Theor. Appl. Genet. 59, 123-128 (1981)

Genotype-Environment Interaction Effects on Reproductive Performance in *Tribolium castaneum*

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Summary. Three lines of *Tribolium castaneum* were raised totally on a yeast-free or yeast-supplemented diet, or raised to pupation on a yeast-free diet and then on a yeast-supplemented diet, and vice versa, to study the effects of genotype × environment interaction and diet changes after pupation on reproduction.

Feeding the yeast-supplemented diet generally resulted in earlier sexual maturation, heavier adult weights and higher egg production. The diets had no effects on larval viability. Changes in diet after pupation had no effects on age at sexual maturity or adult weight. Egg production was determined largely by the environment just prior to and during egg laying. However, egg production on the yeast-free diet was influenced by the pre-pupation diet.

There was significant line × environment interaction effects on age at sexual maturity, mature egg production and adult weight ($P < 0.01$). There was also a sire × environment effect on egg production ($P < 0.05$).

Key words: Genotype-environment Interaction – Reproduction – Eggproduction – *Tribolium*

Introduction

Genotype × environment interaction has been studied by many geneticists and breeders from different points of view. A review of the relevant papers and their opposing views was presented by McBride (1958).

In the genus *Tribolium* temperature, humidity and nutrient medium are among the environmental factors that affect various aspects of the life cycle (Park and Frank 1948; Howe 1962; Frey and Bell 1972; Hawk et al. 1974), and their effects on reproductive performance have been reported. Kidwell et al. (1964) found significant genotype × temperature and genotype × humidity interactions on a number of pupae and larvae 23 days after egg laying, a measure of reproductive performance. Orozco and Bell (1974a, 1974b) studied egg production of virgin females at different temperatures and found large and positive genetic correlations which suggested the possibility of genotype × environment interaction.

In an attempt to further explore the effects of genotype × environment interactions in *Tribolium castaneum*, a five-replicate experiment was performed to study the effects of nutrient media before and after pupation on growth and reproduction in three genotypes. The results of the first in these series which deal with growth traits have been reported by Benyi and Gall (1978). This paper reports the effects of pre- and post-pupation nutrient media on reproductive performance in three lines of *Tribolium castaneum*.

Materials and Methods

Genotypes and Environment

Two lines of *Tribolium castaneum* selected for large and small 21-day pupal weight (lines 6 and 2L, respectively) and their cross were used in the investigation. There were five replicates. The selected lines have been described by Gall (1970, 1971).

Two diets were formulated. One diet, referred to as poor (P), consisted of 100% white unbleached wheat flour. The other diet consisted of 90% white wheat flour supplemented with 10% dried brewers' yeast and was referred to as the good diet (G). The approximate compositions of the diets have already been given by Benyi and Gall (1978). Four environments were formed by dividing the life cycle of *Tribolium* into the active larval and the adult periods and feeding the two diets in various combinations. The four environments were:

1. Diet P for both periods of the life cycle,
2. Diet P for the larval period and diet G for the adult period,

0040/5752/81/0059/0123/$ 1.20

3. Diet G for the larval period and diet P for the adult period, and
4. Diet G for both periods of the life cycle.

Experimental Procedure

For each replicate, a random sample of approximately 100 adults each were taken from populations on lines 6 and 2L, kept in the laboratory, and set for a 24-hour egg collection on diet G. Eighteen to twenty-one days later, 5 male pupae were sampled from each of lines 6 and 2L and mated to 3 randomly-sampled females of its own line. In addition, each of 5 male pupae of line 2L was mated to 3 female pupae of line 6 to form the Line Cross. On day 31, each female was placed in a 4-dram vial containing diet P for a 24-hour egg collection. The following day (day 32), the same females were transferred into vials containing diet G for a second 24-hour egg collection, after which the females were discarded. The conditions under which all cultures were kept have been described by Benyi and Gall (1978).

