GENOTYPE × ENVIRONMENT INTERACTIONS [1]

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SUMMARY

A genotype x environment interaction may be defined as a change in the relative perfor-mance of a « character » of two or more genotypes measured in two or more environments. Inter-actions may therefore involve changes in rank order for genotypes between environments and changes in the absolute and relative magnitude of the genetic, environmental and phenotypic variances between environments.

The genetic correlations for performance of genotypes between environments are assumed to be based on both linkage and pleiotropy and in this respect are similar to genetic correlations between traits in the same genotypes and environments.

Interactions are probably not eliminated if only the low performance environments are exclu-ded. However, there is evidence that heritability increases with increases in levels of performance though the change may be the result of increases in genetic variation or decreases in environ-mental variation or both.

Within the usual range of environments found amongst commercial production units, the changes in variance may be sufficiently large and interactions sufficiently small to warrant a choice of environments used for selection.

There are now many reports of the magnitude of genetic correlation between environments for characters of economic importance in cattle, sheep, pigs and particularly poultry. The corre-lations do not deviate so far from 1 as was perhaps originally suspected and the environments included have to differ considerably for rank order changes to be important. Extreme differences in environmental rainfall, temperature, photoperiod, space, diet and feeding method, and disease exposure are the conditions most likely to result in low genetic correlations.

INTRODUCTION

A genotype x environment interaction may be defined as a change in the relative performance of a « character » of two or more genotypes measured in two or more environments. Interactions may therefore involve changes in rank order for genotypes

between environments and changes in the absolute and relative magnitude of the genetic, environmental and phenotypic variances between environments. These changes in rank order and in variances (an important distinction to be referred to later) are found separately and together and are illustrated in figure I. They have important implications for the animal breeder in designing his selection programmes.
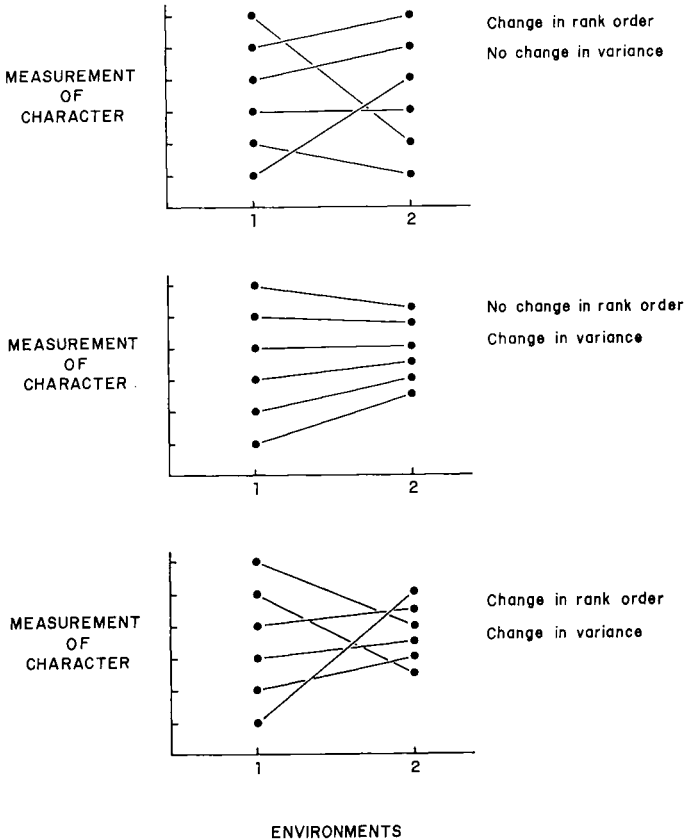

FIG. I. — *Genotype x environment interactions*
Interactions entre le génotype et l'environnement

An early effort to classify genotype-environment interactions was made by HAL-DANE (1946). It would seem that of the four groups of interactions which he proposed, his first group is not an interaction as defined above. A later effort at classification was made by McBRIDE (1958) who did not give a definition but implied that he was discussing non additive relationships between genotype and environment which therefore included both rank order and variance changes. McBRIDE proposed four groups of interactions, namely

Type A	Intra-population micro environnement	
Type B	Intra-population macro	—
Type C	Inter-population micro	—
Type D	Inter-population macro	—

He gave a number of examples which he suggested justified the form of classification though he realized that it was difficult to so clearly define the classes as to avoid borderline cases. He also indicated that HALDDANE's suggested interactions would apply to all four of his own classes. In terms of the design of selection programmes and practical animal breeding there seems little to be gained from either of the schemes of classification. It is however important to distinguish rank order and variance changes and this distinction will be made clear throughout this paper.

