A STATISTICAL STUDY OF QUANTITATIVE CHARACTERS WITH SPECIAL REFERENCE TO PLANT BREEDING

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CONTENTS

1. INTRODUCTION

APPRECIABLE progress has been made in recent years in the development of suitable statistical techniques for the genetic analysis of data concerning quantitative characters on plant material. Methods are now available for the estimation of genetic component of observed variability, the possible number of genetic factors producing variability, dominance effects, etc. The bearing of these aspects of the genetic situation on the advance by selection and the prediction of the magnitude of advance expected from a given intensity of selection have been considered by Panse (1940 *a*). He developed for this purpose an approach of great potential value (Panse, 1940 *b*). The present investigation was undertaken to extend the application of this approach to a somewhat wider range of conditions than those examined by Panse.

2. GENETIC MODELS

Panse studied the effects of selection in five model F_2 populations resulting from self-fertilization of heterozygotes with hypothetical systems of genetic factors leading to certain statistical and genetical consequences. The amounts of genotypic and environmental variabilities in F_2 were assumed to be 1·5 units each in all the five models and

three as the effective number of factors in each case (with the exception of Model V in which it was 32/11), these values being adopted as agreeing with the analysis of fibre-length data from three cotton crosses within the species *G. arboreum.* The models studied were as follows:—

I. No dominance, factors in a geometric series and represented as,

$$\left.\begin{array}{llll} AA + \sqrt{\tfrac{3}{2}} & BB + \sqrt{\tfrac{3}{4}} & CC + \sqrt{\tfrac{3}{8}} \\[4pt] Aa \quad\;\; 0 & Bb \quad\;\; 0 & Cc \quad\;\; 0 \\[4pt] aa \;\; -\sqrt{\tfrac{3}{2}} & bb \;-\sqrt{\tfrac{3}{4}} & cc \;\; -\sqrt{\tfrac{3}{8}} \end{array}\right\}$$ etc., with the common ratio $= \dfrac{1}{\sqrt{2}}$.

II. No dominance, three equal factors

$$\begin{array}{llll} AA + 1 & BB + 1 & CC + 1 \\ Aa \quad 0 & Bb \quad 0 & Cc \quad 0 \\ aa \;-1 & bb \;-1 & cc \;-1 \end{array}$$

III. Balanced dominance, factors in two geometric series with complete dominance in opposite directions.

Series I.—

$$\left.\begin{array}{lll} AA + \dfrac{2}{\sqrt{5}} & BB + \dfrac{2}{5} & CC + \dfrac{2}{5\sqrt{5}} \\[8pt] Aa + \dfrac{2}{\sqrt{5}} & Bb + \dfrac{2}{5} & Cc + \dfrac{2}{5\sqrt{5}} \\[8pt] aa - \dfrac{2}{\sqrt{5}} & bb - \dfrac{2}{5} & cc - \dfrac{2}{5\sqrt{5}} \end{array}\right\}$$ etc.,

Series II.—

$$\left.\begin{array}{lll} A'A' + \dfrac{2}{\sqrt{5}} & B'B' + \dfrac{2}{5} & C'C' + \dfrac{2}{5\sqrt{5}} \\[8pt] A'a' - \dfrac{2}{\sqrt{5}} & B'b' - \dfrac{2}{5} & C'c' - \dfrac{2}{5\sqrt{5}} \\[8pt] a'a' - \dfrac{2}{\sqrt{5}} & b'b' - \dfrac{2}{5} & c'c' - \dfrac{2}{5\sqrt{5}} \end{array}\right\}$$ etc.,

each with common ratio $= 1/\sqrt{5}$.

IV. Balanced dominance, three factors with equal F_2 genotypic variance, one without dominance and the other two with complete dominance in opposite directions.

$$\begin{array}{lll} AA + \sqrt{\tfrac{2}{3}} & BB + 1 & CC + \sqrt{\tfrac{2}{3}} \\ Aa + \sqrt{\tfrac{2}{3}} & Bb \quad 0 & Cc - \sqrt{\tfrac{2}{3}} \\ aa - \sqrt{\tfrac{2}{3}} & bb - 1 & cc - \sqrt{\tfrac{2}{3}} \end{array}$$

V. Balanced dominance, three factors of equal magnitude with dominance as in the last case.

$$AA + \sqrt{\tfrac{3}{4}} \quad BB + \sqrt{\tfrac{3}{4}} \quad CC + \sqrt{\tfrac{3}{4}}$$

$$Aa + \sqrt{\tfrac{3}{4}} \quad Bb \quad 0 \quad Cc - \sqrt{\tfrac{3}{4}}$$

$$aa - \sqrt{\tfrac{3}{4}} \quad bb - \sqrt{\tfrac{3}{4}} \quad cc - \sqrt{\tfrac{3}{4}}$$

In this last case the effective number of factors is 32/11.

Results of selection of 10% of the F_2 individuals with highest phenotypic values were worked out in respect of five F_3 properties, namely, (1) the mean value of the progenies, (2) the mean genotypic variance within the progenies, (3) the covariance of means and variances of the progenies, (4) the variance of the mean values of the progenies, and (5) the variance of the genotypic variance within progenies. The analysis assumed additive gene action, independence of segregation of various factors and independence of the environmental variability and the genotype.

The results showed that the values of most of these properties for the various models did not differ appreciably from one another. The most striking difference was observed between the mean values of progenies from dominance and no dominance models, which arises from the reason that a part of the genotypic variance in F_2 is non-additive. The effect of actual number of factors was observed to be small. This is explained by the fact that owing to the restriction imposed on the effective number of factors, the magnitudes of factors in the geometric series in Models I and III decreased rapidly and the results for the selected portion of the population were determined principally by the first few factors thereby negativing to some extent the purpose of setting up models with a large number of factors. In the present investigation the effective number of factors was consequently varied in the different models, the factors being assumed to be of equal magnitude. To study the effect of variation in the proportion of genotypic and environmental variabilities in F_2, different values of the genotypic variance were assumed keeping the magnitude of environmental variance constant. Again while Panse had assumed dominance of the balanced type which permitted the study of dominance effects in one direction on selection, without affecting the relative simplicity of the calculations, models consisting of factors showing dominance in one direction only were set up in the present investigation in order to study explicitly unsymmetrical dominance effects as are evidenced by the phenomenon of heterosis.

F_2 and F_3 data on fibre-length, measured as halo-length, obtained from 16 inter-racial cotton crosses in the species *G. arboreum* were examined to find a suitable range of values to be expected in actual segregating materials of this type of the variants considered, namely, F_2 genotypic variability and the effective number of factors. On the basis of the range of variability observed, models were set up with F_2 genotypic variances of $0 \cdot 5$, $1 \cdot 5$ and $2 \cdot 5$ units, the environmental variance being $2 \cdot 0$ units in each case. The estimates of the effective number of factors obtained from the halo-length data were far from satisfactory being subject to rather large sampling errors. It appeared, however, that the numbers 2, 8 and 32 would cover a sufficiently wide and useful range of the effective number of factors, representing situations involving a small, a moderate and a large number of such factors. There were thus nine combinations of F_2 variability and effective number of factors. In all 18 models were studied, nine with no dominance of factors and nine others similar to these but in which the higher value of the character was assumed fully dominant for all factors. Full dominance was assumed in order to bring out clearly the unsymmetrical effects of dominance.

Models with no dominance were as follows:—

I.	F_2 genotypic variance		$= 0 \cdot 5$ and number of factors		$= 2$
II.	,,	,,	$= 0 \cdot 5$	,,	,,	$= 8$
III.	,,	,,	$= 0 \cdot 5$	,,	,,	$= 32$
IV.	,,	,,	$= 1 \cdot 5$	,,	,,	$= 2$
V.	,,	,,	$= 1 \cdot 5$	,,	,,	$= 8$
VI.	,,	,,	$= 1 \cdot 5$	,,	,,	$= 32$
VII.	,,	,,	$= 2 \cdot 5$	,,	,,	$= 2$
VIII.	,,	,,	$= 2 \cdot 5$	,,	,,	$= 8$
IX.	,,	,,	$= 2 \cdot 5$	,,	,,	$= 32$

A second set of models with dominance will be referred to with the same numbers.

3. METHOD OF STATISTICAL ANALYSIS

As stated earlier the statistical approach adopted in this study is that developed by Panse (1940 *a* and *b*). To start with, the joint distribution of three variates, (1) the phenotypic value of F_2 parent, x_1, (2) the genotypic variance within F_3 progeny, x_2 and (3) the genotypic mean of F_3 progeny, x_3, was studied with the help of moment generating functions and various moments and product-moments of the three variates were obtained for each model. Two types of moment gene-

rating functions were necessary in the present study for the two groups of models with no dominance and with full dominance. The method of obtaining these is described by Panse (1940 b) and the expression given by him for the cumulant function for a single factor with no dominance has been used for obtaining the moments and product-moments given in Tables I–VI below.

TABLE I

Moments of x_1, F_2 phenotypic value for models with no-dominance

Model \ Power of x_1	x_1^2	x_1^4	x_1^6	x_1^8
I	2·50	18·62500000	229·81250000	3946·531250
II	2·50	18·71875000	233·21093750	4061·123779
III	2·50	18·74218750	234·08251953	4091·344845
IV	3·50	35·62500000	587·43750000	13216·031250
V	3·50	36·46875000	628·57031250	15056·151123
VI	3·50	36·67968750	639·44677734	15577·143368
VII	4·50	57·62500000	1171·56250000	31912·031250
VIII	4·50	59·96875000	1315·11718750	39876·112060
IX	4·50	60·55468750	1353·75244141	42234·981137

All odd moments $= 0$ for all models.

TABLE II

Product-moments of x_3, genotypic mean of F_3 progeny and powers of x_1, the F_2 phenotypic value, for models with no-dominance

Model \ Power of x_3 & x_1	$x_3 x_1$	$x_3 x_1^3$
I	0·5000	3·62500000
II	0·5000	3·71875000
III	0·5000	3·74218750
IV	1·5000	14·62500000
V	1·5000	15·46875000
VI	1·5000	15·67968750
VII	2·5000	30·62500000
VIII	2·5000	32·96875000
IX	2·5000	33·55468750

$x_3 = 0$; $x_3 x_1^2 = 0$ and $x_3 x_1^4 = 0$ for all models.

