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Analysis of hybrid combining ability for growth and multiple stress tolerance traits in the Pacific white shrimp, *Litopenaeus vannamei*

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To identify optimal mating combinations for *Litopenaeus vannamei*, a linear mixed model was used to estimate the general combining ability (GCA) and specific combining ability (SCA) for growth and multiple stress tolerance [high salt (35‰), low pH (6 ± 0.1), and high ammonia nitrogen (70 mg/L) co-stress] traits in 47 combinations of *L. vannamei*. The results showed that the SCA in the parents played a dominant role in the offspring traits. The highest GCAs were observed for females of strain O and males of strain B (0.602 and 8.889, respectively), indicating that the dams of strain O and sires of strain B could be used as maternal and paternal lines to increase multiple stress resistance in the next generation. The growth traits of the hybrid combination strain G♂ × strain H♀ exhibited the highest degree of heterosis (9.838%–46.518%) and a generally high SCA (0.643–8.596) among all mating combinations. The SCA was the highest for the strain N♂ × strain O♀ multiple stress tolerance (30.131), while the heterosis for that combination strain was the third-highest. The combinations of strain G♂ × strain H♀ and strain N♂ × strain O♀ can be used as candidate combinations for rapid growth and multiple stress tolerance, respectively.

KEYWORDS

Litopenaeus vannamei, growth traits, multiple stress-tolerance, combining ability, heterosis

Introduction

The Pacific white shrimp, *Litopenaeus vannamei*, is the most commonly farmed shrimp worldwide (Huang et al., 2022). This species was introduced to China in 1988. In 2020, the seawater production of *L. vannamei* in China reached 119.774 × 10^4 t, constituting more than 80.50% of the total national production of marine shrimp aquaculture. *L. vannamei* has thus become the marine shrimp species with the highest level of production in China (Bureau of Fisheries, 2021). Because *L. vannamei* is not a species native to China, most farmed populations are produced using parents imported from abroad or cultured over multiple generations (Lu et al., 2016). The small effective population sizes after multiple generations of culture may pose a risk of decline in important economic traits because of inbreeding (De Donato et al., 2005; Lu et al., 2017a).

Hybridization is one of the effective methods to solve the above problems (Lu et al., 2016), and it is an important way to create variation. Crossbreeding can produce super-parent vigor (obtain heterosis) that the parents never showed (Maluwa and Gjerde, 2006), thereby significantly improving the viability of the progeny. At present, there are many reports of genetic improvement using selective breeding programs in shrimp (Lu et al., 2016; Sui et al., 2016; Lu et al., 2017b; Zhang et al., 2017b; Yuan et al., 2018). This approach has yielded considerable increases in worldwide shrimp production, from 13% in 1993 to 45% in 2008 (Gjedrem, 2012). After only one generation of selection, the selected strain showed 12% greater growth, compared with the control strain (Argue et al., 2002). Nine improved strains of *L. vannamei* have been bred in China, including Kehai No. 1, Zhongxing No. 1, and Xinghai No. 1 (Zhang et al., 2017b; Kong et al., 2020). However, the research and application of cross-breeding in prawns are less (Lu et al., 2016; Kong et al., 2020), and there are more reports on cross-breeding of other aquatic animals. Examples: in abalone (Deng et al., 2008; Deng et al., 2010), clam (Dai et al., 2014; Huo et al., 2015), and oyster (Yao et al., 2015; Yan et al., 2017). Thus, heterosis has not been extensively explored in shrimp, resulting in insufficient utilization of heterosis. Combining ability analysis is important in studies of aquatic animal hybrid breeding, which is an important genetic improvement approach; combining ability analysis is also a prerequisite for the utilization of heterosis (Hedgecock and Davis, 2007). There have been many reports regarding combining abilities in aquatic animals (Deng et al., 2010; Bosworth and Waldbieser, 2014; Costa et al., 2019; Chaivichoo et al., 2020). Chaivichoo et al. (2020) reported that the total combining ability was higher in male catfish than in female catfish 0.25 to 362.64 vs. 0.23 to 190.32, suggesting that the growth performance of a hybrid is largely dependent on additive genetic variation from its male parent, followed by variation from its female parent.

Combining ability analysis is one of the important tasks in the research of aquatic animal hybrid breeding, an important means of genetic improvement, and a prerequisite for the utilization of heterosis (Hedgecock and Davis, 2007). However, there have been few reports regarding the combining ability of *L. vannamei*; published reports have mainly focused on growth and resistance to a single environmental stress factor (Wang et al., 2013; Hu et al., 2016; Wang et al., 2022), Wang et al. (2022) found P♂ × XH♀ combination had obvious heterosis in growth and high salt tolerance traits. Therefore, the application of the combination in breeding and production shall be promoted in the future. However, in real-world aquaculture production, shrimp usually experience stress from multiple environmental factors. For example, intensive high-density shrimp farming has become increasingly common; however, this approach increases ammonia nitrogen content and reduces pH in the aquaculture water environment (Zhou et al., 2009; Yuan et al., 2018). Ammonia nitrogen concentrations as high as 46.11 mg/L have been reported in the late stage of high-density shrimp farming (Chen et al., 1988). In addition, high temperatures in summer lead to increased salinity in aquaculture water (Colombani et al., 2017). The above changes in water quality indicators are likely to simultaneously expose shrimp to multiple stresses of high ammonia nitrogen, low pH, and high salt concentration. In water with a high ammonia nitrogen content, low pH, or high salinity, shrimp survival should be could lead to reduced because of slow growth, decreased immunity, and increased pathogen susceptibility (Pillai and Diwan, 2002; Ye et al., 2009; Cui et al., 2017; Joseph and Philip, 2020; Yu et al., 2020). Compared with a single stressor, exposure to multiple stresses may be more harmful to shrimp. The genetic parameters of shrimp resistance to multiple stresses have not yet been identified. Thus, there is a need to investigate the combining ability for multiple stress tolerance in *L. vannamei*.

