and B. I. HAYMAN: The analysis of diallel crosses. Maize Genetics News Letter **27**, 48—54 (1953). — 6. JINKS, J. L., and B. I. HAYMAN: The analysis of heritable variation in a diallel cross of *Nicotiana rustica* varieties. Genetics **39**, 767—788 (1954). — 7. KEMPTHORNE, O.: The theoretical values of correlations between relatives in random mating populations. Genetics **40**, 153—167 (1955). — 8. MATHER, K.: Biometrical Genetics. London: Methuen 1949. — 9. SEYFFERT, W.: Untersuchungen über die Vererbung quantitativer Charaktere an *Arabidopsis thaliana* (L.) Heynh. Z. f. Pflanzenzüchtung **42**, 356—401 (1960).

An Experimental Test of Quantitative Genetic Theory

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Summary. An experiment was conducted with *Drosophila melanogaster* to test a theory of quantitative inheritance. The covariances among half and full sibs did not increase with increasing levels of F. The results pose the question "Why did inbreeding not behave as expected?" Some possible causes include: (1) selective elimination of particular genotypes during inbreeding, (2) inbreeding and/or selection within the reference population, (3) maternal age effects, (4) linkage. Linkage and selective elimination of some genotypes appear most likely to be of greatest importance.

A theory of quantitative inheritance applicable to diploid populations with an arbitrary number of segregating loci and arbitrary epistacy has been described in detail by KEMPTHORNE (1957, Ch. 19). This theory is due to FISHER (1918), WRIGHT (1935), COCKERHAM (1952, 1954), ANDERSON (1953), ANDERSON and KEMPTHORNE (1954), HORNER (1952), and KEMPTHORNE (1954). The formulation considered here does not take account of linkage, although COCKERHAM (1956) has extended it to include linkage in a special case and SCHNELL (1961) and VAN AARDE (1963) have made extensive theoretical investigations. The incorporation of linkage parameters in data interpretation presents considerable difficulties. KEMPTHORNE (1957, Ch. 20) also considered inbreeding in a diploid population with arbitrary epistacy, and no linkage. The formulation provides the basis for a reasonable experimental check on the theory based on absence of linkage, which is one of the main interpretive tools of much plant and animal breeding. The results of such an experiment are presented herein.

The Theory and Test

The relevant essential features of the theory are briefly outlined for convenience. The original sources must be consulted for complete development.

The theoretical expectation for the partition of the total genetic variance, (σ_G^2) is:

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAA}^2 + \sigma_{AAD}^2 + \text{- - - +} \text{ etc.},$$

where:

σ_A^2 is the variance due to average effects of genes.

σ_D^2 is the variance due to interactions among allelic gene effects (dominance).

σ_{AA}^2, σ_{AAA}^2, etc. is the variance due to interactions among average effects of two or more non-allelic genes (epistacy).

σ_{DD}^2, σ_{DDD}^2 etc. is the variance due to interactions of two or more non-allelic dominance effects (epistacy).

σ_{AD}^2, σ_{AAD}^2, etc. is the variance due to interactions among dominance and average effects (epistacy).

Knowledge of these components is useful for many purposes, e.g., applied breeding studies and problems of evolution. They can be estimated from the covariances among relatives.

In a large panmictic population (specifically, if there is zero probability that the two genes possessed by an individual at any locus are identical by descent) it has been shown that:

$$\text{Cov (H.S.)} = 1/4\,\sigma_A^2 + 1/16\,\sigma_{AA}^2 + 1/64\,\sigma_{AAA}^2 + \cdots + \text{etc.}$$

$$\text{Cov (F.S.)} = 1/2\,\sigma_A^2 + 1/4\,\sigma_D^2 + 1/4\,\sigma_{AA}^2 + 1/8\,\sigma_{AD}^2 + 1/16\,\sigma_{DD}^2 + 1/8\,\sigma_{AAA}^2 + \cdots + \text{etc.}$$