TABLE III

Product-moments of x_2, genotypic variance within progeny and powers of x_1, the F_2 phenotypic value, for models with no-dominance

Power of x_2 & x_1 Model	$x_2 x_1^2$	$x_2 x_1^4$
I	—0·06250000	— 0·87500000
II	—0·01562500	— 0·23046875
III	—0·00390625	— 0·05834961
IV	—0·56250000	—10·12500000
V	—0·14062500	— 2·84765625
VI	—0·03515625	— 0·73168945
VII	—1·56250000	—34·37500000
VIII	—0·39062500	—10·05859375
IX	—0·09765625	— 2·60620117

$x_2 = 0$, $x^2 x_1 = 0$ and $x_3 x_1^3 = 0$ for all models.

TABLE IV

Product-moments of x_3^2 and powers of x_1, for models with no-dominance

Power of x_3^2 & x_1 Model	x_3^2	$x_3^2 x_1^2$	$x_3^2 x_1^4$
I	0·5000	1·62500000	14·56250000
II	0·5000	1·71875000	16·27343750
III	0·5000	1·74218750	16·72314452
IV	1·5000	8·62500000	114·18750000
V	1·5000	9·46875000	140·13281250
VI	1·5000	9·67968750	147·21240234
VII	2·5000	20·62500000	350·31250000
VIII	2·5000	22·96875000	451·67968750
IX	2·5000	23·55468750	479·76806625

$x_3^2 x_1 = 0$ and $x_3^2 x_1^3 = 0$ for all models.

TABLE V

Product-moments of $x_2 x_3$ *and powers of* x_1 *for models with no-dominance*

Power of $x_2 x_3$ & x_1 / Model	$x_2 x_3 x_1$	$x_2 x_3 x_1^3$
I	−0·06250000	− 0·62500000
II	−0·01562500	− 0·13671875
III	−0·00390625	− 0·03491211
IV	−0·56250000	− 6·75000000
V	−0·14062500	− 2·00390625
VI	−0·03515625	− 0·52075195
VII	−1·56250000	−25·00000000
VIII	−0·39062500	− 7·71484375
IX	−0·09765625	− 2·02026367

$x_2 x_3 = 0$, $x_2 x_3 x_1^2 = 0$ and $x_2 x_3 x_1^4 = 0$ for all models.

TABLE VI

Product-moments of x_2^2 *and powers of* x_1, *for models with no-dominance*

Power of x_2^2 & x_1 / Model	x_2	$x_2 x_1^2$	$x_2 x_1^4$
I	0·0312500000	0·0781250000	0·59375000
II	0·0078125000	0·0195312500	0·14752197
III	0·0019531250	0·0048828125	0·03669453
IV	0·2812500000	0·9843750000	10·96875000
V	0·0703125000	0·2460937500	2·66802978
VI	0·0175781250	0·0615234375	0·65194416
VII	0·7812500000	3·5156250000	52·34375000
VIII	0·1953125000	0·8789062500	12·51373292
IX	0·0488281250	0·2197265625	3·01220416

$x_2 x_1 = 0$ and $x_2 x_1^3 = 0$ for all models.

To obtain moments and product-moments for models with dominance, the cumulant function for a single factor with full dominance was obtained as for no dominance model. This is given in Table VII below. In this table which corresponds to Table II in the reference, Panse, 1940 b, the symbols a and V stand for the magnitude of the factor and the environmental component of the F_2 variance respectively.

TABLE VII

Cumulant function for a single factor model with full dominance

Powers of t_2 & t_3 / Powers of t_1	0	t_2	$t_2{}^2$	t_3	$t_2 t_3$	$t_3{}^2$
0	..	..	$\dfrac{9a^4}{128}$	..	$\dfrac{3a^3}{32}$	$\dfrac{9a^2}{32}$
1	..	$\dfrac{3a^3}{16}$	..	$\dfrac{5a^2}{8}$	$-\dfrac{3a^4}{16}$	$-\dfrac{a^3}{4}$
2	$\dfrac{3a^2}{8}+\dfrac{V}{2}$	$-\dfrac{3a^4}{32}$	$-\dfrac{9a^6}{512}$	$-\dfrac{5a^3}{16}$	$-\dfrac{3a^5}{128}$	$-\dfrac{9a^4}{128}$
3	$-\dfrac{a^3}{8}$	$-\dfrac{a^5}{64}$	$\dfrac{9a^7}{512}$	$-\dfrac{5a^4}{96}$	$\dfrac{17a^6}{128}$	$\dfrac{83a^5}{384}$
4	$-\dfrac{a^4}{64}$	$\dfrac{5a^6}{128}$	$-\dfrac{3a^8}{2048}$	$\dfrac{25a^5}{192}$	$-\dfrac{25a^7}{512}$	$-\dfrac{35a^6}{512}$
5	$\dfrac{a^5}{32}$					
6	$-\dfrac{13a^6}{1920}$					
7	$-\dfrac{11a^7}{1920}$					
8	$\dfrac{823a^8}{215040}$					

With the help of this cumulant function moments and product-moments for the nine models with dominance were calculated and these are presented in Tables VIII–XIII.

From the moments and product-moments given in Tables I–VI and VIII–XIII fourth degree equations for the regression of five F_3 properties on x_1, the phenotypic value of the F_2 parent, were calculated for each model. The five F_3 properties are—(1) x_3, the genotypic

TABLE VIII

Moments of x_1, the F_2 phenotypic value, for models with dominance

Power of x_1 Model	x_1^2	x_1^3	x_1^4	x_1^5	x_1^6	x_1^7	x_1^8
I	2·5000	−0·28867513	18·66666667	− 6·73575314	231·72222222	− 164·57690173	4021·518518
II	2·5000	−0·14433757	18·72916667	− 3·54829853	233·77951389	− 91·49748836	4086·810836
III	2·5000	−0·07216878	18·74479167	− 1·79670201	234·33036024	− 46·95414141	4098·245152
IV	3·5000	−1·50000000	36·00000000	− 45·00000000	616·50000000	−1396·50000000	14775·000000
V	3·5000	−0·75000000	36·56250000	− 25·31250000	638·29687500	− 892·70000000	15732·427730
VI	3·5000	−0·37500000	36·70312500	− 13·00781250	642·03222610	− 473·17163086	15767·747955
VII	4·5000	−3·22748612	58·66666667	−118·34115780	1285·27777778	−4430·621226	39306·851852
VIII	4·5000	−1·61374306	60·22916667	− 69·25647303	1354·93923611	−3094·884630	43510·383753
IX	4·5000	−0·80687153	60·61979167	− 35·88897328	1364·42003038	−1672·557306	43283·133336

TABLE IX

Product-moments of x_3 and powers of x_1 for models with dominance

| Power of x_3 & x_1 / Model	$x_3 x_1$	$x_3 x_1^2$	$x_3 x_1^3$	$x_3 x_1^4$
I	0·41666667	—0·24056261	3·05555556	— 3·68862672
II	0·41666667	—0·12028131	3·10763889	— 1·99466499
III	0·41666667	—0·06014065	3·12065972	— 1·01612645
IV	1·25000000	—1·25000000	12·50000000	—27·50000000
V	1·25000000	—0·62500000	12·96875000	—16·09375000
VI	1·25000000	—0·31250000	13·08593750	—8·33984375
VII	2·08333333	—2·68957177	26·38888889	—77·10105735
VIII	2·08333333	—1·34478588	27·69097222	—46·95544045
IX	2·08333333	—0·67239294	28·01649305	—24·52833420

$x_3 = 0$ for all models

TABLE X

Product-moments of x_2 and powers of x_1 for models with dominance

Power of x_2 & x_1 / Model	$x_2 x_1$	$x_2 x_1^2$	$x_2 x_1^3$	$x_2 x_1^4$
I	0·07216878	—0·04166667	0·52923775	— 0·63888889
II	0·03608439	—0·01041667	0·26912942	— 0·17274306
III	0·01804219	—0·00260417	0·13512853	— 0·04399957
IV	0·37500000	—0·37500000	3·75000000	— 8·25000000
V	0·18750000	—0·09375000	1·94531250	— 2·41406250
VI	0·09375000	—0·02343750	0·98144531	— 0·62548828
VII	0·80687153	—1·04166667	10·89276566	—29·8611111
VIII	0·40343576	—0·26041667	5·36233371	— 9·
IX	0·20171788	—0·06510417	2·60417833	

$x_2 = 0$ for all models
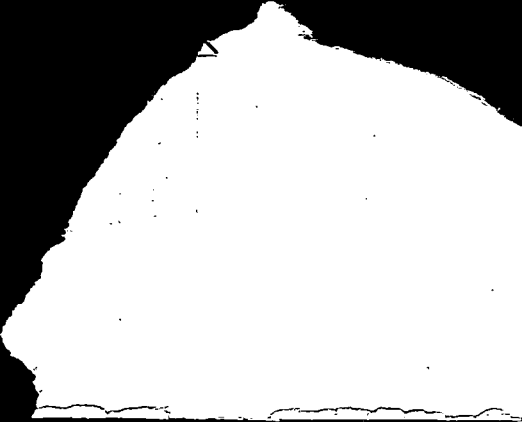
709288194

− 2·37494575

TABLE XI

Product-moments of $x_2{}^2$ and powers of x_1 for models with dominance

Power of $x_2{}^2$ & x_1 Model	$x_2{}^2$	$x_2{}^2x_1{}^2$	$x_2{}^2x_1{}^3$	$x_2{}^2x_1{}^4$
I	0·03125000	0·08333333	—0·01804220	0·66319444
II	0·00781250	0·02180990	—0·00310100	0·18069119
III	0·00195312	0·00551351	—0·00041605	0·04608451
IV	0·28125000	1·12500000	—0·84375000	13·21875000
V	0·07031250	0·30761719	—0·14501953	3·87817383
VI	0·01757812	0·07855246	—0·01936340	1·00384140
VII	0·78125000	4·16666667	—5·04294707	64·49652777
VIII	0·19531250	1·16373698	—0·86675653	19·57261827
IX	0·04882812	0·29856364	—0·11573170	5·09676403

$x_2{}^2x_1 = 0$ for all models

TABLE XII

Product-moments of x_2x_3 and powers of x_1 for models with dominance

Power of x_2x_3 & x_1 Model	x_2x_3	$x_2x_3x_1$	$x_2x_3x_1{}^2$	$x_2x_3x_1{}^3$	$x_2x_3x_1{}^4$
I	0·03608439	—0·04166667	0·14433757	— 0·36805556	1·50351633
II	0·01804220	—0·01041667	0·07442406	— 0·10308160	0·78464758
III	0·00902110	—0·00260417	0·03749394	— 0·02646213	0·39423255
IV	0·18750000	—0·37500000	1·50000000	— 5·43750000	25·31250000
V	0·09375000	—0·09375000	0·78515625	— 1·65820312	13·35058594
VI	0·46875000	—0·02343750	0·39697266	— 0·43322754	6·65908813
VII	0·40343576	—1·04166667	4·84122918	—21·00694444	110·40692108
VIII	0·20171788	—0·26041667	2·54668827	— 6·63519965	58·34479632
IX	0·10085894	—0·06510417	1·28910334	— 1·74526638	28·94947101

