

GENETIC ANALYSIS OF CORRELATED SEQUENTIAL CHARACTERS

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I. INTRODUCTION

WHERE stresses (internal, inter-trait correlations) between sequential characters exist the more "influential" characters in the sequence may project their form of environmental and genetic control into subsequent characters through the medium of these intercorrelations. The character so affected will thus have two main determinants influencing its expression—that induced by the influence of the stresses and that operating over and above those stresses. In genetic analysis of sequential characters we generally analyse only the observed values and ignore the presence or influence of correlations. In the present paper we will subject to genetic analysis both the observed expression of a character and that part of the variation operating over and above the influence of correlations. To obtain this "remainder" variation, not ascribable to correlation, the influence of correlation as a contributory source of variance may be removed from all characters in the sequence, excluding the first, by a technique which has been previously summarised (Thomas, Grafius and Hahn, 1970a).

We have already applied the method of removing correlations to simple genotype \times environment experiments (Thomas, Grafius and Hahn, 1970b). Presently we wish to extend the treatment to consideration of a more sophisticated and purely genetic analysis and will consider a situation where the environment may be presumed constant. The genetic analysis applied here—the diallel analysis of Jinks and Hayman (1953)—allows a detailed examination of the genetic system. A 4×4 diallel analysis is applied to four sequential untransformed (correlated) and transformed (uncorrelated) multiplicative characters in wheat. The four characters, which are components of yield, are in their chronological developmental sequence: heads per plant, spikelets per head, seeds per spikelet and weight/grain. Consideration is also given to progeny prediction of the complex character yield. The raw data are taken from a published source, Whitehouse, Thompson and Valle Ribeiro (1958). Both their F_1 and F_2 diallel sets are considered.

2. METHODS AND MATERIALS

The experiment has been fully described by Whitehouse *et al.* (*loc. cit.*) and their material consequently needs no redescription. Transformation was applied separately to the F_1 and F_2 diallel sets as described by Thomas, Grafius and Hahn (1970a). The intercomponent covariances (or correlations) and variances used in the transformation were calculated from the cross mean values of the entire diallel set under consideration (F_1 or F_2). We would have preferred utilising the correlations or covariances within

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crosses to remove the stresses within cells of the diallel table. The present procedure must therefore rest on the assumption that the inter-cell correlations are representative of the intra-cell situation and that for the latter corresponding r 's are homogeneous over cells. Indirect evidence for this assumption is forthcoming from the established similarity between corresponding inter-cell r 's calculated from the complete diallel and those obtained from the parental sets.

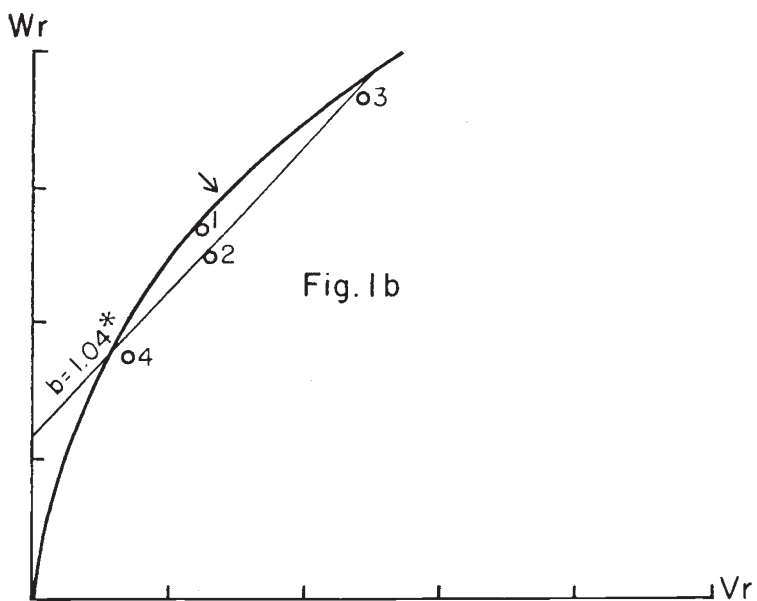
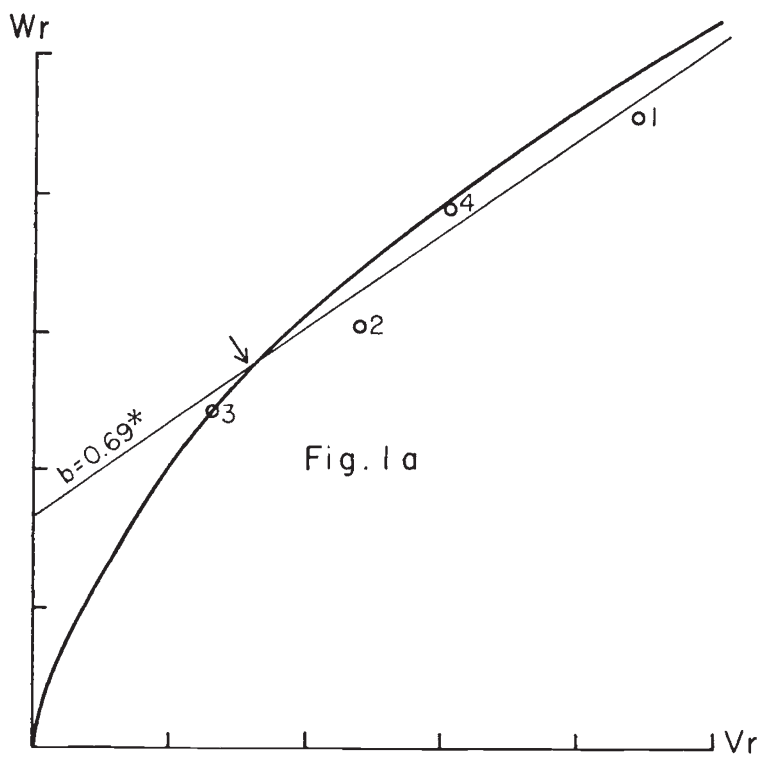
TABLE 1