From the 15th day onwards, following the individual egg collections in the two diets, each vial was inspected twice daily (9 a.m. and 9 p.m.) for pupae. All male pupae were discarded while female pupae were weighed and placed in individual vials. After emergence, four daughters were randomly sampled from each full-sib group. Two daughters remained on their pre-pupation diet while the other two were transferred to the other diet. Each daughter was mated to a mature male from a random-mating population since the presence of the male has been found to stimulate egg production in *Tribolium castaneum* (Gall and Bentley 1970). Each daughter was checked twice daily (9 a.m. and 9 p.m.) for age at sexual maturity, indicated by the first time she was observed to have laid an egg. Twenty-four-hour egg collections were made for all females that had reached sexual maturity on days 36 and 40 and these were summed and called mature egg production. The eggs collected on day 40 were retained for larval count 13 days later to measure larval viability. All females were weighed after the completion of the 40th day egg collection.

Statistical Methods

For age at sexual maturity, adult weight and larval viability data on all daughters alive were used. For mature egg production, data from sterile matings were excluded. A sterile mating was regarded as one that resulted in no egg production or the production of infertile eggs.

In all, 1370 observations were made on age at sexual maturity and 1230 on mature egg production, adult weight and larval viability. The data were analysed by least squares (Harvey 1960) using the following model:

$$Yi_{jklmn} = U + L_i + R_j + LR_{ij} + E_k + LE_{ik} + RE_{jk} + S_{l(ij)} + ES_{kl(ij)} + D_{m(ijl)} + ED_{km(ijl)} + e_{ijklmn}$$

where Y_{ijklmn} = an observation on the nth offspring of mth dam and lth sire in the kth environment, ith line and jth replicate; U = population mean; L_i = effect of the ith genetic line (i = 1, 2, 3); R_j = effect of the jth replicate (j = 1, 2, ..., 5); LR_{ij} = interaction of the ith line and jth replicate; E_k = effect of the kth environment (k = 1, 2, 3, 4); RE_{jk} = interaction of the jth replicate and kth environment; LE_{ik} = interaction of the ith line and kth environment; $S_{(ij)}$ = effect of the lth sire within the ith line and jth replicate l = (1, 2, ..., 5); $ES_{kl(ij)}$ = interaction of the kth environment and the lth sire; $D_{m(ij)}$ = effect of the mth dam, mated to the th sire within the ith line and jth replicate (m = 1, 2, 3); $ED_{km(ijl)}$ = interaction of the kth environment and the mth dam; e_{ijklmn} = random error assumed to be NID. The effects L_i, R_j and E_k were assumed fixed whereas $S_{(ij)}$, $D_{m(ij)}$ and e_{ijklmn} were assumed random.

Least squares means were compared by Duncan's Multiple Range Test. The harmonic mean number of offspring per dam was computed for each trait and used to calculate the contributions of the main effects and interactions to the total variance. The values were 1.47 for age at sexual maturity and 1.37 for mature egg production, adult weight and larval viability. Linear comparisons (Cochran and Cox 1962) were made to test the significance of heterosis and the effect of change in diets on post-emergence traits.

Results and Discussion

Means

Table 1 shows the least squares means for line x environment cells as well as overall line and environment means and standard errors. Averaged over all environments, line 6 daughters were heaviest in adult body weights and line 2L daughters the lightest. Line Cross daughters reached sexual maturity about 4 days earlier than line 6 daughters and about 1 day earlier than line 2L daughters. Line 2L daughters in turn matured about 2 days earlier than line 6 daughters. All the differences were significant ($P < 0.05$). Line 6 daughters laid the largest number of eggs followed closely by the Line Cross though the difference was statistically significant ($P < 0.05$). Line 2L daughters laid about half as many eggs as line 6 and Line Cross daughters. Larval viability was not significantly different between line

