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Genetic differences between the Chinese and European races of common carp

5. Differential adaptation to manure and artificial feeds

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Summary. Common carp of the Chinese and European races and their cross were tested in different environments. The test groups were either stocked together into the same pond, or each group was stocked separately. Mean growth, taken as a measure of the quality of the environment, varied widely between treatments. Genotype-environment interactions were estimated by the regression of growth of different genetic groups on this measure of environment. Proportional growth differences between the European and European × Chinese crossbreds, were several times higher in manured ponds than in ponds with artificial feed. The Chinese fish showed the fastest relative growth in poor conditions, with manure as the major nutrient input, while the European fish showed the fastest relative growth under improved conditions and irrespective of its source of food. The Chinese × European crossbred is heterotic over a range of intermediate conditions with manure as the principal nutrient.

Key words: Common carp – Genotype × environment interactions – Manure utilization

Introduction

The divergent domestication of the common carp (*Cyprinus carpio* L.) in response to differing aquaculture techniques, which gave rise to the Chinese and European races of this species, was described by Wohlfarth et al. (1975).

Genotype-environment interactions involving common carp of the Chinese and European races and their cross have been investigated by manipulating stocking rates and nutrient inputs, and stocking samples of these groups together into differently managed ponds. The quality of environment was estimated as mean growth of all groups in each pond. The regressions of growth on the environment showed clear differences in response to an improving environment between each of the races and their cross (Moav et al. 1975; Wohlfarth et al. 1983). These analyses involved pooled results of a number of yearly experiments. In some of these only supplemental feed was applied, while in others manure was the principal nutrient input. In this paper the results of tests in which only supplemental feed was applied and tests in which manure was the principal nutrient input (with or without some supplemental feed) are analyzed separately.

Materials and methods

The genetic stocks and their crossbreds

The genetic stocks have been described by Moav et al. (1975) and Wohlfarth et al. (1983). They include two isolates of the Chinese ('Big Belly') carp from Taiwan and Hong Kong. Two European strains were used, 'Nasice', introduced from Yugoslavia in 1970 and 'Dor-70', a selected Israeli strain (Wohlfarth et al. 1980). The genetic groups tested in this investigation were crossbreds in order to avoid confounding genotype-environment interactions with growth differences due to inbreeding.

The different types of crossbreds tested include:

1. European × European, produced by reciprocal crossing of 'Dor-70' × 'Nasice'.
2. Chinese × Chinese, produced by crossing Taiwanese × Hong Kong isolates.
3. European × Chinese. Two types of the inter-racial crossbreds were tested. One was the F_1 crossbred between the Taiwanese isolate and 'Dor-70'. In the other, the Chinese parent used was the product of an introgression program aimed at replacing the dominant (S) allele, determining full scale cover of the Chinese carp, by the recessive (s) allele, determining partial ("mirror") scale cover present in the European carp (Wohlfarth et al. 1963). The introgression was initiated in 1971 by crossing the Taiwanese isolate with a mirror carp not related to 'Dor-70'. By a program of recurrent backcrossing to the Chinese parent, 'selfing' and selecting the

Table 1. Details of the test carried out in communal and separate ponds with different nutrient inputs

Year	Testing system	Nutrient inputs	No. of days	No. of replicates[a]	Common carp				Other fish stocked
					No. stocked/ ha	Survival (%)	Weight (g)		
							Initial	Final	
1971	Communal	High protein pellets	133	4	10,730	84.1	25	375	None
				4	6,500	94.0	25	497	
				4	6,500	90.4	25	519	
				4	1,300	87,9	25	812	
1973	Communal	High protein pellets	124	4	8,800	87.2	25	603	Tilapia
				4	8,800	81.5	26	471	
				4	8,800	85.2	25	523	Tilapia, Silver carp,
				4	8,800	82.1	25	377	Grass carp
1974	Communal	High protein pellets	126	4	11,450	79.8	22	486	Tilapia, Silver carp, Grass carp
				4	3,300	81.9	22	1,024	
		Grain pellets		4	11,450	84.2	22	214	
				4	3,300	92.0	22	609	
		Cattle manure		2	3,050	96.7	22	479	
1975	Communal	Cattle manure + grain pellets	126	4	9,050	84.6	30	436	Tilapia, Silver carp, Grass carp
				4	4,800	91.7	30	732	
		Cattle manure		4	9,050	90.6	30	258	
				4	4,800	89.1	30	546	
1976	Communal	Different manures	124	6	6,930	82.2	24	235	Tilapia, Silver carp, Grass carp
		Manures + pellets		6	7,630	76.9	24	390	
	Separate	Different manures		6	6,930	88.8	23	222	
		Manures + pellets		6	7 630	86.4	24	363	
1977	Separate	Poultry manure	124	4	4,000	88.8	35	726	Tilapia, Silver carp, Grass carp
		High protein pellets		4	4,000	92.4	34	1 341	Silver carp
1978	Communal	Poultry manure	126	3	4,900	90.6	24	284	Tilapia, Silver carp, Grass carp
	Separate	Poultry manure	123	4	5,000	89.0	24	394	Tilapia, Silver carp,
				4	4,000	92.5	25	597	Grass carp
Spring 1978	Separate	High protein pellets	61	3	4,000	99.4	452	973	Tilapia, Silver carp
1979	Communal	Poultry manure + high protein pellets	109	9	5,000	82.8	36	627	Tilapia, Silver carp, Grass carp
				9	4,000	85.2	35	816	
1980	Communal	Poultry manures + grain pellets	115	11	5,200	88.6	25	414	Tilapia, Silver carp, Grass carp
		Poultry manure + high proteins pellets		11	5,200	86.6	25	467	