Transformed and untransformed diallel cross values for the four sequential characters in wheat.
Untransformed values are taken from Whitehouse *et al.* (1958)

F ₁ generation	Ears/Plant observed	Spikelets/Ear		Grains/Spikelet		Weight/Grain	
		Observed	Trans- formed	Observed	Trans- formed	Observed	Trans- formed
Apu; 1	24.2	19.4	23.6	2.67	12.31	30.2	109.6
Fram 2; 2	26.5	20.2	24.8	2.13	12.26	30.6	102.3
Glendowe; 3	19.0	21.6	24.9	2.46	12.63	35.4	105.9
Peko; 4	21.7	21.6	25.4	1.69	12.05	52.4	111.0
1 × 2	27.8	20.1	24.9	2.51	12.69	32.9	113.1
1 × 3	20.5	20.9	24.4	2.65	12.64	35.7	111.2
2 × 3	22.7	21.2	25.1	2.47	12.74	31.8	106.2
1 × 4	24.4	20.8	25.0	2.11	12.33	41.4	110.7
2 × 4	24.9	21.3	25.6	2.02	12.48	41.3	109.5
3 × 4	19.6	21.6	25.0	2.08	12.29	46.7	110.6
Average	23.32	20.98	24.87	2.307	12.442	37.77	109.01
F ₂ generation							
1	3.29	14.4	12.9	1.40	1.11	37.9	94.9
2	4.88	16.8	14.6	1.23	0.99	35.5	89.3
3	3.24	17.7	16.2	1.46	1.02	36.6	89.5
4	3.76	16.3	14.5	1.08	0.75	58.2	99.2
1 × 2	4.05	15.8	13.9	1.27	0.99	36.8	89.5
1 × 3	3.31	16.5	14.9	1.43	1.05	39.3	93.7
2 × 3	4.30	17.4	15.4	1.51	1.19	37.5	99.8
1 × 4	3.45	16.0	14.3	1.20	0.86	45.3	91.2
2 × 4	4.18	16.4	14.9	1.20	0.91	46.2	95.2
3 × 4	3.83	17.2	15.4	1.23	0.87	47.6	94.3
Average	3.868	16.55	14.70	1.307	0.974	42.11	93.66

The transformed and untransformed F₁ and F₂ values are shown in table 1, and these data are subjected to the diallel graph analysis of Jinks and Hayman (1953) and the outcome shown in figs. 1a to 4b.

For the first character in the sequence the situation is unchanged from that shown by Whitehouse *et al.* (*loc. cit.*). The remaining characters are, however, transformed and both transformed and untransformed analysis of any one character within a particular generation are included in one figure. Also included in the figures are: the limiting parabolas (dotted curve for the transformed values); the limiting points on these parabolas, indicating the point of complete additivity ($Wr = \frac{1}{2} Vp$, $Vr = \frac{1}{4} Vp$) and marked by an arrow; lastly the regression line of Wr on Vr , where significant, is drawn and its slope value and significance level indicated (+ = <10 per cent.; * <5 per cent.; ** <1 per cent. and *** <0.1 per cent.) (dotted line for transformed values).



Figs. 1a and 1b.— Wr/Vr graph analysis of heads per plant in the F_1 (1a) and F_2 (1b).

3. RESULTS

(i) *Type of genetic control over the sequential characters—the W_r/V_r graph analysis*

The four multiplicative characters are considered in the order of their development.

