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GENETIC DIFFERENCES BETWEEN THE CHINESE AND EUROPEAN RACES OF THE COMMON CARP

I. ANALYSIS OF GENOTYPE-ENVIRONMENT INTERACTIONS FOR GROWTH RATE

ROM MOAV and G. HULATA
Department of Genetics, The Hebrew University of Jerusalem, Jerusalem, Israel
and
G. WOHLFARTH
Fish and Aquaculture Research Station, Dor, Israel

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SUMMARY

Growth rate of 12 groups of common carp was measured at five experimental environments. Three of the 12 tested groups were strains of the domesticated European race of the common carp, one group was a representative of the *Big-Belly* Chinese race, and the remaining eight groups were F_1 crossbreds among the European strains and between the European and the Chinese races. The average growth rate over the five environments of the Chinese *Big-Belly* was considerably poorer than that of the European carp. All the inter-race crossbreds and the crossbreds among the European strains showed heterosis. When the genotype-environment interaction was presented as a linear function of the quality of the environment, the regression coefficient (the overall responsiveness parameter) assumed relatively low values in the *Big-Belly* and two to two-and-a-half fold higher values in the European carp. The overall responsiveness of crossbreds was, on the average, intermediate between the two parents. When, however, it was partitioned into a scale function of the average genotype and specific independent responsiveness, the two components showed a high degree of heterosis but in opposite directions. An explanation of this genetic system in terms of adaptive evolution to the diverse modes of carp domestication in Europe and China was given.

1. INTRODUCTION

THE common carp (*Cyprinus carpio* L.) has been cultivated in ponds in China as a food fish for nearly three thousand years (Hoffman, 1934). Its present cultivation extends throughout mainland China and South-East Asia (Bardach, Ryther and McLarney, 1972). In Europe the common carp has been cultivated in ponds for several hundred years (Hickling, 1962), and its present cultivation extends from Siberia (Kirpichnikov, 1971) to the Mediterranean (Bentram, 1946). The Chinese and European races of the common carp have been separated from each other for a very long time, and they are known to differ in many characteristics, among them: body shape, growth rate, seine escapability, fecundity and hardiness (Lin, personal communication).

In Israel carp farming was initiated in 1939 through a number of introductions, mainly from Europe (Tal and Sheluvsky, 1952; Yashouv, 1955; Moav, Wohlfarth and Lahman, 1964). Commercial breeding of carp in Israel is based on strain crossing and testing, in this way, exploiting the high degree of heterosis for growth rate found in carp (Wohlfarth, Lahman,

Moav and Ankorion, 1965). The first commercially useful F_1 crossbred was found in 1960. Since then an extensive crossing and testing programme has turned up several equally successful crossbreds, but none that surpassed the first successful crossbred of 1960. Until 1970 our testing was limited to the Israeli carp population with the exception of one introduction from the Netherlands (Moav *et al.*, 1964). In an attempt to broaden the genetic base of our testing programme new introductions were made from Taiwan and Yugoslavia. The two imported stocks, two local stocks and eight crossbreds were tested in 1971 under varying environmental conditions. In this paper we report on differences in growth rate between the various strains and their crosses as a function of the quality of the environment. The genotype-environment interactions are analysed in terms of scale effects and specific responsiveness, and the evolutionary implications of the differences between the European and Chinese carp are discussed.

2. The genetic stocks

Four genetically distinct closed groups and eight crossbreds were tested in the present experiment (table 1). One of the four closed groups (strains)

Table 1

The tested groups of carp and details of their spawnings

Group designations		Females		Males		Place of spawning and nursing
		Strain	No.	Strain	No.	
1	*BB*	*Big-belly*	16	*Big-belly*	16	Dor
1×2	*BB*×*Nas*	*Big-Belly*	16	*Našice*	5	Dor
1×3	*BB*×*G*	*Gold*	4	*Big-belly*	16	Dor
1×4	*BB*×*Dor*	*Dor-70*	19	*Big-belly*	18	Gan-Shmuel
2	*Nas*	*Našice*	16	*Našice*	4	Dor
2×3	*Nas*×*G*	*Gold*	4	*Našice*	4	Dor
2×4	*Nas*×*Dor*	*Dor-70*	14	*Našice*	5	Dor
3*	*G*	*Gold*	4	*Gold*	10	Yehiam
L*	*G*×*B*	*Blue*	5	*Blue*	9	Yehiam
3×4	*G*×*Dor*	*Dor-70*	15	*Gold*	7	Dor
4	*Dor*	*Dor-70*	15	*Dor-70*	18	Dor
V†		T	29	*Hol-B*	12	Gan-Shmuel

* All the listed *Gold* plus *Blue* males and females were used in a single spawn. *Gold*×*Gold* produced *Gold* offsprings (G), *Gold*×*Blue* produced normally coloured crossbreds **L**, and *Blue*×*Blue* produced *Blue* offsprings that did not participate in the tests.

† The group V is a widely used commercial crossbred that resulted from a three-way cross between a local crossbred designated **T**, and a strain imported from Holland.

was the Chinese *Big-Belly* carp, and the remaining three (*Našice*, *Gold* and *Dor-70*) belonged to the European race of the common carp. Description of these four groups follows:

(i) *Group 1—the Chinese carp, (BB)*

This group was sent to us as fry from Taiwan in 1970. It has a Chinese origin and is known as the *Big-Belly* carp. Its full scale cover (wild-type) differs from the *mirror* scales pattern of the European domesticated carp by a single dominant allele (Kirpichnikov, 1971). At sexual maturity the fish

are so full of gametes that their bellies appear inflated, hence the name *Big-Belly*. This is, apparently, the only race of common carp grown by the Chinese fish farmers and it is widely distributed over Mainland China, Taiwan, Hong Kong, Singapore, Thailand, Malaysia and other Far-Eastern countries (Hoffman, 1934; Hickling, 1962; Alikunhi, 1966; Bardach *et al.*, 1972; Lin, personal communication).

(ii) *Group 2—Našice, (Nas)*

This group was also sent to us, from Yugoslavia, as fry, in 1970. It belongs to a selected inbred strain of carp known as *Našice* (Fijan, personal communication), which has an outstandingly high ratio of height to length. This characteristic was selected because it was considered desirable for cultivated carp. A high proportion of the *Našice* introductants showed skeletal deformations—a probable result of their high degree of inbreeding.

(iii) *Group 3—Gold, (G)*

Gold body colouration in carp is controlled by a single recessive gene (Wohlfarth and Moav, 1970). Gold individuals were found in the fish farm of Maagan-Michael in Israel in 1963. They were transferred to Dor and became founders of the inbred line called *Gold*.

(iv) *Group 4—Dor-70, (Dor)*

This group was developed at Dor from a selection experiment for fast growth rate initiated in 1965 and carried out until 1970. Since 1965 it has been kept as a closed population.

