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Genotype × environment interaction in dairy cattle and its role in breeding programmes

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Summary. Eighty thousand, one hundred and eleven records of the Israeli dairy herdbook for the period of 1973–1977 were studied and examined to determine the existence of Genotype × Environment Interaction (G × E) as affecting milk yield in kg per day between calvings. Various quantitative measures of environment were used while the genotypes were evaluated as the average performance of each sire's daughters in a whole range of environments.

When the environment was evaluated as level of production, the relative importance of the interaction was found to be very low. Furthermore, the linear dependence on the interaction of the individual sires with the environments was found to be inconsistent with time, meaning that no justification was found for using specific adaptation patterns of genotypes to these environments.

When lactation number and given time periods were used as environments, significant interactions were found between genotypes and environments. Results of the analyses of Genotype × Lactation interaction imply that the interaction values, to a certain degree, confused the differences between the sires when based on first lactation records. We therefore conclude that the need exists to expand the basis of sire evaluation, including the addition of data on successive lactation periods beyond the first one.

We maintain that the genetic characteristic for this phenomenon is the "lactations development" of a sire, *i.e.*, the performance of its daughters during the different lactations. The "maturing rhythm" of a sire may be regarded as a dynamic expression of the genetic makeup controlling lactation development. Furthermore, the prospect of selecting sires of bulls for early or late maturing could provide a new tool for the dairy cattle breeder.

Key words: Lactation – Milk yield – Herd production – Adaptation – Dairy cattle

Introduction

The classical approach of improving animal production is based on the average genetic level to which improved management levels are simultaneously adapted. This approach excludes the possible existence of Genotype × Environment interactions (G × E). Considering farm animals in general, G × E seems to make a small contribution to the phenotypic variance (Robertson et al. 1960; Averduct 1971); nevertheless, ignoring it may increase the error variance which leads to reduction in the reliability of progeny tests (Bar Anan 1975).

Two main objectives exist for taking G × E into account in dairy cattle breeding:

1. The prediction of the differential response of genotypes (genotype = average performance of daughters of a given sire) to various environmental conditions so as to direct the sires' semen differently.
2. Increase of the accuracy of genetic evaluations of sires and cows.

These objectives require an understanding of the magnitude and nature of G × E under certain conditions and it is to this end that this study is intended to explore.

Two main approaches to the examination and analysis of G × E have been suggested. Falconer (1952) and Robertson (1959) considered the expression of a genotype in different environments as different traits of the same genotype. Achieving a complete genetic correlation means that no change in rank of genotypes' performance in the varying environments should be expected, while lower correlation indicates changes in ranking of the genotypes under various conditions and thereby implies the existence of G×E (Dickerson 1962).

The second approach, based on regression analysis, has been suggested by Yates and Cochran (1938) and was further developed by Perkins and Jinks (1968) and Moav et al. (1975), the main features of which are:

1. Testing linear dependence of G×E of individual genotypes on the environmental effects. These regression coefficients enable prediction of specific genotypic responses to a series of environmental conditions.
2. Differences between regression lines of the varying genotypes measure their differential responses to the varying environments.

These regressions of G×E values on the environments may be further complicated by non-linear relationships and by scale effects, but these are beyond the scope of this research.

G×E in dairy cattle has been investigated by several authors. Lytton et al. (1966); Petersen (1975); Powell and Dickinson (1977) were among those who classified the environments according to geographic regions while Robertson et al. (1960); Kelleher et al. (1967) and Averduct (1971) explored G×E through levels of herd and production. However, only Thomas et al. (1968) reported findings of significant interaction.

Description of the data

The data consisted of 80, 111 lactation milk records of Isreali-Friesian dairy cows for the years 1973–1977. Dairy cattle in Israel are kept in either Kibbutzim (collective farms) or Moshavim (small holder farms) with the two herd types showing considerably different management procedures. Artificial insemination is carried out by two regional associations. On and Hasherut, which serve the northern and southern parts of Israel, respectively. The two herd types and the two regions were analysed during two time periods.

The analyses in this study were based on a single quantitative trait: milk yield per day between calvings. The data were screened by means of logical tests aimed at assuring their reliability and resulting in the following two sets of data:

1. Records were adjusted to the equivalent of a 5th lactation, calving in January and age of 24 months in first calving. These adjustments were carried out using least squares constants.
2. The original (unadjusted) data was used for the analysis of G×E involving lactation number as an environmental factor.

