academicJournals

Vol. 12(22), pp. 3514-3521, 29 May, 2013
DOI: 10.5897/AJB12.2201
ISSN 1684-5315 ©2013 Academic Journals
http://www.academicjournals.org/AJB

African Journal of Biotechnology

Full Length Research Paper

Estimates of combining ability and heterosis for growth traits in a full diallel cross of three strains of common carp, Cyprinus carpio L.

Shengyan Su[1,2], Pao Xu[1,2,3]* and Xinhua Yuan[1,2,3]*

[1]Wuxi Fisheries College, Nanjing Agricultural University, Wuxi 214081, PR China.
[2]Key Laboratory of Freshwater Fisheries and Germplasm Resources Utilization, Ministry of Agriculture, Freshwater Fisheries Research Center, Chinese Academy of Fishery Sciences, Wuxi 214081, China, PR China.
[3]Fish genetic and breeding, shanshui western road No.9, 214081, wuxi, Jiangsu, PR China.

Accepted 29 May, 2013

We attempted to determine the combining ability and heterosis of body weight by performing 3 × 3 complete diallel crosses derived by crossing three common carps (*Cyprinus carpio* var. jian, *Cyprinus carpio* haematopterus Temminck et Schlegel and *Cyprinus carpio* haematopterus). In total, 1650 fish were tagged when they were 1.5 months of age. After five months, Jian carp (♂) × Huanghe carp (♀) attained greater weight than pure and other hybrids. By crossing with Jian, Huanghe and Heilongjiang carps have improved body weight compared to their purebred. Significant principal components (PCs) were generated from growth performance data and their statistical loadings. The first principal component had the highest Eigen value of 2.81 and accounted for 70.31% of the variability in the data set. Two crosses, Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) showed high SCA with regard to body weight. Both Heilongjiang carp (♂) × Jian carp (♀) and Heilongjiang carp (♂) × Huanghe carp (♀) had higher heterosis compared to their purebreds. Significant positive phenotypic correlations were also observed between body weight and body length, thickness and height. The aforementioned results listed were identified as the foundation for common carp selective breeding programs.

Key words: Common carp, cross-breeding, heterosis.

INTRODUCTION

Common carp, Cyprinus carpio is a major cultured fish worldwide (FAO, 2007). Common carp is mainly reared in ponds with extensive or intensive management. In China, Jian carps performed better in growth and are favorite strains to customers compared with other carp varieties. However, the growth performance of Jian carp still needs to be improved. Genetic improvements could be an effective way to increase the growth of Jian carp. Generally, crossbreeding is a widely accepted practice used for improving the productivity of commercial fish up

*Corresponding authors. E-mail: yuanxh@ffrc.cn, xup@ffrc.cn. Tel: +86 510 85555796, Fax: +86 510 85555796.

Abbreviations: GCA, General combining ability; **SCA,** specific combining ability; **PIT,** passive integrated transponder; **FFRC,** freshwater fisheries research center; **PCA,** principal component analysis; **PCs,** principal components.

Table 1. Full diallel cross of three strains of common carp.

Cross		Female		
		h	j	y
Male	H	Hh	Hj	Hy
	J	Jh	JJ	Jy
	Y	Yh	Yj	Yy

H, Huanghe carp; J, Jian carp; Y, Heilongjiang carp.

to 20 to 25% productivity compared to the traditional races (Bakes and Gorda, 1995; Vandeputte et al., 2002; Nielsena et al., 2010). The level of heterosis (cross versus purebred) also were measured; varied from 14 to 29% for weight traits, 1.7 to 8.3% for length traits and 8 to 37% for pond survival (Nielsena et al., 2010). Results from plant (Shukla and Pandey, 2008) and warm-blood animals (Abdel-aziz et al., 2003; Shikano et al., 2000) confirmed that hybridization is an economically viable option because hybrids may have better growth performance than pure bred.

The main use of crossbreeding is to generate heterosis. Heterotic studies can provide the basis for exploitation of valuable hybrid combinations. Meanwhile, combining ability, defined by Griffing (1956) can provide a method for screening germplasm and can be used along with heterosis analysis to determine the usefulness of genotypes to be included in a breeding program. Usually, it is preferred to General Combining Ability (GCA), specific combining ability (SCA) and reciprocal effects. Knowledge of combining ability allows producers to use additive effects to match their practical production situation and to gain further increases in productivity through non-additive gene action. The additive and non-additive genetic effect estimated from crossbreeding can be used to improve breeding programs (Shukla and Pandey, 2008; Thanh et al., 2010; Mohamed et al., 2001). In order to increase the efficiency of such application, Qi et al. (2012) also observed five loci which can si-multaneously control GCA and SCA recently.