The remaining eight groups participating in the present tests were crossbreds: 1×2, 1×3, and 1×4 (table 1) were F_1 crossbreds between the *Big-Belly*, and the three European groups, while groups 2×3, 2×4, and 3×4 were F_1 crossbreds between the European groups. Group 9 was a commercial F_1 crossbred between the *Gold* inbred and another local inbred group marked by two recessive body colouration genes *Blue* and *Grey* (Wohlfarth and Moav, 1970). Note that groups 3 (*Gold*) and L (a commercial crossbred) were derived from a single spawn whose offspring segregated into three groups, distinguishable by their body colouration: *Gold* inbreds, *Blue-Grey* inbreds and *Gold* × *Blue-Grey* crossbreds (L). Since the three genetic markers are recessive, the crossbreds had the wildtype colour. Only the *Gold* parent and the crossbred segregants were introduced into the present tests. One of the parents of the last group (V, another commercial crossbred) was introduced to Israel from Holland and the second parent (T) was an excellent local crossbred. V has been the most widely used commercial crossbred in Israel since 1965. The two commercial crossbreds (L and V) served as a control for comparison of the present results with those of earlier tests.

3. Experimental procedures

(i) *Spawning and growing of fry*

The male and the female parents of the various breeding stocks were maintained throughout the winter (November to April) in separate ponds.

Towards the end of April they were introduced into spawning ponds filled with fresh water. As a rule, the fish spawned within 24 hours, and hatching started 2 days later. When the fry reached the minimal size permitting their handling (about 0·1 g), random samples of each spawn were transferred to separate nursery ponds where they were raised to a size enabling their marking (20 to 30 g). After marking by branding (Moav, Wohlfarth and Lahman, 1960*a* and *b*), they were ready for the comparative tests carried out in mixed ponds (Moav and Wohlfarth, 1973).

(ii) *The experimental ponds and their management*

Counted and weighed samples of marked fingerlings of each group were stocked all mixed together into a series of replicated *mixed* ponds filled with fresh water. Sixteen mixed ponds were located at Dor. These were all small ponds of 400 m². Two larger ponds were located at the fish farms Yehiam and Gan-Shmuel (Wohlfarth *et al.*, 1965). At Dor the fish were fed daily with fodder pellets and at the fish farms with grains. At 2-week intervals each pond was seined and the caught fish sorted according to their brand marks. Each group was counted and weighed separately and returned to the pond. This procedure enabled the measurement of growth curves and seine escapability of the tested groups (Moav and Wohlfarth, 1970). The tests started at the beginning of July and were terminated in November. Upon termination of the experiment the ponds were completely drained and all the fish were counted and weighed according to progeny and sex.

(iii) *Correction for differences in initial weight*

Table 2 shows the variation in mean initial weights between the 12 tested groups (11·1 g to 28·2 g). These differences were due, primarily, to random variation in stocking density and fertility of the nursery ponds. Since weight gain is highly correlated with body weight, the groups with higher mean initial weights tend to show larger weight gains than those with lower initial weights. To correct for this bias the following transformation of weight gains was used (Wohlfarth and Moav, 1972).

$$Y = Y' - b(x - x.)$$

Where Y = corrected weight gain,
Y' = observed weight gain,
b = the coefficient of the linear regression of weight gain on initial weight (the correction term),
x = initial weight,
$x.$ = mean initial weight of all the tested groups.

Weight gains corrected in this way have been shown to be independent of variation in initial weight and may, therefore, serve as an estimate of the growth capacity of the tested stocks. In the present tests an estimate of the correlation coefficient between the initial weights and *corrected* weight gains was 0·09.

(iv) *The design of the experiment at Dor*

The 16 experimental ponds at Dor were divided into four sets of four ponds per set, each set receiving a different treatment of water management and fish density. Water management had two levels: standing water and re-circulating water. Stocking density had three levels: low (125 fish per pond), medium (265 fish per pond) and high (426 fish per pond). After the completion of the experiment it was found that water recirculation had

TABLE 2

Weight gains (corrected for differences in initial weights) of the 12 tested groups

Group designation		Initial wt.	"Environmental treatments" at Dor				Yehiam	Mean
			1	2	3	4		
		g	g	g	g	g	g	g
1	*BB*	24·3	264	297	367	468	283	336
1×2	*BB*×*Nas*	27·6	378	454	505	725	395	491
1×3	*BB*×*G*	22·2	321	401	495	726	405	470
1×4	*BB*×*Dor*	11·1	383	457	535	740	386	500
2	*Nas*	30·7	279	352	479	795	292*	439
2×3	*Nas*×*G*	25·7	397	520	590	891	397	559
2×4	*Nas*×*Dor*	26·0	399	477	594	918	403	558
3	*G*	28·2	301	391	478	726	317	443
3×4	*G*×*Dor*	19·2	353	472	587	780	388	516
4	*Dor*	23·2	394	517	593	874	403	556
V		27·7	356	456	589	877	416	539
L	*G*×*B*	26·7	360	444	551	816	397	514
Mean			349	437	530	778	373	494
Mean no. of fish/group/pond†			31	21	19	9·5	—	—
s_e^2 = Error variance‡			529	606	1429	3688	—	1738
s_g^2 = Between groups variance			2075	4168	4446	13513	—	4207
s_g mean			0·13	0·15	0·13	0·15	—	0·13

* Value computed for the missing plot from the regression of weight gain on the quality of the environment (equation 2).

† On termination of the tests.

‡ s_e^2 = "interaction" *MS* of a "Randomised Block" design.

no effect on growth rate (due to technical difficulties the recirculation was rather limited), hence this factor was ignored. The eight ponds with medium density were divided into two equal sets, one set, henceforth called "environment 2" included the four ponds with the lower weight gains and the second set—"environment 3"—included the four ponds with the higher weight gains. The set of four ponds with the high density was called "environment 1" and the set with the low density "environment 4". Note that the difference between treatments 2 and 3 was due to chance variation in fish density caused by mortality, errors, predation and pond fertility.

4. ANALYSIS

Following the notations of Moav and Wohlfarth (1974), the mean performance (corrected weight gain) of the jth genotype in the ith environment may be presented by the following equation:

$$Y_{ij} = \mu + g_j + (1+\beta_j)a_i + \delta'_{ij} + e_{ij} \qquad (1)$$

when, μ is the overall mean; g_j is the mean deviation of the jth genotype (group); a_i is the deviation of the ith environment, or the " environmental effect "; $(1+\beta_j)$ is the coefficient of regression of group j on environment i; β_j being the coefficient of regression of the genotype-environment interaction effect (GE) on the environment; δ'_{ij} is the non-linear component of GE which is linearly independent of a_i, and e_{ij} is the residual " error " associated with Y_{ij}.