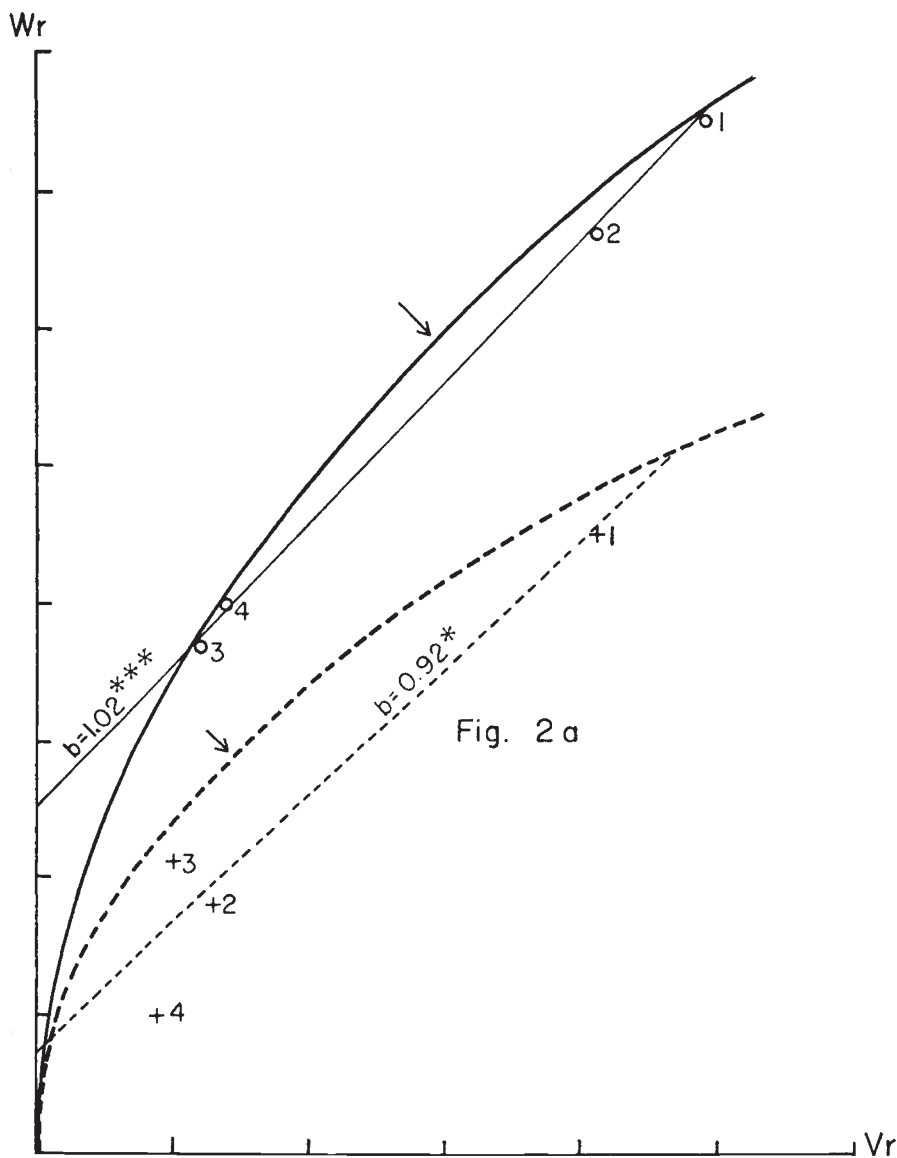


FIG. 2a

(a) *Ears per plant*. The closeness of the regression line and the four array points to the limiting parabola and limiting point in figs. 1a and 1b indicates that little or no dominance is present for this component in either the F_1 or the F_2 .

(b) *Spikelets per ear*. For the untransformed data in both the F_1 and F_2 the genetic situation exhibited in figs. 2a and 2b again appears, from the closeness of the regression line and the array points to the parabola, to represent an additive scheme. The situation is almost unchanged from that