The measurements which are made on the « same » genotypes maintained in two or more environments, frequently are assumed to be measurements of the same character even though different genes may affect the character in different environments. It is clear from some experiments (e. g. FALCONER and LATYSZEWSKI, 1952) that the same measurements are estimating different compound characters in different environments. Care is therefore essential in interpreting the results of genetic analyses and selection programmes involving the same measurements and genotypes in different environments, and it is perhaps inappropriate to talk of these measurements as a single character, unless they have been shown to be so. The genetic correlations for performance of genotypes between environments are assumed to be based on both linkage and pleiotropy and in this respect are similar to genetic correlations between traits in the same genotypes and environments.

CHANGES IN VARIANCE BETWEEN ENVIRONMENTS

Theoretically there could be differences between environments in the intraenvironmental genetic and environmental sources of variation. Increases in the genetic components particularly the additive genetic component and decreases in the environmental components would result in higher values of heritability. It was the late Sir John HAMMOND (1947), who suggested that the more suitable the environment for the expression of a character the greater the progress likely to be achieved by selection. He was assuming that heritability is highest in those environments producing the highest performance for the character under selection. He also assumed that genotype x environment interactions are either small or occur in those environments (low performance) having little importance for most producers. In one aspect he was right but in another he was wrong. Interactions are probably not eliminated if only the low performance environments are excluded. However, there is evidence that heritability increases with increases in levels of performance though the change may be the result of increases in genetic variation or decreases in environmental variation or both (ROBERTSON, O'CONNOR and EDWARDS, 1960 ; BOWMAN and POWELL, 1964).

QUANTITATIVE ESTIMATION
OF GENOTYPE × ENVIRONMENT INTERACTIONS

This subject has been discussed at length by DICKERSON (1962). For several genotypes whose performance is measured in two environments an appropriate product-moment estimate of genetic correlation (r_G) can be calculated from the

genetic components of variance and covariance. For the situation involving more than two environments it is more convenient to calculate the intra-class genetic correlation r_{G_t} from the components of variance for genotypes (σ_G^2) and for genotype x environment interaction (σ_{GE}^2) such that

$$r_{G_t} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2}$$

DICKERSON has shown that the intra class genetic correlation has to be adjusted for differences in genetic scale between environments, so that

$$\text{adj.} \quad r_{G_t} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 - (V\sigma_{G_i})}$$

Where $V\sigma_{G_t}$ = the interenvironmental variance of the intraenvironmental genetic standard deviation (σ_{G_i}).

The adjusted intra class genetic correlation is equivalent to the pooled estimate of product-moment genetic correlations between all possible paired combinations of environments. DICKERSON emphazises that « the variance component for average genetic raenking across all environments is interpreted as the average covariance for the same genotype in different environments (i. e. $\sigma_G^2 = \bar{\sigma}_{G_{ij}}^2$) to include the possibility of negative genetic correlation ». Thus for two environments the value of the product-moment genetic correlation can be between — 1 and + 1 whilst for more than two environments the value of the intra class genetic correlation can be between 0 and + 1.

THE THEORETICAL CONSEQUENCES FOR SELECTION
OF GENOTYPE-ENVIRONMENT INTERACTIONS

Measurements of « the same character » in two different environments should for the purposes of predicting response to selection be considered as two characters. Then, as shown by FALCONER (1952) and ROBERTSON (1959) and as further developed by DICKERSON (1962) the ratio of response for one character in one environment by selection in that environment to the response for the same character in the same environment by selection in a second environment is

$$\frac{R_1}{CR_1} = \frac{1}{r_{G_t}} \frac{i_1 h_1}{i_2 h_2}$$

where R_1 = response in environment 1 by selection in environment 1
$\quad CR_1$ = response in environment 1 by selection in environment 2
i_1 and i_2 = selection intensity in environments 1 and 2 respectively
h_1 and h_2 = square root of the heritability of « character » in environments 1 and 2 respectively.
$\quad\quad r_{G_t}$ = adjusted genetic correlation between the « character » in the two environments.
Frequently the animal breeder is concerned not with just two environments but

with several. DICKERSON (1962) has shown that the genetic response in average per formance in all environments is dependent in the following way on the number of environments used for selection.

Thus
$$\frac{\Delta G_t \text{ when } k > 1}{\Delta G_t \text{ when } k = 1} = \sqrt{\frac{1}{1 + (k - 1)r_{G_t}^1}}$$

where ΔG_t = genetic response in average performance in all enrironments.

k = number of environments.

This expression applies when there is replication of a similar number of individuals of each genotype at each environment irrespective of the number of environments. When the total number of individuals per genotype is fixed and the number at each environment varies, depending on the numbre of environments, then the expression becomes :

$$\frac{\Delta G_t \text{ when } k > 1}{\Delta G_t \text{ when } k = 1} = \sqrt{\frac{1 + (nk - 1)h_w^2}{1 + (n - 1)h_w^2 + n(k - 1)r_{G_t}^1 \cdot h_w^2}}$$

where n = number of individuals per environment

h_w^2 = the heritability of individual variation within environments.