The environments were defined in four different ways:

1. Rank of production: 5 groups (within period, region and herd type).
2. Herd type: Moshav versus Kibbutz (within period and region).
3. Period of time: 1973–75 versus 1975–77 (within region and herd type).
4. Age of the cow: 1st, 2nd, 3rd and 4th lactation (within period, region and herd type).

A set of sires (genotypes) was selected in the two regions and in each of them, two-way tables (environments × genotypes) were prepared using the four definitions of environment. The criterion for selection of sires at any region was their prevalence in the specific determined environment.

Statistical methods

The linear model of the yield (Y) of cow (k) being daughter of sire (i) in environment (j) is defined for two-way fixed effects' model with repeated measurements:

$$Y_{ijk} = A + g_i + e_j + C_{ij} + W_{ijk} \tag{1}$$

where

A	sample average
g_i	additive genotypic effect of Sire i ($i = 1 \ldots m$)
e_j	additive environmental effect of environment j ($j = 1 \ldots n$)
C_{ij}	interaction between genotype i and environment j
W_{ijk}	Intracell random effect of cow k, daughter of Sire i in environment j ($k = 1, \ldots p_{ij}$).

By applying the mixed model for the analysis, as accepted in sire evaluations, dummy interactions may be created due to weighting for unequal number of daughters of a sire in the different environments. In order to avoid this confounding of effects, the fixed effects' model for both sires and environments was assumed.

Two-way analysis of variance was used to provide an overall interaction test for each set of data and thereby, values of g_i, e_j and C_{ij} were derived. Interaction values of a given sire i can be defined as a linear function (β_i) of the additive environmental effects:

$$C_{ij} = \beta_i e_j + \delta_{ij} \tag{2}$$

where δ_{ij} are deviations from the regression line of sire i. Symmetrically, the interaction values of a given environment j may be defined as a linear function (γ_j) of the additive genotypic effects:

$$C_{ij} = \gamma_j g_i + \varkappa_{ij} \tag{3}$$

where $\varkappa_{ij}$ are deviations from the regression line of environment j. Thus, β and γ are characteristics of a given sire and a given environment, respectively. Those two statistics were estimated as weighted regression coefficients.

Incorporating equations 2 and 3 into equation 1 and working with expected values of cell means provides two alternative models:

$$E(y_{ij}) = A + g_i + e_j(1 + \beta_i) \tag{4}$$

$$E(y_{ij}) = A + e_j + g_i(1 + \gamma_j). \tag{5}$$

These two models are not independent, therefore, they were used separately in each of the 24 two-way tables.

Thus, for the first model (equation 4), the interaction values of a given sire $y_{ij.} - (A + g_i + e_j)$ in the various environments are the dependent values of a simple linear regression model, e_j is the independent variable, $A + g_i$ is the intercept ($\bar{G}_i$) and $1 + \beta_i$ is the slope of the line.

Similary, in the second model (equation 5), the interaction values of a given environment across the sires are the dependent values, g_i is the independent variable in the regression, $A + e_j$ is the intercept ($\bar{E}_j$) and $1 + \gamma_j$ is the slope of the line.

Perkins and Jinks' (1968) paper provides a deeper understanding of the β_i and γ_j including statistical background and breeding implications.

When β_i significantly differs from zero, the greater values of β_i indicates a stronger linear response of daughters of sire i above or below the average response of all sires (depending on the sign of β_i) to changing environments. On the other hand, when β_i is zero, one can predict that daughters of sire i are stable in their additive performance and their response to changing environments is similar to the average response of all sires. The same interpretation may be given to γ_j as characteristic and predictor of response of environment j to genetic change.

Results

In each of the 24 two-way analyses of variance, significant general differences were found between the means of environments and the means of genotypes. In addition to the overall interaction test, the models presented in the previous chapter were used to explore the source of interaction, its characteristics and breeding potential.

Due to the large number of analyses performed in this study, only the most important results will be reported for each of the four defined environments separately:

1 Level of production (herd production)

Herd means were calculated for 80, 111 records in each of the eight combinations (2 herd types × 2 regions × 2 periods). A Moshav herd was defined as all recorded cows in a village despite their distribution among several farms. The herds were classified in 5 groups of equal number according to yield level. Of the eight combinations presented in Table 1, only in southern Kibbutz farms, during the period 1975–77, was a significant overall interaction found between genotypes and level of production. Examination of that interaction has shown that interaction was linearily dependent in only two out of the 20 sires. The opposing signs of the significant β_i coefficients of the sires Arbas ($\beta=0.252$) and Ari ($\beta=-0.356$) are presumably the source of the significantly overall interaction in this case. In order to discover whether this is a random phenomenon or is caused by a consistent factor, an analysis involving the successive period was carried out and showed the inconsistency of the two β_i's. Finally, none of the γ_j statistics was significant in the eight data groups.