TABLE XIII

Product-moments of x_3^2 and powers of x_1 for models with dominance

Power of x_3^2 & x_1 Model	x_3^2	$x_c^2 x_1$	$x_3^2 x_1^2$	$x_3^2 x_1^3$	$x_3^2 x_1^4$
I	0·37500000	−0·19245009	1·22222222	−1·82025710	11·36574074
II	0·37500000	−0·09622504	1·26909722	−1·03492040	12·06669560
III	0·37500000	−0·04811252	1·28081597	− 0·53305918	12·19920971
IV	1·12500000	−1·00000000	6·50000000	−16·37500000	96·87500000
V	1·12500000	−0·50000000	6·92187500	−10·13281250	105·67578125
VI	1·12500000	−0·25000000	7·02734375	− 5·30957031	106·72241211
VII	1·87500000	−2·15165741	15·55555556	−50·11568728	314·05092592
VIII	1·87500000	−1·07582871	16·72743056	−32·03392041	345·42028356
IX	1·87500000	−0·53791435	17·02039930	−16·88896980	347·92204680

mean of F_3 progeny; (2) x_2, the genotypic variance within F_3 progeny; (3) $x_2 x_3$, the product of progeny mean and variance within progeny; (4) x_3^2, the square of the progeny mean and (5) x_2^2, the square of the genotypic variance within F_3 progeny. The last three quantities are basic to the calculation of the covariance of F_3 progeny mean and variance within progeny, the variance of progeny mean and the variance of variance within progeny respectively. Since equations for the regression of five dependent variates on the same independent variate are to be calculated, it is convenient to obtain the covariance matrix for each model from the moments of x_1, the independent variate. This was done for all the eighteen models. In models with no dominance the odd moments are all zero and consequently alternate C-coefficients in the matrices are also zero.

By taking product-moments corresponding to a model and a particular dependent variate, we obtain the coefficients, A, B, C, D and E in a regression equation of the type

$$Y = A + Bx_1 + Cx_1^2 + Dx_1^3 + Ex_1^4$$

where Y stands for one of the five properties to be studied. These coefficients were obtained for all the eighteen models for each of the five properties.

It is found that in no-dominance models the coefficients A, C and E turn out to be zero for properties x_3 and x_2x_3 while coefficients B and D are zero in equations for the remaining three properties giving equations of the form

$$Y = Bx_1 + Dx_1^3$$

and

$$Y = A + Cx_1^2 + Ex_1^4$$

in the two cases respectively. In dominance models, however, none of the coefficients are zero and consequently equations for all five properties take the form

$$Y = A + Bx_1 + Cx_1^2 + Dx_1^3 + Ex_1^4$$

The regression coefficients for the various properties are given below, for no-dominance models in Tables XIV and XV and for dominance models in Tables XVI–XX.

TABLE XIV

Regression coefficients for x_3 *and* x_2x_3 *for models with no-dominance*

| | (Equations of the type $Y = Bx_1 + Dx_1^3$) | | | |
| Model | x_3 | | x_2x_3 | |
	B	D	B	D
I	0·20818175	—0·00109822	—0·01196033	—0·00175029
II	0·20201159	—0·00026866	—0·00466273	—0·00021199
III	0·20050073	—0·00006679	—0·00111165	—0·00006014
IV	0·45767558	—0·00285935	—0·11432954	—0·00455710
V	0·43530807	—0·00064653	—0·01760032	—0·00216689
VI	0·43022237	—0·00015753	—0·00378589	—0·00059721
VII	0·59656974	—0·00320384	—0·19982744	—0·01151022
VIII	0·56452399	—0·00067298	—0·02199530	—0·00486330
IX	0·55772318	—0·00016108	—0·00131036	—0·00131036

TABLE XV

Regression coefficients for x_2, $x_2{}^2$ and $x_3{}^2$ for models with no-dominance

(Equations of the type $Y = A + Cx_1{}^2 + Ex_1{}^4$)

Model	x_2			$x_2{}^2$			$x_3{}^2$		
	A	C	E	A	C	E	A	C	E
I	0·01367478	—0·00589456	0·00005700	0·03149328	—0·00019584	0·00001322	0·41795131	0·03536736	—0·00034200
II	0·00319611	—0·00130384	0·00000339	0·00783840	—0·00002074	0·00000138	0·40411676	0·03911509	—0·00010174
III	0·00078566	—0·00031583	0·00000021	0·00195490	—0·00000142	0·00000009	0·40100721	0·03979477	—0·00002636
IV	0·09643736	—0·03124617	0·00036278	0·29271989	—0·00674515	0·00034072	0·92137584	0·18747705	—0·00217671
V	0·02097342	—0·00618118	0·00001812	0·07142080	—0·00063812	0·00003085	0·87079736	0·18543541	—0·00054352
VI	0·00507577	—0·00146140	0·00000107	0·01765227	—0·00004245	0·00000203	0·86045334	0·18413661	—0·00013445
VII	0·21918501	—0·05632519	0·00059485	0·84170778	—0·02826324	0·00115795	1·18488994	0·33795116	—0·00356911
VIII	0·04573103	—0·01049861	0·00002522	0·20065062	—0·00240321	0·00009132	1·12806917	0·31495822	—0·00075675
IX	0·01098904	—0·00246119	0·00000142	0·04917695	—0·00015553	0·00000580	1·11538065	0·31011008	—0·00017961

TABLE XVI

Regression coefficients for x_3 for models with dominance

Model	A	B	C	D	E
I	0·04428068	0·17348043	−0·01980691	−0·00111987	0·00026321
II	0·01993925	0·16858620	−0·00821887	−0·00031387	0·00003004
III	0·00971642	0·16716050	−0·00391958	−0·00008056	0·00000409
IV	0·13361213	0·38785969	−0·04468278	−0·00428017	0·00045437
V	0·05402966	0·36675372	−0·01585626	−0·00123593	0·00001480
VI	0·02585539	0·35960409	−0·00742770	−0·00031035	0·00000069
VII	0·18892491	0·51677480	−0·04910556	−0·00644199	0·00019190
VIII	0·07045438	0·47922775	−0·01562876	−0·00168832	−0·00004731
IX	0·03361551	0·46688100	−0·00744302	−0·00039421	−0·00000726

TABLE XVII

Regression coefficients for x_2 for models with dominance

Model	A	B	C	D	E
I	0·00766964	0·03004250	−0·00343066	−0·00019397	0·00004559
II	0·00172679	0·01459999	−0·00071178	−0·00002718	0·00000260
III	0·00042073	0·00723826	−0·00016972	−0·00000349	0·00000018
IV	0·04008364	0·11635788	−0·01340483	−0·00128405	0·00013631
V	0·00810445	0·05501306	−0·00237844	−0·00018525	0·00000222
VI	0·00193915	0·02697031	−0·00055708	−0·00002328	0·00000005
VII	0·07571521	0·17242232	−0·02325244	−0·00006891	0·00040660
VIII	0·01364343	0·09280105	−0·00302650	−0·00032694	−0·00000916
IX	0·00286282	0·04804617	−0·00050963	−0·00025337	−0·00001277

TABLE XVIII

Regression coefficients for x_3^2 for models with dominance

Model	A	B	C	D	E
I	0·31956784	−0·19898022	0·02333770	−0·00222992	−0·00019048
II	0·30937824	−0·02042714	0·02647182	−0·00221593	−0·00004686
III	0·30646854	−0·00917320	0·02749004	−0·00123888	−0·00001510
IV	0·77771351	−0·13000651	0·10878463	−0·01241392	−0·00144668
V	0·70079319	−0·01584263	0·12512824	−0·00999405	−0·00058086
VI	0·68371513	−0·00409676	0·12723010	−0·00517839	−0·00016245
VII	1·12862284	−0·11297408	0·18408978	−0·02328753	−0·00267931
VIII	0·95088241	0·02210012	0·21461444	−0·01502116	−0·00109397
IX	0·91893946	0·01181074	0·21515365	−0·00706067	−0·00029409

TABLE XIX

Regression coefficients for $x_2 x_3$ for models with dominance

Model	A	B	C	D	E
I	0·02278062	−0·00855267	0·00670705	−0·00045105	−0·00019254
II	0·01225949	−0·00261197	0·00233362	−0·00019034	−0·00000421
III	0·00604145	−0·00060616	0·00119525	−0·00005354	−0·00000066
IV	0·07529732	−0·06227353	0·03531635	−0·00346736	−0·00046127
V	0·02930853	−0·00787770	0·01900708	−0·00148058	−0·00008735
VI	0·01368168	−0·00165577	0·00957011	−0·00038722	−0·00001219
VII	0·90547265	−0·09543215	0·07620822	−0·00837502	−0·00105688
VIII	0·02100192	−0·00770102	0·04195063	−0·00286663	−0·00021066
IX	0·00807868	−0·00177444	0·02087868	−0·00068118	−0·00002843

TABLE XX

Regression coefficients for $x_2{}^2$ for models with dominance

Model	A	B	C	D	E
I	0·03031422	0·00065894	0·00042568	−0·00008242	−0·00000206
II	0·00735488	0·00013880	0·00018430	−0·00001716	−0·00000030
III	0·00182672	0·00001916	0·00006984	−0·00000236	−0·00000003
IV	0·25961429	0·01622530	0·00657346	−0·00142542	−0·00009749
V	0·06125411	0·00294432	0·00267268	−0·00023598	−0·00001294
VI	0·01512491	0·00038151	0·00070735	−0·00002948	−0·00000091
VII	0·69856155	0·06311230	0·02000607	−0·00449112	−0·00037216
VIII	0·16202243	0·01010896	0·00774539	−0·00059599	−0·00004194
IX	0·03994643	0·00124086	0·00199905	−0·00006715	−0·00000277

The regression equations for x_3, the genotypic mean of F_3 progeny and x_2, the genotypic variance within F_3 progeny are presented graphically in Figs. 1–4 these two properties being directly relevant to selection. Figures 1 and 2 give the results for x_3, for no-dominance and dominance models respectively and Figs. 3 and 4 represent the results for x_2 similarly.