This study was performed to analyze the combining ability and heterosis of growth and multiple stress tolerance traits in *L. vannamei*. The findings will provide insights regarding crossbreeding and stress resistance breeding of *L. vannamei*; they will also help to improve growth and stress resistance traits in this species.

Materials and methods

All shrimps used in this study were from the experimental base of the Zhanjiang Guoxing Aquatic Technology Co., Ltd. (Zhanjiang City, Guangdong Province, China). All animal experimental procedures for the current study were approved by Animal Ethical and Welfare Committee of Guangdong Ocean University, China.

Origin of the base population and rearing

In 2019, five populations (four imported and one cultured) were collected and shipped to Zhanjiang Guoxing Aquatic Technology Co., Ltd. The four imported populations were from Thailand (strains W and L) and the USA (strains K and M); the farmed population was *L. vannamei* Xinghai No. 1, cultivated in our laboratory for six consecutive generations. The core group of new varieties (GX: including six different strains) reached 10 generations by 2021; the above 10 strains had 24 parents, which were used to construct 47 combinations (Table 1).

TABLE 1 Incomplete diallel crosses of 24 parents of *L. vannamei*.

Parents	A♂	B♂	C♂	D♂	E♂	F♂	G♂	H♂	I♂	J♂	K♂	L♂	M♂	N♂	O♂	P♂	Q♂	R♂	S♂	T♂	U♂	V♂	W♂	X♂
A♀	1	1																						
B♀		1		1											1									
C♀			1																					
D♀		2		1	1		2							1										
E♀	1				1						1												1	
F♀						1																		
G♀							2																	
H♀							1	1																
I♀			1						1															
J♀										2														
K♀					3						1					1		1						
L♀												3												
M♀	1												2											
N♀			1	1										1										
O♀		1												1	1									
P♀							1									1		1						
Q♀					1												2							
R♀																1		2						
S♀																								
T♀																				1				
U♀																					2			
V♀																						1		
W♀																							1	
X♀																								1
Total	3	5	3	3	6	1	6	1	1	2	2	3	2	3	2	3	2	5		1	2	1	2	1

All populations were kept separately at a stocking density of eight individuals per square meter in a 25-m^2 concrete pond. Two months before the spawning season, using body weight as the criterion, the top 30% of the females (100 individuals) and top 15% of the males (50 individuals) were selected as broodstock from each population. The selected shrimp were individually tagged by numbered rings placed on one ocular peduncle and were raised in concrete tanks, with males and females placed in separate ponds for condition. During the acclimation period, male and female broodstock were fed a condition diet of frozen squid, oysters, artemia, and bloodworms to accelerate the gonadal maturation process (Zhang et al., 2017a). Families were produced by an incomplete diallel cross, mature females of each population were selected and transferred into the pond where male broodstock of a single population was placed for mating, a total of 60 families (47 combinations) were obtained. Mated females were place in individual 500-L tanks for spawning. After hatched, approximately 3500 were randomly selected and cultivated in nursery buckets to postlarval stage 15 (PL15); they were then moved to an independent cement pond for culture and were fed a mixed diet of Chaetoceros and Aremia. When the shrimp reached 3cm length, in total, 383 shrimp were randomly selected from each combination for fluorescent labeling (two visible implant elastomer VIE tags were employed either on the left or right-hand side of the first and sixth segments); all labeled shrimp were placed in a pond measuring 13 m × 15 m × 1 m in length, width, and height, respectively, in the common environment for 60 days, all individuals in the pond were reared under standard commercial conditions during the growth-out phase and were feed with commercial prawn pellet containing 40% crude protein. The pond had a water exchange rate of 15–30% of the total water volume per day (Zhang et al., 2017a; Zhang et al., 2017b; Yuan et al., 2018).

Multiple-stress experiment

In 2019, Zhanjiang Guoxing Aquatic Products Technology Co., Ltd. monitored the bottom water quality indicators of the pond used for *L. vannamei* aquaculture.

The upper limit of salinity was 35‰, and the nadir pH was 6. In a previous study (Yuan et al., 2018), we determined that the median lethal concentration (LC_{50}) of ammonia nitrogen for *L. vannamei* (at PL15) was 120 mg/L for 48 h. We set the high salinity and low pH conditions to 35‰ and pH 6 ± 0.1, respectively. Reduce the LC_{50} (120 mg/L) for 48 h under high ammonia nitrogen stress by half (60 mg/L), and then decrease in the direction of 1 mg/L or increase in the direction of 120 mg/L at intervals of 1 mg/L, and can be divided into 120 gradients. A group of experiments is difficult to complete, divided into 40 gradients as a group (total, 3 groups). Group 1: salinity and pH constant at 35‰ and 6 ± 0.1, ammonia nitrogen concentration decreased from 60mg/L by 20 (60, 59, 58, 57, 56, 55, 54, 53, 52, 51, 50, 49, 48, 47, 46, 45, 44, 43, 42, 41mg/L); ammonia nitrogen concentration increased by 20 from 60mg/L (61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80 mg/L). Groups 2 and 3 pre-experiments will continue to be added or subtracted in the future.

The materials used for high salt, low pH, and high ammonia nitrogen measurements were coarse salt (Salinity Meter Refractometer, HT211ATC), 1 mg/L HCl, 1 mg/L NaOH (Duan et al., 2019) (High-Precision pH Test Pen, ATC), and NH4Cl analytical pure crystals (water quality analyzer). In a preliminary experiment, three replicates (30 shrimp per replicate) per gradient were placed in the adjusted experimental seawater. Because low pH in a water column slowly returns to normal, the experimental seawater pH was adjusted at 2-h intervals and deaths were counted. The dissolved oxygen content was maintained at > 6.0 mg/L. At a salinity of 35‰, pH of 6 ± 0.1, and ammonia nitrogen level of 70 mg/L (because the concentration of multiple-stress was found in group 1 of pre-experiments, we didn't need to proceed to group 2 and group 3 of pre-experiments), the median lethal time (LT50) was 47.31 h (close to 48 h). Therefore, we used a salt concentration of 35‰, pH of 6 ± 0.1, and ammonia nitrogen concentration of 70 mg/L in the multiple stress experiment.