2 Herd types – Kibbutz, Moshav

Using the above definition of environment, the cows were classified into two groups of the four combinations of 2 regions × 2 periods. Table 2 shows that in only one case was a significant G × E found. Further analysis utilizing the regression method was not possible due to the absence of degrees of freedom (only two environments).

3 Time scale

Time scale was considered as an environmental factor by using data of two periods of time (1973–75, 1975–77).

Four sets of data (2 herd types × 2 regions) were used separately as bases for two-way analyses.

In one of the four sets, a significant interaction between the average milk production of the sire's daughters and periods of time (Table 3), was found signifying the relative performance of the various sires as inconsistent with time. Examination of the means and deviations from additivity reveals that this interaction may be attributed mainly to four sires: Charodi, Lochem, Zamir and Bashan. These four sires are used in Fig. 1 (as full circles) to show the implications of this kind of interaction on the accuracy of progeny testing.

4 Lactation number (age of the cow)

Eight sets of data were used as the source of the analyses (2 herd types × 2 periods × 2 regions). In each set, the data were classified into four categories according to the number of lactation of the cows during

Table 1. Distribution of sires, herds and daughters in five production levels (as environments) in each of the eight sets of data

	Kibbutz				Moshav			
	North		South		North		South	
	1973-5	1975-7	1973-5	1975-7	1973-5	1975-7	1973-5	1975-7
No. of sires	20	20	20	20	13	13	5	5
Mean no. of herds/group	25	25	14	14	35	35	13	13
Mean no. of daughters/group	3,000	2,600	1,260	1,160	580	500	170	150
Overall no. of daughters and significance of G × E	15,066	13,093	6,321	5,798*	2,923	2,563	859	748

* Sire × level of production interaction is significant at $0.01 < P < 0.05$

Table 2. Distribution of sires and daughters in two herd types: Kibbutz and Moshav (as environments) in each of the four sets of data

	North		South	
	1973-5	1975-7	1973-5	1975-7
No. of sires/group	13	13	5	5
Overall no. of daughters and significance of G × E	17,092	14,029	4,531	3,959**

** $0.001 < P < 0.01$

Table 3. Distribution of sires, herds and daughters in two periods of production (as environments) in each of the four sets of data

	Kibbutz		Moshav	
	North	South	North	South
No. of sires/group	20	20	12	5
No. of herds/group	125	70	175	65
Overall no. of daughters and significance of G × E	28,159***	12,119	5,228	1,607

*** $P < 0.001$

Table 4. Distribution of daughters and significance of G × E in four lactations (as environments) in each of four sets of data for the five most prevalent sires. (All the original files for all sires were significant for G × E)

	North		South	
	1973-5	1975-7	1973-5	1975-7
1st lactation	3,708	1,300	1,001	708
2nd lactation	2,532	1,893	1,114	987
3rd lactation	875	1,530	958	763
4th lactation	407	797	549	392
Total	7,522***	5,520	3,622***	2,850

*** Interaction of sires × lactation no. is significant at level $P < 0.001$

the specified time period of the analysis. These lactation groups represent four distinct environmental levels. The above definition created a situation where the number of daughters of many sires was highly varied at the different age levels and enabled us to analyse the "Kibbutz" data in the following two ways:

a) As original data for all sires. The G × E interactions in the four sets of data based on 12–16 sires, were highly significant; however, due to space limitation, they are not presented in this paper.

Table 5. Interaction values in kg milk per day between calvings (C_{ij}) and number of daughters (f_{ij}) for five sires in each of first four lactations (E_1 to E_4) in the file: Kibbutz, South in 1973-75. The characteristics for the sires are listed in the right marginals: genotypic average ($\bar{G}_i$), genotypic effect (g_i), number of daughters (n_i), weighted regression coefficient (β_i) and its standard error, culling rates (CR_i), in % at first lactation in the previous year (1972/3). The characteristics of the einvironment are listed on the lower marginals: environmental average ($\bar{E}_j$), environmental effect (e_j), number of daughters (m_j), weighted regression coefficient (γ_j) and its standard error