Covariances between half and full sibs can be estimated by use of a simple and well-known genetic experiment. Each of a number of sires, s (numbered from $i = 1$ to s) is mated to a random sample of dams $(i\,j)$ where j runs from 1 to m_i. Each mating of sire i by dam $i\,j$ produces n_{ij} progeny. The observations can be represented by the model

$$y_{ijk} = \mu + s_i + d_{ij} + e_{ijk}$$

in which

$$E(s_i) = E(d_{ij}) = E(e_{ijk}) = 0$$

and the s, d, and e quantities are uncorrelated and $E(s_i^2) = \sigma_s^2$, $E(d_{ij}^2) = \sigma_d^2$ and $E(e_{ijk}^2) = \sigma_e^2$ then

$$E(Y_{ijk} - \mu)(Y_{ijk'} - \mu) = \sigma_s^2 + \sigma_d^2 = \text{Cov (F.S.)}, (k' \neq k)$$

$$E(Y_{ijk} - \mu)(Y_{ij'k'} - \mu) = \sigma_s^2 = \text{Cov (H.S.)}, (k' \neq k), (j' \neq j)$$

$$E(Y_{ijk} - \mu)^2 = \sigma_s^2 + \sigma_d^2 + \sigma_e^2 = \sigma_p^2$$

Hence

$$\sigma_e^2 = \sigma_p^2 - \text{Cov (F.S.)},$$

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$\sigma_d^2 = \text{Cov (F.S.)} - \text{Cov (H.S.)}$,
$\sigma_s^2 = \text{Cov (H.S.)}$.

Estimates of σ_s^2, σ_d^2, and σ_e^2 are obtained by equating the mean squares to their expectations in the analysis of variance:

Source of variation	D.F.	M.S.	E.M.S.
Sires	$s-1$	S	$\sigma_e^2 + k_2\,\sigma_d^2 + k_3\,\sigma_s^2$
Dams within sire	$\sum_i (m_{ij}-1)$	D	$\sigma_e^2 + k_1\,\sigma_d^2$
Progeny within dam and sire	$\sum_{ij} (m_{ij}-1)$	E	σ_e^2

Mean squares and k values are computed in the usual way. It is important to note that in order to equate the estimates of the covariances among sibs to the theoretical genotypic covariances it is necessary to assume that environmental deviations are associated at random with genotypes and that the non-environmental part of the phenotype of an individual is determined solely by the genotype of the individual and not, for example, partially by maternal effects or other possible causes.

The structure of covariances between relatives under an inbreeding system with epistacy has been investigated theoretically by HARRIS (1964), but the formulation is quite complex. A large number of parameters is involved, and only a very large experiment would be informative in terms of the model he used. However, with random mating of individuals of a population which results by inbreeding a random mating population to a definite F value (WRIGHT, 1922), very simple expressions exist for the genotypic variance of the progeny, the genotypic variance in the original random mating population and the covariance of half-sibs and of full-sibs. It is possible to express the covariance of any two relatives, neither of whom is inbred, in the population resulting from random mating of the inbred population. The experiment already described may be generalized by requiring that the sires and dams be random members of the population resulting by pure inbreeding without selection to an extent measured by F, from a random mating population. The case F equal to zero corresponds to the situation when sires and dams are chosen from a non-inbred random mating population, and when F equals unity they are random homozygous individuals resulting from inbreeding to homozygosity of a random mating population. The genetic interpretation of the resulting estimates follows:

$$\text{Cov (H.S.)} = \left(\frac{1+F}{4}\right)\sigma_A^2 + \left(\frac{1+F}{4}\right)^2\sigma_{AA}^2 + \left(\frac{1+F}{4}\right)^3\sigma_{AAA}^2 + \cdots + \text{etc.}$$

$$\text{Cov (F.S.)} = \left(\frac{1+F}{2}\right)\sigma_A^2 + \left(\frac{1+F}{2}\right)^2\sigma_D^2 + \left(\frac{1+F}{2}\right)^2\sigma_{AA}^2 + \left(\frac{1+F}{2}\right)^3\sigma_{AD}^2 + \left(\frac{1+F}{2}\right)^4\sigma_{DD}^2 + \cdots + \text{etc.}$$

These results form the basis for an experimental test of theory. Prior inbreeding raises the coefficients of the higher order terms, e.g. if F is equal to unity,

$$\text{Cov (F.S.)} = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \cdots + \text{etc.}$$

i.e., every coefficient becomes unity.