The multiple stress [simultaneous high salt (35‰), low pH (6 ± 0.1), and high ammonia nitrogen (70 mg/L) stress] experiment was designed based on findings in the preliminary experiment. The seawater concentration was adjusted to the multiple stress concentration. Sixty fishing nets were placed in cement ponds (width, length, and height of 5 m × 8 m × 1 m, respectively); 30 experimental shrimp were randomly selected from each family (Zhang et al., 2017a; Dong, 2018; Liu et al., 2019; Li et al., 2021) and placed into fishing nets (pool water level, 30 cm). The experimental seawater pH was adjusted at 2-h intervals. The number of deaths was counted, the survival time (ST) was recorded, and growth-related traits were measured. An analytical balance (0.01-g accuracy) connected to a computer was used to automatically determine body weight (BW). Shrimp were photographed using a digital camera; total length (TL), body length (BL), carapace length (CL), carapace width (CW), and abdomen length (AL) measurements were performed using ImageJ (NIH). The experiment ended when all shrimp had died.

Statistical analyses

We used the following analytical model for combining growth ability and integrated stress tolerance traits (Bosworth and Waldbieser, 2014; Tran et al., 2021):

$$y_{ijk} = \mu + g_i + g_j + s_{ij} + Age_k + Sex_k + e_{ijk} \tag{1}$$

Where y_{ijk} is the trait value of the k-th hybrid offspring, μ is the population mean, g_i is the general combining ability (GCA) of the i-th parent, g_j is the GCA of the j-th maternal line, s_{ij} is the specific combining ability (SCA) of the i-th sire crossed with the j-th dam, Age_k is the age covariate, $Sex_k$is the sex fixed effect, and e_{ijk} is the random error effect. Variance component division and combining ability estimation were performed using ASReml4 software (Butler et al., 2017).

We used the following heterosis formula for growth and combined stress tolerance traits (Lu et al., 2016):

$$H(\%) = \frac{F_1 - 1/2(P_1 + P_2)}{1/2(P_1 + P_2)} \tag{2}$$

Where F_1, P_1, and P_2 represent the first generation of reciprocal offspring of parent 1 and parent 2, the mean value of inbred offspring of parent 1, and the mean value of the representative type of inbred offspring of parent 2, respectively; *H* (%) is the reciprocal offspring heterosis rate.

In this study, it was difficult to distinguish between males and females at the time of the experiment. Furthermore, the model did not converge after the addition of the fixed effect of sex. Therefore, we removed the sex-fixed effect from the model in our analysis.

Results

GCA of *L. vannamei* parents

The GCAs for each trait of *L. vannamei* are shown in Table 2. The GCAs for six growth traits (BW, TL, BL, CL, CW, and AL) and multiple stress tolerance traits in female parents ranged from -2.088×10^{-6} to 3.210×10^{-6} and from −0.531 to 0.602, respectively; those values in male parents ranged from -9.061×10^{-6} to 1.298×10^{-5} and from −8.755 to 8.889, respectively. Thus, the GCAs for the six growth traits in male and female parents were close to 0. The highest GCAs were observed for females of strain O and males of strain B (0.602 and 8.889, respectively), indicating that they were resistant to multiple stressors.

SCAs of the mating combinations of *L. vannamei*

The SCAs for growth and integrated stress tolerance traits in the offspring of 47 combinations of *L. vannamei* are shown in

TABLE 2 General combining ability for seven traits in *L. vannamei* at 15 week old.

