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RESEARCH ARTICLE

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Effect of ecological environments on subspecies characteristics and economic traits in filial generations of cross between *indica* and *japonica* rice

Abstract Two recombinant inbred lines (RILs) populations, RILSA derived from the cross between "Zhongyouzao8" (*indica*) and "Toyonihiki" (*japonica*) rice cultivars, and RILSB derived from the cross between "Qishanzhan" (*indica*) and "Akihikari" (*japonica*) rice cultivars, were grown in Liaoning and Sichuan Provinces, China to understand the effects of ecological environments on the subspecies characteristics and economic traits in filial generations of cross between *indica* and *japonica*. The results showed that both the subspecies characteristics and economic traits changed significantly. The effects of ecological environments on Cheng's index and six subspecies characteristics were different on the basis of populations or characteristics. The distribution of Cheng's index in RILSA was *japonicalinous* in Liaoning and Sichuan. The distribution of Cheng's index in RILSB approached to normal distribution in Liaoning, but it was *japonicalinous* in Sichuan. As a whole, the two populations were more *japonicalious* in Sichuan than in Liaoning. The panicle number, seed setting rate and per-thousand-grain weight were decreased significantly in Sichuan. The grain number per panicle showed no significant change. A significant positive correlation was found between Cheng's index and the economic traits, including six subspecies traits. It suggested that the reason that the filial generation of cross between *indica* and *japonica* in northern China showed *japonicanous* subspecies characteristics might be the artificial selection by breeders on the economic traits. In addition, *indica-japonica* differentiation and the relationship with ecological environments were discussed.

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1 Introduction

The cultivated Asian rice species is composed of two subspecies, *indica* and *japonica*, which are apparently different in biological characteristics and have their advantages and disadvantages respectively in rice production (Chinese Academy of Agriculture Science, 1984; Yuzo Futsuhara, 1990). Great heterosis and variations can be created from crossing between *indica* and *japonica* (Yang and Zhao, 1959). The intersubspecies heterosis and its utilization have become a hot point on rice breeding either in northern China or in southern China (Xiong et al., 1989; Yang et al., 1996; Yuan, 1997; Zhou et al., 1997; Zhou and Lu, 2005). From the investigation on rice pedigree, the most widely used cultivars in northern China were bred through the cross between *indica* and *japonica*, as well as in southern China (Lin and Min, 1991). In the study, we studied the vascular bundles (Xu et al., 1996), Cheng's index (Xu et al., 2003a) and stomata in leaves (Chen et al., 2003). The results showed that cultivars derived from the cross between *indica* and *japonica* in northern China did not combine the subspecies characteristics. In contrast, they remained the *japonica* characteristics, which suggested that the results might be correlated with ecological adaptability or reproductive isolation without conscious direct selection. Up to now, most studies have always focused on the relationships between *indica-japonica* differentiation and heterosis, and F_1 subspecies classification, whose object was to probe the method of utilization interspecies heterosis, genetics mechanism and parent selection (Yang and Liu, 1991; Li and Xu, 1998; Sun et al., 2000). Recently, it have been found that there was no significant correlation between Cheng's index, subspecies characteristics and economic characters in F_1 or cultivars that derived from the cross between *indica* and *japonica*. However, there was a significant correlation in F_2 population (Xu et al., 2003b). The distribution of *indica-japonica* differentiation in double haploid (DH) or RILs showed continuous normal distribution (Mei et al., 1997; Chen et al., 2001). Conversely, few study reports can be found on the relationship between subspecies characteristics and economic traits in segregative population of high generation (Wu et al., 2003), especially the patterns of changes and their relationships under different ecological environments.

2 Materials and methods

Materials used in this study contained two RILs, RILSA and RILSB. RILSA derived from the cross between "Zhongyouzao8" (*indica*) and "Toyonihiki" (*japonica*), including 175 lines. RILSB derived from the cross between "Qishanzhan" (*indica*) and "Akihikari" (*japonica*), including 180 lines. Two RILs were numbered on lines and one line was divided into two, grown in Deyang, Sichuan Province (N30°31′–31°42′, E103°45′–105°15′) and Shenyang, Liaoning Province (N41°11′–43°2′, E122°25′–123°48′) in 2005, respectively. In Sichuan, materials with 20 plants grown per line, sowed on April 26 and transplanted on May 27, with row spacing and plant spacing being 26.6 and 16.5 cm, respectively. In Liaoning, the same materials were grown by ten plants per line, sowed on April 13, transplanted on May 15, with 30 cm row spacing and, 13.3 cm plant spacing. Cultivation and management practices were the same as those in the local rice fields.

Cheng's index method (Cheng, 1993) was used to discriminate the subspecies characteristics. The glume color and leaf pubescence were investigated at the heading stage. The average panicle number was investigated at the ripe stage by randomly sampling ten plants per line, and sampling five middle plants for indoor analysis after being air dried. The length of the first and the second rachis, and the length/width ratio of spikelets, glume pubescence and phenol reaction were investigated and the scores were evaluated on the basis of Cheng's index method. Panicle weight, biomass and harvest index were also investigated (Biomass and harvest index were not investigated in Sichuan due to the limitation of the experimental conditions there). The detailed information including grains per panicle, number of filled grains, number of empty-unfilled grains, seed setting rate and thousand-grain weight was investigated by sampling ten panicles on the mode of primary branches.