Qu et al. (2012) identified several quantitative trait loci (QTLs) that responded to combining ability and heterosis of agronomic traits, which provided valuable information for dissecting genetic basis of combining ability. The research began by comparing the progeny growth of Huanghe, Heilongjiang and Jian carps full diallel cross in a monoculture pro-duction environment at FFRC. Another purpose of this study was to estimate the magnitude of heterosis for growth when crossing with Jian carp. Such information about Jian carp is lacking but is needed to decide the type of breeding strategy to be used to improve Jian carp. This information was obtained by performing two 3 × 3 complete diallel crosses using Huanghe, Heilongjiang and Jian carps. This paper presents the analyses of these crosses.

MATERIALS AND METHODS

Stocks, mating design and rearing of fry

Three varieties (Jian, Huanghe and Heilongjiang carps) were obtained from FFRC freshwater station in Wuxi, China. Three full diallel crosses were made using these strains with an average of 2 kg per cross and the abbreviations were also listed (Table 1) and 5 males and five females per strain were used to produce 30 full-sib families. Purebred strains assigned for normal group were made by crossing only one male and female each, resulting in 33 different families in total. For each stock, females were stimulated for spawning using oxytocin and fertilized with the milt from each male brooder. The fertilized eggs were transferred to separate hatching hapas in the same pond until they can be tagged.

Tagging and production environment

After nearly 1.5 months, 50 fish were randomly sampled from each family and tagged individually with passive integrated transponder (PIT) tags. The tags were implanted into the abdominal cavity. In order to determine the effect of combination, spawning time, family ID, body weight, body length, thickness and height were recorded. Reproduction and fry rearing prior to tagging were conducted in fine-mesh hapas inside concrete tanks. Each tank was installed with two rows of hapas, leaving a 40 cm passage along the middle of the tank for inspection feeding. In this study, 33 hapas were used, each for one combination. Hapas were sized by 120 × 80 × 100 cm (length × width × depth) and made with nylon net cloth. The tanks were supplied with filtered well water and equipped with air stones for continuous aeration. During the experiment period, the dissolved oxygen ranged from 3.8 to 8.6 mg/l, and pH from 7.2 and 8.5, pond water temperature was from 18 and 20°C. After that, they were stocked into an earthen pond (2 mu, 1.5 to 1.8 m water depth).

On July 16, 2008, the growth traits performance on all fish in the pond were recorded and stocked for wintering in the same pond. After wintering, the same recordings were repeated on November 26, 2009 (harvesting). Fish were fed a commercial feed with 30% of protein. No severe disease outbreaks were found during the experiment. The research was carried out in accordance with the Code of Ethics of the World Medical Association for animal experiments.

Statistical analysis

Variance analysis of body weight gain was done using the following model:

Where show the ith combination, jth family, kth individual, instead of the mean value, instead of the ith combination, present the ith combination, jth family and is the residual error. Analysis of variance by the least significant difference (LSD) significant test at P< 0.05 was used to test the effects of hybrids and families (random effect: sire, dam and individual). PCA and cluster analysis were performed using SAS 8.0. To estimate the combining ability and heterosis (dominance genetic effect) for body weight, a previously reported generalized linear model was applied (Tave, 1993; Zhang and Kang, 1997).

Highlights

1) Higher bodyweight compared to purebred can be obtained by special cross.

Table 2a. Description statistics of harvest growth traits.