Parents		General combining ability						
		BW(g)	TL (mm)	BL (mm)	CL (mm)	CW (mm)	AL (mm)	ST (h)
Dam	A	9.655×10^{-8}	9.055×10^{-8}	8.452×10^{-8}	2.517×10^{-7}	2.095×10^{-6}	7.554×10^{-8}	0.127
	B	-1.266×10^{-7}	-2.938×10^{-7}	-2.683×10^{-7}	-1.369×10^{-7}	-9.583×10^{-7}	-2.296×10^{-7}	0.322
	C	1.149×10^{-7}	3.337×10^{-7}	3.000×10^{-7}	1.040×10^{-7}	7.251×10^{-7}	2.552×10^{-7}	0.277
	D	-1.975×10^{-7}	-2.885×10^{-7}	-2.594×10^{-7}	-1.378×10^{-7}	-1.278×10^{-6}	-2.305×10^{-7}	-0.050
	E	4.871×10^{-8}	1.263×10^{-7}	1.186×10^{-7}	8.016×10^{-9}	-9.326×10^{-8}	9.616×10^{-8}	0.178
	F	1.456×10^{-7}	3.723×10^{-7}	3.350×10^{-7}	3.963×10^{-7}	2.921×10^{-6}	2.906×10^{-7}	0.139
	G	-1.721×10^{-8}	4.183×10^{-8}	3.278×10^{-8}	5.282×10^{-9}	-3.530×10^{-8}	2.489×10^{-8}	0.069
	H	2.525×10^{-7}	6.125×10^{-7}	5.531×10^{-7}	1.874×10^{-7}	1.361×10^{-6}	4.762×10^{-7}	-0.076
	I	-1.540×10^{-7}	-3.651×10^{-7}	-3.270×10^{-7}	-1.349×10^{-7}	-1.098×10^{-6}	-2.856×10^{-7}	-0.134
	J	-2.011×10^{-7}	-6.503×10^{-7}	-5.885×10^{-7}	-2.421×10^{-7}	-1.551×10^{-6}	-4.987×10^{-7}	0.164
	K	-2.270×10^{-7}	-5.779×10^{-7}	-5.267×10^{-7}	-2.464×10^{-7}	-1.776×10^{-6}	-4.484×10^{-7}	-0.531
	L	-1.082×10^{-7}	-2.066×10^{-7}	-1.845×10^{-7}	-7.262×10^{-8}	-6.469×10^{-7}	-1.627×10^{-7}	0.047
	M	-1.119×10^{-7}	-2.908×10^{-7}	-2.525×10^{-7}	-1.261×10^{-7}	-8.713×10^{-7}	-2.115×10^{-7}	-0.140
	N	8.354×10^{-8}	3.004×10^{-7}	2.746×10^{-7}	6.906×10^{-8}	3.470×10^{-7}	2.335×10^{-7}	0.362
	O	-3.005×10^{-7}	-7.429×10^{-7}	-6.609×10^{-7}	-2.703×10^{-7}	-2.088×10^{-6}	-5.720×10^{-7}	0.602
	P	7.300×10^{-7}	1.388×10^{-6}	1.256×10^{-6}	3.793×10^{-7}	3.210×10^{-6}	1.105×10^{-6}	-0.109
	Q	1.171×10^{-7}	3.848×10^{-7}	3.393×10^{-7}	1.059×10^{-7}	7.025×10^{-7}	2.882×10^{-7}	-0.415
	R	2.097×10^{-7}	6.440×10^{-7}	5.715×10^{-7}	1.869×10^{-7}	1.319×10^{-6}	4.912×10^{-7}	-0.193
	T	2.788×10^{-8}	8.933×10^{-8}	7.028×10^{-8}	-3.582×10^{-9}	-1.361×10^{-8}	6.913×10^{-8}	-0.077
	U	-2.365×10^{-7}	-6.518×10^{-7}	-5.824×10^{-7}	-2.043×10^{-7}	-1.198×10^{-6}	-5.113×10^{-7}	0.010
	V	-7.129×10^{-8}	-9.921×10^{-8}	-9.085×10^{-8}	-4.576×10^{-8}	-4.053×10^{-7}	-7.791×10^{-8}	-0.327
	W	-1.392×10^{-8}	-1.663×10^{-8}	-1.854×10^{-8}	-8.064×10^{-9}	-1.545×10^{-7}	-2.120×10^{-8}	0.061
	X	-6.086×10^{-8}	-2.005×10^{-7}	-1.757×10^{-7}	-6.503×10^{-8}	-5.127×10^{-7}	-1.566×10^{-7}	-0.307
Sire	A	8.739×10^{-7}	2.133×10^{-7}	2.015×10^{-7}	1.392×10^{-6}	2.613×10^{-6}	2.487×10^{-6}	-0.609*
	B	-1.076×10^{-6}	-3.555×10^{-7}	-3.140×10^{-7}	-7.161×10^{-7}	-1.538×10^{-6}	-4.075×10^{-6}	8.889
	C	-1.468×10^{-6}	-5.006×10^{-7}	-4.345×10^{-7}	-9.445×10^{-7}	-1.941×10^{-6}	-5.517×10^{-6}	8.416
	D	1.817×10^{-6}	7.665×10^{-7}	6.765×10^{-7}	1.152×10^{-6}	1.980×10^{-6}	8.455×10^{-6}	1.060*
	E	-2.074×10^{-6}	-6.551×10^{-7}	-5.844×10^{-7}	-1.274×10^{-6}	-2.621×10^{-6}	-7.401×10^{-6}	1.286*
	F	8.167×10^{-7}	3.337×10^{-7}	2.936×10^{-7}	1.820×10^{-6}	3.224×10^{-6}	3.707×10^{-6}	3.000
	G	1.729×10^{-7}	-3.376×10^{-8}	-3.544×10^{-8}	-3.049×10^{-7}	-5.063×10^{-7}	-3.614×10^{-7}	-6.028**
	H	-9.343×10^{-7}	-3.144×10^{-7}	-2.738×10^{-7}	-5.555×10^{-7}	-1.119×10^{-6}	-3.465×10^{-6}	3.726
	I	2.728×10^{-7}	1.009×10^{-7}	8.989×10^{-8}	1.032×10^{-7}	2.447×10^{-7}	1.149×10^{-6}	1.319*
	J	-1.128×10^{-6}	-5.827×10^{-7}	-5.158×10^{-7}	-1.112×10^{-6}	-1.712×10^{-6}	6.363×10^{-6}	3.553
	K	3.375×10^{-7}	1.815×10^{-8}	1.860×10^{-8}	-2.116×10^{-7}	-3.578×10^{-8}	4.382×10^{-7}	0.209*
	L	-6.070×10^{-7}	-1.852×10^{-7}	-1.617×10^{-7}	-3.335×10^{-7}	-7.141×10^{-7}	-2.075×10^{-6}	1.009*
	M	-2.030×10^{-6}	-8.271×10^{-7}	-7.283×10^{-7}	-1.490×10^{-6}	-2.584×10^{-6}	-9.061×10^{-6}	2.865
	N	1.150×10^{-6}	5.622×10^{-7}	4.903×10^{-7}	8.224×10^{-7}	1.386×10^{-6}	6.093×10^{-6}	5.103
	O	-1.517×10^{-6}	-7.010×10^{-7}	-6.124×10^{-7}	-1.364×10^{-6}	-2.203×10^{-6}	-7.564×10^{-6}	5.066
	P	3.036×10^{-6}	1.174×10^{-6}	1.029×10^{-6}	1.752×10^{-6}	3.195×10^{-6}	1.298×10^{-5}	-8.755**
	Q	4.261×10^{-7}	2.144×10^{-7}	1.866×10^{-7}	3.317×10^{-7}	5.233×10^{-7}	2.284×10^{-6}	-3.220*
	R	2.300×10^{-6}	9.151×10^{-7}	8.049×10^{-7}	1.408×10^{-6}	2.441×10^{-6}	1.005×10^{-5}	-4.840**
	T	1.564×10^{-7}	8.006×10^{-8}	6.160×10^{-8}	-1.645×10^{-8}	-1.503×10^{-8}	8.819×10^{-7}	-1.671*
	U	-1.327×10^{-6}	-5.842×10^{-7}	-5.105×10^{-7}	-9.380×10^{-7}	-1.322×10^{-6}	-6.523×10^{-6}	0.222*
	V	-4.000×10^{-7}	-8.892×10^{-8}	-7.962×10^{-8}	-2.101×10^{-7}	-4.474×10^{-7}	-9.940×10^{-7}	-7.070**
	W	1.543×10^{-6}	6.303×10^{-7}	5.523×10^{-7}	9.879×10^{-7}	1.718×10^{-6}	6.870×10^{-6}	-6.878**
	X	-3.414×10^{-7}	-1.797×10^{-7}	-1.540×10^{-7}	-2.986×10^{-7}	-5.659×10^{-7}	-1.998×10^{-6}	-6.650**