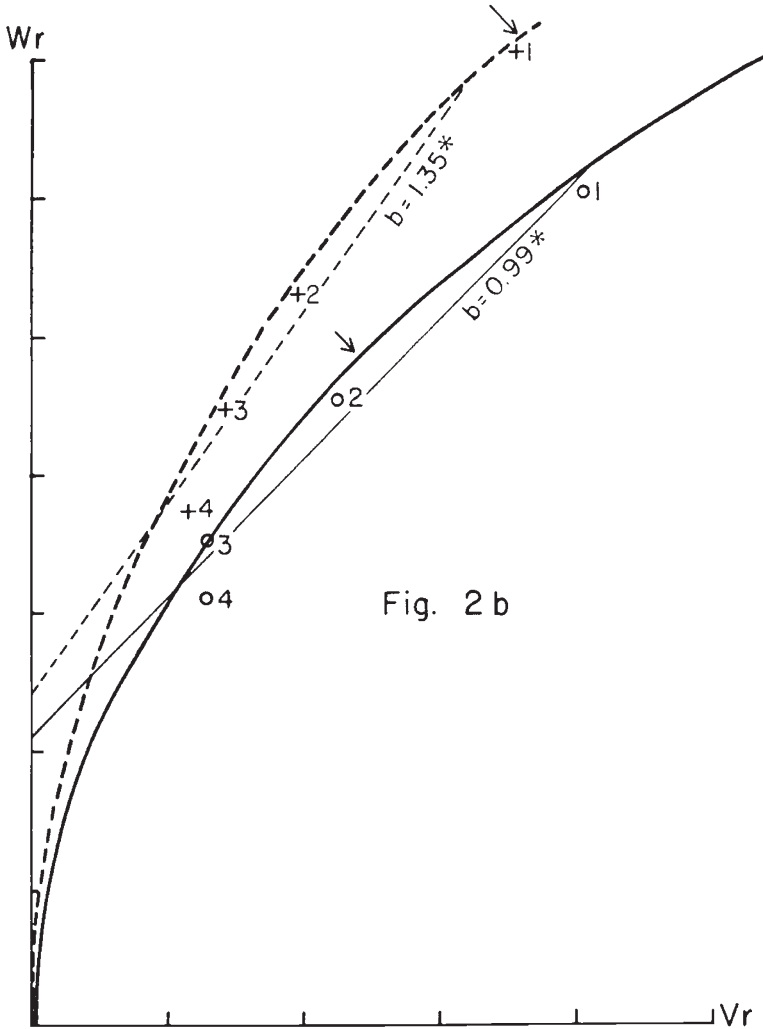


FIG. 2b

Figs. 2a and 2b.— W_r/V_r graph analysis of transformed (crosses) and untransformed (open circles) spikelets per ear in the F_1 (2a) and F_2 (2b).

of the untransformed values when the transformed F_2 graph is considered. However, the graph of transformed F_1 values indicates that partial dominance is present.

(c) *Grains per spikelet*. The untransformed data for F_1 in fig. 3a again indicates a highly additive genetic control. The transformed F_1 data, in the same graph, implies a high level of dominance. The situation is somewhat different in the F_2 , in fig. 3b, for both transformed and untransformed

data. Neither regression line is significant and the pattern of distribution of the array points suggests genic interaction. This suggestion is somewhat stronger for the transformed data as may also be the mean level of dominance since the array points are generally distributed at a greater distance from the relevant limiting parabola.

(d) *Weight per grain.* A high level of additivity again apparently holds for untransformed data in figs. 4*a* and 4*b* for both generations. On the other hand, the closeness to the Vr axis of the array points for the transformed values in both generations could be taken as a measure of gene interaction or as an indication of a lack of genetic control over this last character in the sequence.

(e) *Summary of Wr/Vr graphs findings.* The interpretation of untransformed data appears straightforward and strongly indicates that all components are under predominantly additive control. On the other hand, the transformed data appear to exhibit deviation from an additive scheme—toward a higher dominance and/or genic interaction level and this tendency increases as we progress along the developmental sequence. Removing the influence of correlation appears to have revealed a somewhat different type of genetic control than that surmised from analysis of untransformed data.

(ii) *Degree of genetic control over the sequential characters*

There are differences in the *degree* as well as the differences discussed above in the *type* of control over these sequential characters when correlations are removed and compared with the untransformed data. This may be surmised easily from the relative positions of the limiting point in figs. 2*a* to 4*b*. The position of this point indicates the degree of parental variance, since here $Wr = \frac{1}{2}Vp$ and $Vr = \frac{1}{4}Vp$. In turn, Vp , the variance of parents, is a convenient measure of genetic variation (in fact, the additive variance) and therefore we must conclude that there are differences in the amount of genetic variation exhibited by a character when expressed with and without correlation. In the process of comparing the genetic variance of the transformed and untransformed values let us assume that environmental variance does not contribute, a reasonable view since it must at least be constant across transformed and untransformed values for a character and lastly assume that the narrow sense heritability of all characters, untransformed, is 100 per cent.