Except for the different notations, equation 1 is identical to that of Perkins and Jinks (1968) and several subsequent workers (*i.e.* Hill and Samuel, 1971; Fripp, 1972; Freeman, 1973; and others). The present β_j is identical to β_i of Perkins and Jinks (1968) and $(1+\beta_j)$ is identical to b of Finlay and Wilkinson (1963).

β_j may be divided into two components: a scale effect caused by the correlation between the intra-environment variation and the environment's mean, and a second component of responsiveness (sensitivity) to an underlying environmental variable that cannot be expressed as a scale function (Dickerson, 1962; Moav and Wohlfarth, 1974). Thus,

$$\beta_j = sg_j + \beta'_j$$

when s is a scale effect and $\beta'_j = (\beta_j - sg_j)$ measures the specific responsiveness, *i.e.* it is a function of the environment after elimination of the scale effect. Substitution into equation 1 and pooling the last two terms $(\delta_{ij} = \delta'_{ij} + e_{ij})$ yields (after Moav and Wohlfarth, 1974),

$$Y_{ij} = \mu + g_j + (1 + \beta'_j + sg_j)a_i + \delta_{ij} \qquad (2)$$

Separation of the term sg_ja_i is basically identical to the method used by Tukey (1949) when he developed a procedure for testing for the presence of non-additivity in a two-way Analysis of Variance data.

Positive correlation between an environment's mean performance $(\mu + a_i)$ and a linear responsiveness to the environment (β_j of equation 1) has been found in numerous studies of both plants and animals (for example: Dickerson, 1962; Perkins and Jinks, 1968; Bucio-Alanis *et al.*, 1969; Fripp and Caten, 1971; Hill and Samuel, 1971; Paroda and Hayes, 1971). Several authors expressed the need for separation of the scale effect (sg_j) from the independent or specific responsiveness regression (β'_j). When $\beta'_j = 0$, specific interaction is absent; $\beta'_j > 1$ indicates specific adaptation to improved environment (responsiveness to increased inputs) and $\beta'_j < 1$ indicates specific adaptation (tolerance) to poor environmental circumstances.

The $(1+\beta_j)$ of equation 1 was estimated separately for each one of the 12 tested groups by computing the regression coefficients of corrected weight gains (Y_{ij}) on the environmental means $(Y_{i\cdot})$ following the procedure suggested by Bucio-Alanis (1966). Here, the fact that Y_{ij} is non-independent of $Y_{i\cdot}$ presents a statistical problem (Freeman and Perkins, 1971; Perkins and Jinks, 1973) in that, the computed regression tends to be an underestimate of $(1+\beta_j)$. However, it has been found that the bias becomes smaller with increased number of tested genotypes (Fripp, 1972; Hardwick and Wood, 1972; Freeman, 1973). Thus, under the common assumptions of " fixed effects " (model I) Analysis of Variance, the expectation of b_j (the least-squares regression of Y_{ij} on $Y_{i\cdot}$) for a given j is,

$$E(b_j) = 1 + \frac{(\beta'_j + sg_j)\sigma_a^2}{\frac{\sigma_\delta^2}{J} + \sigma_a^2} \xrightarrow[J\to\infty]{} (1 + \beta'_j + sg_j) \qquad (3)$$

when J is the number of tested genotypes. This relationship was similarly shown by Hardwick and Wood (1972, fig. 1). The scale parameter s may

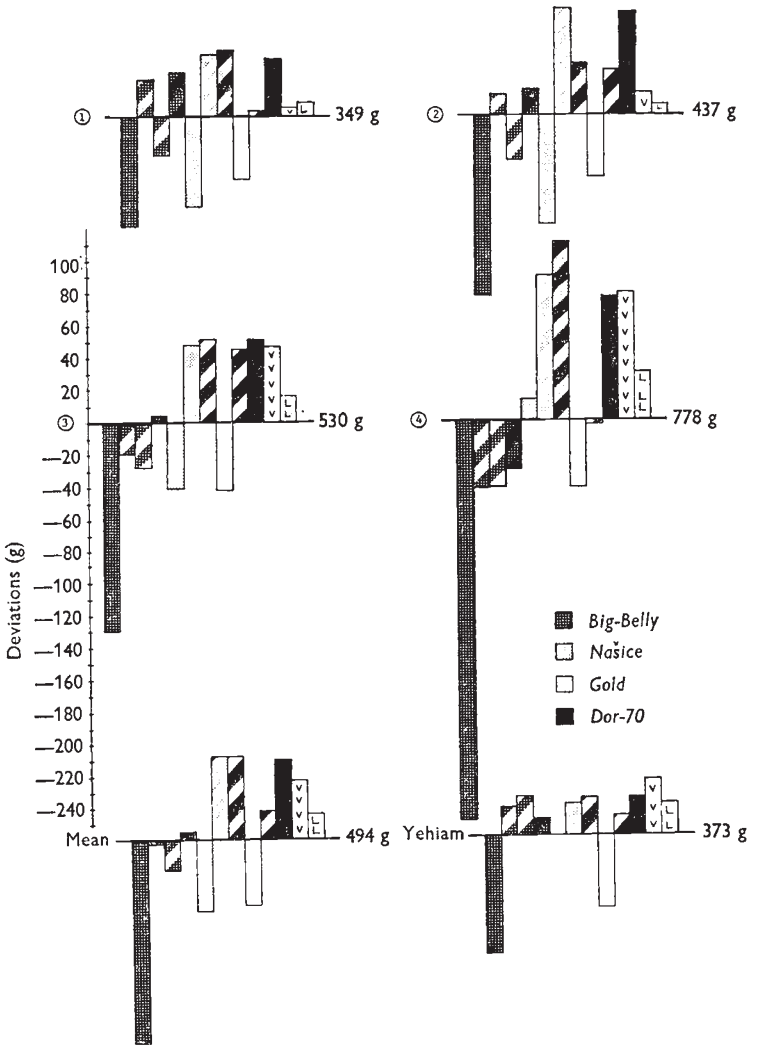

FIG. 1.—Weight gains of the 12 tested groups expressed as deviations from the five environmental treatment means, and from the overall mean. (The weight gains were corrected for differences in initial weights (table 2). Values on the right of the horizontal axis are the treatments means from which the deviations were measured. Columns with a single marking represent parental lines, and columns with alternate markings represent crossbreds.)

be estimated by the Least-Squares regression coefficient of b_j on $Y_{.j}$ (the mean of the jth genotype over all the environments) to be designated $\hat{s}_1$,

$$\hat{s}_1 = \text{regression } (b_j \text{ on } Y_{.j}) \qquad (4)$$

The expectation of $\hat{s}_1$ being,

$$E(\hat{s}_1) = \frac{s\sigma_a^2\sigma_g^2}{\left[\frac{\sigma_\delta^2}{J}+\sigma_a^2\right]\left[\frac{\sigma_\delta^2}{J}+\sigma_g^2\right]} \xrightarrow[J\to\infty]{} s \tag{5}$$

Hence, $\hat{s}_1$ tends to be an under-estimate of s.

