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Genotype × environment interaction in *Tribolium castaneum**

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A knowledge of the existence and nature of genotype × environment interaction is essential to an understanding of genetic changes in natural populations and to the formulation of effective breeding plans for domestic species. The results of selection experiments in different environments have not always appeared to agree fully with theoretical expectations (Falconer, 1960, p. 324). Experiments are required to test existing theory and provide a basis for extended theoretical development. This paper describes the analysis of an experiment with the flour beetle, *Tribolium castaneum*, designed to detect and investigate the nature of genotype X environment interaction. The environments relate to temperature and relative humidity and the genotype expression to reproductive performance.

1. EXPERIMENTAL DESIGN

Temperature and relative humidity exert a strong influence on growth and on the reproductive rate of *T. castaneum* (Bray, 1960; Bray *et al.*, 1962), and they were used to create two environments. One, designated E_1, was provided by an incubator maintained at a temperature of 33·3°C. and 45% relative humidity. These are generally considered optimum or near optimum conditions for maximum reproduction and growth. The other environment, E_2, was at room conditions where the temperature varied between 22·2°C. and 26·7°C. and the relative humidity varied from 30% to 35% during the experiment. Conditions as divergent as those of E_2 are within the range commonly encountered by natural populations of *T. castaneum*. These environments are subject to control, and are considered as fixed effects.

A large sample from a panmictic population of wild-type beetles was obtained from Dr A. E. Bell of Purdue University. It was expanded and maintained as a panmictic population with an estimated effective size of several thousand. Approximately 100 male and 300 female pupae were isolated to initiate the experiment. Each sex was maintained separately in the incubator for 10 days when the adults had emerged and matured. Ninety-two matings of one male and three females

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were made and placed in the incubator. Four days later, the females were transferred to individual $\frac{3}{4}$ oz. creamers and returned to the incubator until pupae were produced.

Six daughters were taken as pupae from each dam for experimental treatment and measurement. It was not possible to determine exactly the age of pupae, but the procedure used was designed to minimize age variation in a practical manner. Each group of six full sibs was maintained in the incubator for 8 days at which time adult beetles had emerged and matured. Three of each group were assigned to the incubator, E_1, and the other three to room conditions, E_2. Each adult female was individually mated to an unrelated male immediately prior to being placed in the appropriate environment. The female and her mate were discarded after 72 hours. The number of pupae and of larvae produced by each female were counted 23 days after removal of the adults in E_1, and 34 days after their removal in E_2.

Two related measures of reproductive performance were studied, the number of pupae and the number of pupae and larvae. These traits are not statistically independent since they form a part-whole relation. This design and the statistical analysis are similar to those described by Lowry *et al.* (1956) in which half and full poultry sibs were divided among two environments.

2. RESULTS AND DISCUSSION

The range in pupa number produced by an individual female in the incubator was 0 to 68 with an average of 13·4, while under room conditions the range was 0 to 29 and the average 3·3. The range for pupae plus larvae in the incubator was 0 to 93, with an average of 20·1; comparable data under room conditions were 0 to 32, and an average of 9·2.

The variance within full-sib families was larger in E_1 than in E_2 for both traits. A transformation to $(X+1)^{\frac{1}{2}}$ equalized the variances, and subsequent analyses were made employing the transformed data.

The analysis of variance is presented in Table 1. In some instances only one or two of the three females mated to each sire produced pupae. The desired six pupae were not available from a few dams. Analyses were computed considering the coefficients of the expected mean squares that would have been zero in the balanced case as zero and calculating the proper coefficients for the remainder. Ignoring the slight imbalance did not materially alter the estimates of the variance components. The expectations of the mean squares are given in Table 1. The coefficients indicate the degree of imbalance was slight. The F values required for approximate tests of significance are readily deduced from Table 1.

Estimates of the components of variance are presented in Table 2. Since the environmental factors are controllable, the variation attributable to them was not included in σ_T^2 in Table 2. Differences among sires account for 17·5 and 14·2% of the total variance for the two traits.