This expression can be used to choose the appropriate number of environments for selection depending on the specific values of the heritability and the genetic correlation.

PRACTICAL CONSEQUENCES

OF GENOTYPE-ENVIRONMENT INTERACTIONS

FOR THE ANIMAL BREEDER

A. — *Changes in variance between environments*

Within the usual range of environments found amongst commercial production units, the changes in variance may be sufficiently large and interactions sufficiently small to warrant a choice of environments used for selection. In those cases where selection is based on an index of several characters it is usually not necessary to record all characters in all environments and further, though less likely, it may be advantageous to record the different characters each in a different set of environments. The animal breeder is often required to carry out a selection programme on the basis of records from commercial units and his choice of environments is then determined not by considerations of programme design and efficiency but solely by the number of producers who can be persuaded to undertake the necessary recording.

Perhaps of greater future interest are the consequences of selection in environments not included amongst current commercial production units, and in which the genetic variance may be increased considerably. For example, the results of the following experiments will be particularly interesting ; selection for egg production in chickens maintained on continuous light and in which regular ovulation cycle lengths of 22 hours have been recorded ; selection for length of oestrus season in sheep maintained on constant daylength ; selection for growth and conversion efficiency of various species on diets deficient in some normally required constituent

where the feed intake can be controlled so that the animal cannot compensate for the deficiency by increased intake. Such selection programmes may make it possible to markedly change the efficiency and performance of the domesticated species.

B. — *Rank order changes between environments*

There are now many reports of the magnitude of genetic correlation between environments for characters of economic importance in cattle, sheep, pigs and particularly poultry. The correlations do not deviate so far from 1 as was perhaps originally suspected and the environments included have to differ considerably for rank order changes to be important. Extreme differences in environmental rainfall, temperature, photoperiod, space, diet and feeding method, and disease exposure are the conditions most likely to result in low genetic correlations.

In determining the number of environments, in which to select in those cases where the genetic correlation is much less than 1, the breeder should ask first three nongenetic questions. What proportion of commercial production is represented by each of the distinguishably different environments and are any of them relatively unimportant? In the economic circumstances likely to prevail in the near future (5-15 years depending on species) are any of the existing environments used for commercial production likely to be abandoned because they are unsuitable for economic or other reasons? Would it be easier (in terms of persuasion, economics or other practical considerations) to persuade some producers to change their environments/systems of production to but one or two standard forms to suit one or two selected genotypes rather than to select many genotypes to suit the many production environments/systems?

Answers to these questions, coupled with the magnitude of the genetic parameters usually enables the breeder to reduce the number of separate strains to meet specific environmental/production systems requirements to very few (2 or 3). However, it does emphasize the advantages to be gained from closer collaboration between breeders and workers in other disciplines (e. g. nutrition, behaviour, environment) in finding the optimum cobimnation of genotype and environment.

RÉSUMÉ

INTERACTIONS GÉNOTYPE × MILIEU

On peut définir une interaction génotype-milieu comme un changement dans les performances relatives, pour un « caractère », de un ou plusieurs génotypes, performances mesurées dans deux ou plusieurs milieux. Les interactions peuvent ainsi impliquer des changements dans l'ordre de classification des génotypes selon les milieux et des changements dans les valeurs absolues et relatives des variances génétiques, des variances de milieu et des variances phénotypiques entre milieux.

On suppose que les corrélations génétiques des performances des génotypes entre milieux résultent à la fois du linkage et de la pléiotropie et, de ce point de vue, elles ressemblent à des corrélations génétiques entre caractères à génotypes et milieux constants.

Les interactions ne sont probablement pas éliminées si on exclut seulement les milieux à faibles performances. Cependant on a pu montrer que l'héritabilité augmente lorsqu'augmente le niveau des performances, bien que cette évolution puisse provenir d'un accroissement de la

variation génétique ou d'une diminution de la variation due au milieu ou des deux phénomènes.

A l'intérieur de l'intervalle normal de variation de milieu des unités commerciales de production, les changements de variance peuvent être suffisamment grands et les interactions suffisamment petites pour garantir un choix de milieux utilisables en sélection.

Il y a maintenant de nombreux travaux établissant la valeur de la corrélation génétique entre milieux pour des caractères économiquement importants chez les Bovins, le Mouton, les Porcs et, spécialement, la Volaille. Les corrélations s'écartent moins de l'unité qu'on ne l'avait peut-être pensé au départ et les milieux mis en comparaison doivent être très différents pour que les changements d'ordre de classification soient importants. Des écarts extrêmes dans la pluviométrie, la température, le photopériodisme, la densité de peuplement, le régime et les méthodes d'alimentation ainsi que l'exposition à la maladie sont les conditions les plus susceptibles d'entraîner de faibles corrélations génétiques.

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