To compare the amount of variance present in the transformed and untransformed data we could simply express the parental variance of the former as a percentage of the latter. However, as may be seen from table 1, the means of untransformed characters and their transformed values are different and thus the variances are not directly comparable. Therefore, in our comparison we chose to weigh each variance with its specific mean—and use this weighted variance as a measure of genetic variation. In table 2 the parental means, variances and weighted variances for transformed and untransformed characters are given. In this table the parental means and variances of the transformed data were obtained from the transformation of the parental set only and not from the complete diallel set transformation. Also, for each character a comparison of the weighted variances for transformed and untransformed data is indicated, the former being expressed as a percentage of the latter; this column is interpreted as the “amount” of genetic variance operating on the character over the apparent variance

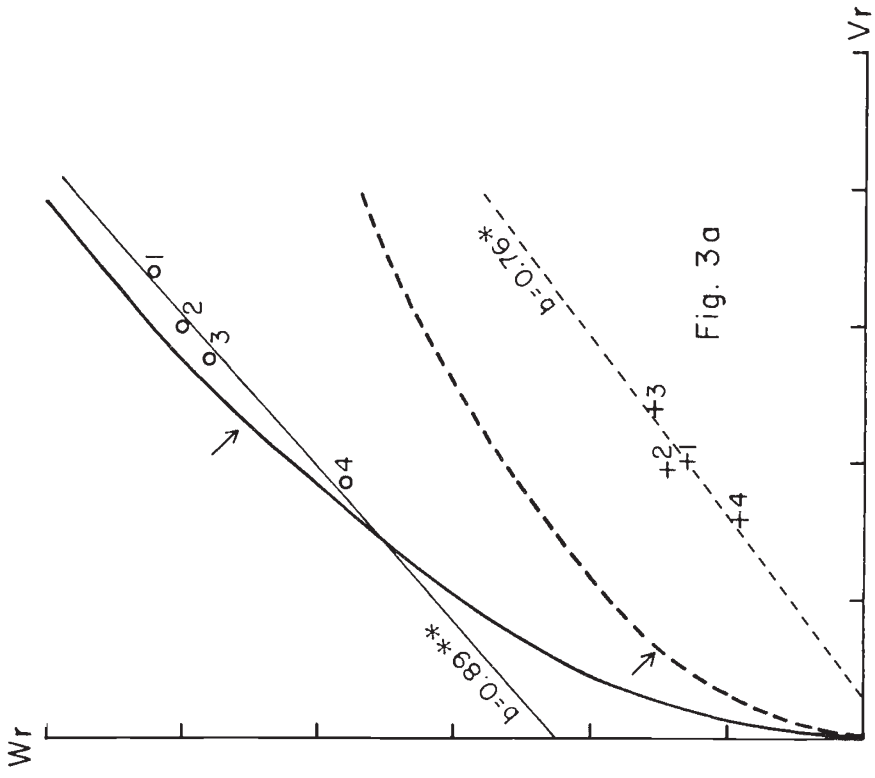


Fig. 3a

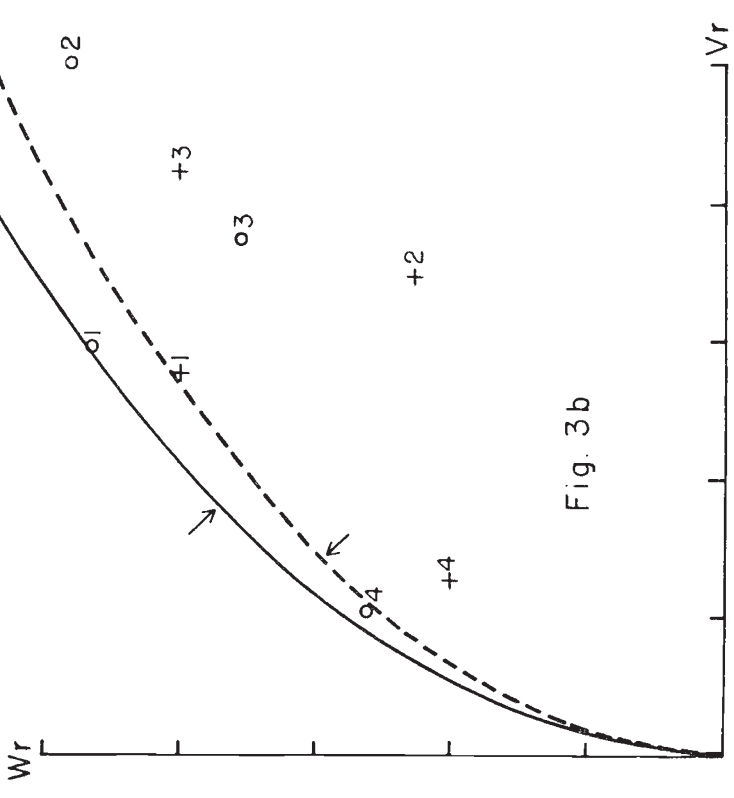


Fig. 3b

Figs. 3a and 3b.— W_r/V_r graph analysis of transformed (crosses) and untransformed (open circles) grains per spikelet in the F_1 (2a) and F_2 (2b).