[a] No. of replicates = number of ponds in communal testing or number of ponds per tested group in separate testing

mirror segregants, each two-year cycle produced mirror segregants more closely resembling the Chinese parent. In different experiments half Chinese and three-quarter Chinese parents were used for crossing with 'Dor-70'.

Experimental procedures

All tests were carried out in earthen ponds of 400 m², except for two tests which also included 1,000 m² ponds. Experimental techniques were described by Moav et al. (1975). In most tests, common carp were grown in polyculture with tilapias, silver carp and grass carp. The carp were young-of-the-year fingerlings, except for the test carried out in the spring of 1978. Ponds were stocked in July and tests terminated in November. The experimental periods varied between 110 to 130 days. A series of tests run between 1971 to 1980 is described. The different genetic groups of the common carp were either stocked together into a series of "communal ponds", or separately into replicated "separate ponds" (Wohlfarth and Moav 1985). Nutrient inputs consisted of a pelleted feed (25% protein or sorghum) or of manure (cow or poultry), often supplemented by relatively small amounts of feed. These nutrient inputs were applied six days per week, at amounts increasing with increasing fish biomass (Wohlfarth 1978). All treatments were replicated, usually with a minimum of four replications. Further technical details are shown in Table 1.

Presentation of results

Results of communal testing are presented in units of daily growth per fish since variation in effective number of fish, due to unequal mortalities, has an equal influence on all groups co-stocked into the same pond. Those of separate testing are shown as yields (mean daily weight increment per unit area), due to the possible bias resulting from variation in the number of fish at the end of the tests.

In previous investigations, the mean growth of all carp growing in a given pond was taken as a quantitative estimate of the environment (Moav et al. 1975; Wohlfarth et al. 1983). Differences between groups in coefficients of regression of growth on the environmental mean show the differential responses of these groups to a progressively improving environment: i.e., these differences estimate genotype environmental interactions. In this paper *growth differences* are regressed directly on the environmental mean. The total regressions of growth or growth differences on the environmental mean include two components, a scale effect resulting from correlation between growth or growth differences and environmental mean, and a specific component of responsiveness independent of this scale effect (Moav et al. 1975). Regressions of *proportional* growth differences between genotypes on environmental means were computed to isolate this independent component. In communal testing, the proportional difference is the difference in growth between tested groups, divided by mean growth of tested groups. In separate testing, the proportional difference is yield difference divided by mean yield of the tested groups.

Results

The tests, carried out between 1971 and 1980, are divided into four unequal groups according to testing method, communal or separate, and nutrient inputs applied, either feed only or manure (with or without a relatively small amount of feed). All tests included the European crossbred and one or two European × Chinese crossbreds. The last three tests also included the Chinese crossbred in communal ponds with manure or manure plus feed.

1 Communal testing, manure or manure plus feed

Results (Table 2) were generated from 12 replicated observations, five with manure only and seven with manure plus supplemental feed. Growth of the European × Chinese crossbred exceeded that of the European crossbred in 10 observations. Only under conditions of the fastest growth (1979, manure plus feed, low stocking rate) did the European crossbred show the fastest growth. The Chinese crossbred showed the slowest growth in four observations, growing faster than the European crossbred only under conditions of the slowest growth (1978, manure only, high stocking rate).

The regressions of growth on the environmental mean (Fig. 1 a) show the stronger response to an improving environment of the European relative to the Chinese crossbred. They also show heterosis of the European × Chinese crossbred in intermediate environments (between 1 to 6 g/fish/day). The slopes of these response curves (Fig. 1 a), computed jointly over all observations are similar to those computed separately for manure plus feed and manure alone.

Regression of growth *differences* between pairs of groups on environmental mean (Fig. 1 b) for the European minus Chinese, European × Chinese minus Chinese, European minus European × Chinese were 0.74, 0.47, 0.22, respectively. The coefficients of regression of differences between the European and the European × Chinese crossbreds are similar when computed over all observations or for the observations in which manure plus feed were applied ($b=0.22$ or 0.27, respectively). But for the observations in which manure only was applied, this regression is close to zero ($b=-0.04$). This means that with manure plus supplemental feed, absolute differences in growth between the European and European × Chinese crossbreds increase with improving environment, from negative to positive values. However, with manure as the only nutrient input, the European × Chinese is expected to grow faster than the European independently of conditions.