Table 1. Least squares means and standard errors*

Line	Environment	Age at sexual maturity (days) $\bar{x}$	s.e.	Mature egg production (no.) $\bar{x}$	s.e.	Adult weight (mg) $\bar{x}$	s.e.	Larval viability (%) $\bar{x}$	s.e.
6	1	31.4^{a}	0.18	35.5^{d}	0.75	3.08^{d}	0.024	0.78^{a}	0.018
	2	31.0^{a}	0.19	$52.4^{a,b}$	0.83	3.09^{d}	0.021	0.81^{a}	0.020
	3	$26.7^{b,c}$	0.20	41.3^{c}	0.86	3.28^{e}	0.28	0.80^{a}	0.20
	4	$26.6^{b,c}$	0.19	53.0^{a}	0.79	3.33^{e}	0.25	0.77^{a}	0.19
2L	1	26.9^{b}	0.18	18.5^{g}	0.77	1.29^{a}	0.025	0.90^{b}	0.018
	2	$26.7^{b,c}$	0.20	25.4^{f}	0.87	1.30^{a}	0.028	0.89^{b}	0.021
	3	$26.2^{c,d}$	0.21	20.2^{g}	0.95	1.28^{a}	0.023	0.90^{b}	0.023
	4	$26.2^{c,d}$	0.20	24.5^{f}	0.90	1.25^{a}	0.029	0.88^{b}	0.021
Line Cross	1	$25.7^{d,e}$	0.17	33.0^{e}	0.72	2.16^{b}	0.023	0.92^{b}	0.017
	2	25.6^{e}	0.18	50.1^{b}	0.79	2.21^{b}	0.025	0.93^{b}	0.019
	3	25.0^{f}	0.18	38.8^{e}	0.80	2.38^{c}	0.026	0.90^{b}	0.19
	4	24.6^{f}	0.17	$51.3^{a,b}$	0.76	2.36^{c}	0.025	0.90^{b}	0.018
		Line means							
6		28.9^{a}	0.10	45.6^{a}	0.49	3.20^{a}	0.019	0.79^{a}	0.012
2L		26.5^{b}	0.09	22.3^{b}	0.28	1.28^{b}	0.008	0.89^{b}	0.010
Line Cross		25.2^{c}	0.06	43.3^{c}	0.36	2.28^{c}	0.009	0.91^{b}	0.006
		Environmental means							
	1	28.0^{a}	0.09	29.0^{a}	0.41	2.14^{a}	0.012	0.87^{a}	0.011
	2	27.8^{a}	0.09	46.2^{b}	0.46	2.20^{a}	0.013	0.88^{a}	0.009
	3	25.8^{b}	0.15	33.4^{c}	0.44	2.31^{b}	0.020	0.80^{a}	0.012
	4	25.8^{b}	0.09	46.9^{b}	0.52	2.31^{b}	0.016	0.85^{a}	0.012

* In a column means carrying the same superscript are not significantly different at $P < 0.05$

2L and the Line Cross. Line 6 had a significantly lower larval viability than either line 2L or the Line Cross ($P < 0.05$).

The general reproductive performance of the lines as measured by age at sexual maturity, mature egg production and larval viability showed that line 6 daughters matured about 4 days later in environments 1 and 2 than in 3 and 4. In each pair of environments, age at sexual maturity was about equal. In line 2L and the Line Cross, there was a difference of less than a day between the ages at sexual maturity of females raised on the yeast-free and yeast-supplemented diets. The yeast-free diet, thus, had a greater detrimental effect on line 6 than on line 2L and the Line Cross. In each environment, the Line Cross was the earliest to reach sexual maturity and line 6 the latest. Though the difference between line 2L and the Line Cross were not more than 1.5 days over all environments, the difference between line 6 and the mean of line 2L and the Line Cross was dependent on the environment.

Line 6 females reached sexual maturity about 5 days later than 2L and the Line Cross in environments 1 and 2 but only a day later in environments 3 and 4. This would suggest a higher level of heterosis for this trait in environments 1 and 2 than in 3 and 4.