Sire	$C_{ij}(f_{ij})$ Lactation								
	E_1	E_2	E_3	E_4	$\bar{G}_i(n_i)$	g_i	β_i	$S(\beta_i)$	CR_i
Chaviv	0.811 (32)	−0.513 (90)	−0.986 (85)	0.688 (64)	17.563 (271)	−1.632	−0.071	0.451	7.3
Niron	−0.243 (725)	0.09 (653)	0.522 (423)	−0.369 (109)	19.338 (1910)	0.143	0.161	0.119	3.8
Bigtan	−0.009 (22)	−0.174 (113)	0.829 (221)	−0.645 (189)	19.426 (545)	0.231	−0.173	0.502	0.9
Ari	−0.171 (71)	0.544 (154)	−0.182 (179)	−0.191 (169)	19.802 (573)	0.607	−0.09	0.182	2.5
Elem	−0.388 (151)	0.053 (104)	−0.183 (50)	0.517 (18)	19.846 (323)	0.651	0.159	0.079	5.2
$\bar{E}_j$	17.018	18.975	19.993	20.794	19.195				
m_j	1,001	1,114	958	549	3,622				
e_j	−2.177	−0.22	0.798	1.599					
γ_j	−0.455*	0.36	0.474	−0.416					
$S(\gamma_j)$	0.134	0.164	0.461	0.277					

b) As selected data consisting of the five most prevalent sires (Table 4).

Comparison of the results of Table 4 and former Tables evidencing a phenomenon new to this study; a regression coefficient, γ_j, characterizing an "environmental specificity" to genotype change, was found to be significant in both regions for the first lactation:

in the north: $\gamma_1 = -1.064 \pm 0.302$
in the south: $\gamma_1 = -0.455 \pm 0.134$.

Attention should be drawn to the similarity of the results obtained independently from two files, consisting of different sets of sires, mainly because thousands of daughters were involved in each analysis. (See Table 5 for full description of the results for the southern region.) The results of the northern region are not presented, again due to space limitations.

That the sire rank may change between first and following lactations might be evidence of an important phenomenon which should be considered in progeny tests.

Discussion

By investigating the characteristics of G×E, attention should be directed towards two main fields of application:

1. Adaptation of genotypes to environments.
2. The effect of G×E on the accuracy of estimating the genetic merits of individual cows and sires.

G×E was analysed in orientation of "specific adaptation" of genotypes to environments; it was carried out by applying the regression technique to characterize the genotypic reaction to environmental change (β_i). Several cases were found to demonstrate this pattern in practice and based on the results of the same genotypes in two time periods, it may be concluded that there is no consistency in respect to the "behavior" of G×E in the two time periods (an indication for three-way interaction). The lack of substantial G×E associated with different production levels agrees with earlier analyses.

The existence of Genotype×Time and Genotype×Lactation interactions (G×T, G×L) indicate important implications concerning breeding strategy and accuracy of progeny tests. The interpretation of G×T can be visualized by plotting the genotypic effects of the later period (1975–77) against those of 1973–75. Generally, one would expect to obtain a positive correlation if the relative later performance of the sires' daughters is in full agreement with the evaluation of these sires based on an earlier period of time. The relevant findings are presented in Fig. 1 and emphasized by the following points:

1. The similarity of the genetic values between the two time periods is not perfect as expressed by the regression (b) and correlation (R) coefficients (for 18 degrees of freedom) which are significantly less than 1.

$b = 0.359 \pm 0.156$
$R = 0.474$.

2. Most of the G×T is based on four sires (see Results). Those sires are presented in Fig. 1 as full circles, and after their removal, the accordance is much more convincing as expressed by the following values (for 14 degrees of freedom) which do not differ significantly from 1.

$b = 0.812 \pm 0.12$
$R = 0.873$.

The findings may be interpreted to mean that in the edited group of sires, there was neither interaction as scale effect nor as change in rank. Nevertheless, the exceptions in Fig. 1 symbolize a random unpredictable interaction to which the breeding program is exposed.

Although the extent of G×T is limited, the validity of the phenomenon may lead the breeder to include two sequential periods in progeny testing, ignoring the cost of effect at this point. But since in a sequential period of time, data can be attained by both first and second lactating cows, further consideration of this subject seems warranted.