From Figs. 1 and 2 it would be seen that the regression of progeny mean on parental value is approximately linear over a wide range of F_2 phenotypes especially for the models with larger number of factors. This can also be judged from the small values of the regression coefficients for higher powers of x_1. The ideal curves become parallel to the axis of x at values of Y represented by the maximum and minimum genotypic values. A polynomial can represent such curves only over a certain range. It is easy to see that after the polynomials have turned back the fit is poor. It can be seen from Fig. 1 that this happens within the range of plotted values only for models with two factors and it may be pointed out that even here the fraction of F_2 outside the range beyond which the curves turn back is less than 0·0001. From Fig. 2 it is seen that the curves turn back sooner on the right of origin, *i.e.*, for positive values of deviation from the F_2 mean, than they do on the other side of the mean. This is due to the fact that the maximum genotypic value is much nearer the mean of F_2 than the minimum in the presence of dominance of high value. Even so the

fraction of F_2 population beyond the points at which the curves turn back is less than $0 \cdot 001$ in all cases.
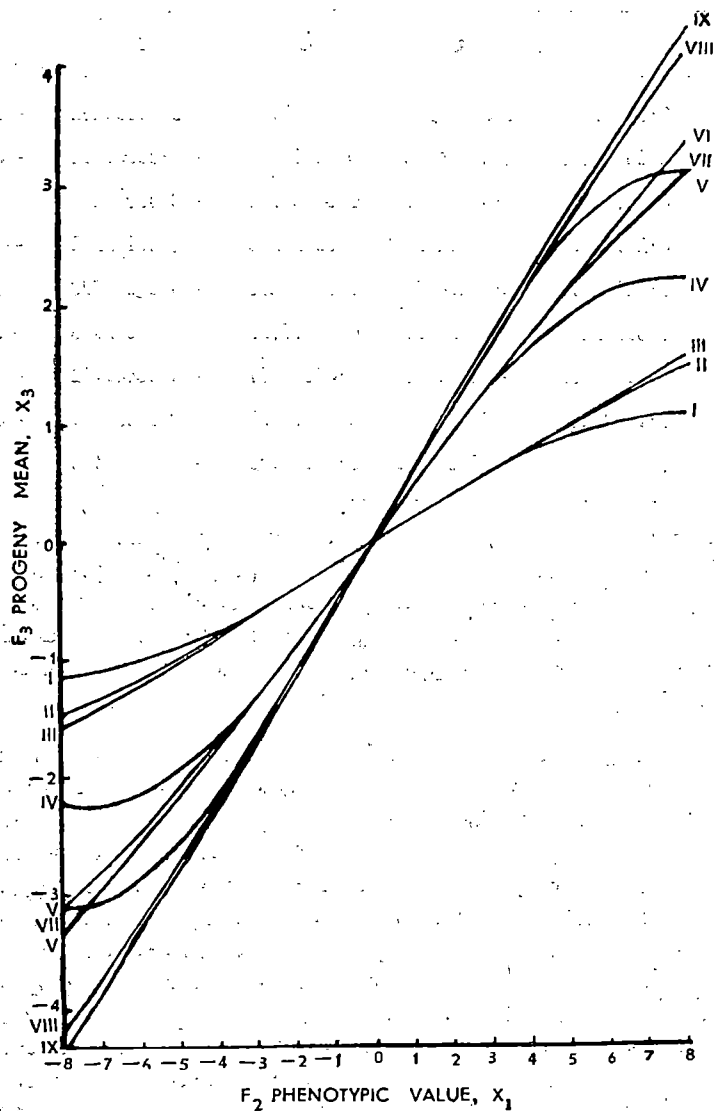

FIG. 1. Relation between x, the genotypic mean of F_3 progeny and x_1, the F_2 phenotypic value (No-dominance models).

Effects of various characteristics of the models on the relation between the phenotypic value of F_2 parent and the genotypic mean of the resulting progeny can be seen from these figures. The most striking

point about the curves is, perhaps, the considerable divergence between the curves for models with different F_2 genotypic variances. This is to be expected. The corresponding curves obtained by Panse (1940 b).
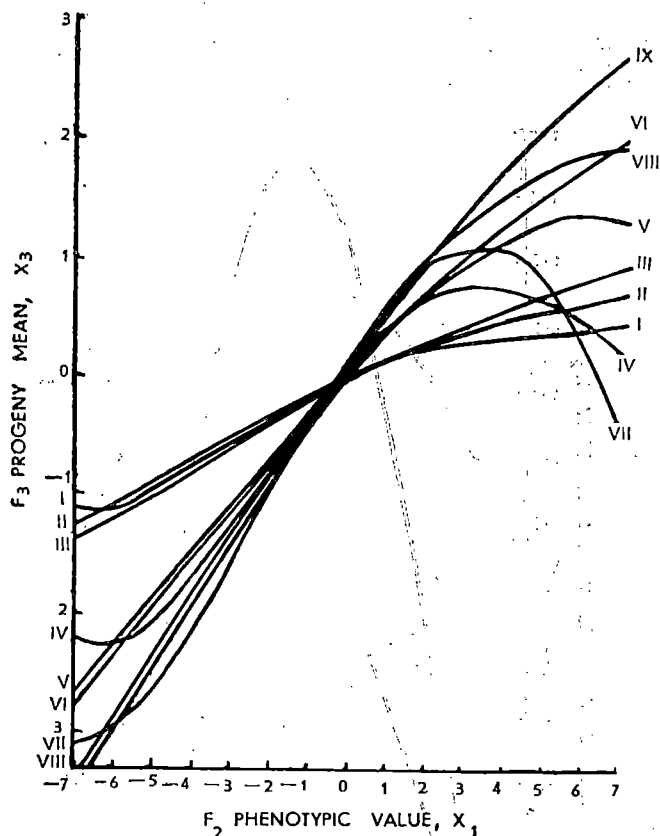
FIG. 2. Relation between x_3, the genotypic mean of F_3 progeny and x_1, the F_2 phenotypic value (Dominance models).

differed very little from model to model on account of the fact that F_2 genotypic variance was the same in all models. The curves also indicate the effect of dominance in lowering the advance by selection, for by comparing the curves for the corresponding no-dominance and dominance models in Figs. 1 and 2 we find that the slope is steeper for the former, *i.e.*, selection of individuals having any particular phenotypic value would give F_3 progenies having a higher mean value on an average in the no-dominance case than when dominance is present. The effect of asymmetrical nature of dominance on the relation of progeny mean (x_3) and parental value (x_1) is seen from the different behaviour of curves in Fig. 2 on the right and the left of the origin, an effect.

already remarked upon in the previous paragraph. The effect of the number of factors on the relation, however, seems to be small especially for curves in Fig. 1 for the no-dominance models. Even in dominance models, it will be seen from Fig. 2, that the difference between curves for models with 8 and 32 factors is much less than that between these and the 2-factor models.
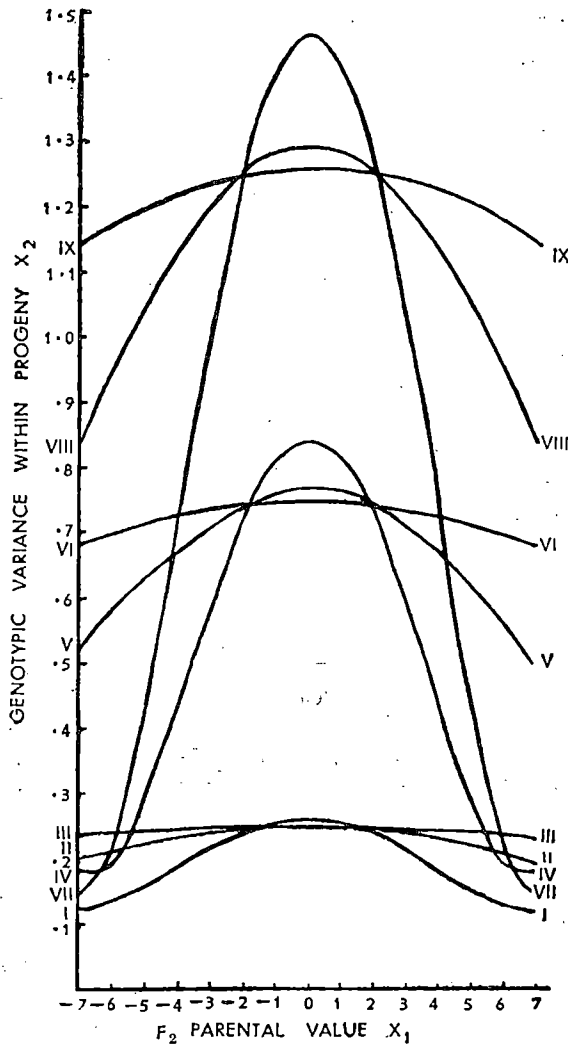

FIG. 2. Relation between x_2, the genotypic variance within F_3 progeny and x_1, the F_2 phenotypic value (No-dominance models).

In drawing curves in Figs. 3 and 4 the mean value of genotypic variance within F_3 progeny for the particular model has been added to the values calculated from the regression equation in the case of each curve. The values of variance represented in Figs. 3 and 4 are
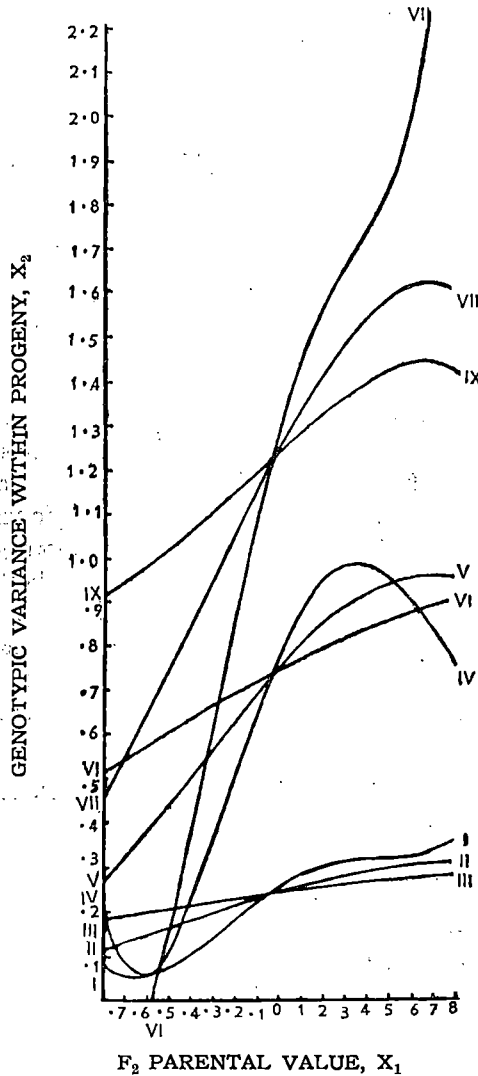
FIG. 4. Relation between x_2, the genotypic variance within F_3 progeny and x_1, the F_2 phenotypic value (Dominance models).