The regressions of proportional growth differences on environmental mean (Fig. 1 c) for European versus Chinese, European versus European × Chinese, European × Chinese versus Chinese were 11.9, 9.7, 4.5, respectively. For European versus European × Chinese this regression is larger for observations in which only manure was applied ($b=10.8$), than for manure plus feed ($b=6.8$). This means that the largest difference in specific response to an improving environment is between European and Chinese crossbreds and the smallest between the European × Chinese and Chinese crossbreds. The difference in specific response between the European and European × Chinese crossbreds is higher with manure only than with manure plus feed.

2 Communal testing, supplemental feed

The results (Table 3) consisting of 12 replicated observations show that the European × Chinese had a faster growth than the European in only one observation. The regressions of growth on the environmental mean (Fig. 2 a) show the better response of the European crossbred to an improving environment ($b=1.27$ compared to 1.02). These regression coefficients as well as those of growth differences on the environmental mean (Fig. 2 b) are similar to those generated from manured ponds but intersect at a lower environmental mean (approximately 2.5 g compared to approximately 6 g). This means that growth of the European is expected to exceed that of the European × Chinese under worse environmental conditions when feed rather than manure is the major nutrient input. The

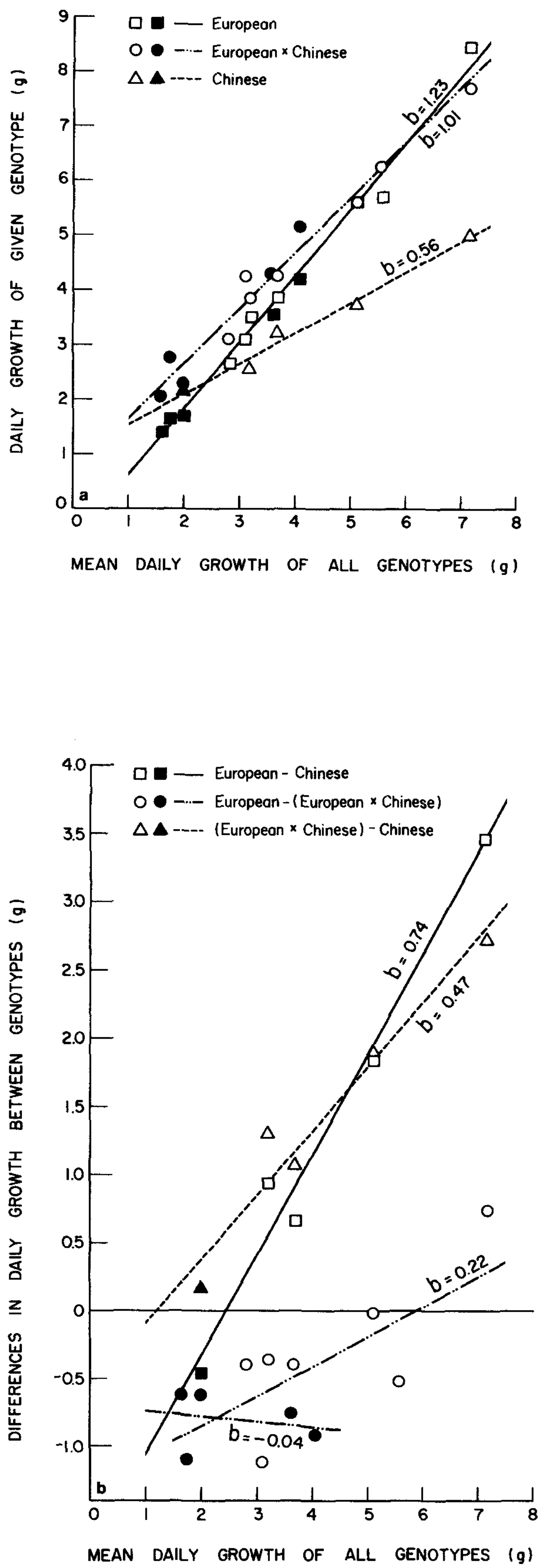
Table 2. Communal testing with manure or manure plus feed as nutrient inputs.
a. Growth of different genotypes