Partitioning the G×L interaction into components, by using the models of linear dependence, shows that the interaction values in first lactation are linearily dependent (negative γ_1) on the genotypic values (g_i) (see Table 5). In other words, the best genotypes involve negative interaction values in first lactation

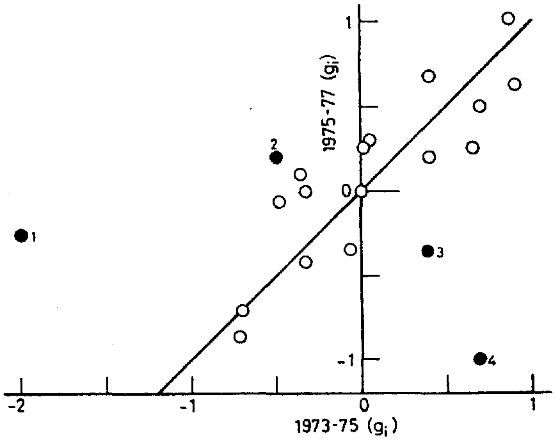

Fig. 1. The genetic values (g_i) of 20 sires in 1975–77 versus their genetic values in 1973–75. The diagonal line represents regression with slope b = 1, the full circles stand for sires which express significant interaction with the change of time

Table 6. Transmitting values and repeatability values in percent of selected sires in the first three lactations (L_1 to L_3) representing production types

Production type		Name of sire	No. of sire	Transmitting values			Repeatability		
				L_1	L_2	L_3	L_1	L_2	L_3
High	High	Pere	286	+570	+599	+680	99	97	87
High	Low	Lochem	149	+405	+154	+ 96	91	94	90
Low	High	Eilon	401	+ 91	+299	+522	99	97	90
Low	Low	Luz	133	+ 66	− 77	− 48	96	98	98

and vice versa. The negative value of γ_1 has a major implication on progeny tests; the chance for wrong decisions based on first lactation is much higher when the γ_1 coefficient is negative and vice versa. Powell et al. (1981) also found that the first lactation had the lowest predictive value for future performance of a sire.

Analyses involving different sets of sires imply that interaction values tend to confuse, to a certain degree, the differences between the sires on the basis of first lactation records. For example, the sire, Zamir from the northern region, with genotypic effect (g_i) of −1.1 kg milk per day between calvings, had a relative advantage (of 0.4 over the other sires) only during the first lactation whereas at second and following lactations, its performance relatively declined. Considering that the results are based on thousands of daughters, complete reliance on the heifers' records may prove to be dangerous as this could lead to a biased estimate for genetic evaluation for persistency of production.

Theoretically, it may be claimed that the reported Genotype × Lactation interaction is based on two main sources:

1. Biological interaction – differential maturing of the daughters of various sires.
2. Statistical interaction – differential culling rates of the daughters of various sires; e.g., a sire with a large proportion of daughters culled after the first lactation will be relatively better in milk production in the second lactation.

In order to distinguish between these two sources, the culling percentages (for milk production) of the sires at first lactation in 1972–73, which predetermine the number of daughters at second lactation, were recorded (Bar-Anan, personal communication) and are presented in Table 5 (last column).

Judging by this information, one can infer that these culling rates are quite similar except for the sire Chaviv. This sire is characterized by the lowest genetic value and his daughters were subjected to the highest culling rate between the first and second lactation. One would expect that the interaction at second lactation would be positive due to the selection impact, but in effect, it is highly negative (Table 5). Another example reinforcing this finding is illustrated by the sire Ari, who while having a low culling rate at first lactation shows the highest positive interaction in the second.

These results do not support a possible bias in interaction due to differential culling levels.

We maintain that the genetic characteristic for this phenomenon is the "lactations development" of a sire, i.e. the performance of its daughters at the different lactations. For example, the lactation effect (L2–L1) of the sire Zamir is lower than that of the other sires; his daughters are distinguished by a very high performance at first lactation, whereas at the following lactations, production development is relatively low. Note that the seven sons of the sire Zamir are characterized by the same pattern of "lactations development" (Bar-Anan and Ron, unpublished). The results of the Israeli progeny tests in 1981 seem to support the finding of different production types of sires; the Israeli sire evaluation procedure estimates separate sire transmitting values for each of the first three lactations of its daughters. The ranking of sires with high repeatability values changed considerably due to sire × number of lactation interactions (Table 6).

Heiman (1968) presented sires of the Friesian breed showing the early and late maturing types. The "maturing rhythm" of a sire may be regarded as a dynamic expression of the genetic make-up controlling the lactations' development. Furthermore, the prospect for selection of sires of bulls early or late maturing may provide a new tool for the dairy cattle breeder.

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