thus absolute values and not deviations from the mean variance within progeny. On account of the differences in these means for the three groups of models having common genotypic variance in F_2 the curves

are far separated. The curves thus differ from one another more widely than the corresponding curves for Panse's models (1940 b, Fig. 2). This is to be expected since all the five models studied by Panse assumed a common genotypic variance in F_2. The curves for our dominance models in Fig. 4 are seen to differ very notably, both from the curves for no-dominance models in Fig. 3 and from the curves for Panse's models, just referred to, in being unsymmetrical. While both the latter sets of curves slope symmetrically downwards as we move away from the F_2 mean, the curves in Fig. 4 rise on the right of the origin and fall on the left of it. As pointed out earlier in connection with curves in Figs. 1 and 2 a polynomial connot represent the ideal curves towards the extremes. This, however, is not of much consequence in our study of the effects of selection as the fraction of F_2 population having such extreme phenotypic values is quite small. It will also be noted from Figs. 3 and 4 that curves for models having a common genotypic variance but differing in the number of factors differ appreciably amongst themselves both for dominance and no-dominance models, which again is unlike curves for Panse's models. The difference is due to the fact that, unlike the models considered by Panse, the present models differ in the effective number of factors. With a larger value for the effective number of factors the fall of genotypic variance within progeny (x_2) as we move away from the mean is more gradual in no-dominance models (Fig. 3). In dominance models, both the rise on the right of the origin and the fall on the left of it are more gradual with increasing number of factors. Thus with a larger number of factors variance is conserved at the extremes of the F_2 distribution owing to the presence of a larger number of heterozygotes in the corresponding F_3 progenies.

4. F_3 STATISTICAL PROPERTIES OF SELECTED PORTION OF F_2 POPULATION

After obtaining the regression equations of the five quantities on x_1, the F_2 phenotypic value, as described in the last section, the mean values of five F_3 properties corresponding to the selected portion of the F_2 population were obtained by the method used by Panse. However, certain changes were necessary in the expressions given by Panse in order to take into account the asymmetrical nature of the F_2 distributions in dominance models. It was also intended to study the effect of selection at both ends of the F_2 populations with dominance in one direction.

Corresponding to each model, the deviate of the F_2 distribution, ξ, was calculated for two levels of selection, viz., 10% and 5%; in the

case of dominance models this deviate was calculated for selection at both ends. The deviate ξ is expressible in terms of the normal deviate x for the same probability by means of polynomials in x and coefficients a, b, c, d, e, etc., which depend on the cumulants, k_1, k_2, etc., of the distributions under study by the relations $k_1 - m = av^{\frac{1}{2}}$, $k_2 - v = bv$, $k_3 = cv^{3/2}$, etc. m and v being respectively the mean and variance of the normal distribution (Cornish and Fisher, 1937). We choose $m = 0$ and $v = k_2$ and so the expression for ξ reduces to

$$\xi = x + \frac{1}{6} c (x^2 - 1) + \frac{1}{24} d (x^3 - 3x) - \frac{1}{36} c^2 (2x^3 - 5x)$$

$$+ \frac{1}{120} e (x^4 - 6x^2 + 3) - \frac{1}{24} cd (x^4 - 5x^2 + 2)$$

$$+ \frac{1}{324} c^3 (12x^4 - 53x^2 + 17) + \frac{1}{720} f (x^5 - 10x^3 + 15x)$$

$$- \frac{1}{384} d^2 (3x^5 - 24x^3 + 29x) - \frac{1}{180} ce (2x^5 - 17x^3 + 21x)$$

$$+ \frac{1}{288} c^2 d (14x^5 - 103x^3 + 107x)$$

$$- \frac{1}{7776} c^4 (252x^5 - 1688x^3 + 1511x)$$

Substituting for x and polynomials in x corresponding to the two levels of selection we obtain

$$\xi = 1 \cdot 28155 \quad + 0 \cdot 10706\, c \quad - 0 \cdot 07249\, d$$
$$+ 0 \cdot 06106\, c^2 - 0 \cdot 03464\, e \quad + 0 \cdot 14644\, cd$$
$$- 0 \cdot 11629\, c^3 + 0 \cdot 00227\, f \quad + 0 \cdot 00776 d^2$$
$$+ 0 \cdot 01086\, ce - 0 \cdot 10858 c^2\, d + 0 \cdot 09585 c^4$$

for the 10% level of selection, i.e., $P = 0 \cdot 1$ and

$$\xi = 1 \cdot 64485 + 0 \cdot 28426\, c - 0 \cdot 02018\, d - 0 \cdot 01878\, c^2$$
$$- 0 \cdot 04928\, e + 0 \cdot 17532\, cd - 0 \cdot 11900\, c^3$$
$$- 0 \cdot 01082 f + 0 \cdot 05985\, d^2 + 0 \cdot 09462\, ce$$
$$- 0 \cdot 39517\, c^2 d + 0 \cdot 25623\, c^4$$

for the 5% level of selection or $P = 0 \cdot 05$.

In the case of no-dominance models the coefficients c and e are also zero and for those models the expressions reduce further to

$$\xi = 1 \cdot 28155 - 0 \cdot 07249\, d + 0 \cdot 00227\, f + 0 \cdot 00776\, d^2$$

and

$$\xi = 1 \cdot 64485 - 0 \cdot 02018\,d - 0 \cdot 01082\,f + 0 \cdot 05985\,d^2$$

respectively for the two levels of selection. By substituting the numerical values of the coefficients c, d, e, etc., corresponding to each model, the values of ξ, were obtained for all models. For selection of low value, *i.e.*, at the lower end of the F_2 distribution, the values of ξ, were obtained by giving to the odd cumulants negative values, changing the sign of the corresponding terms in the above expression and taking this as the numerical value of ξ. Actually the deviate would be negative being on the other side of the mean. The values of ξ are given in Table XXI.

TABLE XXI

Values of ξ for 10% and 5% selection

Model	10% Selection ($P = 0 \cdot 1$)			5% Selection ($P = 0 \cdot 05$)		
	Dominance models		No-dominance models	Dominance models		No-dominance models
	High value	Low value		High value	Low value	
I	1·273447	−1·292081	1·283020	1·622041	−1·667923	1·645195
II	1·277773	−1·285967	1·281910	1·634241	−1·655546	1·644951
III	1·279654	−1·283610	1·281640	1·639639	−1·650087	1·644879
IV	1·256096	−1·320916	1·288450	1·565315	−1·720025	1·646360
V	1·269821	−1·297017	1·283230	1·610318	−1·679210	1·645295
VI	1·275728	−1·288324	1·281970	1·628389	−1·661330	1·644968
VII	1·246880	−1·343474	1·293310	1·522478	−1·755004	1·647538
VIII	1·265499	−1·304721	1·284380	1·593885	−1·695032	1 645605
IX	1·273219	−1·291695	1·282250	1·620484	−1·669167	1·645047

The above values of ξ are in standard measure. The values of the actual deviates of the F_2 distribution will be given by $\xi\sigma$, where σ is the standard deviation of the distribution. The mean value of any F_3 property Y for the selected portion of the population is obtained from the integral

$$\int_{\xi\sigma}^{\infty} Y f(x_1)\,dx_1$$

where $f(x_1)\,dx_1$ is the frequency element, by dividing this integral by the fraction of the F_2 population selected, *i.e.*, by 0·1 and 0·05 for the two levels of selection. Putting

$$Y = A + Bx_1\ Cx_1{}^2 + Dx_1{}^3 + Ex_1{}^4$$

we have the integral equal to

$$\int_{\xi\sigma}^{\infty}(A + Bx_1 + Cx_1{}^2 + Dx_1{}^3 + Ex_1{}^4)f(x_1)\,dx_1$$

Following the method by which Panse (1940 b) deduced the expression for this integral in terms of the Hermite polynomials and the coefficients a, b, c, A, B, C, etc., we get the following expression

$$P\,(A + C\sigma^2 + D\sigma^3 c + E\sigma^4 \cdot \overline{3 + d})$$

$$- Z\Big[\ A\Big\{-\frac{c}{6}\ \xi_2 + \frac{d}{24}\,\xi_3 - \frac{e}{120}\,\xi_4 + \Big(\frac{f}{720} + \frac{c^2}{72}\Big)\xi_5$$

$$-\Big(\frac{g}{5040} + \frac{cd}{144}\Big)\xi_6 + \ldots\Big\}$$

$$+ B\sigma\Big\{-1 + \frac{c}{6}\,(\xi_3 + 3\xi_1) - \frac{d}{24}\,(\xi_4 + 4\xi_2) + \frac{e}{120}\,(\xi_5 + 5\xi_3)$$

$$-\Big(\frac{f}{720} + \frac{c^2}{72}\Big)(\xi_6 + 6\xi_4) + \Big(\frac{g}{5040} + \frac{cd}{144}\Big)(\xi_7 + 7\xi_5)$$

$$-\Big(\frac{h}{40320} + \frac{d^2}{1132} + \frac{ce}{720}\Big)(\xi_8 + 8\xi_6)\Big\}$$

$$+ C\sigma^2\Big\{\xi_1 - \frac{c}{6}(\xi_4 + 7\xi_2 + 6) + \frac{d}{24}\,(\xi_5 + 9\xi_3 + 12\xi_1)$$

$$- \frac{e}{120}\,(\xi_6 + 11\xi_4 + 20\xi_2)$$

$$+ \Big(\frac{f}{720} + \frac{c^2}{72}\Big)(\xi_7 + 13\xi_5 + 30\xi_3)$$

$$- \Big(\frac{g}{5040} + \frac{cd}{144}\Big)(\xi_8 + 15\xi_6 + 42\xi_4)$$

$$+ \Big(\frac{h}{40320} + \frac{d^2}{1132} + \frac{ce}{720}\Big)(\xi_9 + 17\xi_7 + 56\xi_5)\Big\}$$

$$+ D\sigma^3\Big\{-\xi_2 - 3 + \frac{c}{6}(\xi_5 + 12\xi_3 + 21\xi_1)$$

$$- \frac{d}{24}\,(\xi_6 + 15\xi_4 + 48\xi_2 + 24)$$

$$+ \frac{e}{120}(\xi_7 + 18\xi_5 + 75\xi_3 + 60\xi_1)$$

$$- \left(\frac{f}{720} + \frac{c^2}{72}\right)(\xi_8 + 21\xi_6 + 108\xi_4 + 120\xi_2)$$

$$+ \left(\frac{g}{5040} + \frac{cd}{144}\right)(\xi_9 + 24\xi_7 + 147\xi_5 + 210\xi_3)$$

$$- \left(\frac{h}{40320} + \frac{d^2}{1132} + \frac{ce}{720}\right)(\xi_{10} + 27\xi_8 + 192\xi_6 + 336\xi_4)\Big\}$$

$$+ E\sigma^4 \Big\{\xi_3 + 6\xi_1 - \frac{c}{6}(\xi_6 + 18\xi_4 + 435\xi_2 + 180)$$

$$+ \left(\frac{f}{720} + \frac{c^2}{72}\right)(\xi_9 + 30\xi_7 + 255\xi_5 + 660\xi_3 + 360\xi_1)$$

$$- \left(\frac{g}{5040} + \frac{cd}{144}\right)(\xi_{10} + 34\xi_8 + 339\xi_6 + 1092\xi_4 + 840\xi_2)$$

$$- \left(\frac{h}{40320} + \frac{d^2}{1132} + \frac{ce}{720}\right)(\xi_{11} + 38\xi_9 + 435\xi_7 + 1680\xi_5 + 1680\xi_3)\Big\}\Big]$$

where P is the proportion given by $\int_{\xi}^{\infty} Z d\xi$ which is $0\cdot1$ and $0\cdot05$ for the two levels of selection and Z is the ordinate of the normal distribution corresponding to ξ.