The experiment is essentially as follows. A large panmictic reference population is established. A number of subpopulations inbred to particular values of F, with replication of the inbreeding process by the same and different methods of reaching each F value, are formed. The resulting material is evaluated by several independently replicated experiments for each replicate of each F population. This permits estimates of the various components of genotypic variance, and checks on the negligibility of high-order components. It can then be determined whether there is a reasonable partition of genetic variance which holds over all values of F. If so, a partial verification of the partition of genetic variance and the role of inbreeding in application of the theory of quantitative inheritance is provided. The experiment was also designed with a view to obtaining a better idea than has so far been given, of the role of interlocus interactions in quantitative inheritance. It is perhaps unnecessary to recall that no amount of verification will prove a theory correct; it can only indicate that it gives a reliable representation of prescribed situations. If a reasonable partition of the genetic variance over all values of F is not found, various possible causes exist, e.g., elimination of some genotypes by the inbreeding, and remain to be investigated. Estimates should also be obtained from covariances for different relationships under random mating.

The test actually conducted is described as follows. A large sample of a wild-type stock of *Drosophila melanogaster* designated as Princeton was obtained from Dr. J. W. GOWEN. It had been maintained by mass mating in one-pint culture bottles for about 25 years. Preliminary experiments indicated a reasonable amount of genetic diversity for the traits measured, body weight and the number of chaeta on the 4th and 5th abdominal segments. Only females were measured. The population was expanded to sixteen bottles. In each of 10 generations preceding the test, the bottles were isolated and the next generation of parents obtained by including in each of the 16 new culture bottles a sample of males and virgin females from each of the 16 bottles of the previous generation.

Seven levels of F were arbitrarily selected: 0.000, 0.250, 0.375, 0.500, 0.734, 0.859 and 1.000. Three levels of F, 0.000, 0.375, and 0.500 were replicated. The populations with F equal unity were produced as isogenic lines for all four chromosomes by a marked-inversion outcross technique (KIDWELL 1963). The populations for each of the other F values were formed as follows. A large number (Table 6) of single pair matings were made from the reference population. Mates were paired at random, except that mating of flies from the same culture was prohibited. The progeny of these matings were used for the zero level of F. Single pair full sib mating was practiced until the specified level of F was reached in the other levels. It is important to note that a distinct set of lines was formed for each level of F.

At each level of F, one-third of the lines were randomly chosen, and a single male selected. Each male was mated with two females, each randomly chosen from one of the remaining lines. An attempt was made to obtain measurements on six female pro-

Table 2. *Analysis of Variance of Body Weight and Abdominal Chaeta Number.*
Parental Inbreeding, F