Parameter		Time	Weight (g)	Length (mm)	Thickness (mm)	Height (mm)
Pure bred	Hh	Tagging	9.21±1.06	59.62±6.23	10.18±0.74	20.60±1.80
	Hh	Harvesting	237.76±12.23	200.66±7.33	32.74±0.66	60.88±1.01
	Hh	Gain	228.55±11.76	141.04±9.12	22.56±0.85	40.28±1.85
	Jj	Tagging	13.521±1.09	67.77±6.43	11.98±0.76	29.19±1.85
	Jj	Harvesting	302.2±12.61	220.77±7.56	37.04±0.68	64.3±1.04
	Jj	Gain	288.67±12.13	153.0±9.41	25.06±0.87	35.11±1.90
	Yy	Tagging	8.3±0.94	56.92±5.55	9.75±0.66	18.38±1.60
	Yy	Harvesting	236.78±10.90	199.4±6.53	32.65±0.59	59.1±0.90
	Yy	Gain	228.48±10.48	220.77±21.3	22.90±0.75	64.3±11.95
Cross bred	Hj	Tagging	11.28±0.47	64.87±2.79	11.24±0.33	21.14±0.80
	Hj	Harvesting	310.12±5.48	222.95±3.29	36.7±0.30	66.53±0.45
	Hj	Gain	298.84±5.27	158.08±4.09	25.46±0.38	45.39±0.83
	Hy	Tagging	13.03±0.43	72.01±2.52	11.23±0.30	22.11±0.73
	Hy	Harvesting	262.74±4.95	217.34±2.97	33.8±0.27	62.02±0.41
	Hy	Gain	249.70±4.76	145.33±3.69	22.57±0.34	39.91±0.75
	Jh	Tagging	13.51±0.43	68.19±2.53	10.75±0.30	21.72±0.73
	Jh	Harvesting	312.01±5.48	225.69±2.98	36.57±0.27	66.90±0.41
	Jh	Gain	298.49±4.78	157.50±3.71	25.82±0.34	45.18±0.75
	Jy	Tagging	10.12±0.40	60.76±2.38	10.23±0.28	20.21±0.68
	Jy	Harvesting	289.8±4.66	212.42±2.80	35.51±0.25	65.44±0.39
	Jy	Gain	279.69±4.48	151.66±3.48	25.28±0.32	45.23±0.70
	Yh	Tagging	8.82±0.46	64.76±2.73	10.05±0.32	19.88±0.79
	Yh	Harvesting	271.08±5.35	213.15±3.21	34.39±0.29	63.21±0.44
	Yh	Gain	262.26±5.15	148.39±3.99	24.34±0.37	43.33±0.81
	Yj	Tagging	4.0±0.44	26.98±2.58	4.20±0.30	8.27±0.74
	Yj	Harvesting	297.36±5.06	215.45±3.03	36.35±0.27	66.65±0.42
	Yj	Gain	293.36±4.87	188.47±3.77	32.16±0.35	58.38±0.765

2) Two combinations had higher SCA about body weight, one strain had higher GCA.
3) Phylogram tree in the data partitioned by 4 traits related to growth in common carp.

RESULTS

Difference between the four traits related to growth performance

The mean body weight, length, thickness, and height of both pure bred and cross bred fish at tagging, harvesting and body weight gain are listed in Table 2a. The body weight gain showed no difference between pure bred and cross bred fish for Jian carp; although, cross bred had higher body weight at harvesting; jian carp (♂) × Huanghe carp (♀) attained greater weight than pure and cross other bred carp. By crossing with Jian, Huanghe and Heilongjiang carp improved body weight compared to their purebred (Table 2b).

Difference in body weight between the families of different groups as related to growth

In order to further family selection, differences between the families of different groups as related to growth performance are showed in Table 3. Only one significant difference in different family can be found for cross Heilongjiang carp (♂) with Jian carp (♀), while other group had bigger significant differences between different families. The significant differences for 4th, 5th, 14th, 16th, 29th and 30th families were observed compared to the other families in its own combinations.

Body weight gain variance analysis

From the aforementioned description, the family and the line can influence the body weight gain; thus, the general linear model was established based on the significant test. The combination and family in special combination can affect the body weight gain. Combination and family

Table 3. Difference between the families of different groups with regard to body weight gain.

Group	Difference between the families of different group related to growth				
	Family	**2 (g)**	**3 (g)**	**4 (g)**	**5 (g)**
Jy	1	1.58	3.61**	6.31**	-3.97**
	2		1.95	4.59**	-5.38**
	3			2.67**	-7.35**
	4				-9.92**
		7 (g)	8 (g)	9 (g)	10 (g)
Yj	6	-0.30	-1.57	-2.26*	-1.04
	7		-1.22	-1.83	-0.67
	8			-0.48	0.64
	9				1.23
		12 (g)	13 (g)	14 (g)	15 (g)
Hy	11	-2.86**	0.09	-5.31**	-0.97
	12		3.11**	-2.45*	1.85
	13			-5.69**	-1.11
	14				4.25**
		17 (g)	18 (g)	19 (g)	20 (g)
Yh	16	4.30**	5.11**	3.99**	4.19**
	17		1.01	0.23	0.19
	18			-0.68	-0.77
	19				-0.05
		22 (g)	23 (g)	24 (g)	25 (g)
Hj	21	1.49	-0.92	-3.54**	-3.89**
	22		-2.47*	-5.0**	-5.46**
	23			-2.83**	-3.16**
	24				-0.04
		27 (g)	28 (g)	29 (g)	30 (g)
Jh	26	-1.30	-0.97	-5.09**	-3.41**
	27		0.31	-3.92**	-2.11*
	28			-4.14**	-2.39*
	29				2.06*