BW, body weight; TL, total length; BL, body length; CL, carapace length; CW, carapace width; AL, abdomen length; ST, survival time. The symbols * and ** indicate significance at 0.05 and 0.01 probabilities, respectively.

Table 3. The highest SCA-ranked combinations for six growth traits (BW, TL, BL, CL, CW, and AL) of 47 combinations were: R♂ × P♀ (3.023), R♂ × P♀ (9.725), R♂ × P♀ (8.685), F♂ × F♀ (1.707), F♂ × F♀ (0.791), and R♂ × P♀ (7.216), respectively. The combinations with the second-highest SCA values were G♂ × H♀ (2.572), G♂ × H♀ (8.596), G♂ × H♀ (7.648), R♂ × P♀ (1.466), R♂ × P♀ (0.716), and G♂ × H♀ (6.344), respectively. The ratios of GCA variance to phenotypic variance for parental growth and multiple stress tolerance traits ranged from 1.006×10^{-6}% to 4.536×10^{-5}% and from 0.253% to 6.502%, respectively. The ratios of variance of the SCA to the phenotypic variance of the growth and multiple stress tolerance traits of the parents were 10.125% to 11.351% and 6.502%, respectively. In addition, the ratio of GCA variance to the phenotypic variance was less for the female parent (0.253%) than for the male parent (Table 4). And the parental P-value ranged from 2.69×10^{-63} to 2.19×10^{-6}(Table 4).

Heterosis of growth and integrated stress tolerance traits in *L. vannamei* hybrid combinations

Figure 1 shows growth and multiple stress tolerance heterosis in *L. vannamei*. The heterosis ranges of seven traits (BW, TL, BL, CL, CW, AL, and multiple stress tolerance) in 24 hybrid combinations were −18.977% to 46.518%, −7.508% to 15.288%, −7.483% to 15.214%, −4.815% to 9.838%, −5.504% to 10.964%, −8.408% to 17.116%, and −50.42517% to 68.462%, respectively. In terms of BW, TL, BL, CL, CW, and AL, heterosis was highest in the combination G♂ × H♀: 46.518%, 15.288%, 15.214%, 9.838%, 10.964%, and 17.116%, respectively. The three best combinations of heterosis were R♂ × P♀ (68.462%), P♂ × R♀ (43.077%), and N♂ × O♀ (24.500%). In addition, the heterosis of seven traits in 24 hybrid combinations had both positive and negative values, indicating that heterosis could be obtained by crossing and that harmful alleles can be exposed by hybridization.

Discussions

General combining abilities

Combining ability includes GCA (general combining ability) and SCA(Specific combining ability) (Hayman, 1957; Costa et al., 2019). GCA represents the average performance of parental lines in hybrid combinations, which is mainly improved by pure propagation; it provides information concerning the magnitude of additive genetic effects, which can be used to identify superior parents in breeding programs. High positive GCA values contribute to increased character expression, while negative values tend to have a reducing effect (Hayman, 1957; Eisen et al., 1983). To our knowledge, this is the first attempt to analyze the combining ability for multiple stress tolerance traits in *L. vannamei*. Our results showed that the GCAs of O strain females and B strain males were highest (0.602 and 8.889, respectively). Thus, females of strain O and males of strain B could be used as the maternal and paternal lines, respectively, to increase multiple stress resistance in the next generation. The GCAs for six growth traits (BW, TL, BL, CL, CW, and AL) in male and female parents ranged from -9.061×10^{-6} to 1.298×10^{-5} and from -2.088×10^{-6} to 3.210×10^{-6}, respectively; these values were close to 0. Similar results were previously reported for agricultural papaya (Eisen et al., 1983), maize (Khamphasan et al., 2020), cotton (Hinze et al., 2011), rice, and tilapia (Lin et al., 2016), where the traits had GCAs of 0 or close to 0. The observation of a GCA close to 0 for the growth traits of *L. vannamei* indicated that there is little potential for continued selection to achieve genetic improvement; crossbreeding should be performed in combination with the results of SCA for strain improvement.