Source of Variation	0.000		0.250		0.375		0.500		0.734		0.859		1.000	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Body Weight:														
Among Sires	131	18,910.0	124	13,152.3	129	9,534.6	109	11,135.3	148	17,575.7	129	9,083.0	88	19 208.8
Among Dams/Sires	127	7,442.6	125	5,971.9	128	4,940.7	110	5,998.2	143	9,996.2	128	3,921.2	88	8,881.6
Among Full Sibs	1253	3,139.7	1226	2,028.3	1277	1,639.1	1085	1,794.9	1406	2,145.2	1262	1,824.8	847	3,373.0
Chaeta Number:														
Among Sires	131	10.89	124	9.36	128	9.93	109	8.61	148	11.59	129	14.46	87	7.10
Among Dams/Sires	131	8.34	124	8.03	128	7.23	110	9.75	144	8.12	128	9.90	87	6.36
Among Full Sibs	1307	6.66	1233	5.50	1278	6.17	1095	6.35	1421	6.84	1266	6.86	847	5.68
Replicates														
Body Weight:														
Among Sires	116	16,190.5			114	10,593.0	119	7,186.1						
Among Dams/Sires	114	5,721.7			108	6,730.1	119	4,609.7						
Among Full Sibs	1149	1,829.7			1079	1,707.1	1190	1,732.2						
Chaeta Number:														
Among Sires	117	10.08			114	9.16	119	13.37						
Among Dams/Sires	118	8.30			114	6.99	120	7.91						
Among Full Sibs	1167	6.74			1128	6.89	1193	6.85						

geny of each dam. The traits measured include body weight and the number of chaeta on the 4th and 5th abdominal segments. Body weight was observed on one sample of progeny and chaeta number on another sample. Body weight was measured on a Mettler microbalance four to six hours post emergence. All the weights were taken by one person. Chaeta counts were made by three people, whose counts were frequently cross checked and found to be in close agreement.

The flies were maintained at a temperature of 22 °C, which resulted in a 12-day generation interval. The tests were conducted during a 120-day period. The entire population for each F level was formed and tested at one time. A system of blocking wherein a part of the population for each F level is measured at the same time is obviously preferable. It was precluded by the size of the test and the available assistance. The F level tested at any given time was chosen at random, except for $F = 0.859$, which required the longest to produce and was tested last.

A standard nested analysis of variance was completed for each level of F for body weight. The same analysis was completed for abdominal chaeta number on the 4th abdominal segment, the 5th abdominal segment and the sum of the two. Only the data for the sum of the chaeta number on the 4th and 5th segments are reported.

Results and Discussion

The mean, error standard deviation and coefficient of variation for body weight and chaeta number for each level of inbreeding of the parents are presented in table 1. Differences among the means are small and non-significant. There is no evidence of a relation between the means and the inbreeding of the parents or a relation between the means and the chronological order of testing. It is concluded that no detectable environmental changes occurred during the experiment.

The analysis of variance was completed for each level of inbreeding and the variance components estimated. They are presented in tables 2, 3 and 4 for body weight and chaeta number. Estimates of the half-sib and full-sib covariances are presented in table 5 for body weights and chaeta number. These results are drastically different from those predicted by the theory. The components of variance do not behave as expected. Both σ_s^2 and σ_d^2 are expected to

Table 1. *Mean, Standard Deviation and Coefficient of Variation of Body Weight and Chaeta Number for each Level of Inbreeding of the Parents.*

F	Body Weight			Chaeta		
	gm. × 10⁻⁶	S.D.	C.V.	Number	S.D.	C.V.
0.000	1100	56.03	5.09	42.4	2.58	6.09
0.250	1090	45.04	4.13	42.6	2.34	5.51
0.375	1123	40.49	3.60	42.7	2.48	5.82
0.500	1150	42.37	3.68	42.5	2.52	5.92
0.734	1094	46.32	4.24	42.5	2.62	6.15
0.859	1125	42.72	3.80	41.8	2.62	6.26
1.000	1113	50.08	5.22	42.2	2.38	5.65
Replicates						
0.000	1110	42.77	3.64	42.9	2.60	6.05
0.375	1183	41.32	3.72	42.2	2.62	6.21
0.500	1177	41.62	3.52	42.4	2.62	6.16