Another approach to the estimation of s is to make use of the finding that the coefficient of variation of the genotypes means within all the five environments were almost identical (table 2, last row). In other words, the differences between the groups means in each environment were proportional to the environment's mean. Consequently,

$$s_2 = 1/\mu \tag{6}$$

and its estimate, $\hat{s}_2$ is,

$$\hat{s}_2 = \frac{1}{Y_{..}}. \tag{7}$$

As was already explained, $E(b_j)$ has two components (equation 3). The first $(1+sg_j)$ is due to the average genotype (g_j) and its scale effect, and the second (β'_j) is due to an independent sensitivity (responsiveness). b_j was partitioned, accordingly, into

$$\bar{b}_j = (1+\hat{s}(Y_{.j}-Y_{..}) = \text{an estimate of } (1+sg_j) \tag{8}$$

and

$$\beta'_j = (b_j-\bar{b}_j) = \text{an estimate of } \beta'_j. \tag{9}$$

Two estimates of $\bar{b}_j$ were made, employing, respectively, the two different estimates of s (equations 4 and 7).

5. Experimental results

(i) *Average weight gains*

Weight gains (corrected for differences in initial weights) of the twelve tested groups of carp are presented in table 2 and in fig. 1, according to the four " treatments " at Dor (four ponds per treatment), plus the pond of Yehiam. In order to emphasise the differences between the groups, the column heights of fig. 1 represent deviations from treatment means. The means over all the five environments are listed in the right hand column of table 2, and are illustrated in fig. 1.

The Error variances of the mean weight gains per pond of the tested groups (s_e^2, table 2) were computed, separately, for each of the four environments at Dor from the differences between the four replicated ponds of each environment. Thus, s_e^2 is equal to the " Interaction Mean-Square " of Randomised Block Design-Analysis of Variance of the 12 groups in the four ponds of each environment. The Randomised Blocks analysis of the results of each environment at Dor also yielded " between-groups " Mean-Squares (MS_g). From these and the Error variances (s_e^2), estimates of the variance components between group means, were computed for each environment in the traditional way:

$$s_g^2 = \frac{MS_g - s_e^2}{4}$$

TABLE 3

Estimates of the overall regression of weight gain on the quality of the environment (b_j), and its two components—one due to variation in mean genotypes and their scale effects ($\bar{b}_j$), and a second due to specific sensitivity to changes in the environment ($b_j - \bar{b}_j$)

(For explanations of the column heads see text)

Group designation	Mean (g)	Mid-point (g)	b_j	Regression due to mean genotypes and their scale effects				Specific regression independent of the mean genotypes			
				$\bar{b}_{1j}$	$\bar{b}'_{1j}$	$\bar{b}_{2j}$	$\bar{b}'_{2j}$	$b_j - \bar{b}_{1j}$	$b_j - \bar{b}'_{1j}$	$b_j - \bar{b}_{2j}$	$b_j - \bar{b}'_{2j}$
1	336	370	0·479	0·604	0·543	0·680	0·655	−0·125	−0·064	−0·201	−0·176
1×2	491	549	0·806	0·997	0·966	0·944	0·972	−0·191	−0·160	−0·188	−0·158
1×3	470	533	0·890	0·944	0·928	0·951	0·943	−0·054	−0·038	−0·061	−0·033
1×4	500	561	0·852	1·020	0·944	1·012	0·998	−0·168	−0·142	−0·160	−0·101
2*	439	527	1·229	0·865	0·914	0·889	0·933	0·364	0·315	0·340	0·296
2×3	559	642	1·167	1·170	1·186	1·132	1·136	−0·003	−0·019	0·035	−0·019
2×4	558	647	1·245	1·167	1·198	1·129	1·145	0·078	0·047	0·116	0·047
3	443	514	1·000	0·875	0·883	0·897	0·910	0·125	0·117	0·103	0·123
3×4	516	587	0·990	1·060	1·056	1·044	1·039	−0·070	−0·066	−0·054	−0·063
4	556	636	1·130	1·162	1·172	1·125	1·126	−0·032	−0·042	0·005	−0·041
V	539	624	1·196	1·119	1·143	1·091	1·104	0·077	0·053	0·105	0·054
L	514	589	1·060	1·055	1·060	1·040	1·042	0·005	0·000	0·020	0·002
Means	494	565	1·003	1·003	1·003	0·997	1·000	0·000	0·000	0·005	−0·005

* Estimates here are based only on the four environments of Dor (the observation of Yehiam was missing).

s_g^2 is an estimate of the genetic variance between the groups means. It will be inflated by any variance component arising from the " common environment " of all the individuals of each group. Here again (table 2) the Standard Deviation (s_g) is proportional to the mean so that the coefficient of variation (s_g/mean; table 2) is very similar for all the five environments.

A Randomised Block analysis was also performed on the means of all the five treatments. This yielded estimates of 1783 and 4207 for the " interaction " (s_e^2) and " between groups " (s_g^2) variances, respectively, and an estimate of the Standard Error of the group means of 19 g ($\sqrt{1738/5} \cong 19$). With the help of this Standard Error the 12 tested groups could be divided into four distinct classes: *Class 1*: The *Big-Belly* (336 g); *Class 2*: The two European inbreds *Našice* and *Gold* (441 g); *Class 3*: The three crosses between the Chinese and the European races (487 g); *Class 4*: All the five European crossbreds plus *Dor-70* (540 g).

(ii) *Genotype-environment interactions*

The four environmental treatments of Dor plus the pond of Yehiam constituted five different environments. The quality of the environment was measured by the average performance (weight gain) of all the tested genotypes in each environment. Thus, the best environment (treatment 4, 778 g) was more than twice as good as the poorest environment (treatment 1, 349 g). The presence of genotype-environment interactions is clearly seen in fig. 1 from the differences in ranking of the tested groups at the different environments, especially striking are the differences between the extreme treatments 1 and 4.

The environment effect (a_i) plus the genotype-environment interaction (GE) components were partitioned according to equation 2. b_j (equation 3) the linear regression coefficient of weight gain (Y_{ij}) on the environments means (Y_i) served as a measured of the *overall* responsiveness (sensitivity) of each group to the quality of the environment, as was explained in the section " Analysis ". The 12 computed b_j's are listed in the fifth column from left of table 3. The coefficients of correlation between the groups weight gains (Y_{ij}) and the mean weight gain of the environments ($Y_{i\cdot}$) were higher than 0·99 in all the groups. This shows that the assumption of linearity of the function of the environment for all the groups was amply justified. Fig. 2 illustrates these functions for most of the tested groups. Fig. 2A illustrates the regressions of the three strains *Big-Belly*, *Našice* and *Dor-70* plus the two crossbreds *Big-Belly* × *Našice* and *Dor-70* × *Našice*. The third cross *Big-Belly* × *Dor-70* was omitted because it was very similar to the cross *Big-Belly* × *Našice*. Each one of the figs. 2B and 2C shows two European strains and the crossbred between them. From these figures and column 5 of table 3 we see that the purebred *Big-Belly* and its three crossbreds with European carp all had b_j values smaller than one, while all the European groups had values around, or higher, than one. This indicates that the *Big-Belly* is specifically adapted to poor conditions while the European carp is relatively more adapted to environments of higher quality. The intersection of the regression lines of *Našice* and the *Big-Belly* (fig. 2A) is a good demonstration of reversed adaptations.

