

## NOTES AND COMMENTS

### THE 2×2 GENOTYPE-ENVIRONMENT TABLE

J. H. VAN DER VEEN

*Laboratory of Genetics, Agricultural University, Wageningen, The Netherlands,  
and A.R.C. Unit of Biometrical Genetics, Department of Genetics,  
University of Birmingham, England*

Received 4.ix.58.

If two genotypes or groups of genotypes,  $G_0$  and  $G_1$ , are raised in each of two environments,  $E_0$  and  $E_1$ , the four resulting phenotypes may, in respect

TABLE 1

	$G_0$	$G_1$	Mean
$E_0$ . . . . .	$m+d+e+g$	$m-d+e-g$	$m+e$
$E_1$ . . . . .	$m+d-e-g$	$m-d-e+g$	$m-e$
Mean . . . . .	$m+d$	$m-d$	$m$

of any quantitative character, be expressed in terms of four parameters. In table 1,  $m$  stands for the overall mean,  $d$  represents the average genotypic

TABLE 2

	$G_0$		$G_1$	
$E_0$ .	00	$d+e+g$	01	$e$
$E_1$ .	10	$d$	11	$g$

effect,  $e$  the average environmental effect, and  $g$  the genotype-environment interaction. These parameters were recently used by Mather and Morley Jones (1958) in their study of genotype-environment interactions in quantitative inheritance.

In the following we will compare in terms of  $d$ ,  $e$  and  $g$  the *relative* magnitudes of the phenotypic values, to be labelled 1, 2, 3 and 4 in descending order. For ease of inspection table 1 may be transformed into table 2 by adding to its elements  $-m+d+e+g$  and dividing by 2.

Haldane (1946) compared the relative magnitudes without the use of parameters, and dealt with  $3! = 6$  situations, left after assigning the largest phenotypic value to 00. This implies (table 2)  $e+g > 0$ ,  $d+g > 0$ , and  $d+e > 0$ , *i.e.* not more than one of the parameters is allowed to become

negative, and its absolute value must be smaller than the value of the two positive ones. Haldane's six types can be described as follows :—

1a	$\begin{array}{cc} 1 & 3 \\ 2 & 4 \end{array}$	3	$\begin{array}{cc} 1 & 4 \\ 2 & 3 \end{array}$	4a	$\begin{array}{cc} 1 & 4 \\ 3 & 2 \end{array}$
	$d > e >  g $		$d > g >  e $		$g > d >  e $
1b	$\begin{array}{cc} 1 & 2 \\ 3 & 4 \end{array}$	2	$\begin{array}{cc} 1 & 2 \\ 4 & 3 \end{array}$	4b	$\begin{array}{cc} 1 & 3 \\ 4 & 2 \end{array}$
	$e > d >  g $		$e > g >  d $		$g > e >  d $

Mather and Morley Jones (*loc. cit.*) took all three parameters as positive in that they omitted the modulus sign from the inequalities, and therefore did not cover all possible situations.

The present author proposes a modified approach as (1) it seems more consistent to take the same two parameters as positive in all cases, and as (2) it is customary in biometrical genetics to define  $d$  as non-negative. Let us define  $d$  and  $e$  as non-negative and consequently allow only  $g$  to take sign. This means that the four phenotypic values must be arranged in table 1 so that  $00+10 \geq 01+11$ , as  $d \geq 0$ , and  $00+01 \geq 10+11$ , as  $e \geq 0$ . Then with  $g < 0$  four new sequences of magnitude arise, *viz.*  $3'$  ( $d > -g > e$ ) as a counterpart of 3 ( $d > g > e$ ), etc., in which  $00$  is not the largest phenotype. The  $6+4 = 10$  types have been listed in table 3. Inspecting this table with the help of table 2 we see :—

1. Table 3 is symmetrical for  $d > e$ , *i.e.*  $10 > 01$ , and  $e > d$ , *i.e.*  $10 < 01$ .
2.  $g > 0$  implies that  $00$  is the largest phenotype,  $g < 0$  that  $11$  is the smallest.
3. If  $g > 0$ , then  $00-10 > |01-11|$  and  $00-01 > |10-11|$ . This means that  $G_0$  is the less stable genotype and at the same time  $E_0$  the most differentiating environment. If  $g < 0$  this holds for  $G_1$  and  $E_1$  respectively.
4. If  $d > |g|$  and  $d > e$  (cases 1a, 3 and 3'), then  $G_0$  is the highest "yielder" irrespective of environment:  $G_0$  shows *unconditional superiority*. If in addition  $|g| > e$  (cases 3 and 3'), then  $G_0$  and  $G_1$  have their highest values in different environments. Thus the superiority of the environment is conditioned by the genotype. This may be described as *conditional superiority of the environment*.