By substituting appropriate values for the Hermite polynomials and the coefficients a, b, c, A, B, C, etc., the mean values of various properties were calculated for each model at each level of selection and for selection at two ends in respect of models with dominance. The properties, genotypic mean of selected F_3 progeny and mean genotypic variance within F_3 progeny, i.e., $\bar{x}_3$ and $\bar{x}_2$ are directly calculated, while for the properties, variance of the F_3 progeny mean, the covariance of F_3 progeny mean and genotypic variance within progeny and variance of the genotypic variance within progeny the mean values are obtained by calculating the mean values of the quantities; x_3^2, $x_2 x_3$ and x_2^2, i.e., $\overline{x_3^2}$, $\overline{x_2 x_3}$ and $\overline{x_2^2}$ and subtracting from them respectively the quantities $(\bar{x}_3)^2$, $(\bar{x}_3)(\bar{x}_2)$ and $(\bar{x}_2)^2$.

A difficulty was noticed in calculating the results for dominance models consisting of two factors. The mean value of x_3^2, i.e., $\overline{x_3^2}$,

was found to be less than $(\bar{x}_3)^2$ in some cases and the variance of F_3 progeny mean could not be calculated in those cases. This was apparently a result of approximations involved in the calculations.

With two factor models, however, it is possible to enumerate the genotypes and thus calculate the results of selection directly. Thus denoting the factors by A and B, the nine genotypes and their relative frequencies in the F_2 can be set down as follows:—

AABB	1/16	AAbb	1/16	aabb	1/16
Aa BB	1/8	Aa bb	1/8		
AABb	1/8	aa BB	1/16		
Aa Bb	1/16	aa Bb	1/8		
Total	9/16		3/8		1/16

The genotypic value, the F_3 progeny mean and the genotypic variance within progeny are known for each of these genotypes. The phenotypic values of these genotypes will be scattered about their genotypic values with variance represented by the environmental component of F_2 variance. Knowing the actual deviate, $\xi\sigma$, beyond which the F_2 individuals are selected in the different cases, we can obtain the proportion of different genotypes in the selected portion of the population and from these the mean values for various properties. Taking Model IV with dominance where the magnitude of each factor is one unit as the simplest case, the genotypic value of the first four genotypes, $AA\,BB$, $AaBB$, $AABb$ and $AaBb$, is $+2$, of the next four, $AAbb$, $Aabb$, $aaBB$ and $aaBb$, 0 and of the remaining genotype, $aabb$, -2. The actual deviate for 10% selection of the highest phenotypes is $2\cdot349440$ measured from the F_2 mean which is 1 on the scale of genotypic values.

To find the proportion of the four genotypes belonging to the first group above which is selected we calculate the normal deviate given by

$$\frac{3\cdot349440 - 2\cdot000000}{\sqrt{2}}$$

the factor 2 in the denominator representing the value of the environmental component of the F_2 variance assumed.

$$\therefore \text{ The normal deviate} = \frac{1\cdot349440}{\sqrt{2}} = 0\cdot954552$$

From the table of normal probability integral (Pearson, K., 1930) we find by entering the table against the above value of the normal

deviate and using interpolation that $0 \cdot 1699021$ of the individuals belonging to this group are selected. These constitute

$$\frac{9}{16} \, (0 \cdot 1699021) = 0 \cdot 0955699 \text{th}$$

of the F_2 population. Similarly we find that the selected portions of the other two groups constitute $0 \cdot 0034185$ and $0 \cdot 0000049$th parts of the F_2 population. These total up to $0 \cdot 0989933$ which is quite close to the fraction $1/10$ as might be expected. By calculating the mean values of the five properties for each of the genotypic groups and taking into account the relative frequencies of the different groups calculated above, we get the mean values of the F_3 properties for the selected portion of the population. Results for the 5% selection as also for the selection of low values for the dominance models were obtained similarly. The results were obtained for all the three 2-factor models and the resulting values are included in the tables of results presented later in place of those calculated by the general method as the former would be more accurate. Similar calculations made for the no-dominance models with two factors verified the correctness of the values obtained for these models by the general method.

5. RESULTS OF SELECTION AND CONCLUSIONS

The results of selection obtained as described earlier are discussed below.

The first property we consider is, x_3, the genotypic mean of the selected progenies. This property is of considerable practical interest as showing the immediate gain from selection. The results are presented in Table XXII below which gives the means of the selected F_3 populations measured as deviations from the means of unselected F_3 populations, i.e., the values of genotypic advances due to selection. For models with dominance the advances are given for selection for high as well as for low value.

For a proper appreciation of effects of dominance on selection it is necessary to take into consideration the effects of dominance on F_1, F_2 and F_3 means of unselected populations. To facilitate this consideration the mean values for unselected F_1, F_2 and F_3 measured from the respective midparental values are given for the various models in Table XXIII.

The F_1 means represent the hybrid vigour as also the maximum possible genetic advance in models with dominance. In no-dominance models on the other hand the F_1, F_2 and F_3 means as well as hybrid

vigour are zero.   For these models therefore only the values of maximum genotypic advance are given.

TABLE XXII

Genotypic advances over F_3 *mean*

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·358815	−0·556763	0·550740	0·383270	−0·670766	0·636445
II	0·411083	−0·511540	0·553936	0·459971	−0·621417	0·648423
III	0·437437	−0·486917	0·554676	0·502720	−0·582923	0·651327
IV	0·767806	−1·441881	1·393375	0·792340	−1·722842	1·580886
V	0·996041	−1·308247	1·404495	1·064666	−1·663096	1·637439
VI	1·089032	−1·204765	1·406615	1·228106	−1·520699	1·649857
VII	1·012878	−2·078664	2·051569	1·025709	−2·530193	2·304136
VIII	1·441254	−1·982463	2·065798	1·499056	−2·499955	2·404575
IX	1·593004	−1·849073	2·068517	1·777449	−2·262164	2·424622

TABLE XXIII

F_1, F_2, F_3 *means and maximum advance*

Model	Models with dominance			Models with no-dominance	
	F_1 mean (Also maximum advance)	F_2 mean	F_3 mean	Maximum advance	
I	1·154700	0·577350	0·288675	1·414236	
II	2·309400	1·154700	0·577350	2·828472	
III	4·618800	2·309400	1·154700	5·656944	F_1 mean
IV	2·000000	1·000000	0·500000	2·449490	= F_2 mean
V	4·000000	2·000000	1·000000	4·898980	= F_3 mean
VI	8·000000	4·000000	2·000000	9·797960	= 0 for all no-dominance models
VII	2·581989	1·290994	0·645497	3·162278	
VIII	5·163978	2·581989	1·290994	6·324556	
IX	10·327956	5·163978	2·581989	12·649112	

It would be observed from the table that the values of hybrid vigour are, in general, large, especially for models with 8 and 32 factors. This is a consequence of the type of dominance assumed, namely, full-dominance in one direction for all factors. Such a situation may not exist, perhaps, in any plant material. Nevertheless, the present set of models would serve to bring out clearly, because in a magnified form, the effects of dominance in one direction. It would also be observed from this table that owing to loss of hybrid vigour the fall in the mean of the unselected F_3 from the F_2 mean is more than the genotypic advances for 10% and 5% selection in certain cases and therefore the mean of selected F_3 would be less than the F_2 mean under the conditions assumed.

The most striking effect to be observed from Table XXII is that of the magnitude of genotypic variance in F_2. This is, of course, expected. The results are more useful, however, in enabling us to observe the effects of the proportion of genotypic and environmental components of variance on the response to selection. To facilitate this the results have been transformed to the basis of unit genotypic variance in F_2 by dividing the results for models with the F_2 genotypic variance of 0·5, 1·5 and 2·5 units by $\sqrt{0·5}$, $\sqrt{1·5}$ and $\sqrt{2·5}$ respectively. These transformed values are presented in Table XXIV.

TABLE XXIV

Genotypic advances on the basis of unit genotypic variance in F_2

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·507441	−0·787382	0·778864	0·542026	−0·948606	0·900069
II	0·581359	−0·723427	0·783384	0·650497	−0·878816	0·917009
III	0·618629	−0·688605	0·784430	0·710953	−0·824378	0·921115
IV	0·626911	−1·177291	1·137686	0·646943	−1·406695	1·290543
V	0·813264	−1·068179	1·146765	0·869296	−1·357912	1·336963
VI	0·889191	−0·983687	1·148496	1·002744	−1·241646	1·347103
VII	0·640600	−1·314662	1·297526	0·648715	−1·600234	1·457263
VIII	0·911529	−1·253820	1·306525	0·948086	−1·581110	1·520787
IX	1·007504	−1·169456	1·308245	1·124157	−1·430718	1·533466

The effect of the environmental component in reducing the immediate advance by selection will be very clearly seen from this table. The effects of the number of factors and that of dominance can also be observed from this table. It is seen that the advances in the presence of dominance are appreciably less than in its absence which is to be expected since only 2/3rd of the genotypic variance is *genetic* in these models. The effect of the number of factors appears to be small particularly in the absence of dominance. The results given in this table could therefore be used for the prediction of advance from a knowledge of the magnitudes of genotypic and environmental components in the F_2 in the absence of appreciable dominance effects. Again, as might be expected, the advances due to selection are appreciably smaller for selection in the same direction as that of the dominance than for selection in the opposite direction. It may also be noted that whereas the selected populations are expected to maintain their mean values in the no-dominance models in the absence of any further selection, the mean values of the selected portions would fall progressively in the succeeding generations under similar circumstances. The ultimate value that may be expected to be reached in any model is represented by its genetic mean.