The two components, σ_{ES}^2 and $\sigma_{ED/S}^2$ provide an estimate of the magnitude and in part the nature of the interaction. They account for 6·7 and 3·7%, respectively,

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Table 1. *Analysis of variance of* $(pupae+1)^{\frac{1}{2}}$ *and* $(pupae+larvae+1)^{\frac{1}{2}}$

Source of variation	Degrees of freedom	Mean squares		Expected mean squares
		$(\text{Pupae}+1)^{\frac{1}{2}}$	$(\text{Pupae}+\text{larvae}+1)^{\frac{1}{2}}$	
Environments, E	1	1157·694**	799·445**	$\sigma^2_W + 2{\cdot}96\sigma^2_{ED/S} + 8{\cdot}45\sigma^2_{ES} + 758{\cdot}51\sigma^2_E$
Sires, S	91	6·015**	6·519**	$\sigma^2_W + 5{\cdot}86\sigma^2_{D/S} + 16{\cdot}34\sigma^2_S$
Dams in Sires, D/S	168	1·720**	2·411**	$\sigma^2_W + 5{\cdot}80\sigma^2_{D/S}$
Environments × Sires, ES	91	1·934**	0·998	$\sigma^2_W + 2{\cdot}95\sigma^2_{ED/S} + 8{\cdot}24\sigma^2_{ES}$
Environments × Dams in Sires, ED/S	168	1·105*	1·214	$\sigma^2_W + 2{\cdot}92\sigma^2_{ED/S}$
Within, W	997	0·943	1·105	σ^2_W

* 5% level of significance.
** 1% level of significance.

of the total variance for $(\text{pupae}+1)^{\frac{1}{2}}$ and both mean squares are significantly different from zero. There is no indication of interaction of non-additive genetic effects with environment since $\sigma^2_{ED/S}$ is actually smaller than σ^2_{ES}. Corresponding values for $(\text{pupae}+\text{larvae}+1)^{\frac{1}{2}}$ are 8·3 and 2·1%, but neither mean square is significant. This unexpected result indicates that the interaction was due to differences among genotypes in their relative rate of reaching pupation in the two environments, but that there are no such differences for total production.

Table 2. *Components of variance estimated from analysis of variance of* $(\text{pupae}+1)^{\frac{1}{2}}$ *and* $(\text{pupae}+\text{larvae}+1)^{\frac{1}{2}}$

	$(\text{Pupae}+1)^{\frac{1}{2}}$		$(\text{Pupae}+\text{larvae}+1)^{\frac{1}{2}}$	
Component	Value	% Total	Value	% Total
σ^2_W	0·943	63·12	1·105	62·64
$\sigma^2_{ED/S}$	0·055	3·68	0·037	2·10
σ^2_{ES}	0·100	6·69	0·147	8·33
$\sigma^2_{D/S}$	0·134	8·97	0·225	12·76
σ^2_S	0·262	17·54	0·250	14·17
σ^2_T	1·494	100·00	1·764	100·00

The nature of the interaction may also be indicated by a comparison of the average production, on both the actual and transformed scale, of each sire's daughters in one environment with the average production of his daughters in the other environment. Part of the interaction is due to an increasing difference in production between environments associated with increasing breeding values of the sires. In addition there are some differences in rank of breeding value of individual sires in the two environments. These rank changes result in selection of different sets of sires in the two environments.