Table 3. *Estimates of Variance Components, Body Weight.*

	σ_T^2	σ_s^2	%	σ_d^2	%	σ_e^2	%
Parental F Level							
0.000	4,878.05	992.60	20.34	745.74	15.28	3,139.72	64.36
0.250	3,304.42	602.33	18.22	673.77	20.38	2,028.32	61.38
0.375	2,583.13	386.34	14.95	557.70	21.58	1,639.09	63.45
0.500	2,936.51	427.99	14.57	713.63	24.30	1,794.89	61.12
0.734	4,160.67	640.48	15.39	1,374.94	33.04	2,145.25	51.56
0.859	2,622.17	437.98	16.70	359.40	13.70	1,824.79	69.59
1.000	5,222.89	878.72	16.82	971.19	18.59	3,372.99	64.58
Replicates							
0.000	3,368.78	886.65	26.31	652.48	19.36	1,829.65	54.31
0.375	2,911.45	325.64	11.18	878.68	30.18	1,707.13	58.63
0.500	2,429.88	216.19	8.89	481.42	19.81	1,732.26	71.28

increase with the level of F. Clearly, they do not. In the case of body weight there is a slight suggestion of curvilinearity, with a decrease as F increases to 0.500 and then an increase. No pattern can be discerned for chaeta number.

Both σ_s^2 and σ_d^2 with F equal to unity should be at least twice as great as when F is equal to zero, and they are not. In the case F equal to unity the offspring of a given sire and dam are genetically identical. The error mean square should provide a reasonable estimate of environmental variation. The sequence of error mean squares should fit

$$\sigma_E^2 + \sigma_G^2 - \text{Cov (F.S.)}$$

and should decrease with increasing F, but it does not.

Table 4. *Estimates of Variance Components, Chaeta Number.*

	σ_T^2	σ_s^2	%	σ_d^2	%	σ_e^2	%
Parental F Value							
0.000	7.158	0.213	2.98	0.282	3.94	6.662	93.07
0.250	6.034	0.109	1.79	0.430	7.11	5.496	91.08
0.375	6.571	0.226	3.43	0.179	2.72	6.166	93.83
0.500	6.919	−0.097	0.00	0.570	8.24	6.349	91.75
0.734	7.359	0.299	4.05	0.221	3.00	6.839	92.93
0.859	7.760	0.386	4.97	0.519	6.68	6.855	88.34
1.000	5.861	0.060	1.02	0.118	2.01	5.683	96.96
Replicates							
0.000	7.154	0.148	2.06	0.264	3.68	6.742	94.24
0.375	7.091	0.184	2.58	0.017	0.23	6.890	97.17
0.500	7.482	0.457	6.10	0.179	2.38	6.846	91.50

These results preclude plausible estimates of the partition of the total genetic variance. Rather, attention is directed toward a possible elucidation of the anomalous results. Here, unfortunately, the element of speculation becomes large. The results pose the important question, "Why did inbreeding behave not at all as expected?" These data cannot provide an answer, but there are some factors to be considered.

While this experiment was in progress, Dr. G. C. TANEJA, a National Research Council (Canada) Post Doctoral Fellow, became interested in it. When he returned to India, he took a sample of the Princeton stock and with S. NEGI conducted a similar experiment (TANEJA, G. C. and S. NEGI, 1963). Only four levels of F (0.000, 0.250, 0.500, and 0.734) were used, and only 150 pairs were started at each level of F. Abdominal chaeta number and wing length were measured. They found that the half and full sib covariances increased linearly with F in the case of chaeta number, but their results were similar to ours for wing length. In a larger later experiment, TANEJA (personal communication) reports results similar to ours. In view of the size of our experiment and the generally similar results of TANEJA, it seems that these results must be accepted as representative of some "real" situation and cannot be dismissed as due to sampling error or inaccurate technique.

It is reasonable to review the assumptions, to attempt to determine whether they were violated and the possible results. Possible effects of gross environmental changes during the experiment that might have been different for the different levels of F have already been considered, and found unlikely to be important. There is no evidence that the requirement that environmental deviations be associated at random with genotypes has been violated.