As might be expected, more intense selection leads to greater progress which is seen by comparing the corresponding results for 10% and 5% levels. However, the differences are not very large for these two levels. The effects of environmental variability, dominance and the number of factors are more pronounced at the higher level of selection.

The genotypic mean of F_3 progeny tells us the progress made by selection in F_2. Other properties are of interest from the point of view of potentiality of the selected F_3 to respond to further selection. The variance of the progeny mean in the selected F_3 is, perhaps, the most important quantity for this purpose. In view of the greater stability of the progeny mean in comparison to the individual plant value it is the more dependable criterion for further selection and the importance of the variance of the progeny mean is therefore clear. The results for this property are given in Table XXV.

As in the case of the mean of selected progeny considered earlier the results may be transformed to the basis of unit genotypic variance in F_2. This is done by multiplying the results for Models I-III by 2, those for Models IV-VI by 2/3 and those for Models VII-IX by 2/5. The results thus obtained are given in Table XXVI.

TABLE XXV

Variance of F_3 *progeny mean*

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·143896	0·416676	0·375032	0·122448	0·400883	0·353664
II	0·234258	0·381037	0·406098	0·218135	0·382591	0·398684
III	0·277429	0·352421	0·411876	0·268384	0·354547	0·409372
IV	0·206288	0·894803	0·773159	0·170206	0·801296	0·694188
V	0·500717	0·862406	0·918364	0·473498	0·751438	0·884171
VI	0·640278	0·950630	0·943335	0·626709	0·791597	0·928096
VII	0·264293	1·307897	1·007807	0·241491	1·062423	0·897000
VIII	0·691054	1·132824	1·269576	0·694387	0·763330	1·200170
IX	0·914490	1·156384	1·322492	0·928266	1·005488	1·277697

TABLE XXVI

Variance of F_3 *progeny mean on the basis of unit genotypic variance in* F_2

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·287792	0·833352	0·750064	0·244896	0·801766	0·707328
II	0·468516	0·762074	0·812196	0·436270	0·765182	0·797368
III	0·554858	0·704842	0·823752	0·536768	0·709094	0·818744
IV	0·137525	0·596535	0·515439	0·113470	0·534197	0·462792
V	0·333811	0·574937	0·612243	0·315665	0·500959	0·589447
VI	0·426852	0·633753	0·628890	0·417806	0·527731	0·618731
VII	0·105717	0·523159	0·403123	0·096596	0·424969	0·358800
VIII	0·276422	0·453130	0·507830	0·277755	0·305332	0·480068
IX	0·365796	0·462554	0·528997	0·371306	0·402195	0·511079

It is seen from the table that greater environmental variability in relation to the genotypic leads to a greater variance of the F_3 progeny mean. This is to be expected, for greater environmental variability would bring together more diverse genotypes into the selected portion of the population. From a comparison of values for dominance and no-dominance models it would appear that the former values are smaller owing to only 2/3rd of the genotypic variance in the F_2 being genetic. It is also seen that in the dominance models the values of the variance of F_3 progeny mean are smaller for selection at the higher end than at the lower. This is explained by the fact that for any factor the difference between the means of progenies arising from the heterozygote and the dominant homozygote is smaller than that between the progenies arising from the heterozygote and the recessive homozygote.

The effect of the number of factors is clear in the results for no-dominance models and for selection at the higher end in dominance models, the magnitude of the variance increasing appreciably with increase in the number of factors. The trend is, however, not clear for the results of selection at the lower end in dominance models. The values at this end seem to decrease progressively with increase in the number of factors in models I–III but reach a minimum and then increase in the remaining models. The result is difficult to explain unless it is considered to be due to the approximations involved in the method of calculation.

The above results are true with regard to both levels of selection. As is to be expected the values for more intense selection are smaller except in two cases (Models VIII and IX with-dominance). Probably this is also to be explained by the approximations involved in the method.

The results for mean genotypic variance in the selected progenies may be considered next. This variance is an index of scope for improvement through single plant selection within progeny, just as the variance between progenies indicates the scope for improvement at the stage of progeny selection. The results are given in Table XXVII.

The results given in the above table can be transformed to the basis of unit genotypic variance in F_2 by multiplying the results for Models I–III by 2, those for Models IV–VI by 2/3 and those for Models VII–IX by 2/5. These transformed results are given in Table XXVIII.

From this table it is seen that the increase of environmental component of variance in the F_2 has the effect of increasing the genotypic variance within progeny in the selected F_3 in no-dominance models and for selection of low value in the dominance models. For selection

TABLE XXVII

Mean genotypic variance within F_3 progeny

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·312148	0·153566	0·220641	0·316384	0·138820	0·207037
II	0·285601	0·205699	0·242964	0·289834	0·196183	0·239372
III	0·268942	0·228916	0·248269	0·271769	0·224759	0·247360
IV	0·980342	0·317436	0·550618	0·987702	0·233147	0·468582
V	0·899405	0·549492	0·703662	0·909700	0·500535	0·681173
VI	0·831677	0·659642	0·738625	0·842237	0·635947	0·732917
VII	1·642286	0·444937	0·805124	1·647256	0·288060	0·636529
VIII	1·529094	0·866102	1·149136	1·540288	0·765891	1·100712
IX	1·401836	1·073236	1·225404	1·414636	1·037592	1·213047

TABLE XXVIII

Mean genotypic variance within progeny on the basis of unit genotypic variance in F_2

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·624296	0·307132	0·441282	0·633768	0·277640	0·414074
II	0·571202	0·411398	0·485928	0·579668	0·392366	0·478744
III	0·537884	0·457832	0·496538	0·543538	0·449518	0·494720
IV	0·653561	0·211624	0·367079	0·658468	0·155431	0·312388
V	0·599604	0·366328	0·469108	0·606466	0·333690	0·454115
VI	0·554451	0·439761	0·492417	0·561491	0·423964	0·488611
VII	0·656914	0·187975	0·322050	0·658902	0·115224	0·254512
VIII	0·611638	0·346441	0·459654	0·616115	0·307356	0·440285
IX	0·560734	0·429294	0·490162	0·565854	0·414036	0·485219

of high value on the other hand, the variance within progeny decreases slightly. This is a consequence of the fact that as a result of full dominance the largest proportion of heterozygotes which determines the genotypic variance within progeny occurs at the upper extreme of the range of F_2 genotypic values. With an increase of the environmental component of variance, genotypes producing smaller genotypic variance also shift in a greater proportion into the selected range as a result of which the mean genotypic variance within progeny goes down. Another consequence of the same fact is that with more intense selection the variance increases in the progenies selected for high value unlike the results for no-dominance models and at the lower end of the range of the dominance models.

By a comparison of the results for selection at the two extremes in the dominance models it is seen that for a given model the variance within the selected progeny is appreciably greater at the upper end. This is obviously due to the accumulation of the heterozygotes, which produce the genotypic variance within progeny, at the upper end of the range. In comparing the results for dominance models with those of no-dominance models it should be remembered that only 2/3rd of the genotypic variance in the former is genetic, while in the latter the whole of it is genetic. Taking into account this fact we find that not withstanding the greater value of the genotypic variance residual within progenies selected for high value the scope for permanent improvement by selection at the single plant stage would be smaller in the case of dominance models than in the absence of dominance.

Again from Table XXVIII it can be seen that the number of factors have an appreciable effect on this property especially in models with a higher proportion of genotypic variance in F_2. In no-dominance models and in selection for low value in dominance models the value of within progeny variance increases with increasing number of factors. In selection for high value on the other hand it decreases with an increase in the number of factors.

The results for the covariance between F_3 progeny mean and the variance within progeny are given in Table XXIX.

It can be seen from the above table that a greater value of the initial genotypic variance leads in general to a larger numerical value of the covariance between progeny mean and the variance within progeny. The most striking effect that can be observed is, perhaps, the decrease of the covariance with increase in the number of factors. The effect is quite regular in no-dominance models and in selection for low value in dominance models. In selection for high value it

TABLE XXIX

Covariance of progeny mean and variance within progeny

| Model | 10% Selection, models with | | | 5% Selection, models with | | |
| | Dominance | | No-dominance | Dominance | | No-dominance |
	High value	Low value		High value	Low value	
I	−0·011321	0·054426	−0·061163	−0·015319	0·053969	−0·078382
II	0·003893	0·021010	−0·014400	0·002471	0·021485	−0·016434
III	0·004273	0·008626	−0·003640	0·003853	0·008786	−0·004212
IV	−0·132672	0·204593	−0·288216	−0·145267	0·193365	−0·275624
V	−0·015842	0·079435	−0·083326	−0·014789	0·057249	−0·091952
VI	0·006817	0·037868	−0·021404	0·005995	0·026279	−0·024315
VII	−0·309308	0·393362	−0·526344	−0·320123	0·387080	−0·468327
VIII	−0·058792	0·100795	−0·168955	−0·047859	0·031733	−0·182657
IX	0·002881	0·045629	−0·044239	0·015329	0·041742	−0·049273

appears that for a small number of factors the covariance is negative but tends to positive values and increases still further with increase in the number of factors. The trends as between dominance *versus* no-dominance and with increase in the number of factors are the same at the higher level of selection. The effect of the level of selection itself is, however, a little curious in that more intense selection decreases numerically the value of covariance in some cases and increases it in others although slightly. No explanation can be offered and the result may be due to approximations involved in the method of calculation.

It is clear, however, that the correlation between progeny mean and variance within progeny would serve as a good index of the number of factors operating in the F_2 segregation particularly where the initial genotypic variance is large. If the value of this coefficient is small, whether positive or negative, it might be inferred that the number of factors is rather large. If the correlation is significant it indicates a rather small number of factors. Significant positive correlation could occur in selection for low value either in the presence or absence of dominance whereas for selection for high value it should be negative. Thus the covariance will not be useful for distinguishing existence or absence of dominance in the material. It may also be pointed out here that the decrease of covariance between the progeny mean and the

genotypic variance within progeny with increase in the number of factors has an important bearing on plant breeding; for with a low value for the covariance it becomes possible to select simultaneously progenies with high mean and with considerable genotypic variance within them, this variance representing further scope for advance through single plant selection in the selected progenies.