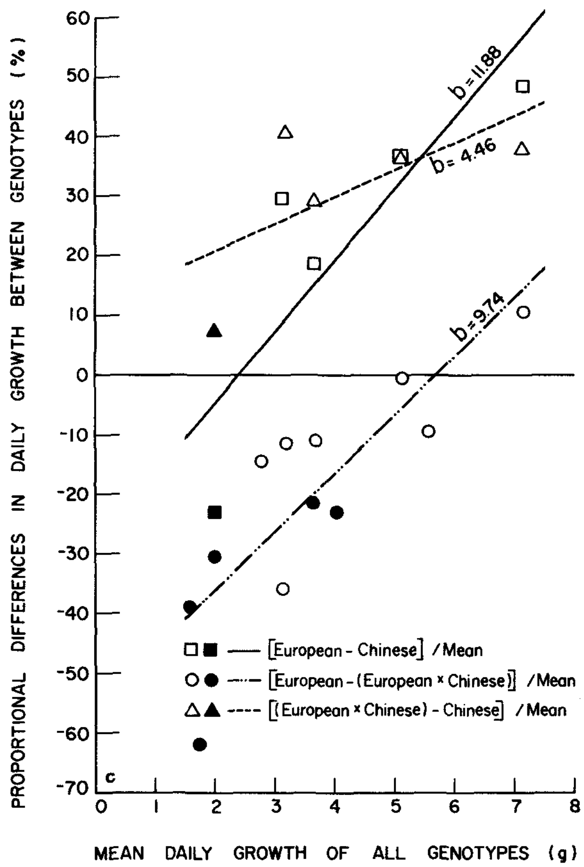
Year	Nutrient inputs	Stocking rate	Mean daily corrected weight gain (g/fish)						Further details in:
			European × European	Chinese × European	3/4 Chinese × European	Mean C×E, 3/4 C×E	Chinese × Chinese	Mean of all carp stocked[a]	
1974	Cattle manure	Low	3.55	4.52	4.12	4.32		3.60	Moav et al. 1977
1975	Cattle manure + Grain pellets	High	3.13	3.92	4.57	4.25		3.12	
		Low	5.71	5.75	6.71	6.23		5.54	
	Cattle manure	High	1.64	2.94	2.52	2.73		1.76	
		Low	4.21	5.08	5.18	5.13		4.05	
1976[b]	Manures + feed pellets	Mean of High and Low	2.67		3.08			2.78	
	Manures		1.42		2.04			1.58	
1978	Poultry manure	High	1.69	2.30			2.15	2.02	
1979	Poultry manure + feed pellets	High	5.60	5.62			3.75	5.11	Wohlfarth et al. 1983
		Low	8.43	7.70			4.98	7.13	
1980	Poultry manure + grain pellets	High	3.48	3.85			2.54	3.22	
	Poultry manure + feed pellets		3.85	4.25			3.18	3.65	

[a] Mean weight gain differs from mean of groups in table due to unequal numbers of fish in different groups and due to stocking further groups of fish into these ponds, not appearing in table
[b] Different type of cattle and poultry manure, different feed pellets

Table 2b. Absolute and proportional differences in growth between genotypes

Year	Nutrient inputs	Stocking rate	Differences in mean daily corrected weight gains					
			(European × European − Chinese × European)		(European × European) − (Chinese × Chinese)		(European × Chinese) − (Chinese × Chinese)	
			Absolute (g)	Proportional (%)	Absolute (g)	Proportional (%)	Absolute (g)	Proportional (%)
1974	Cattle manure	Low	−0.768	−21.34				
1975	Cattle manure + grain pellets	High	−1.119	−35.88				
		Low	−0.524	− 9.46				
	Cattle manure	High	−1.095	−62.15				
		Low	−0.921	−22.75				
1976	Manures + feed	Mean of high and low	−0.408	−14.70				
	Manures		−0.621	−39.28				
1978	Poultry manure	High	−0.613	−30.41	−0.462	−22.92	+0.151	+ 7.49
1979	Poultry manure + feed pellets	High	−0.017	− 0.33	+1.853	+36.27	+1.870	+36.60
		Low	+0.732	+10.27	+3.450	+48.40	+2.718	+38.13
1980	Poultry manure + grain pellets	High	−0.368	−11.44	+0.941	+29.25	+1.309	+40.69
	Poultry manure + feed pellets		−0.401	−10.98	+0.669	+18.32	+1.070	+29.30





◄ **Fig. 1 a–c.** Communal testing with manure (*solid symbols*) or manure plus feed (*open symbols*). **a** The regressions of growth on the quality of the environment; **b** the regressions of growth differences between genotypes on the quality of the environment. (The *interrupted line* shows the regression of the growth difference between the European and European × Chinese crossbreds with manure only); **c** the regressions of proportional growth differences between genotypes on the quality of the environment

regression of the proportional difference between the two crossbreds on environmental mean (b = 3.24; Fig. 2c) is much lower than the parallel regression coefficient in manured ponds (b = 9.74; Fig. 1c).