Table 5. *Estimates of Half Sibs and Full Sib Covariances, Body Weight and Chaeta Number.*

	Body Weight		Chaeta Number	
	Cov (H.S.)	Cov (F.S.)	Cov (H.S.)	Cov (F.S.)
Parental F Value				
0.000	992.60	1738.34	0.213	0.495
0.250	602.33	1276.11	0.109	0.539
0.375	386.34	944.04	0.226	0.405
0.500	437.99	1141.61	−0.097	0.473
0.734	640.48	2015.42	0.299	0.520
0.859	437.98	797.39	0.386	0.805
1.000	878.72	1849.90	0.060	0.178
Replicates				
0.000	886.65	1539.12	0.148	0.412
0.375	325.64	1204.32	0.184	0.201
0.500	216.19	697.62	0.457	0.636

Table 6. *Percent of Original Matings Available for Testing at each Level of F.*

	0.000	0.250	0.375	0.500	0.734	0.859	0.000R	0.375R	0.500R
Number started	480	480	540	600	1080	1080	450	600	600
Number remaining	420	402	435	402	540	414	439	454	426
Percent	87.50	83.75	80.56	67.00	50.00	38.33	97.56	75.67	71.00

It is assumed that sires and dams are random individuals from the population resulting by pure inbreeding without selection. It is possible that inbreeding did not result in the degree of homozygosity measured by F, i.e., that some genotypes were selectively eliminated. In the development of all the populations, including F equal zero but excluding F equal unity, only part of the pairs started survived to the test generation. No attempt was made to distinguish among the causes of loss. Some lines were lost because flies escaped or became trapped in the media prior to reproduction. These are included with cases of sterility and infertility, and no investigation was made as to their cause. The number of lines started and the number and percent available for test are presented in table 6. Losses are of course greater at the higher levels of F. However, the per-generation loss rate was quite uniform. Chaeta number is not generally regarded as an important component of fitness, and it is difficult to conceive of a reason why homozygosity would not increase linearly with F. However, the results of LEVINE and DOBZHANSKY (1958) may be noted. Very extensive inbreeding in *Dros. pseudoobscura* did not produce homozygosity. There may be a relation between body weight and fitness. In *Dros. pseudoobscura*, TANTAWY and VETUKHIV (1960) found that females larger in a number of body measurements laid more eggs. TANTAWY and REEVE (1956) found evidence that natural selection against homozygosity at some loci reduces the rate of fixation and that the genotype becomes more sensitive to the effects of further fixation as it becomes more homozygous. Selection against fixation appeared to become more intense as the genetic background became more homozygous. While it seems likely that some genotypes were selectively eliminated, it is doubtful that this could completely account for the observed results.

It is possible that the reference population was already inbred to a high level of F. It had been maintained by mass culture in one-pint milk bottles for more than 25 years prior to this experiment. It is possible that at one or more points the effective number of parents was small enough for random drift to become effective. It is also possible that natural selection under laboratory conditions had resulted in peculiar gene frequencies. Preliminary tests had indicated a heritability of the order of 0.4 for body weight and 0.6 for chaeta number. However, in these data at the F equal zero level the heritability estimated as $(4\,\sigma_s^2/\sigma_p^2)$ is of the order of 0.8 for body weight and 0.1 for chaeta number. It is possible, therefore, that peculiarities of the reference population have influenced the results.

It is also assumed that the non-environmental part of the phenotype of an individual is determined solely by the genotype of the individual and not, for example, partially by maternal effects. Large maternal effects have been observed for body weight (KIDWELL et al., 1965) in this population. It is possible that the size of the females tended to decrease with increasing levels of F and that this influenced the weight of the non-inbred progeny. There is, however, no evidence of maternal effects for chaeta number.

Linkage has not been taken into account in this development. Since there are only four pairs of chromosomes, one of which is very small, it is possible that linkage is important in quantitative inheritance in *Drosophila melanogaster*.