Table 3. *Within environment estimates of heritability*

	E_1		E_2	
h^2 estimated by	$(\text{pupae}+1)^{\frac{1}{2}}$	$(\text{pupae}+\text{larvae}+1)^{\frac{1}{2}}$	$(\text{pupae}+1)^{\frac{1}{2}}$	$(\text{pupae}+\text{larvae}+1)^{\frac{1}{2}}$
$4\sigma^2_S/\sigma^2_T$	0·68 ± 0·17	0·64 ± 0·16	1·15 ± 0·18	0·51 ± 0·15
$4\sigma^2_{D/S}/\sigma^2_T$	0·67 ± 0·18	0·66 ± 0·18	0·25 ± 0·14	0·69 ± 0·19
$2(\sigma^2_S+\sigma^2_{D/S})/\sigma^2_T$	0·68 ± 0·09	0·65 ± 0·09	0·70 ± 0·10	0·60 ± 0·09

Three estimates of the heritability of each trait were computed within each environment. The three estimates were made by using the sire and dam-within-sire components for computing the intra-class correlations given in Table 3. The standard errors of the estimates as defined by Osborne & Patterson (1952) are also shown. There is no evidence that heritability is different in the two environments.

In each instance the sire component was larger than the dam-within-sire component, indicating that there is probably not much non-additive genetic variance in the population or that there are little or no environmental effects common to full sibs within half-sib families that are not common to paternal half sibs. Consequently, estimates of heritability from these two components may be considered equally reliable and their combination seems to provide the best estimate, since it has smaller variance.

It has been shown (Falconer, 1952; Lowry *et al.*, 1956; Robertson, 1959) that the genotype X environment interaction may be expressed as a genetic correlation. Therefore, another measure of the importance of these interactions may be obtained from the magnitude of the genetic correlation, r_G, between the measurements of the trait in the two environments. Two estimates of r_G for each trait are available from Table 2, these are $\sigma_S^2/(\sigma_S^2+\sigma_{ES}^2)$ and $\sigma_{D/S}^2/(\sigma_{D/S}^2+\sigma_{ED/S}^2)$ which when evaluated are 0·72 and 0·71 for (pupae + 1)$^{\frac{1}{2}}$ and 0·63 and 0·86 for (pupae + larvae + 1)$^{\frac{1}{2}}$.

When the same selection differential is applied on the two environments, and the heritabilities are equal, as in these data, the ratio of the correlated response of selection to the direct response is the genetic correlation. Hence, selection in one environment for production in the other is only 71 to 72% as effective as direct selection for pupa number, and 63 to 86% as effective for total production. In terms of percent of total variance the interaction is small, but it has a rather large effect on the correlated selection response. Moreover, this effect increases with increasing selection intensity.

SUMMARY AND CONCLUSIONS

An experiment was conducted with the flour beetle, *Tribolium castaneum* to investigate genotype-environment interaction. Ninety-two matings of one male and three females were made at random from a large panmictic population. The females were transferred to individual containers after 4 days. Six daughters were randomly selected from each sire–dam pair and individually mated to unrelated males. Three of the six were placed in an incubator (33·3°C., 45% relative humidity) and three in a cabinet at room conditions (22·2–26·7°C., 30–35% relative humidity) and allowed to produce eggs during a 3-day period. Progeny were counted as pupae and larvae. The traits studied were number of pupae and number of pupae plus number of larvae. A transformation to (X + 1)$^{\frac{1}{2}}$ was required. A conventional least-squares model was employed, and a large environmental effect was observed. In the incubator the mean number of pupae was 13·4 and of pupae + larvae was 20·1 while the corresponding figures for room conditions were 3·3 and 9·2. Genotype-environment interaction accounted for 3·7 to 6·7% of the total variance for (pupae + 1)$^{\frac{1}{2}}$ and 2·1 to 8·3% for (pupae + larvae + 1)$^{\frac{1}{2}}$. Heritability of the traits was essentially the same in both environments. The interaction was due to an increasing difference between environments in production associated with increasing breeding values of the sire, and to small changes in rank of breeding values on the two environments. As a result of the interaction, selection in one

environment for production on the other would be expected to be only 71 to 72% as effective as direct selection for (pupae + 1)$^{\frac{1}{2}}$ and 62 to 86% for (pupae + larvae + 1)$^{\frac{1}{2}}$ even though the fraction of the total variance attributed to genotype-environmental interaction was less than 10%.

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