The overall function of the environment (b_j) was partitioned into a scale function ($1 + sg_j$, equations 2 and 3) and specific adaptation independent of

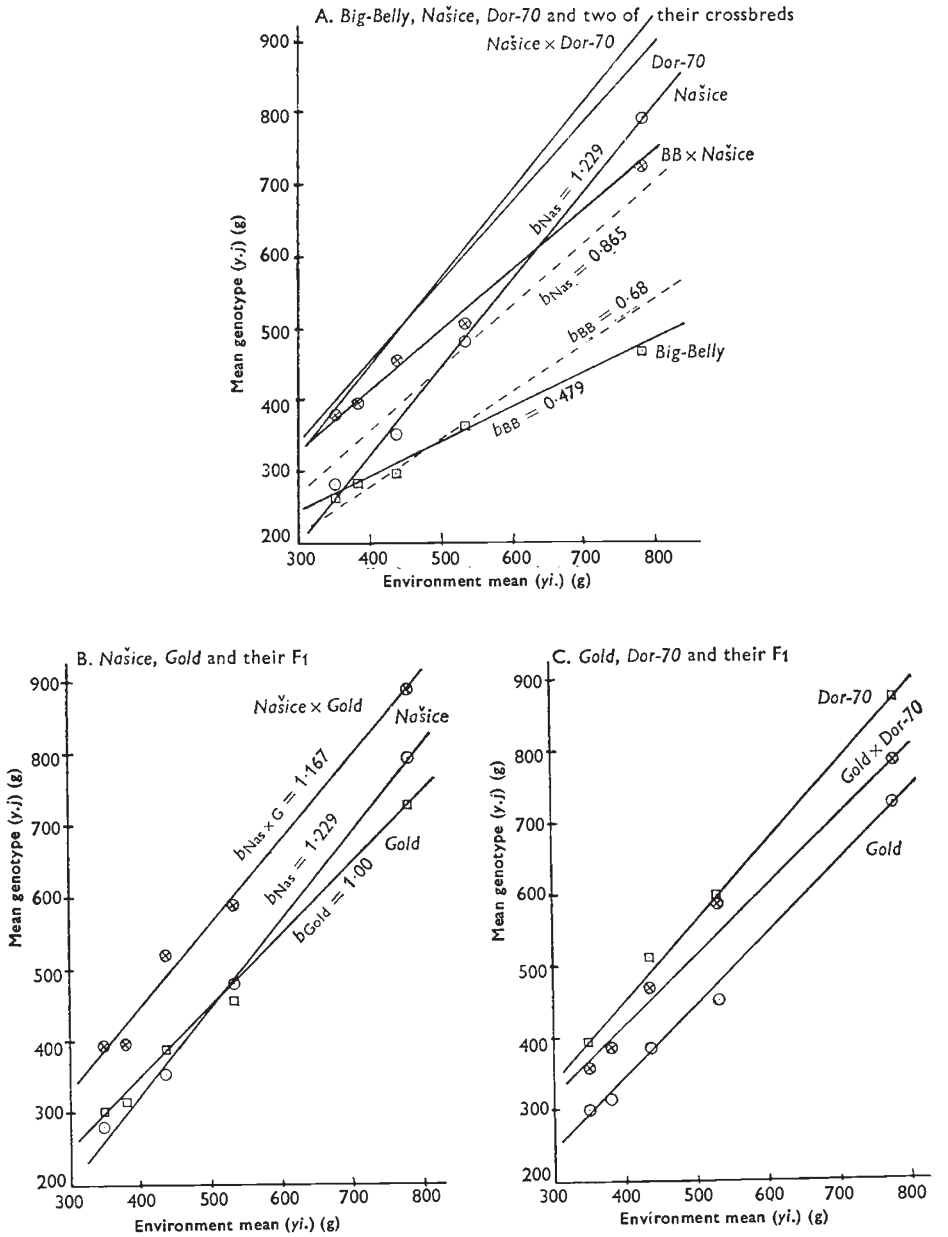

FIG. 2.—The regression of weight gain on the quality of the environment. (For definitions of b, $\hat{b}$ and further explanations see text.)

scale (β'_j), as was explained in the section "Analysis". However, the magnitudes of the estimate $\hat{s}$ (equations 4 and 7) and consequently of $\hat{b}_j$ (equation 8) and of β'_j (equation 9) are dependent on the choice of the environments mean μ, *i.e.* $Y_{.j}$ of equation 4 is evaluated at the point $\hat{\mu} = Y_{..}$, and $Y_{..}$ appears directly in equation 7. When the environments presented

in a given test can be justifiably considered to be a random sample of environments drawn from a definable population of environments then there is no ambiguity about the choice of $\bar{Y}_{..}$ as an estimate of μ. When, however, this condition is not met, evaluation of s at the point $\bar{Y}_{..}$ is not necessarily the best choice.

For trivial causes three of the five environmental treatments of the present study fell below the mean (table 2), therefore the overall mean (494 g) does not coincide with the mid-range point (565 g) and evaluation of s at the mid-range appears at least as reasonable as evaluation at the mean ($\bar{Y}_{..}$). Since a clear criterion for choice was not evident, evaluation was made at the two points, and at each point by two methods of estimation, namely $\hat{s}_1$ (equation 4) and $\hat{s}_2$ (equation 7). Hence the four estimates of $\bar{b}_j$ in table 3. s of $\bar{b}_{1j}$ was estimated by equation 4, at $\bar{Y}_{..} = 494$ g, s of $\bar{b}'_{1j}$ was similarly estimated by equation 4, but at the mid-range (565 g). In $\bar{b}_{2j}$, and $\bar{b}'_{2j}$ s was estimated by equation 7, again at $\bar{Y}_{..}$, and the mid-range, respectively. Each estimate of the scale function yielded a different estimate of the specific adaptation parameter β'_j (equation 9). These are also listed in table 3 (the four right-hand columns).