Each point represents an average of n = 50 observations.*, ** Significant at P = 0.05 and = 0.01 within each column, respectively.

Table 4. Variance analysis of body weight gain.

Source	Mean square	Pr>F
combination	106290.04	<0.0001
Combination (family)	70372.85	<0.0001

cannot affect directly the body weight gain together (Table 4).

Pearson correlation coefficients and covariance of 4 traits related to growth

The Pearson correlation coefficients (upper triangular) and covariance of four traits (lower triangular) related to growth are showed in Table 5. High correlation was found among the 4 traits. Covariances for the four traits are listed in Table 5. Significant differences were found between traits related to growth based on the complete dataset.

PCA and cluster analysis

The most significant PCs generated from the growth performance data and their statistical loadings in the current study is shown in Table 6. A new set of four orthogonal variables (PCs) was generated by PCA. The first principal component had the highest Eigen value of 2.81 and accounted for 70.31% of the variability in the data set. The second and third PCs (PC2 and PC3) had Eigen values of 0.74 and 0.28 and accounted for 18.5 and 6.9% of the variance in the data, respectively. PC1 describes 70.31% of the variance in the data set, and its loadings indicate that it has high contributions from weight (0.54), thickness (0.53) and height (0.54) variables. PC2 showed a high positive loading for length (0.92); and PC3 was most described by thickness (-0.84). Beside this, PC4 showed a high loading for weight (-0.68)

Table 5. Pearson correlation coefficients and covariance of 4 traits related to growth.

Group	Parameter	Weight	Length	Thickness	Height
All	Weight	7914.74	0.41**	0.74**	0.83**
	Length	1899.94	2717.40	0.45**	0.36**
	Thickness	316.40	113.17	23.22	0.85**
	Height	54974	138.37	26.85	55.85
Hh	Weight	8028.06	0.70**	0.88**	0.90**
	Length	2303.84	1370.31	0.68**	0.65**
	Thickness	379.10	120.50	23.09	0.88**
	Height	626.32	188.31	32.95	60.84
Hj	Weight	6153.42	0.85**	0.69**	0.69**
	Length	1519.88	514.74	0.62**	0.47**
	Thickness	225.43	58.57	17.30	0.66**
	Height	390.41	76.98	19.64	51.65
Hy	Weight	10450.48	0.24**	0.68**	0.90**
	Length	2863.63	13755.67	0.43**	0.24**
	Thickness	420.32	309.30	36.99	0.69**
	Height	742.90	222.99	34.06	64.97
Jh	Weight	6240.86	0.71**	0.77**	0.85**
	Length	1453.19	671.21	0.65**	0.71**
	Thickness	254.95	70.33	17.55	0.84**
	Height	406.70	111.63	21.27	36.64
Jj	Weight	9418.03	0.94**	0.51**	0.43**
	Length	1935.70	453.84	0.57**	0.35**
	Thickness	333.82	82.03	45.30	0.25
	Height	497.62	88.72	20.33	142.82
Jy	Weight	10741.61	0.85**	0.82**	0.90**
	Length	2358.40	715.66	0.76**	0.79**
	Thickness	422.07	101.99	24.89	0.89**
	Height	709.53	160.93	33.60	57.62
Yh	Weight	5665.02	0.85**	0.76**	0.85**
	Length	1288.53	407.70	0.77**	0.83**
	Thickness	200.30	54.67	12.42	0.80**
	Height	392.36	103.01	17.34	37.37
Yj	Weight	4918.62	0.83**	0.65**	0.85**
	Length	1156.53	392.42	0.65**	0.81**
	Thickness	188.17	53.41	16.96	0.77**
	Height	351.47	94.36	18.53	34.55
Yy	Weight	3951.85	0.53**	0.62**	0.52**
	Length	1007.17	898.57	0.27*	0.26*
	Thickness	118.10	24.37	9.04	0.40**
	Height	294.17	70.12	10.57	81.54

Above the diagonal: Phenotypic correlation. Below the diagonal including the diagonal: covariance. *, ** Significant at P = 0.05 and 0.01, respectively.