induced by the influence of correlation. Were all this genetic variance found to be additive it would also represent the "true relative" heritability of the character—but we know from the Wr/Vr graphs that dominance is

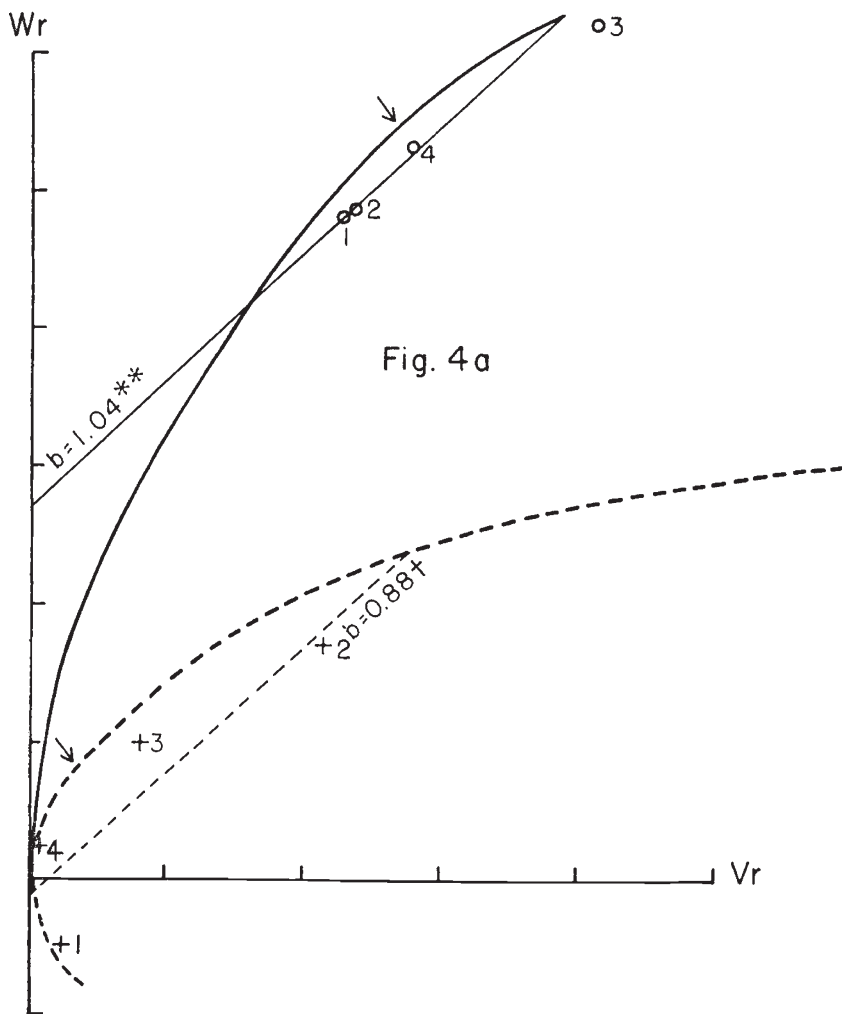


FIG. 4a

generally present for the transformed variable and thus the "true" heritability would generally be somewhat reduced over that indicated in the last column of table 2.

(iii) *The complex character, yield*

We have not subjected the complex character yield to genetic analysis since it is contended that the subject will have been covered in the analysis of the components. Whitehouse *et al.* (*loc. cit.*) did apply the Wr/Vr graph analysis to yield and the described epistatic condition for this trait when

compared with the additive control over its components lends some weight to Grafius (1965) position that the components may interact on a non-genic