The two broken lines of fig. 2A, represent, respectively, the scale functions ($\bar{Y}_{ij} = a + \bar{b}_{1j}\bar{Y}_{i.}$, when a = y-axis intercept) of *Našice* and *Big-Belly*. The differences between the slopes of these broken lines and their corresponding solid lines are due to specific (non-scale) adaptation. The four $\bar{b}$ estimates and their corresponding $(b_j - \bar{b}_j)$ estimates were similar for all the four estimates of $\bar{b}$ (table 3), therefore subsequent presentation and analysis will be restricted to the first estimates ($\bar{b}_{1j}$ and $b_j - \bar{b}_{1j}$).

An Error variance for the specific adaptation parameter $\hat{\beta}'_j = (b_j - \bar{b}_{1j})$ has been computed by dividing, randomly, the four ponds of each treatment at Dor into two sets of two. $(b_j - \bar{b}_j)$ for each group at each treatment were available. The intra-pair variance (0·0033) served as an estimate of the Error variance, and Student's Least Significant difference (0·13) showed the existence of significant differences. (For a test of significance of the overall sensitivity parameter b_j see Perkins and Jinks, 1968.)

(iii) *Dominance of growth rate as a function of the quality of the environment*

The twelve tested groups included four strains (European: *Našice*, *Gold*, *Dor-70*; and Chinese: *Big-Belly*) and six crossbreds between them. To evaluate the heterosis (potence) of growth rate (measured by corrected weight gains), the difference between each pair of parental groups at each environment, was divided by two and designated A_i (A_i = deviation of the parent with the higher value from the mid-parental value evaluated at the ith environment). Similarly, the deviation of the crossbred from the mid-parental value was designated D_i and the ratio D_i/A_i served as a measure of relative potence at the ith environment (Bucio-Alanis *et al.*, 1969).

Bucio-Alanis *et al.* (1969) and Knight (1973) showed how the potence ratio changes as a function of the quality of the environment. Using the present notations, the *potence ratio* equation of Bucio-Alanis *et al.* takes the following form:

$$\frac{D_i}{A_i} = \frac{D + (\beta_h - \bar{\beta}_{12})a_i}{A + (\beta_1 - \bar{\beta}_{12})a_i}. \qquad (10)$$

When D and A are defined at the overall mean (μ), a_i is the environmental deviation (equation 1), β_h and β_1 are, respectively, the deviations of the response parameter β_j (equation 1) of the crossbred and the parent ($j = 1$) with the higher performance at the overall mean, and $\bar{\beta}_{12}$ is the mean response of the two parents.

The response parameter may be further partitioned into its scale component and the *specific* response (equation 2). Thus,

$$\beta_h = sg_h + \beta'_h, \quad \beta_1 = sg_1 + \beta'_1 \qquad\qquad \bar{\beta}_{12} = s\bar{g}_{12} + \bar{\beta}_{12}$$

Substitution into the last equation yields the following equation which shows how the above two components contribute to the potence ratio,

$$\frac{D_i}{A_i} = \frac{D + [s(g_h - \bar{g}_{12}) + (\beta'_h - \bar{\beta}'_{12})]a_i}{A + [s(g_1 - \bar{g}_{12}) + (\beta'_1 - \bar{\beta}'_{12})]a_i}. \tag{11}$$

Table 4 shows the D/A ratios of the six crossbreds evaluated at six environmental points: at the overall mean ($Y_{..} = 494$ g), at environment 1 of Dor (349 g, see table 2), at environment 4 of Dor (778 g), at the mid-range point (565 g) and at two extrapolated points (250 g and 900 g). Evaluation at the first three environments was made directly from the observations, therefore it involved the independent interaction residual component δ_{ij} (equation 2), in addition to the parameters of equation 10. Conversely, evaluation at the last environmental points (250 g, 565 g and 900 g) was made by equation 10, *i.e.* from the responsiveness functions (fig. 2). Table 4 clearly shows that the mean D_i/A_i of all the six crosses becomes smaller as the environment improves, but in each cross this ratio has a different function depending on its specific parameters (equation 10). D_i/A_i attains its maximal (or minimal) value when $A_i = 0$, *i.e.* when the responsiveness curves (fig. 2) of the two parents intersect. Thus, the maximal D_i/A_i of the crossbred *Našice* × *Dor-70* is attained at the environmental point 778 g; that of *Našice* × *Gold* at 494 g; that of *Našice* × *Big-Belly* at 349 g and the remaining three crosses reach maximal values at environmental points lower than 250 g. In order to illustrate the relationship of the potence ratio to the quality of the environment, the computed D_i/A_i of the two crossbreds *Našice* × *Big-Belly* (solid lines) and *Našice* × *Gold* (broken lines) were drawn in fig. 3 together with the observed ratios at the five environmental treatments. The diagrams show the nearly excellent fit of the results to their computed expectations.

(iv) *Dominance of the response (sensitivity) functions*

The potence ratio of the overall regression of performance (corrected weight gains) on the quality of the environment (b_j, equation 3 and table 5, third column from left) had a mean value over all the six crosses, very close to zero (0·16, table 5). The scale component b_j (equation 8) is fully determined by the average genotype g_j; consequently, both have identical potence ratios (D/A of table 4, evaluation at $Y_{..} = 494$ g, and rewritten again, for emphasis, in table 5 under the heading b_{1j}). As we have seen, all the potence ratios of average weight gains (hence of b_j) were positive with a mean of 1·3. This is a reflection of the high degree of hybrid vigour of faster growth rate in carp.

TABLE 4

Potence ratio (equation 10) evaluated at six environmental points

(Evaluation at the lowest (250 g) and the highest (900 g) environments were done by extrapolation.)

Crossbred group	250 g		349 g		Mean = 494 g		Mid-range = 565 g		778 g		900 g	
	A	*D/A*	*A*	*D/A*	*A*	*D/A*	*A*	*D/A*	*A*	*D/A*	*A*	*D/A*
1 × 2	39·5	2·92	2·0	55·5	51·5	2·00	78·5	1·28	158·5	0·56	204·5	0·41
1 × 3	10	4·40	18·5	2·08	53·5	1·50	72	1·26	129	1·00	159·5	0·89
1 × 4	30·5	1·43	65	0·83	110	0·49	133	0·44	203	0·34	242·5	0·30
2 × 3	29·5	3·54	18	6·11	2	59·00	6·5	18·69	31	4·26	45	3·16
2 × 4	70	0·63	65	0·78	58·5	1·03	54·5	1·20	44	1·79	76	0·64
3 × 4	40·5	0·88	46·5	0·12	56·5	0·29	61	0·20	74	−0·27	83	−0·16
Means	36·7	1·76	35·8	1·72	55·3	1·30	67·8	1·11	106·6	0·75	135·1	0·59

The potence direction of the specific adaptation component

$$\hat{\beta}'_j = (b_j - \bar{b}_j)$$

was found to be in the negative side, that is, in the opposite direction to weight gain and $\bar{b}_j$ (table 5). The average potence ratio of $(b_j - \bar{b}_j)$ over all the six crosses was $-1{\cdot}12$, indicating heterosis of high adaption (tolerance) to poor environment (low responsiveness). Since the overall responsiveness b_j is the sum of its two components $\bar{b}_j$ and $\hat{\beta}_j$, and since the potence ratios of the two components have reverse directions of approximately equal magnitudes, therefore the potence ratio of the overall responsiveness b_j is approximately zero.