Table 6. PCA analysis of 4 traits related to the growth in common carp.

Prin	Eigen value	Difference	Proportion	Cumulative	Weight	Length	Thickness	Height
1	2.81220349	2.07189601	0.7031	0.7031	0.544	0.361	0.533	0.538
2	0.74030749	0.46279196	0.1851	0.8881	-0.219	0.921	-0.881	-0.309
3	0.27751553	0.10754204	0.0694	0.9575	0,433	0.126	-0.838	0.307
4	0.16997349		0.0425	1.0000	-0.684	0.072	-0.787	0.722

and height (0.72).

Phylogenetic analysis was done for the 9 combinations with the data of four traits at tagging and harvest. Well-resolved phylogenetic trees for most clades of common carps was created (Figure 1). The cross Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) were found to be monophyletic sister-groups. The predominantly pure bred Jian carp and progeny obtained by reciprocal cross with Heilongjiang carp were shown to be distinct from cross Jian carp (♂) and Heilongjiang carp (♀) associated clades.

Estimates of general, maternal, reciprocal, nonmaternal and specific combining abilities

Estimates of GCA and SCA, and maternal, reciprocal and nonmaternal effect on body weight are listed in Table 7. Estimates of GCA of the 3 genotypes showed that Jian carp was the best combiner for body weight (Table 7). Estimates of SCA from nine crosses for body weight are also presented in Table 7. Two crosses, Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) exhibited high SCA with regard to body weight. Reciprocal, maternal and nonmaternal effects were found to be not significant.

Heterosis of experimental groups of common carp

Heterosis analysis of the experimental groups is showed in Table 8. The result for body weight gain showed that Jian carp can make the Huanghe carp; and Heilongjiang carp had higher parent heterosis by crossing with it. The whole progeny in the F1 group showed the approximate mid parent heterosis. Besides, both Heilongjiang carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Heilongjiang carp (♀) individuals have similar heterosis between parent heterosis and mid parent heterosis.

DISCUSSION

The diallel cross is usually performed to improve growth performance and increase yield and disease resistance (Bakes and Gorda, 1995; Kwaye et al., 2008; Owolade et al., 2009; Wolters and Johnson, 1995). Based on the data of the diallel cross, the strain with highest GCA and SCA can be selected as the best combiner and the most promising specific combiner, respectively (Kwaye et al., 2008). In the present study, complete crosses were carried out in order to identify the combination that exhibited best growth performance.

Differences in body weight between the lines of different groups in terms of growth performances and Pearson correlation coefficients for 4 growth traits

In this study, the complete diallel cross was used to improve growth performance. The mean body weight for the cross Jian carp (♂) and Huanghe carp (♀) was higher than other combinations at harvesting time; although, this difference was not significant; thus, the body weight and body weight gain of Jian carp can be increased by crossing it with Huanghe carp. By crossing with Jian carp, Huanghe carp and Heilongjiang carp have improved body weight compared to their purebred. Differences between families were key for family selection (Casler and Brummer, 2008). Significant differences among families for special combinations indicated that there was considerable genetic variation.

The correlation coefficient between weight and length for purebred Jian carp was greater than that for progeny obtained by cross Jian and Huanghe carp. However, progeny of the Huanghe carp purebred had larger correlation coefficients between weight and thickness, weight and height as compared to crossbred progeny. Notably, the purebred progeny of Heilongjiang carp had lower correlation between length and thickness, length and height.

PCA and cluster analysis

PCA can decrease the number of descriptors associated with the data set analyzed while still explaining the maximum amount of variability present in the data. A new set of four orthogonal variables (PCs) was generated by PCA. The first principal component (PC1) had the highest Eigen value of 2.81. It describes 70.31% of the variance in the data set, and its loadings indicate that it has high contributions from the weight (0.54), thickness (0.53) and height (0.54) variables. Phylogenetic analysis was done for the nine combinations with the data of 4 traits at tagging and harvest showed that different stages produced different trees (data not shown). Hence, data

Table 7. Estimates of general, maternal, reciprocal, non-maternal and specific combining abilities using harvest weight.