If  $e > |g|$  and  $e > d$  (cases 1b, 2 and 2'), then  $E_0$  shows *unconditional superiority*. If in addition  $|g| > d$  (cases 2 and 2'), then

TABLE 3

The possible comparisons in terms of the parameters  $d$ ,  $e$  and  $g$  (cf. Table 1), of four phenotypes obtained by raising two genotypes in each of two environments. The phenotypic values have been labelled 1, 2, 3 and 4 in descending order of magnitude. The parameters  $d$  and  $e$  have been defined as non-negative. A line indicates equality of phenotypic values. Type numbers have been added to the cases where all four values are different.

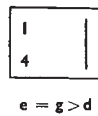
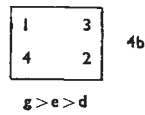
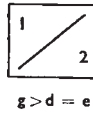
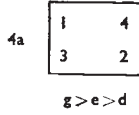
d > e

d = e

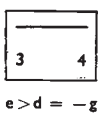
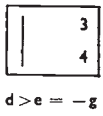
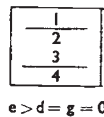
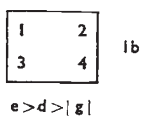
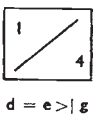
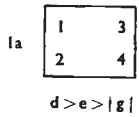
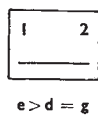
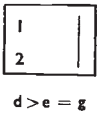
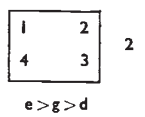
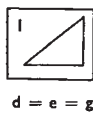
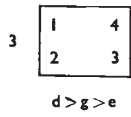
d < e



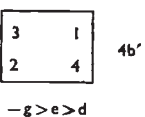
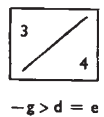
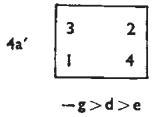
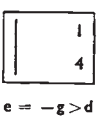
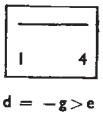
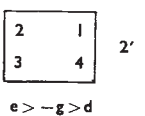
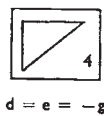
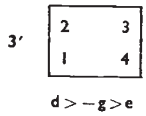
$g > d = e = 0$



g > 0



g < 0



$-g > d = e = 0$

$E_0$  and  $E_1$  induce the "better performance" in different genotypes. Thus the superiority of the genotype is conditioned by the environment: *conditional superiority of the genotype*.

If  $|g| > d$  and  $|g| > e$  (cases  $4a$ ,  $4a'$ ,  $4b$  and  $4b'$ ), then there is no unconditional superiority of either kind: *specific adaptation*.

Turning now to the cases of two or more phenotypic values being equal, we find that each of them corresponds uniquely to a parameter equality (cf. table 2) :—

$$\begin{array}{llll}
 d = -g & \therefore 00 = 01 & e = -g & \therefore 00 = 10 \\
 d = g & \therefore 10 = 11 & e = g & \therefore 01 = 11 \\
 d = g = 0 & \therefore \begin{cases} 00 = 01 \\ 10 = 11 \end{cases} & e = g = 0 & \therefore \begin{cases} 00 = 10 \\ 01 = 11 \end{cases} \\
 d = e & \therefore 10 = 01 & d = e = -g & \therefore 00 = 01 = 10 \\
 d = e = 0 & \therefore \begin{cases} 10 = 01 \\ 00 = 11 \end{cases} & d = e = g & \therefore 01 = 10 = 11 \\
 & & d = e = g = 0 & \therefore 00 = 01 = 10 = 11
 \end{array}$$

It should be noted that  $d = 0$ ,  $e = 0$  or  $g = 0$  does not in itself lead to equality of phenotypic values. The different cases, apart from  $00 = 01 = 10 = 11$ , have been inserted in table 3.

Change in environment or selection in populations of genotypes may cause the different types to pass into each other. When by some selection device  $g$  is increased, e.g. type  $4a'$ , changes into  $3'$ ,  $1a$ ,  $3$  and  $4a$  respectively. Decrease of  $d$  leads from, e.g. type  $1a$  via  $1b$  to  $2$  or  $2'$ , depending on whether  $g > 0$  or  $g < 0$ . When we then allow  $d$  to become negative, we obtain  $e > -d > |g|$  and finally  $-d > e > |g|$ . These types derive from  $1b$  and  $1a$  by interchanging the columns. Having defined  $d$  as non-negative, however, the selection result will under the present approach make the particular population change its label  $G_0$  into  $G_1$  or *vice versa*.

*Acknowledgments.*—I wish to thank Professor K. Mather for helpful discussion and for the opportunity of working in his department. This work was carried out while in receipt of a grant from the Netherlands Organisation for Pure Research (Z.W.O.).

## REFERENCES

- HALDANE, J. B. S. 1946. The interaction of nature and nurture. *Ann. Eugenics*, 13, 197-205.  
 MATHER, K., AND MORLEY JONES, R. 1958. Interaction of genotype and environment in continuous variation. I. Descriptions. *Biometrics*, 14, 343-359.