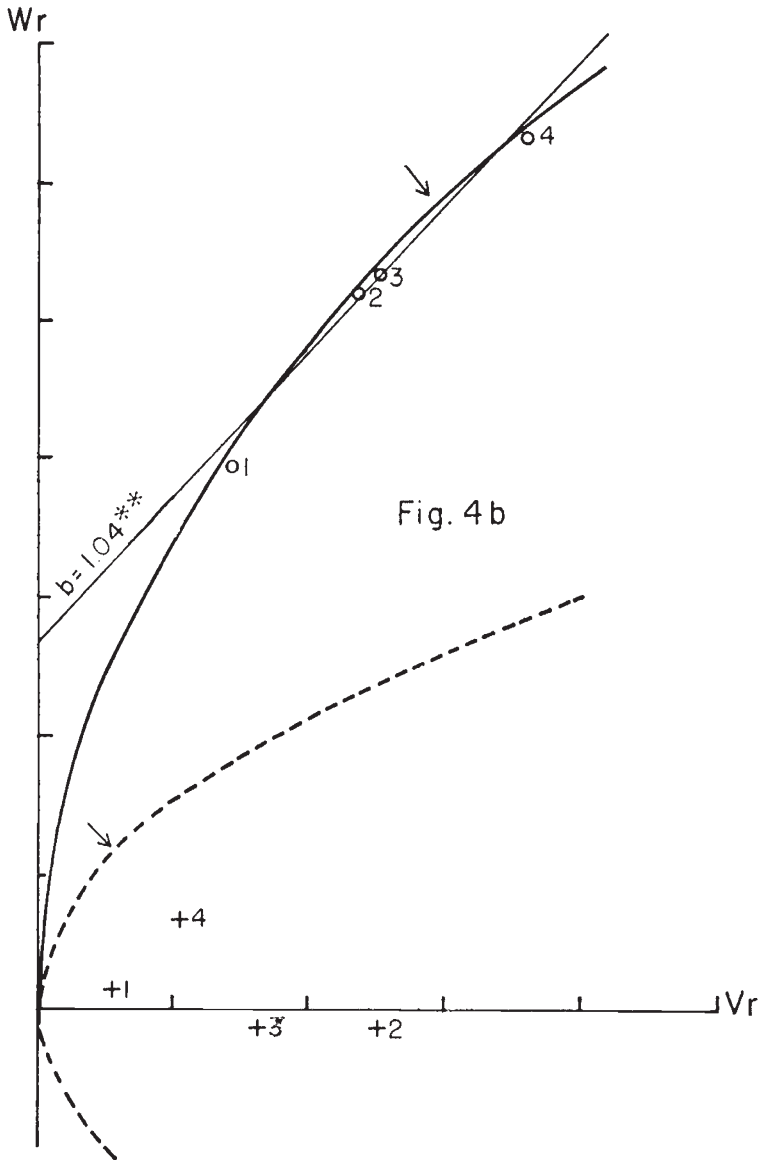


FIG. 4b

Figs. 4a and 4b.— Wr/Vr graph analysis of transformed (crosses) and untransformed (open circles) weight per grain in the F_1 (2a) and F_2 (2b).

level. In addition, the complex inheritance pattern for yield accounts for the fairly low predictive value of midparental yield in determining progeny yield, as indicated by the low correlation values in the last column of table 3. This is in contrast with the high predictive value of component midparents in determining their respective component expression in the progeny, which

may be surmised from the Wr/Vr graphs (figs. 1 to 4). However, naïvely resorting to the components midparents to predict progeny yield does not improve the situation. The value obtained by multiplication of component midparents only slightly improves the correlation with progeny yield in the

TABLE 2
Estimation of "true relative" genetic variance of sequential characters

	Untransformed data			Transformed data			"True relative" genetic variance $\frac{(B_2/A_2)}{(B_1/A_1)} \times 100$
	Parental mean A_1	Parental variance B_1	Weighted parental variance $(B_1/A_1) \times 100$	Parental mean A_2	Parental variance B_2	Weighted parental variance $(B_2/A_2) \times 100$	
F_1							
Heads/plant	22.85	1.04	—	—	—	—	100.00
Spikelets/head	20.70	1.19	5.748	26.60	0.487	1.83	31.83
Seeds/spikelet	2.24	0.18	8.036	16.89	0.032	0.19	2.35
Weight/grain	37.15	108.99	293.405	476.98	0.003	<0.01	<0.01
F_2							
Heads/plant	3.83	0.53	—	—	—	—	100.00
Spikelets/head	16.30	1.93	11.85	14.72	1.936	12.47	105.32
Seeds/spikelet	1.29	0.03	2.32	1.52	0.020	1.32	56.89
Weight/grain	42.05	116.86	277.91	165.91	0.001	<0.01	<0.01

F_2 but drives the correlation to virtually zero in the F_1 (table 3). We may surmise that there is some form of intercomponent interference underlying the situation and we already have examined above the consequences of one form of such interference—the inter-trait correlations. Removal of the correlations allows the recognition of two broad categories of component:

TABLE 3

Correlation and determination coefficients of observed diallel progeny yield with calculated midparent values of individual yield components and yield in the F_1 and F_2 . Yield 1 is calculated from the midparent component values and Yield 2 directly from parental yield

	Heads/ plant	Spikelets/ ear	Grains/ spikelet	Weight/ grain	Yield 1	Yield 2
F_1						
r (4 d.f.)	0.968**	-0.794	-0.033	-0.348	-0.098	0.796
Coefficient of determination	94%	63%	0%	12%	1%	63%
F_2						
r (4 d.f.)	0.449	0.896*	-0.312	0.290	0.810	0.686
Coefficient of determination	20%	80%	10%	8%	66%	47%

"influencing", e.g. heads/plant in the F_1 and spikelets/ear in the F_2 , and "influenced", e.g. the subsequent traits (see table 2). It is not too large a step to hypothesise that "influential" traits should not only strongly affect subsequent traits but contribute "disproportionately" to the variance of the complex trait. This surmise is borne out from the results given in table 3. Here the only midparent component traits which show a significant correlation with progeny yield are, in the F_1 , heads/plant (94 per cent. determination) and in the F_2 , spikelets/head (80 per cent. determination)—the influential rather than influenced characters mentioned above.