The pattern of egg production in all four environments was about the same in all lines. Egg production was lowest in environment 1, slightly improved in environment 3, and comparatively high in environments 2 and 4. The numbers of eggs produced in environments 2 and 4 were about equal within each line. In each environment, line 6 and Line Cross daughters laid the largest number of eggs and line 2L laid half as many eggs as lines 6 and Line Cross females. This may be explained partially in terms of body size. Enfield et al. (1966) reported an increase in the number of offspring produced in *Tribolium* as body size increased. The environment in which a female was raised had no apparent effect on the viability of her offspring, though line 6 females produced larvae of lower viability than lines 2L and Line Cross females.

Linear comparisons of environmental means shows that the change of diet after pupation had no effects on age at sexual maturity, adult weight, or larval viability. For mature egg production, the significant differences observed for all comparisons except that between environments 2 and 4 suggest that egg production was determined largely by the prevailing environment during egg laying. However, for egg laying on the yeast-free diet, females raised on the yeast-supplemented diet pre-pupation laid

more eggs than those raised continuously on the yeast-free diet suggesting that an optimum environment early in life not only hastens sexual maturation but also improves reproduction, generally.

Analyses of Variance and Estimates of Variance Components

Table 2 shows mean squares and estimates of variance components expressed as percentage of total variation from analyses of variance. Age at sexual maturity, mature egg production, and adult weight showed highly significant line, environment and replicate effects ($P < 0.01$). Evidence of genetic differences within lines was indicated by highly significant sire effects on age at sexual maturity and adult weight ($P < 0.01$) and a significant dam effect on larval viability ($P < 0.05$).

There were significant line x environment interaction effects on age at sexual maturity, mature egg production and adult weight ($P < 0.01$); a significant environment x sire interaction for mature egg production ($P < 0.05$); a significant line x replicate and replicate x environment interactions for age at sexual maturity, mature egg production and adult weight ($P < 0.01$). No interactions were observed for larval viability.

Line effects contributed 33.2%, 51.4%, 88.1% and 10.0% to the variation in age at sexual maturity, mature egg production, adult weight and larval viability, respectively. The corresponding environmental effects were 12.3%, 16.9%, 0.5%, and 0.0%, respectively. The other main effects contributed less than 4% to the variation in each trait.

The magnitude of genotype x environment (G x E) interaction was assessed in two ways. First, the contribution of line x environment interaction was compared with the total contribution from line and environment. Second, the total contribution of within line G x E interaction effects (environment x sire + environment x dam) was compared with the total within line genotype effects (sire + dam) to estimate the magnitude of the within-line genotype x environment interaction.

For age at sexual maturity, line and environment contributed 45.5% to the total variation as against 14.6% from their interaction. The interaction effects were, therefore, about 32% as large as the main effects. Within line G x E interaction was about one third as large as within line genotypic variation (0.6% vs 1.8%).

Line and environment contributed 68.2% to variation in mature egg production compared with only 3.1% from line x environment interaction. On the other hand, within line interaction contributed 2.0% to the variation compared with 0.70% from within line genetic effects. Line x environment interaction contributed less than 1% to the total variation in adult weight compared with a total contribution of 88.6% by line and environment. There was no within line interaction effects on adult weight but within line genotypic variation contributed 1%.

The major contribution to the variation in larval viability was from residual effect (76.7%) with line contributing 10.0%. There was no line x environment interaction effect but within line G x E interaction contributed an

Table 2. Mean squares (MS) and variance components expressed as percentage of the total variance (V.C)