Zusammenfassung

Zur Überprüfung einer quantitativen Vererbungstheorie wurde ein Versuch mit *Drosophila melanogaster* durchgeführt. Die Kovarianzen zwischen Halb- und Vollgeschwistern erhöhten sich mit steigendem F-Wert (steigendem Homozygotiegrad) nicht. Die Ergebnisse werfen die Frage auf, warum sich die Inzuchten nicht wie erwartet verhielten. Einige mögliche Gründe dafür dürften sein: 1. selektive Elimination einzelner Genotypen während der Inzucht, 2. Inzucht und/oder Selektion innerhalb der betreffenden Population, 3. Einfluß des mütterlichen Kreuzungsalters, 4. Kopplung. Kopplung und selektive Elimination von Genotypen haben wahrscheinlich die größte Bedeutung.

Literature Cited

1. ANDERSON, V. L.: A model for the study of quantitative inheritance. Ph. D. Thesis. Iowa State Univ. Library (1953). — 2. ANDERSON, V. L., and O. KEMPTHORNE: A model for the study of quantitative inheritance. Genetics **39**, 883–898 (1954). — 3. COCKERHAM, C. C.: Genetic covariation among characteristics of swine. Ph. D. Thesis. Iowa State Univ. Library (1952). — 4. COCKERHAM, C. C.: An extension of the concept of partitioning hereditary variance for analysis of covariance among relatives when epistasis is present. Genetics **39**, 859–882 (1954). — 5. COCKERHAM, C. C.: Effects of linkage on the covariances between relatives. Genetics **41**, 138–141 (1956). — 6. FISHER, R. A.: The correlation between relatives on the supposition of Mendelian inheritance. Trans. roy. Soc. Edinb. **52**, 399–433 (1918). — 7. HARRIS, D. L.: Genotypic covariances between inbred relatives. Genetics **50**, 1319–1348 (1964). — 8. HORNER, T. W.: Non-allelic gene interaction and the interpretation of quantitative genetic data. Ph. D. Thesis. North Carolina State College (1952). — 9. KEMPTHORNE, O.: The correlations between relatives in a random mating population. Proc. roy. Soc. Lond. B. **143**, 103–113 (1954). — 10. KEMPTHORNE, O.: An introduction to Genetic Statistics. New York, N.Y.: John Wiley and Sons 1957. — 11. KIDWELL, J. F.: Genotype X environment interaction with isogenic lines of *Drosophila melanogaster*. Genetics **48**, 1593–1604 (1963). — 12. KIDWELL, J. F., M. M. KIDWELL, W. R. HARVEY, and D. J. NASH: Genotype and temperature effects on body weight and reproduction in *Drosophila melanogaster*. M. S. prepared (1965). — 13. LEVINE, H., and TH. DOBZHANSKY: New evidence of heterosis in naturally occurring heterozygotes in *Drosophila pseudoobscura*. Heredity **12**, 37–49 (1958). — 14. SCHNELL, F. W.: Some general formulations of linkage effects in inbreeding. Genetics **46**, 947–957 (1961). — 15. TANEJA, G. C., and S. NEGI: Estimates of covariances between full sibs and between half sibs for bristle number and wing length in samples of *Drosophila* bred to varying levels of inbreeding. Jour. Genetics **58**, 347–357 (1963). — 16. TANTAWY, A. O., and E. C. R. REEVE: Studies in Quantitative Inheritance. IX. The effects of inbreeding at different rates in *Drosophila melanogaster*. Z. indukt. Abstamm. u. Vererblehre **87**, 648–667 (1956). — 17. TANTAWY, A. O., and M. O. VETUKHIV: Effects of size on fecundity, longevity and viability in populations of *Drosophila pseudoobscura*. Amer. Nat. **94**, 395–403 (1960). — 18. VAN AARDE, I. M. R.: Covariances of relatives in random mating populations with linkage. Ph. D. Thesis. Iowa State Univ. Library (1963). — 19. WRIGHT, S.: Coefficients of inbreeding and relationship. Am. Nat. **56**, 330–338 (1922). — 20. WRIGHT, S.: The analysis of variance and the correlations between relatives with respect to deviations from an optimum. J. Genet. **30**, 243–256 (1935).