The results for the variance of genotypic variance within progeny are given in Table XXX.

TABLE XXX

The variance of genotypic variance within progeny

Model	10% Selection, models with			5% Selection, models with		
	Dominance		No-dominance	Dominance		No-dominance
	High value	Low value		High value	Low value	
I	0·029428	0·024794	0·030316	0·028980	0·022742	0·029401
II	0·006110	0·005621	0·007734	0·005562	0·004996	0·007698
III	0·001472	0·001412	0·001943	0·001328	0·001261	0·001943
IV	0·252036	0·157150	0·234520	0·250913	0·128544	0·201509
V	0·064316	0·053595	0·067147	0·062141	0·050186	0·065303
VI	0·015963	0·015377	0·017227	0·015757	0·014381	0·017144
VII	0·677398	0·371526	0·545859	0·677049	0·302660	0·408281
VIII	0·175118	0·134340	0·181092	0·167276	0·118563	0·172429
IX	0·048935	0·038988	0·047987	0·045207	0·039659	0·047387

Higher initial genotypic variance is seen to increase the values of variance of genotypic variance within selected progenies as might be expected. It can also be shown that an increase of the environmental variability in relation to the genotypic also leads to an increase in the mean value of the variance of variance. The values of this quantity are also greater in no-dominance models than in dominance models with the exception of results for selection of high value in Models IV and VII. The values are also greater with selection for high value than for low value in dominance models. It might be noted that the variation in this quantity is almost inversely proportional to the number of factors, other things remaining the same.

6. DISCUSSION

One of the most important uses of the study of inheritance of quantitative characters with reference to crop plants is its application to plant breeding. The use of statistical techniques in conjunction with appropriately planned experimental data for the study of this subject has become fairly clear in recent years; and the plant breeder has also become conscious of the importance of such studies, as these are likely to lead to the development of more efficient methods for selection. Some of these, such as the replicated progeny row breeding, have already become popular with him. There is, however, a pressing need to evolve techniques by means of which the genetics of quantitative characters could find direct application in plant breeding. The results obtained in the present investigation throw considerable light on the genetic situation in its bearing on selection in self-fertilised crops. The approach was introduced by Panse and the results obtained in his investigation have been amplified and extended here to cover a wider range of the different components of the genetic situation to be suitable for testing in plant breeding practice. Though certain simplifying assumptions are involved, the results would undoubtedly serve in providing a basis for the application of the method to experimental data. We shall consider in some detail how the results could be so applied.

As has been pointed out by Mather (1949), much of the data of experiments on quantitative characters obtained in the past suffer from defects of design or inadequacy. It is clear that the specification of the experimental conditions under which the data need to be obtained is an essential prerequisite for a fruitful analysis of the quantitative characters. Thus, Mather has given a layout for an experiment by which data, suitable for obtaining information regarding scale, number of factors, genotypic variance in F_2 and its partition into components attributable to additive gene-action, dominance and environmental effects, might be collected. His layout consists of blocks of 40 plots sown with parental strains, F_1 and F_2 and 25 F_3 progenies chosen randomly in F_2. From the information obtained from such an experiment, we might by using the results of the present investigation, anticipate the results expected from a selection of 10% or 5% of the highest or lowest individuals in the F_2, with regard to any particular quantitative character. This information obtained from an experiment of the size proposed by Mather might not be very precise and might serve to give only a broad indication of the course of selection. In view of this limitation it might prove more advantageous to seek some indication

of the genetic situation existing in the material, particularly about dominance and the number of factors in segregation on the basis of the results obtained in the present investigation. For this purpose it would suffice to carry out an experiment of the following type.

To start with, the plant breeder could grow the F_1, the parents and the F_2 all in one experiment. Such an experiment would enable him to test the adequacy of the scale as well as help him to estimate the magnitudes of the genotypic and environmental components of F_2. A measure of hybrid vigour will also be available from which he could infer the magnitude of unsymmetrical dominance effects. The plant breeder could next grow a number of F_3 progenies resulting from the highest 10% or 5% of F_2 phenotypes in a randomised and replicated layout. The layout should also include sufficient number of plots sown with the parental and F_1 strains in order to give independent information regarding the environmental variation between and within plots. Plots sown with F_2 should also be included. This would enable the experimenter to obtain a fresh estimate of the genotypic part of F_2 variance, by subtracting the estimate of environmental variance obtained from genetically uniform material from the estimate of gross variance in F_2; and this value would serve as a check on the estimate of the same quantity calculated from the previous experiment. The layout would thus be similar to that proposed by Mather, referred to earlier, with the difference that instead of randomly selected F_3 progenies it would include progenies selected on the performance of the F_2 parent. In the interest of precison of the quantities to be calculated from the data, the number of progenies should be as large as feasible and the F_2 should be sufficiently large to permit such a selection. The number of plots of genetically homogeneous material should also be sufficient, say 20 or 25, to give stable estimates of environmental variance. The data collected from such an experiment could be analysed to give the values of F_3 mean, variance between and within F_3 progenies and the covariance of progeny mean and variance within progeny. These quantities along with estimates of between plot and within-plot variances given by genetically uniform material, would enable the worker to obtain mean values of the statistical properties discussed earlier for the selected F_3 population. A comparison of the results obtained from the analysis with the results obtained in the present investigation would give a good indication about the actual genetic situation existing in the material experimented upon.

The comparison of the experimental results with the theoretical results obtained in the present investigation could be done from two

angles. One way would be to calculate from the initial experiment the ratio of genotypic and environmental components of F_2 variance. In many cases this would be comparable to one of the ratios characterising the three groups of models with common F_2 genotypic variance. The estimates of F_3 properties obtained from the experimental data could next be transformed to the basis of equal genotypic variance in F_2. The transformed values could be compared with the theoretical with the help of suitable tests of significance. It is, however, doubtful whether such test would be efficient since the values obtained experimentally might be susceptible to large sampling errors. The experiment could perhaps provide more usefully a comparison of the relative values of the various statistics in order to indicate against the background of the results obtained in the present investigation which pattern the material follows most closely. Thus, we might by following this approach obtain an indication of the existence and magnitude of dominance or the number of factors. With biased dominance the first effect expected in the material is the manifestation of hybrid vigour. A confirmation of the dominance so revealed will be provided by the relation between the genotypic variance within progeny and the variance of progeny means. It might be recalled that in the absence of dominance the former is appreciably smaller than the latter. In the presence of dominance they would be nearly equal or the former would even exceed the latter. This is true even of balanced dominance (Panse, 1940 a, Table I). Thus the presence of dominance, either balanced or biased could be detected and some idea of the magnitude of dominance effects obtained. An indication of the number of factors operating can be obtained from the magnitude of covariance between progeny mean and within progeny variance. The significance of the covariance can be judged by calculating the coefficient of correlation between the progeny mean and within progeny variance. If this is non-significant even with a large amount of data a rather large value for number of factors would be indicated.

It may be pointed out that the present results are based on a number of simplifying assumptions and are subject to certain limitations. Thus the genes controlling the character are assumed to be independent in segregation. The existence of linkage in the material would make a difference to the results of selection and the results would not be comparable in such a case with the hypothetical results for our models. Another such assumption, common to most of the investigations in the genetics of quantitative characters and also made in the present investigation, is that of absence of fertility or viability disturbances. With the existence of such complicating features in the experimental

material the results obtained from the material will not be in accord with those expected from our models. However, it seems worthwhile to compare the results obtained from experimental data with hypothetical results since such a comparison would itself provide evidence for the existence of such disturbances.

7. SUMMARY

The object of the present investigation was the study of effects of various aspects of the genetic set-up on the results of selection and the utilisation of the results in plant breeding.

With this object genetic models similar to those developed by Panse were set up using for this purpose the numerical results of analysis of experimental data for fibre-length of certain cotton (*Gossypium arboreum*) crosses. On the basis of the quantities representing a range of genotypic variances in F_2, 18 models were set up, 9 with dominance and a corresponding set of 9 models without dominance, with different values for the effective number of factors and genotypic variance in F_2 and a constant value for the environmental variance. Corresponding to each model, the moments and product-moments of the three variates, x_1, F_2 phenotypic value, x_2, genotypic variance within F_3 progeny and x_3 the genotypic mean of F_3 progeny, were obtained and the regression equations of five F_3 properties on the F_2 phenotypic value were calculated. These equations enable the study of the effects of various characteristics of the models on the relation between F_3 properties and F_2 parental value.

With the help of these regression equations the values of each of the five F_3 properties—(1) the genotypic mean of F_3 progeny, (2) mean genotypic variance within F_3 progeny, (3) the variance of the genotypic mean of F_3 progeny, (4) the covariance of the F_3 progeny mean and variance within progeny and (5) the variance of genotypic variance within F_3 progeny—were calculated for each model for two levels of selection, namely 10% and 5%. The results of selection at both ends of the F_2 phenotypic range were obtained for dominance models. To obtain these results the mean value for an F_3 property was expressed in terms of the regression coefficients, corresponding to that property, cumulants of the F_2 distribution and Hermite polynomials corresponding to the level of selection.

It was observed from the results that a higher environmental variance in F_2 relative to the genotypic variance has the effect of reducing the immediate advance by selection but that it increases the variance of the F_3 progeny means. Dominance likewise reduces the immediate

advance by selection and also leads to a fall of the mean value in the succeeding generations owing to the segregation of heterozygotes. It also leads to a smaller variance of the genotypic mean of F_3 progeny, in general, owing to the smaller magnitude of the genetic variance in F_2 and further by reducing the divergence of the progeny means of the dominant homozygotes and the heterozygotes for selection of high value. This last effect is reversed in selection for low value, owing to which the values of this variance are nearer to the values for no-dominance models. With increase in the number of factors the immediate advance due to selection is increased only slightly, but the magnitudes of both the variance of F_3 progeny means and the mean genotypic variance within progeny increase appreciably. Further, the covariance of F_3 progeny mean and the genotypic variance within progeny decreases with increase in the number of factors, thus increasing the scope of further improvement by selection in the next generation. The immediate advance due to selection is greater at the higher level of selection but the variance of F_3 progeny means is smaller.

The utilisation of the results in plant breeding was considered and a layout containing the parental strains, F_1, F_2 and F_3 progenies selected on the basis of the performance of the F_2 parent, is suggested for adoption by the plant breeder in order that the experimental data may provide an indication of the various genetic aspects of his material against the background of results obtained in the present investigation.

8. ACKNOWLEDGEMENT

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