Source	d.f	Age at sexual maturity (days)		Mature egg production (no.)		Adult weight (mg)		Larval viability (%)	
		MS	V.C	MS	V.C	MS	V.C	MS	V.C
Line (L)	2	1625.62[b]	33.23	60175.37[b]	51.38	341.55[b]	88.07	1.66[b]	9.97
Replicate (R)	4	21.21[b]	0.51	1637.47[b]	2.19	3.33[b]	1.35	0.02	0.00[c]
L X R	8	36.38[b]	3.08	486.52[b]	1.70	1.29[b]	1.41	0.06	0.26
Environ (E)	3	452.56[b]	12.29	15003.92[b]	16.86	1.52[b]	0.51	0.03	0.00[c]
L X E	6	181.87[b]	14.65	989.91[b]	3.09	0.62[b]	0.58	0.01	0.00[c]
R X E	12	10.21[b]	1.09	288.44[b]	0.84	0.45[b]	0.69	0.06	0.77
Sires/L X R	60	6.32[b]	1.75	85.69	0.42	0.20[b]	0.84	0.05	1.53
E X S/L X R	180	3.21	0.64	79.44[a]	1.97	0.05	0.00[c]	0.04	6.14
Dam/S/L X R	150	2.90	0.00[c]	68.53	0.31	0.07	0.19	0.04	4.60
E X D/S/L X R	xx	3.10	0.00[c]	56.20	0.00[c]	0.06	0.00	0.03	0.00[c]
Error	xx	3.62	32.76	60.96	21.23	0.06	6.36	0.03	76.73

xx Degrees of freedom for E X D were 387 and 343 for age at sexual maturity and egg production adult weight and larval viability, respectively. The corresponding error degrees of freedom were 532 and 437

[a] $P < 0.05$

[b] $P < 0.01$

[c] Negative estimates were assumed zero

Table 3. Least squares estimates of line by environment interaction effects

Line	Environment			
	Diet P in both periods	Diet P in larval period, diet G in larval period	Diet G in larval period, diet P in adult period	Diet G in both periods
Age at sexual maturity (days)				
6	$1.34^{b} \pm 0.14$	$1.19^{b} \pm 0.15$	$-1.33^{b} \pm 0.15$	$-1.20^{b} \pm 0.16$
2L	$-0.72^{b} \pm 0.14$	$-0.74^{b} \pm 0.16$	$0.72^{b} \pm 0.16$	$0.74^{b} \pm 0.17$
Line cross	$-0.62^{b} \pm 0.13$	$-0.45^{b} \pm 0.14$	$0.60^{b} \pm 0.14$	$0.46^{b} \pm 0.15$
Mature egg production (no.)				
6	$-1.64^{a} \pm 0.72$	0.98 ± 0.80	-0.72 ± 0.81	1.38 ± 0.76
2L	$4.38^{b} \pm 0.75$	$-2.11^{a} \pm 0.83$	1.65 ± 0.91	$-3.92^{b} \pm 0.84$
Line cross	$-2.74^{b} \pm 0.68$	1.13 ± 0.76	-0.93 ± 0.78	$2.54^{b} \pm 0.74$
Adult body weight (mg)				
6	-0.10 ± 0.06	-0.06 ± 0.06	0.14 ± 0.06^{a}	0.01 ± 0.06
2L	0.09 ± 0.06	0.10 ± 0.06	-0.09 ± 0.06	-0.10 ± 0.07
Line cross	0.01 ± 0.05	-0.05 ± 0.06	-0.05 ± 0.05	0.09 ± 0.06
Larval viability (%)				
6	-2.3 ± 2.7	-1.7 ± 3.1	3.4 ± 3.0	0.6 ± 3.2
2L	2.9 ± 2.9	1.4 ± 3.2	-1.9 ± 3.2	-2.4 ± 3.4
Line cross	-0.6 ± 2.7	0.3 ± 2.9	-1.5 ± 2.8	1.8 ± 3.0

[a] $P < 0.05$
[b] $P < 0.01$

amount equal to the within line combined genotype effects (6.1% and 6.2%, respectively).

Table 3 shows estimates of line × environment interaction effects. Significant estimates were observed mainly for age at sexual maturity and mature egg production with considerable changes in sign indicating differences in adaptation of the lines to the environments. The significant estimates tend to suggest that for mature egg production line 6 was poorly adapted to environment 1 but was indifferent to the others. Line 2L was well adapted to environment 1 but poorly adapted to 3 and 4 while the Line Cross was poorly adapted to environment 1 but well adapted to environment 4.