Parent			Cross			
Parent	g	M	Cross	s	r	n
J	22.30**	-1.84	Jj	-22.48**		
H	-8.08*	-0.90	Hj	16.86**	-0.94	0.27
Y	-14.23**	2.73	Yj	5.53		-0.27
			Jh	16.86**		
			Hh	-26.00**		
			Yh	9.23		-0.27
			Jy	5.62	-3.77	
			Hy	9.13	-4.17	
			Yy	-14.75**		

g (GCA), general combining ability; s (SCA), specific combining ability; r, reciprocal; m, maternal; N, non-maternal component. *, ** Significant at P = 0.05 and 0.01, respectively.

Table 8. Heterosis of experimental groups of common carp about body weight gain.

Crossbred	Sire heterosis	Dam heterosis	Midparent heterosis
Hj	0.28	0.02	0.13
Hy	0.10	0.10	0.10
Jh	0.03	0.30	0.15
Jy	-0.02	0.24	0.09
Yh	0.12	0.12	0.12
Yj	0.29	0.02	0.14

Midparent and parent heterosis were calculated as [(F1 - MP)/MP] × 100, [(Fl - DP)/DP] × 100, and [(Fl - SP)/SP] × 100, where, F1 is the cross mean, MP is the average mean index of the 2 parents, DP is the mean of the dam parent and SP is the mean of the sire parent.

on length, thickness and height were standardized by weight. Based on this change, three different data can create the same phylogenetic tree. The cross Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) were found to be monophyletic sister-groups.

The pure bred Jian carp and progeny obtained by reciprocal cross with Heilongjiang carp were shown to be distinct from cross Jian carp (♂) and Heilongjiang carp (♀) -associated clades. These results were consisted with the close performances.

Estimates of general, maternal, reciprocal, nonmaternal, and specific combining abilities and heterosis of experimental groups of common carp

Combining ability analysis was used to identify parents with high GCA and referred to the average performance of a parent in hybrid combinations and parental combinations with high SCA (Sprague and Tatum, 1942; Griffing, 1956). In the present study, Jian carp was the best combiner for body weight. It could be used in hybridization programs to exploit heterosis. Other strains (for example, Heilongjiang carp) were not good general combiners but could be used in three- or four-way crosses or for recurrent selection that allows for random crosses. Two crosses, Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀), exhibited higher SCA for body weight because the performance of a parent was relatively better than expected on the basis of the average performance of the other parents involved. These hybrids indicated additive × dominance type gene interactions in terms of expression of traits. The superiority of these crosses may be due to complementary and duplicate gene actions (Girase and Deshmukh, 2000). Therefore, these hybrids are expected to produce desirable segregants and could be exploited successfully in Jian carp improvement programs. Furthermore, Townsend et al. (2013) demonstrated that combining ability as determined by a diallel cross can be used to identify elite parents for the production of improved A. annus hybrids. Devi and Singh (2010) try to find the interralationships among heterosis, molecular diversity and combining ability in short duration maize (Zea mays L.) across the environments.

The result also showed that Jian carp, Huanghe carp and their progeny in the F1 group favored the crossbreeding group Huanghe carp (♂) × Jian carp (♀).

Therefore, we conclude that efforts to improve Jian carp by crossing have practical significance. However, the current research project has documented substantial additive genetic variation with regard to growth traits. Further genetic improvement of growth traits is possible by additive and non-additive genetic breeding. In addition, the following research of interest is expanding and fixing such hybrid vigor.

Conclusions

Of the 6 hybrids obtained in the present study, Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) exhibited heterosis with respect to body weight (harvest weight). Jian carp was the best combiner for body weight. The heterosis of Jian carp (♂) × Huanghe carp (♀) and Huanghe carp (♂) × Jian carp (♀) obtained in this work supply significant implications for the development of breeding programs of common carp.

ACKNOWLEDGEMENTS

This work was supported by grants from the National Non- profit Institute Research Grant of CATAS-TCGRI (2013JBFM14), Key Projects in the National Science & Technology Pillar Program during the twelfth Five-Year Plan Period (2012BAD26B02) , the Earmarked Fund for Modern Agro-industry Technology Research System (CARS-46) and the Natural Science Foundation of Jiangsu Province of China (BK2010164). We thank the students and staff of Aquatic Genetic Laboratory, FFRC for their kind assistance in the study.

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