3 Separate testing, manure or manure plus feed

The results (Table 4) consist of five replicated observations, four with manure only, and one with manure plus feed. A larger yield was obtained from the European × Chinese in all five observations. The regression of yield on the environmental mean (Fig. 3a) is only a little larger for the European than the European × Chinese crossbreds (b = 2.30 versus 2.09). The single set of observations in which manure plus feed were applied deviate markedly from both these regression lines (as well as that of yield differences on the environmental mean, see Fig. 3b). Deleting these

Table 3. Communal testing, feed only as nutrient input. Growth and growth differences between different genotypes

Year	Treatment	Stocking rate	Mean daily corrected weight gain (g/fish)							Further details in:
			European × European	Chines × European	3/4 Chinese × European	Mean of C×E, 3/4 C×E	Mean of all fish[a]	Difference (E×E – E×C)		
								Absolute (g)	Proportional (%)	
1971	Water exchange	High	2.96	2.87			2.60	0.09	3.15	Moav et al. 1975
		Medium	3.79	3.53			3.47	0.26	7.47	
	Standing water	Medium	4.13	3.83			3.66	0.30	8.28	
		Low	6.80	5.48			5.71	1.32	23.10	
1973	Polyculture	High	3.02	3.24	3.30	3.27	2.75	–0.25	–8.89	
	Polyculture +aeration	High	3.91	3.89	3.86	3.88	3.51	0.03	0.91	
	Monoculture	Low	4.62	4.11	4.29	4.20	3.97	0.42	10.63	
	Monoculture +aeration	Low	5.09	4.40	4.52	4.46	4.25	0.63	14.78	
1974	25% protein pellets	High	4.52	3.98	4.30	4.14	3.65	0.38	10.34	Moav et al. 1977
		Low	9.91	8.07	8.97	8.52	7.90	1.39	17.54	
	Grain pellets	High	1.88	1.75	1.82	1.78	1.51	0.10	6.48	
		Low	5.25	4.86	5.65	5.26	4.62	–0.01	–0.2	

[a] See footnote in Table 2a

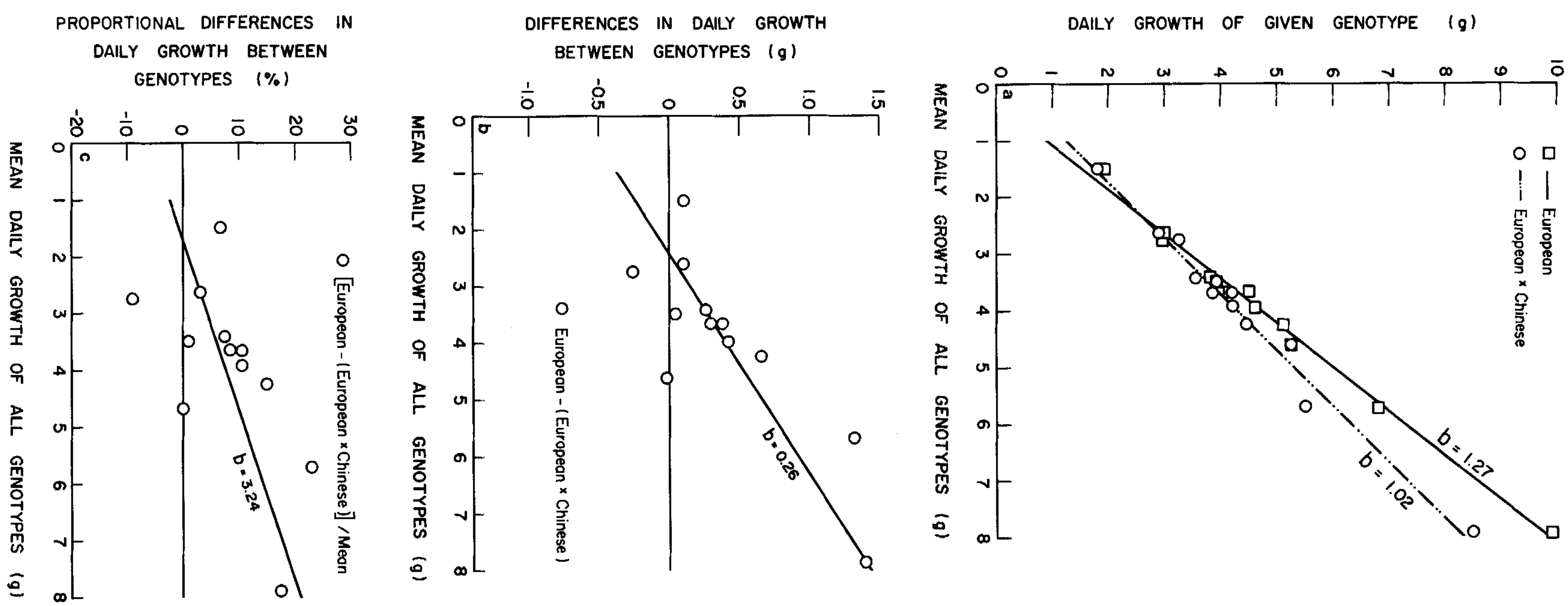
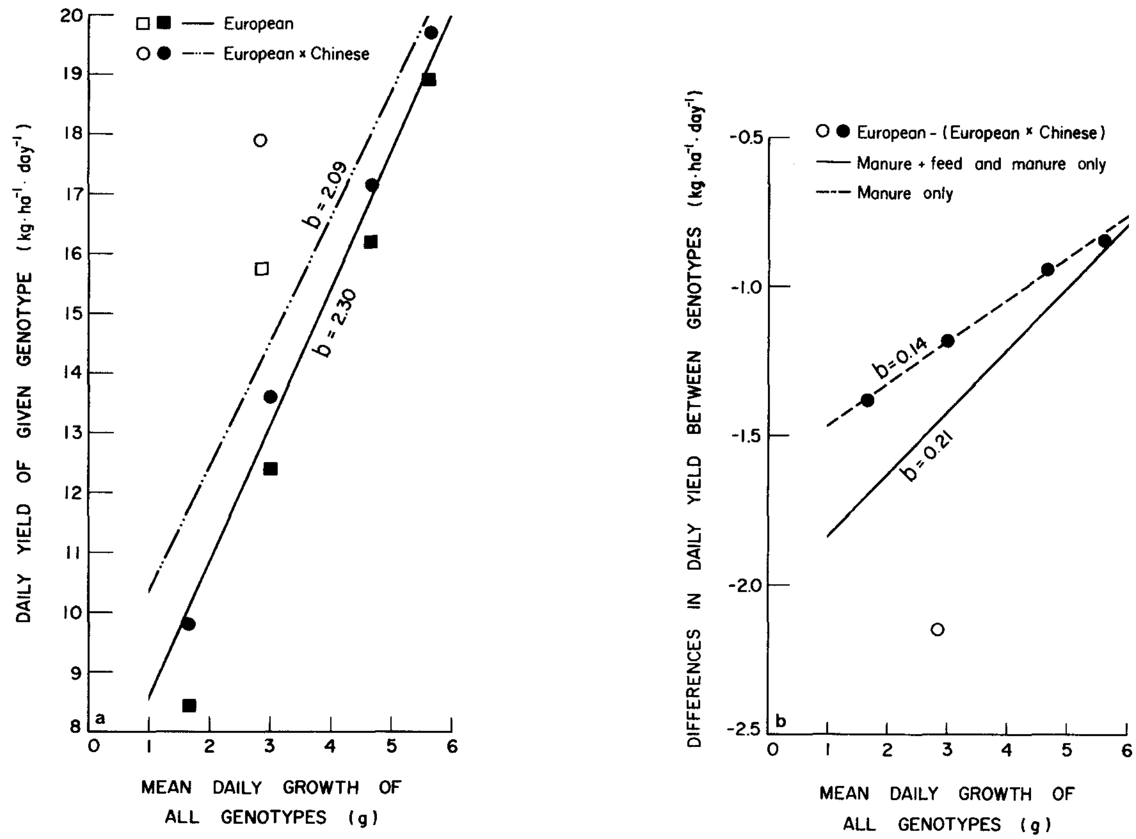