The interpretation of the estimates for age at sexual maturity is different since a bigger mean and therefore a positive estimate is a measure of slow development. The constants suggest that line 6 was poorly adapted to environments 1 and 2 and well adapted to environments 3 and 4 while in line 2L and the Line Cross the situation was reserved.

Line × environment interactions had significant effects on all traits except larval viability (Tables 2 and 3) indicating that the effect of the environment is a function of the line being used. There was also a significant within line G × E interaction effect on mature egg production. This implies that it may be important to test the offspring of sires in different environments for some reproductive traits since it is likely that the offspring will react differently to the environments. Orozco and Bell (1974a, 1974b) suggested that there was genotype × environment interaction in egg production of *Tribolium*. Osman and Bradford (1965) and Carter et al. (1971) concluded that genotype × environment interactions were small and not likely to be important in reproductive traits in sheep. The results of this investigation suggest genotype × environment interactions measured as line × environment effect may have an important effect on developmental rate but not on other traits.

Considering all traits, line effects were the largest for all traits contributing 10 to 88% of the variation observed. Within line genotypic effects were important only for age at sexual maturity and adult weight and larval viability but contributed less that 5% to the variation. The important line effects coupled with the relatively small within line genotypic effects observed for most traits suggest the need to emphasize lines (genetic stock) over sires and dams within lines when choosing animals for reproductive performance.

Heterosis

Table 4 shows the percent heterosis. Heterosis estimates for age at sexual maturity were significant in all environments ($P < 0.01$) and the average value in environments 1 and 2 (11.5%) was about double that in environments 3 and 4 (6.2%). This shows that although the superiority of the F_1 was observed on both diets, the expression was greater on the poor diet where the development of line 6 females was slow. The level of heterosis for mature egg production were similar in environments 2, 3 and 4 averaging 28.4% but was significantly lower ($P < 0.05$) in environment 1 (20.0%). It appears that for egg production, expression of heterosis in the F_1 was supressed by continuously raising the females on the poor diet. Significant heterosis was observed for larval viability ($P < 0.01$). The estimate in environment 3 was significantly lower ($P < 0.05$) than the average in the other three environments. Since environments had no overall effects on larval viability, the latter result may have been due to sampling or random error. There was no heterosis for adult weight in environments 1 and 2, but highly significant heterosis was observed when adults grew in environments 3 and 4. It appears that like egg production, heterosis for adult weight was suppressed by the yeast-free diet.

Considering all reproductive traits collectively, the hybrid females had the best overall reproductive performance. They reached sexual maturity 3 days earlier and laid 20 to 29% more eggs depending on the environment. This observation agrees with the report by Bell (1974) who indicated that hybrids reached sexual maturity about 3 days earlier and laid more than twice as many eggs as the mean of the parental lines. The heterosis reported for egg production in this investigation is considerably lower than the 279.3% reported by Boylan and Wong (1965). In their study, the high level of heterosis was due to the immaturity of the imbred females compared with the hybrids when egg collections were made. In this investigation, egg collections were made after the females had reached sexual maturity in all environments.

Table 4. Percent heterosis in four environments [a]

Environment	Age at sexual maturity (days)	Mature egg production (no.)	Adult weight (mg)	Larval viability (%)
1	11.82[b]	20.00[b]	−1.14	9.52[b]
2	11.27[b]	28.21[b]	−0.64	9.41[b]
3	5.48[b]	27.87[b]	4.39[b]	5.88[b]
4	6.82[b]	29.11[b]	3.06[b]	9.09[b]

[a] Percent heterosis = $\frac{F1 - MP}{MP} \times 100$ (x − 1 for age at sexual maturity)

[b] $P < 0.01$

Acknowledgement

The technical assistance of Mr. Boyd Bentley is greatly appreciated.

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Received August 7, 1980
Communicated by H. Abplanalp

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