Specific combining ability

SCA refers to the heterosis between two specific populations that exceed the GCA. Nonadditive effects can be measured using the SCA to determine the presence of epistasis and heterosis. Our results showed that the highest SCA-ranked combinations for six growth traits (BW, TL, BL, CL, CW, and AL) of 47 combinations were: R♂ × P♀ (3.023), R♂ × P♀ (9.725), R♂ × P♀ (8.685), F♂ × F♀ (1.707), F♂ × F♀ (0.791), and R♂ × P♀ (7.216), respectively. The combinations with the second-highest SCA values were G♂ × H♀ (2.572), G♂ × H♀ (8.596), G♂ × H♀ (7.648), R♂ × P♀ (1.466), R♂ × P♀ (0.716), and G♂ × H♀ (6.344), respectively. Among the 47 combinations, the highest SCA for multiple stress tolerance was observed for N♂ × O♀ (30.131). These results indicate that R♂ × P♀, G♂ × H♀, and F♂ × F♀ could be used as candidate mating combinations to obtain offspring with high growth rates. The combination N♂ × O♀ was selected as the candidate mating combination for the offspring with multiple stress tolerance. In addition, the ratios of the GCA variance to phenotypic variance for parental growth and multiple stress tolerance traits ranged from 1.006×10^{-6}% to 4.536×10^{-5}% and from 0.253% to 6.502%, respectively. The ratios of variance of the SCA to the phenotypic variance of the growth and multiple stress tolerance traits of the parents were from 10.125% to 11.351% and 6.502%, respectively. Moreover, the ratio of the GCA variance to the phenotypic variance was less for the female parent (0.253%) than for the male parent. These observations indicate that the parental SCA played a dominant role in progeny trait performance, and the paternal effect greatly affected the multiple stress tolerance. The dominant role of SCA in the growth and multiple stress tolerance indicates that the *L. vannamei* population has high heterosis, rich genetic diversity, and unstable genetic variation; thus, this

TABLE 3 SCAs for 47 combinations of *L. vannamei* at 15 week old.

Combination	Specific combining ability						
	BW (g)	TL (mm)	BL (mm)	CL (mm)	CW (mm)	AL (mm)	ST (h)
A♂×A♀	-0.261	-1.809	-1.607	0.725	0.385	-1.321	2.700
A♂×E♀	-0.317	-1.707	-1.473	-0.273	-0.142	-1.257	18.417
A♂×M♀	1.535	5.640	5.111	0.855	0.398	4.231	-23.553*
B♂×A♀	0.854	2.617	2.354	0.360	0.183	1.961	8.314
B♂×B♀	-1.321*	-4.140*	-3.733*	-0.676*	-0.356*	-3.127*	13.349
B♂×D♀	-0.140	-0.353	-0.312	-0.090	-0.050	-0.278	-0.103
B♂×O♀	-0.570*	-1.664	-1.475	-0.265	-0.155	-1.266	14.011
C♂×C♀	0.705	2.978	2.650	0.448	0.196	2.165	24.007
C♂×I♀	-1.244*	-4.263*	-3.796*	-0.678*	-0.358*	-3.187*	-16.895
C♂×N♀	-1.068*	-3.700*	-3.234*	-0.656*	-0.315*	-2.646	26.567
D♂×B♀	1.159	4.475	3.976	0.661	0.313	3.284	2.273
D♂×D♀	-0.846*	-2.724	-2.381	-0.473*	-0.240*	-1.971	11.325
D♂×N♀	1.675	5.882	5.225	0.892	0.414	4.310	-9.357
E♂×D♀	0.285	1.699	1.496	0.226	0.093	1.226	13.572
E♂×E♀	-1.077*	-3.115*	-2.757*	-0.516*	-0.280*	-2.305	26.979
E♂×K♀	-1.730**	-6.405*	-5.748*	-1.051*	-0.518	-4.768*	-12.388
E♂×Q♀	0.252	1.299	1.117	0.145	0.062	0.926	-23.019*
F♂×F♀	0.894	3.322	2.960	1.707	0.791	2.465	12.005
G♂×D♀	-2.093**	-7.238**	-6.406**	-1.162**	-0.581**	-5.319*	-5.242
G♂×G♀	-0.106	0.373	0.290	0.023	-0.010	0.211	5.953
G♂×H♀	2.572	8.596	7.648	1.328	0.643	6.344	-21.509*
G♂×P♀	-0.184	-2.068	-1.889	-0.475*	-0.177	-1.476	-3.323
H♂×H♀	-1.022*	-3.130*	-2.761*	-0.521*	-0.275*	-2.304	14.908
I♂×I♀	0.299	1.004	0.906	0.097	0.060	0.764	5.277
J♂×J♀	-1.234*	-5.803*	-5.200*	-1.043*	-0.420*	-4.231*	14.218
K♂×E♀	-0.081	-0.475	-0.455	-0.138	-0.067	-0.371	2.821
K♂×K♀	0.450	0.656	0.643	-0.061	0.058*	0.662	-1.984
L♂×L♀	-0.664*	-1.844	-1.631	-0.313	-0.175	-1.380	4.036
M♂×M♀	-2.221**	-8.235**	-7.343**	-1.398**	-0.634**	-6.025**	11.463
N♂×D♀	1.583	6.042	5.312	0.905	0.431	4.387	-23.868*
N♂×N♀	-0.095	0.499	0.435	0.062	-0.005	0.325	14.158
N♂×O♀	-0.230	-0.943	-0.804	-0.196	-0.087	-0.661	30.131
O♂×B♀	-0.615*	-2.956*	-2.614*	-0.576*	-0.216*	-2.105	12.266
O♂×O♀	-1.045*	-4.023*	-3.561*	-0.704*	-0.324*	-2.925*	8.004
P♂×K♀	-0.058	0.527	0.404	0.034	-0.003	0.321	-22.506*
P♂×P♀	1.641	4.733	4.302	0.644	0.330	3.630	-14.921
P♂×R♀	1.739	6.426	5.667	0.966	0.457	4.678	2.393
Q♂×Q♀	0.466	2.135	1.881	0.311	0.128	1.519	-12.886
R♂×K♀	-0.055	0.066	0.047	0.016	-0.018	-0.019	-9.118
R♂×P♀	3.023	9.725	8.685	1.466	0.716	7.216	8.834
R♂×R♀	-0.452	-0.679	-0.617	-0.161	-0.099	-0.511	-19.086*
T♂×T♀	0.171	0.797	0.621	-0.015	-0.004	0.586	-6.685
U♂×U♀	-1.451*	-5.816*	-5.147*	-0.880*	-0.324*	-4.337*	0.887
V♂×V♀	-0.438	-0.885	-0.803	-0.197	-0.110	-0.661	-28.293*
W♂×E♀	1.774	6.424	5.732	0.961	0.463	4.748	-32.799*
W♂×W♀	-0.086	-0.148	-0.164	-0.035	-0.042	-0.180	5.278
X♂×X♀	-0.374	-1.789	-1.553	-0.280	-0.139	-1.329	-26.612*

BW, TL, BL, CL, CW, AL, ST: see legend in Table 2. The symbols * and ** indicate significance at 0.05 and 0.01 probabilities, respectively.