TABLE 5

Potence ratios of the regression of weight gain on the quality of the environment

(b'_j and b_j = overall regression (for their difference see text); $\bar{b}_{1j}$ = regression due to the mean genotype and its scale effect; $(b_j - b_{1j})$ = specific (non-scale, independent) regression.)

Crossbred group	b_j		$\bar{b}_{1j}$		$(b_j - \bar{b}_{1j})$		b'_j	
	$A \times 1000$	D/A	$A \times 1000$	D/A	$A \times 1000$	D/A	$A \times 1000$	D/A
1×2	375	−0·13	130·5	2·01	244·5	−1·27	440	−0·14
1×3	260·5	0·58	135·5	1·51	125	−0·43	351	0·57
1×4	325·5	0·15	279	0·49	46·5	−1·92	405	0·15
2×3	114·5	0·46	5	60·00	119·5	−2·07	105	0·43
2×4	49·5	1·32	148·5	1·03	198	−0·44	44	1·25
3×4	65	−1·15	143·5	0·29	78·5	−1·48	42	−1·15
Means	198·3	0·16	140·3	1·30	135·3	−1·12	231	0·19

Note that the crossbreds have been included along with their parents in evaluating the environmental values. It may be argued that this procedure could result in biased estimates of potence ratio. Strictly speaking this objection could result in biased estimates of potence ratio. Strictly speaking this objection may be valid. Yet, we assumed that in the present case, our simplifying procedure should not contribute more than a negligible bias. To test our assumption, we estimated b_j in exactly the same method used by Bucio-Alanis *et al.* (1969). That is, for each crossbred the environmental values were estimated separately, as the means of the respective two parents, and potence ratio was defined as,

$$\frac{D}{A} = \frac{(b_h - 1)}{(b_1 - 1)}$$

when b_h, and b_1 are respectively, the regression coefficients (equation 8) of the crossbred and the parent with the higher value. These estimates are presented in the right-hand column of table 5 under the heading b'_j. We can see that all the six b'_j estimates are very similar to the corresponding b_j estimates (on the left side of table 5). Hence, our use of the crossbreds in evaluating the environmental values did not interfere with estimation of the potence ratios.

5. Discussion

The present discussion is limited to growth rate and its responsiveness to the quality of the environment. The genetic diversity of the European and the Chinese races of carp, their evolution under the widely varying domesti-

cation methods, and the implications of these matters to breeding practices will be discussed in the second article of this series.

The differences in growth rate and responsiveness of growth rate to changes in the quality of the environment may be summed up as follows:

(i) The overall response (regression) function of growth rate on the quality of the environment is two to two-and-a-half fold greater in the European than in the Chinese carp (table 3).

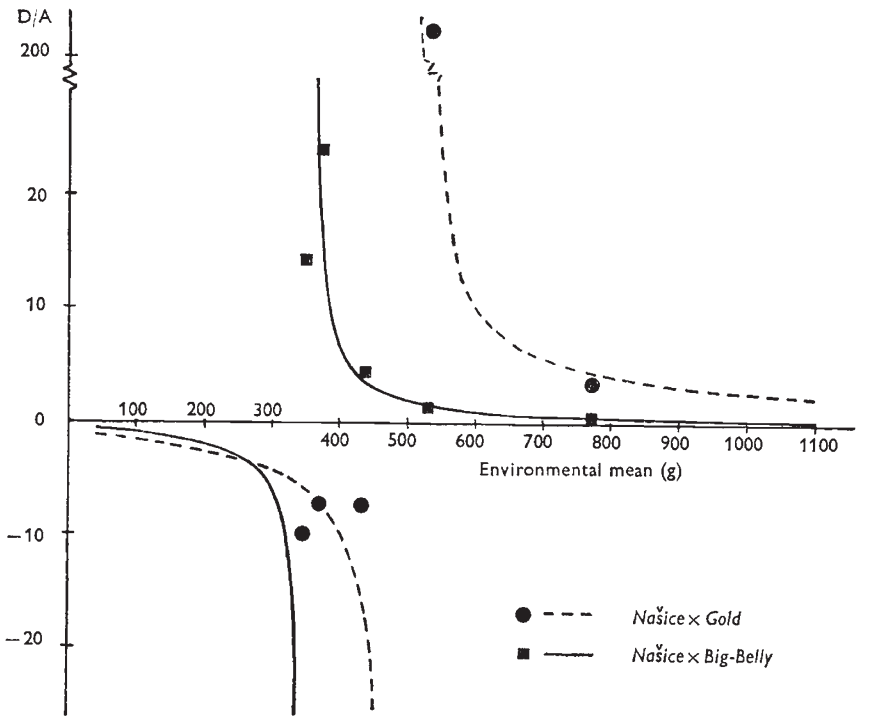

FIG. 3.—The potence ratio of two crossbreds plotted on the environmental values. (The squares and circles represent observations and the curves represent the expected relationships.)

(ii) The inter-racial F_1 crossbreds have intermediate b_j values, *i.e.* responsiveness shows almost complete genetic additivity.

(iii) The Potence Ratio as a function of the quality of the environment had taken the rather complex form of fig. 3 (similar to that shown by Bucio-Alanis *et al.*, 1969).

(iv) The deviations of the overall regression b_j from unity, are partially accounted for by a scale component ($\bar{b}_j$, equation 8). Note that when scale is the only cause for deviations of the slopes of the response lines from unity, the rankings of the genotypes and their proportional differences remain identical throughout the whole environmental range.

(v) The deviations due to specific adaptation (β'_j) have contributed considerably to the variation between the genotypes.

Separation of the overall response function (b_j) into its scale and specific adaptation components is essential for an insight into the genetic determination of variation in response to the quality of the environment and under-

standing of its evolution. The scale component of responsiveness is completely determined by the average genotype (g_j) of growth rate. Hence it does not require a separate genetic control and its evolution can be explained in terms of the relative reproductive fitness of growth rate. Faster growth rate appears to be a major component of high reproductive fitness in carp, and this can explain the high degree of dominance in this direction (Moav and Wohlfarth, 1973). Since the scale function $\bar{b}_j$, is fully determined by mean growth rate (equation 8), the dominance magnitude and direction of the former are fully accounted for by those of the latter. On the other hand, specific tolerance to poor environment (β'_j, equations 2 and 9) has a different and at least partially independent, genetic control than does average growth rate. Here we should expect low values of β'_j, (corresponding to high tolerance to poor environment) to be correlated with high reproductive fitness, and this is exactly what has been found (table 5). Thus, we can understand why the dominance direction of $\bar{b}_j$ and β'_j are in opposite directions, and why their combination—the overall responsiveness (β_j) appears to be genetically additive.