Fig. 2a–c. Communal testing with feed. **a** The regressions of growth on the quality of the environment; **b** the regression of growth differences between genotypes on the quality of the environment; **c** the regression of proportional growth differences between genotypes on the quality of the environment



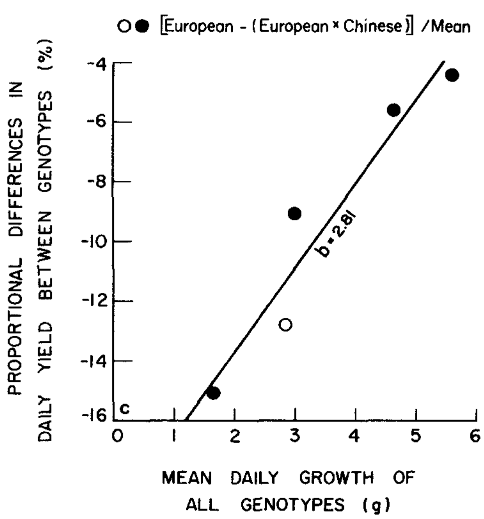


Fig. 3a–c. Separate testing with manure (*solid symbols*) or manure plus feed (*open symbols*). **a** The regressions of yield on the quality of the environment; **b** the regression of yield differences between genotypes on the quality of the environment. (The *interrupted line* shows the regression with manure only); **c** the regression of porportional yield differences between genotypes on the quality of the environment

points from the analyses results in highly significant correlations. With manure as the only nutrient input, the European crossbred is expected to produce a higher yield than the European×Chinese only in environments above 11.5 g/fish/day. Regressions of proportional yield differences on the environmental mean (Fig. 3c) are similar when based on all five observations or on the four manure only observations (b=2.81 and 2.68, respectively).

4 Separate testing, supplement feed

The results (Table 5) consist of only two replicated observations. In 1978 adult fish of a much higher initial weight than in all other tests here described were tested in the spring of their second year and during a short period (61 days). Yields of the two crossbreds were virtually equal (1977) or the European×Chinese crossbred showed a somewhat higher yield (1978).