TABLE 4 Variance components of combining ability for growth and multiple stress tolerance traits in *L. vannamei.*.

Variances		**Traits**						
		BW (g)	**TL (mm)**	**BL (mm)**	**CL (mm)**	**CW (mm)**	**AL (mm)**	**ST (h)**
Dam	Variance of GCA (σ^2_{GCA})	2.870×10^{-7}	2.485×10^{-6}	1.988×10^{-6}	1.448×10^{-7}	5.197×10^{-7}	1.421×10^{-6}	3.243
	Variance ratio of GCA ($\sigma^2_{GCA}/\sigma^2_P$)	1.673×10^{-6}%	1.135×10^{-6}%	1.148×10^{-6}%	2.635×10^{-6}%	4.109×10^{-5}%	1.197×10^{-6}%	0.253%
	P-value	2.19×10^{-6}	1.44×10^{-6}	1.41×10^{-6}	1.75×10^{-11}	2.57×10^{-10}	1.24×10^{-6}	3.55×10^{-59}
Sire	Variance of GCA (σ^2_{GCA})	1.609×10^{-6}	2.227×10^{-6}	1.742×10^{-6}	6.649×10^{-7}	5.737×10^{-7}	1.812×10^{-5}	83.264
	Variance ratio of GCA . ($\sigma^2_{GCA}/\sigma^2_P$).	9.383×10^{-6}%	1.017×10^{-6}%	1.006×10^{-6}%	1.210×10^{-5}%	4.536×10^{-5}%	1.527×10^{-5}%	6.502%
	P-value	2.06×10^{-10}	6.06×10^{-12}	5.78×10^{-12}	1.04×10^{-17}	1.37×10^{-15}	7.14×10^{-12}	2.69×10^{-63}
Variance of SCA (σ^2_{SCA})		1.761	22.174	17.564	0.624	0.141	12.050	331.278
Variance ratio of SCA ($\sigma^2_{SCA}/\sigma^2_P$)		10.265%	10.125%	10.143%	11.351%	11.132%	10.151%	25.870%
Phenotypic variance (σ^2_P)		17.157	218.994	173.160	5.495	1.265	118.712	1280.523

BW, TL, BL, CL, CW, AL, ST: see legend in Table 2.

population is suitable for cross-breeding. Studies on aquatic animals, such as catfish (Bosworth and Waldbieser, 2014), salmon (Vandeputte et al., 2002), rainbow trout (Henryon et al., 2002), sea bass (Wang et al., 2006), and Atlantic cod (Tosh et al., 2010), have shown that the breeding traits of the progeny can be markedly influenced by the maternal genetic effects. This is in contrast to that noted in the present results. However, a previous study showed that the paternal effect was greater than the maternal effect in terms of breeding traits in the sea cucumber (Liu, 2015), tilapia (Tang et al., 2015), and *Sinonovacula constricta* (Li, 2018).

Analysis of heterosis for growth and integrated stress tolerance traits

Heterosis is a phenomenon in which the progeny of a parental cross of two different populations is superior to its parents in terms of reproduction, survival, and growth (Burke and Arnold, 2001; Hua et al., 2003; Hochholdinger and Hoecker, 2007). In commercial production environments, heterosis is analyzed to evaluate the feasibilities of various hybridization schemes. In the present study, the heterosis of 7 traits (BW, TL, BL, CL, CW, AL, and ST) in 24 hybrid combinations had positive and negative values ranging from −18.977% to 46.518%, −7.508% to 15.288%, −7.483% to 15.214%, −4.815% to 9.838%, −5.504% to 10.964%, −8.408% to 17.116%, and −50.42517% to 68.462%, respectively. Therefore, hybridization led to both heterosis and exposure to harmful alleles. This was consistent with the results of a previous study (Lu et al., 2016), in which the heterosis (−13.36% to 13.80%) of the body weight of *L. vannamei* had both positive and negative values. Similar results have been reported in aquatic animals, such as bighead carp growth and survival (−55.9% to 13.8%) (Duong et al., 2022) and abalone growth and survival (−10.8% to 41.4%) (Li et al., 2017). Lu et al. (2016) suggested that a large amount of heterosis may be caused by the accumulation of favorable dominant alleles or dominant alleles that masking recessive deleterious alleles in hybrids. From the perspective that inbreeding exposes harmful genes, heterosis is only a compensation for the decline caused by inbreeding (i.e., a hybrid progeny does not show any advantages but may show disadvantages) (Tian et al., 2007; Yuan et al., 2015). Dunham (2011) argued that crosses between wild and farmed (domesticated) strains could result in positive heterosis, outbreeding suppression (or negative heterosis), or moderate heterosis. In general, crosses can provide information concerning the frequency of heterozygotes among progenies, produce a degree of heterosis, and can help to alleviate inbreeding decline.