Selection operates on the overall responsiveness β_j rather than on its components, and it should favour intermediate values. However, the optimum selected for is determined by the sub-range of the environments at which most of the selection is carried out. Higher values of β_j are preferred at the upper (better) side of the environmental range. Since the European ponds fell into this section we have an evolutionary explanation for the high value of β_j of the European carp, and the opposite holds true for the Chinese carp.

Genetic variation within the European race. Of the three European parental groups, *Našice* and *Gold* suffered conspicuously from severe inbreeding depression in growth rate, viability and adaptation to poor environment. This was reflected in the low rate of growth of these two groups as contrasted with the high degree of heterosis of their F_1 crossbred (fig. 2B). These results fit well with our earlier findings of relatively high degree of inbreeding depression and heterosis (Moav and Wohlfarth, 1973).

A notable exception to the above generalisation is *Dor-70* which, despite some inbreeding in its last five generations, did not show any manifestation of inbreeding depression. Its crossbred with *Našice*, performed almost identically to itself throughout the whole environmental range (fig. 2A), while its crossbred with *Gold* was more or less intermediate (fig. 2C).

The above results constitute additional evidence that relatively large genetic variability in rate of growth exists in the European race of the common carp and that a high proportion of this variation is non-additive.

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6. References

ALIKUNHI, K. H. 1966. Synopsis of biological data on common carp, *Cyprinus carpio* L. 1758, Asia and the Far East. *FAQ Fisheries Synopsis* 31.1.

BARDACH, J. E., RYTHER, J. H., AND MCLARNEY, W. O. 1972. *Aquaculture. The Farming and Husbandry of Freshwater and Marine Organisms*, 868 pp. J. Wiley, N.Y.

BENTRAM, G. 1946. Carp farming in Palestine. *Emp. J. Exp. Agr., 14*, 187-194.

BUCIO-ALANIS, L. 1966. Environmental and genotype-environmental components of variability. I. Inbred lines. *Heredity, 21*, 387-397.

BUCIO-ALANIS, L., PERKINS, JEAN M., AND JINKS, J. L. 1969. Environmental and genotype-environmental components of variability. V. Segregating generations. *Heredity, 24*, 115-127.

DICKERSON, G. E. 1962. Implications of genetic-environmental interactions in animal breeding. *Anim. Prod., 4*, 47-64.

FINLAY, K. W., AND WILKINSON, G. N. 1963. The analysis of adaptation in a plant breeding programme. *Aust. J. Agric. Res., 14*, 742-754.

FREEMAN, G. H. 1973. Statistical methods for the analysis of genotype-environment interactions. *Heredity, 31*, 339-354.

FREEMAN, G. H., AND PERKINS, JEAN M. 1971. Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of the environments. *Heredity, 27*, 15-23.

FRIPP, YVONNE J. 1972. Genotype-environmental interactions in *Schizophyllum commune*. II. Assessing the environment. *Heredity, 28*, 223-238.

FRIPP, YVONNE J., AND CATEN, C. E. 1971. Genotype-environmental interactions in *Schizophyllum commune*. I. Analysis and character. *Heredity, 27*, 393-407.

HARDWICK, R. C., AND WOOD, J. T. 1972. Regression methods for studying genotype-environment interactions. *Heredity, 28*, 209-222.

HICKLING, C. 1962. *Fish Culture*, 287 pp. Faber and Faber, London.

HILL, J., AND SAMUEL, C. J. A. 1971. Measurement and inheritance of environmental response amongst selected material of *Lolium perenne*. *Heredity, 27*, 265-276.

HOFFMAN, W. E. 1934. Preliminary notes on the fresh-water fish industry of South China, especially Kwangtung province. *Lingnan University Science Bulletin, No. 5*, 70 pp. Lingnan Univ., Canton, China.

KIRPICHNIKOV, V. 1971. Genetics of the common carp and other edible fish. Seminar/Study Tour in the USSR on genetic selection and hybridization of cultivated fishes. *Rep. FAO/UNDP(TA) (2926)*, 186-201.

KNIGHT, R. 1973. The relation between hybrid vigour and genotype-environment interactions. *Theor. Appl. Genet., 43*, 311-318.

MOAV, R., AND WOHLFARTH, G. 1970. Genetic correlation between seine escapability and growth capacity in carp. *J. Hered., 61*, 153-157.

MOAV, R., AND WOHLFARTH, G. 1973. Fish breeding in Israel. In: *Agricultural Genetics—Selected Topics* (ed. R. Moav), 352 pp. J. Wiley, N.Y.

MOAV, R., AND WOHLFARTH, G. 1974. Magnification through competition of genetic differences in yield capacity in carp. *Heredity, 33*, 181-202.

MOAV, R., WOHLFARTH, G., AND LAHMAN, M. 1960*a*. Genetic improvement of carp. II. Marking fish by branding. *Bamidgeh, 12*, 49-53.

MOAV, R., WOHLFARTH, G., AND LAHMAN, M. 1960*b*. An electric instrument for brandmarking fish. *Bamidgeh, 12*, 92-95.

MOAV, R., WOHLFARTH, G., AND LAHMAN, M. 1964. Genetic improvement of carp. VI. Growth rate of carp imported from Holland relative to Israeli carp and some crossbred progeny. *Bamidgeh, 16*, 142-149.

PARODA, R. S., AND HAYES, J. D. 1971. An investigation of genotype-environment interactions for rate of ear emergence in spring barley. *Heredity, 26*, 157-175.

PERKINS, JEAN M., AND JINKS, J. L. 1968. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. *Heredity, 23*, 239-256.

PERKINS, J. M., AND JINKS, J. L. 1973. The assessment and specificity of environmental and genotype-environmental components of variability. *Heredity, 30*, 111-126.

TAL, S., AND SHELUVSKI, M. 1952. A review of the fish farming industry in Israel. *Trans. Am. Fish. Soc., 81*, 218-223.

TUKEY, J. W. 1949. One degree of freedom of non-additivity. *Biometrics, 5*, 232-242.

WOHLFARTH, G., AND MOAV, R. 1970. The effects of variation in spawning time on subsequent relative growth rate and viability in carp. *Bamidgeh, 22*, 42-47.

WOHLFARTH, G., AND MOAV, R. 1972. The regression of weight gain on initial weight in carp. I. Methods and results. *Aquaculture, 1*, 7-28.

WOHLFARTH, G., LAHMAN, M., MOAV, R., AND ANKORION, Y. 1965. Activities of the Carp Breeders Union in 1964. *Bamidgeh, 17*, 9-15.

YASHOUV, A. 1955. The Punten carp and its attributes. *Bamidgeh, 7*, 46-55.