4. DISCUSSION

The "true relative" genetic variance of sequential characters when examined with the influence of previous characters in the developmental order removed differs considerably from the apparent genetic variance of the untransformed character (table 2). For the F_1 diallel the actual amount of genetic variance present in the second character in the sequence, spikelets per head, is *c.* 30 per cent. of the apparent genetic variance and this drops off rapidly to 2 per cent. in the third character, seeds per spikelet, and to practically zero for the last, weight per grain. These values are somewhat greater than the "true" heritability estimates for these components since the analysis of the Wr/Vr graph indicates an increase in the degree of dominance as we proceed along the sequence. Thus the true heritability differs quite considerably from the apparent (untransformed) situation. The reason for this lies in the fact that the apparent situation for spikelets/head reflects to some degree (about 70 per cent. = 100 per cent. - 30 per cent.) the observed genetic situation for heads per plant and the apparent situation for seeds/spikelet and weight/grain reflect almost completely (*e.g.* about 97 per cent. = 100 per cent. - 3 per cent.) the variation in the first two characters in the sequence. The mechanism of reflection is, of course, the internal correlations whose removal allows the true genetic control to be observed. In the F_2 the situation is somewhat different. The last character in the sequence possesses practically no true genetic variance and the penultimate character only 55 per cent. of the untransformed variance and even here the heritability would be considerably reduced if we recall fig. 3*b* (transformed data) where there are indications of a deviation from additivity. However, the second character in the sequence does not suffer from a reduction in "true" genetic value. In this case, however, there was little influence of heads per plant on spikelets per head though the medium of correlations, in contrast to the F_1 situation. The reason for the lack of influence of heads per plant in the F_2 may be surmised from table 1, from the very low values of this character and thus its inability to produce stress—see Whitehouse *et al.* (*loc. cit.*) for an explanation of these low values in the F_2 . In the F_2 , and in the F_2 only, we may conclude therefore that the true genetic situation for spikelets per head is revealed in analysis either of transformed or untransformed data and indeed the Wr/Vr graph situation for this character does not differ greatly from transformed to untransformed data.

In summary, we may surmise that both the amount and kind of genetic variance may differ from the apparent situation when the influence of correlations are removed. The analysis of yield components illustrates the point that we might or might not be inspecting the true genetic situation when untransformed sequential characters are analysed. If the characters are strongly correlated there is good evidence that an apparent control over later characters in a sequence is merely a reflection, through stresses, of control by previous characters. It may not be a general rule that the latter characters in a sequence have little or no real direct genetic control—but this possibility will rest with analysis of other sequences. The present findings do however agree with those considered in a similar type of analysis by Thomas, Grafius and Hahn (1970*b*), where yield components in barley and rice were considered, in that the degree of true direct genetic control diminishes as characters further along a sequence are considered.

The possible applications of the present findings to improving breeding techniques are rather exciting. We have already indicated in section (iii) of the Results that yield prediction is feasible in the present data by ignoring unimportant and concentrating on one influential component. The findings may have more general application since the predictive values of midparents may be weighted with the true relative genetic variances as well as the conventional heritability and multiple regression weights proposed by Grafius (*loc. cit.*). Such weighting applied to the present data gave a very slight improvement in determination of progeny yield over that of the best component—which is not surprising since the effectiveness of the latter is so high. What also offers some room for optimism is the finding that the type and degree of stress is under stronger environmental than genetic control (Thomas, Grafius and Hahn, 1970*b*), but that the expression of the primary characters in the sequence is under genetic control. Further reference to prediction will be made in a forthcoming paper (Grafius and Thomas, 1970).

5. SUMMARY

1. Diallel analysis is applied to four sequential, correlated, yield component traits in wheat.

2. Analysis of the untransformed components indicates a mainly additive control of genetic variance. However, with the correlations removed deviations from additivity may be observed. These deviations increase in magnitude with progression from early to late developmental traits.

3. The parental variance of the transformed variables is generally less than the corresponding untransformed characters. This decrease becomes larger with progression along the developmental sequence away from the main influential character.

4. The degree of dropoff is more striking in the F_1 than the F_2 , but in both instances the relative variance of the transformed variable compared with the untransformed variable approaches zero in the last component—seed weight.

5. A means of prediction of the complex trait, progeny yield, is suggested.

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