In addition, this study identified a hybrid combination of G♂ × H♀, which generally has high SCAs for BW (2.572), TL (8.596), BL (7.648), and AL (6.344). The combination of six growth traits [BW (46.518%), TL (15.288%), BL (15.214%), CL (9.838%), CW (10.964%), and heterosis of AL (17.116%)] for G♂ × H♀ was the highest among all combinations. The SCA for the hybrid combination N♂ × O♀ (30.131) was the highest, while it's heterosis (24.500%) was the third-highest. Thus, the combination G♂ × H♀ can be used to achieve rapid growth, while N♂ × O♀ can be used to achieve multiple stress tolerance.

Conclusion

In this study, the parental model was used to analyze the GCA and SCA among six *L. vannamei* germplasm populations; heterosis was analyzed in each population. The results showed that the growth and multiple stress tolerance performance of the hybrid offspring were mainly affected by the parental SCA, which implies that the effect of genetic improvement through cross-breeding will be better. Strain O females and strain B males can serve as the maternal and paternal parental lines for the next generation to achieve multiple stress resistance. The growth

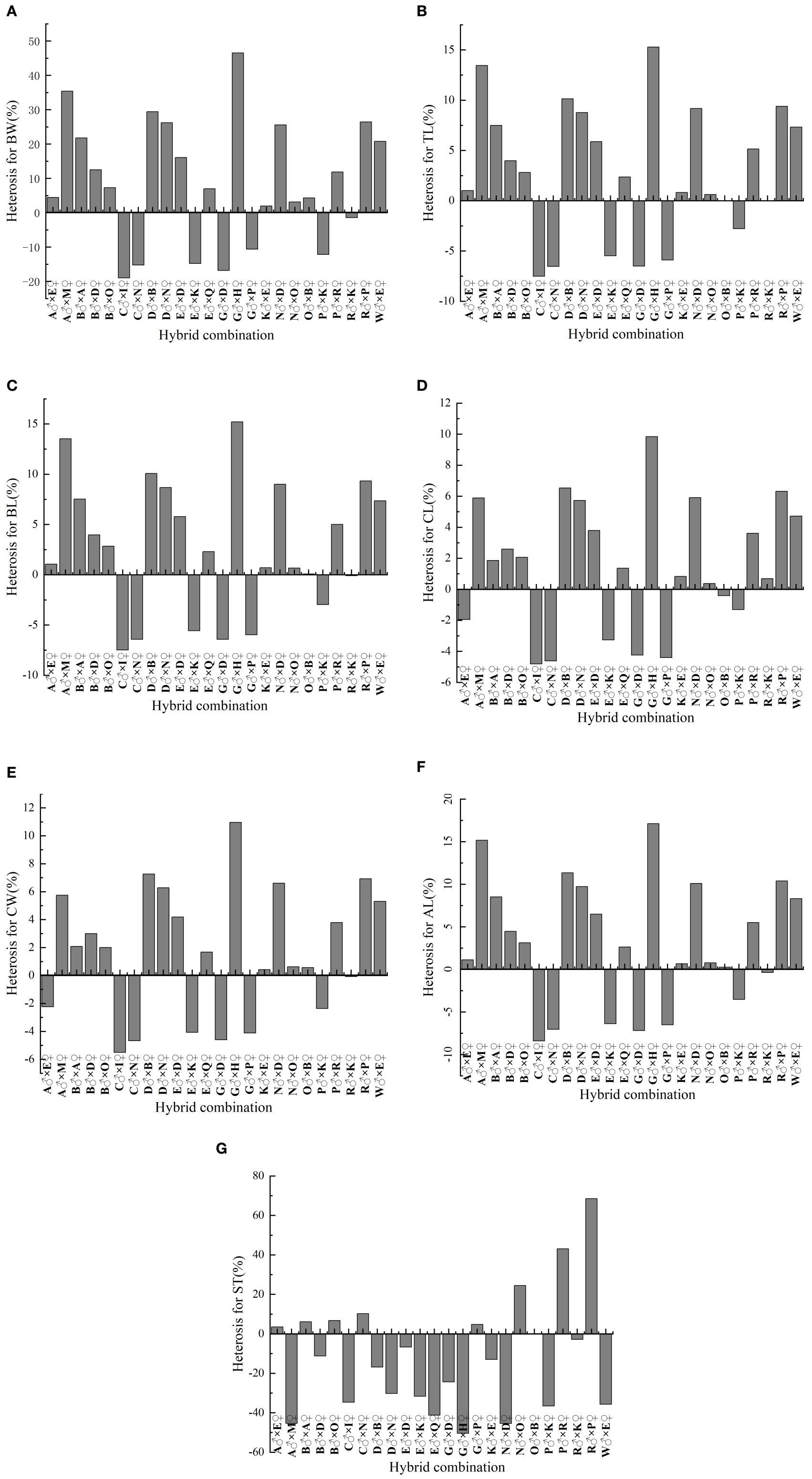

FIGURE 1
Heterosis in 24 hybrid combinations of *L. vannamei*.. **(A)** BW, body weight; **(B)** TL, total length; **(C)** BL, body length; **(D)** CL, carapace length; **(E)** CW, carapace width; **(F)** AL, abdomen length; **(G)** ST, survival time.

traits of the hybrid combination G♂ × H♀ exhibited the highest heterosis and a generally high SCA, compared with other examined mating combinations examined. The N♂ × O♀ combination had the highest SCA for multiple stress tolerance and the third-highest heterosis. Therefore, in the future, G♂×H♀ can be considered the preferred combination to improve the growth rate of the offspring, and N♂×O♀ as the preferred combination to improve the multi-factor stress tolerance of the offspring.

Data availability statement

The raw data used to support the findings of this study are available from the corresponding author upon request: JL, liujy70@126.com.

Ethics statement

This study was carried out in accordance with the requirements of Care and Use of Laboratory Animals in China, Animal Ethical and Welfare Committee of China Experimental Animal Society. The protocol was reviewed and approved by the Animal Ethical and Welfare Committee of Guangdong Ocean University, China.

Author contributions

JL designed the study and provided relative experiment material. LW analyzed data, carried out the experiment and wrote this manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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