Table 4. Separate testing, with manure or manure plus feed as nutrient inputs. Yields and yield differences of different genotypes

Year	Nutrient inputs	Stocking rate	Mean daily yield (kg/ha)		Daily means of both groups		Yield difference (European × European) − (European × Chinese)		Further details in:
			European × European	European × Chinese	Yield (kg/ha)	Individual weight gain (g/fish)	Absolute (kg/ha)	Proportional (%)	
1976	Manures	Means of high and low	8.44	9.82	9.13	1.65	−1.38	−15.12	
	Manures + feed pellets		15.74	17.89	16.82	2.83	−2.15	−12.78	
1977	Poultry manure	Low	18.87	19.71	19.29	5.60	−0.84	−4.35	Wohlfarth 1978
1978	Poultry manure	High	12.41	13.59	13.00	3.01	−1.18	−9.08	Wohlfarth et al. 1980
		Low	16.21	17.15	16.68	4.65	−0.94	−5.64	

Table 5. Separate testing, with feed only as nutrient input. Yield differences of different genotypes

Year	Nutrient inputs	Stocking rate	Mean daily yield (kg/ha)		Daily means of both tested groups		Yield difference (European × European) − (European × Chinese)		Further details in:
			European × European	European × Chinese	Yield (kg/ha)	Individual weight gain (g/fish)	Absolute (kg/ha)	Proportional (%)	
1977	Feed pellets	Low	38.13	38.69	38.41	10.44	−0.56	−1.46	Wohlfarth 1978
Spring 1978	Feed pellets	Low	31.99	35.86	33.93	8.53	−3.87	−11.41	Hepher and Sandbank 1984

Discussion

Analyses of the experimental results are summarized in Table 6, which also shows coefficients of correlation and their significance.

Comparisons between the tested genotypes

In practically all cases the European × Chinese showed a faster growth in manured ponds, while that of European crossbred was faster with supplemental feed. The regressions of growth of the European × Chinese crossbred is a little higher for manure only than for manure plus feed, but the opposite is true for the European crossbred. Regressions of growth differences between European and European × Chinese crossbreds are similar for manure plus feed only, but zero for manure only.

The associations between absolute or proportional growth differences and the environmental mean were positive under all conditions tested. This shows the better response to environmental improvement of the European compared to either Chinese or European × Chinese, and of European × Chinese compared to Chinese. For European × Chinese in communal testing, regression of absolute growth differences on environmental mean (estimating total response to environmental variation including scale effect) are similar with different nutrient inputs. But the regression of proportional growth differences (estimating the component of response not influenced by scale effect) is three times larger for manure than feed. This shows that the specific response function is masked by the scale effect more strongly in environments of supplemental feeding than in manured ponds. The scale effect results from the association between growth and growth differences.

Table 6. The regression equations, coefficients of correlation and their significance

Testing method	Trait	Nutrient inputs[a]	Genotypes[b]	No. of observations	Regression equations	Coefficients of correlation	P
Communal	Growth	M+F, M	EE	12	Y=− 0.673+ 1.228X	0.995	0.0001
		M+F, M	EC	12	Y= 0.636+ 1.007X	0.987	0.0001
		M+F, M	CC	5	Y= 0.955+ 0.561X	0.991	0.0011
		M+F	EE	7	Y=− 0.761+ 1.251X	0.993	0.0001
		M	EE	5	Y=− 0.424+ 1.124X	0.997	0.0002
		M+F	EC	7	Y= 0.707+ 0.983X	0.988	0.0001
		M	EC	5	Y= 0.285+ 1.161X	0.978	0.0038
	Growth differences	M+F, M	EE–EC	12	Y=− 1.309+ 0.220X	0.717	0.0087
		M+F, M	EE–CC	5	Y=− 1.815+ 0.735X	0.987	0.0017
		M+F, M	EC–CC	5	Y=− 0.570+ 0.472X	0.973	0.0054
		M+F	EE–EC	7	Y=− 1.468+ 0.268X	0.765	0.0450
		M	EE–EC	5	Y=− 0.697− 0.039X	0.200	0.7467 (ns)
	Proportional growth differences	M+F, M	(EE–EC)/X.	12	Y=− 56.05 + 9.740X	0.828	0.0009
		M+F, M	(EE–CC)/X.	5	Y=− 28.31 + 11.876X	0.854	0.0655 (ns)
		M+F, M	(EC–CC)/X.	5	Y= 11.61 + 4.457X	0.648	0.2370 (ns)
		M+F	(EE–EC)/X.	7	Y=− 40.22 + 6.844X	0.778	0.0396
		M	(EE–EC)/X.	5	Y=− 63.23 + 10.783X	0.735	0.1568 (ns)
Communal	Growth	F	EE	12	Y=− 0.339+ 1.274X	0.995	0.0001
		F	EC	12	Y= 0.239+ 1.016X	0.989	0.0001
	Growth difference	F	EE–EC	12	Y=− 0.638+ 0.259X	0.834	0.0007
	Proportional growth difference	F	(EE–EC)/X.	12	Y=− 5.044+ 3.243X	0.617	0.0325
Separate	Yield	M+F, M	EE	5	Y= 6.183+ 2.297X	0.897	0.0392
		M+F, M	EC	5	Y= 8.217+ 2.090X	0.832	0.0803 (ns)
		M	EE	4	Y= 4.307+ 2.596X	0.999	0.0011
		M	EC	4	Y= 5.909+ 2.457X	0.999	0.0012
	Yield difference	M+F, M	EE–CC	5	Y=− 2.033+ 0.207X	0.624	0.2604 (ns)
		M	EE–EC	4	Y=− 1.602+ 0.139X	0.998	0.0016
	Proportional yield difference	M+F, M	(EE–EC)/X.	5	Y=− 19.36 + 2.809X	0.962	0.0090
		M	(EE–EC)/X.	4	Y=− 18.52 + 2.675X	0.972	0.0277

[a] M = Manure, F = Feed
[b] E = European, C = Chinese, X. = Mean of all genotypes

Since supplemental food is a more efficient nutrient input than manure, it is expected to increase the scale effect more than manure.

The larger regression of proportional growth differences on the environmental mean, with manure relative to supplemental feeding, means that the true response difference between the European and European×Chinese crossbreds was more pronounced with manure rather than feed. This may be explained by the divergent conditions in which Chinese and European carp were domesticated. These were much harsher in China and with a heavy reliance on manure. Genetic adaptation to these conditions presumably resulted in a relatively fast growth of Chinese carp in poor conditions and with manure, but their slow response to improved conditions. European carp, on the other hand, grow relatively slowly in poor conditions, respond better to improvement in these conditions and are non-specific to their source of food. This lack of specificity may be a result of manure always being present in the ponds (in the form of fish faeces) even when not deliberately applied.

Differences in adaptation to different nutrient inputs are seen by comparing regressions of growth on the environmental mean between the European and European×Chinese crossbreds, with either manure or feed (Figs. 1a and 2a). The points of intersection of these regression lines show that at a mean growth of at least 6 g/fish/day, the European grows faster than the European×Chinese in manured ponds, while with feed this occurs at a mean growth rate of 2.5 g/fish/day or more. Points of intersection of regression lines of growth differences between the European and European × Chinese crossbreds with the X axis (Figs. 1 b and 2 b) show the same result.

In separate testing with manure, the regressions of absolute and proportional yield differences on the environmental mean are about half of the estimate of the growth regressions in communal testing. This is presumably due to competition between groups in communal testing, which increases inter-group growth differences relative to separate testing but does not change relative rankings (Moav and Wohlfarth 1974). In separate testing with feed the two observations showed a slight yield advantage of the European × Chinese over the European crossbred, or their virtual equality in yield. Since with feed the European grows faster than European × Chinese in communal ponds, its yield is also expected to be higher in separate testing. The expected yield difference between the groups is fairly low and the unexpected yield equality is regarded as a random fluctuation.

Application to aquaculture

Choice of stocks depends on management factors, principally nutrient inputs and stocking rates. Prediction of the range of environmental means, at which a given genotype is to be preferred, are given by the points of intersection of response curves of the different genotypes (Figs. 1 a, 2 a and 3 a). With manure as the principal nutrient input, European crossbreds show the fastest relative growth at rates exceeding 6 g/fish/day. The European × Chinese shows the fastest growth between 1–6 g/fish/day, and the Chinese at below 1 g/fish/day. *Yields* of the European × Chinese crossbred exceed those of the European in conditions of up to 10–11 g/fish/day. This difference between growth and yield results is due to the influence of stocking rate. Increasing stocking rate tends to increase yields, especially of Chinese and European × Chinese crossbreds, but depresses growth rate. Hence the higher yields of European × Chinese consist of a larger number of more slowly growing and thus smaller fish. With feed as the only nutrient input, growth of the European × Chinese crossbred exceeds that of the European only up to a mean daily growth rate of 2.5 g/fish.

General conclusions concerning genetic adaptation to different aquaculture conditions are clear. European carp are adapted to European conditions, of low stocking rates resulting in fast growth during the second and third year. The Chinese carp is adapted to the traditional Chinese aquaculture management, consisting of heavy reliance on manures, and high stocking rates. In intermediate managements, European × Chinese crossbreds appear the optimal choice. Their use in a modernized version of Chinese aquaculture has been demonstrated in Hong Kong (Sin 1982).

Dominance relations

The intersections of the response curves of the European and Chinese crossbreds and their inter-racial crossbred (Fig. 1 a) show that their dominance relation is a function of the environment. The use of inter-racial crossbreds for estimating dominance relations was discussed by Moav et al. (1975). In manured ponds, at environments enabling a mean daily growth of 6 g/fish, the European carp is fully dominant over the Chinese for the trait growth rate. At environments of 1 g/fish/day the Chinese carp is dominant over the European. At 2.5 g/fish/day the two races are co-dominant and between 1–6 g/fish/day the crossbred is overdominant. In different conditions these relations change: e.g., with supplemental food the European carp is dominant over the Chinese carp at a mean daily growth rate of 2.5 g/fish (Fig. 2 a).

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