3 Results

3.1 Changes of subspecies characteristics under different ecological environments

All the lines showed continuous variation either in Sichuan or in Liaoning (Fig. 1). It suggested that no obvious boundary between every segregate phenotype on subspecies characteristics. Cheng's index, ranged from 0 to 24, and representing the gradual changes from *indica*, *indicalinous*, *japonicalinous* to *japonica*. Based on Cheng's index, RILSA showed obvious *japonicalinous* distribution, while RILSB showed normal distribution in Liaoning and *japonicalinous* distribution in Sichuan. It could be considered that RILSA and RILSB were more *japonicalinous* in Sichuan than in Liaoning.

Table 1 indicated that glume pubescence approached to normal distribution, and phenol reaction, glume color at heading time and length/width ratio of spikelets were *japonicalinous*, while leaf pubescence was *japonicalinous* in Sichuan and normal distribution in Liaoning. The scores of length of the first and the second rachises, and leaf pubescence were higher in Sichuan than in Liaoning, and the tendency was the same between the two populations. However, the difference was that scores of glume color at heading time and length/width ratio of spikelets in RILSA were lower in Sichuan than in Liaoning, while scores of phenol reaction in RILSB were higher in Sichuan than in Liaoning. There were no significant differences on the other subspecies characteristics.

3.2 Changes of economic characters under different ecological environments

Most economic characteristics changed significantly in RILSA and RILSB under different environments (Fig. 1). Panicle number, seed setting rate and thousand-grain weight in RILSA were significantly less in Sichuan than in Liaoning.

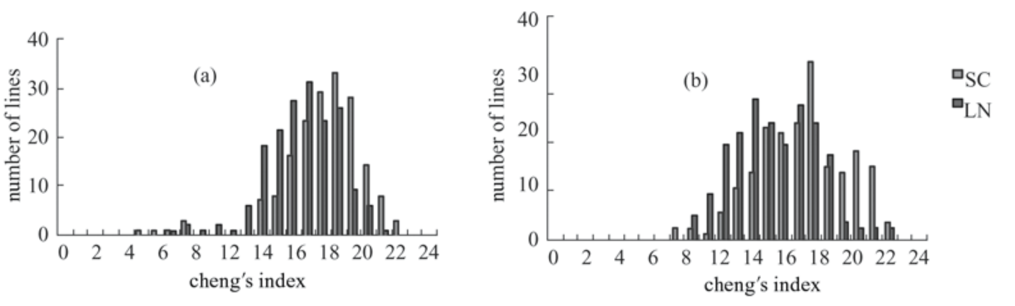

Fig. 1 Frequency distribution of Cheng's index for RILSA (a) and RILSB (b). Note: SC stands for Sichuan and LN for Liaoning

Table 1 Changes of subspecies characteristics under different ecological environments

trait	population	region	scores 0	1	2	3	4	average	standard deviation	coefficient of variation /%	difference (*t* value)
Glume pubescence	RILSA	Sichuan	4	23	82	50	16	2.03	0.83	40.79	−1.11
		Liaoning	3	28	66	60	18	2.08	0.87	41.99	
	RILSB	Sichuan	7	38	64	54	17	1.92	0.99	51.73	1.61
		Liaoning	7	33	66	49	25	1.86	0.99	53.23	
Phenol reaction	RILSA	Sichuan	1	12	7	17	138	3.58	0.92	25.62	−1.07
		Liaoning	2	10	8	13	142	3.61	0.91	25.10	
	RILSB	Sichuan	1	17	31	16	115	3.07	1.25	40.85	4.59**
		Liaoning	10	22	28	17	103	2.84	1.34	47.15	
Length of first and second rachises	RILSA	Sichuan	6	36	81	26	26	2.17	1.03	47.47	7.52**
		Liaoning	25	61	67	14	8	1.54	0.99	64.21	
	RILSB	Sichuan	33	46	50	37	14	1.74	1.20	69.14	9.88**
		Liaoning	67	59	36	14	4	1.05	1.04	99.29	
Glume color at heading time	RILSA	Sichuan	3	22	17	69	64	2.95	1.06	36.09	−2.63**
		Liaoning	0	0	5	111	59	3.13	0.48	15.38	
	RILSB	Sichuan	10	28	11	59	72	2.85	1.25	43.85	−1.92
		Liaoning	1	3	16	100	60	3.00	0.69	22.90	
Leaf pubescence	RILSA	Sichuan	5	3	3	28	136	3.64	0.85	23.22	17.85**
		Liaoning	6	42	56	39	32	2.20	1.17	53.06	
	RILSB	Sichuan	3	5	4	31	137	3.63	0.81	22.44	13.74**
		Liaoning	0	34	40	59	47	2.56	1.12	43.69	
Length/width ratio of spikelets	RILSA	Sichuan	0	9	82	84	0	2.43	0.59	24.35	−7.55**
		Liaoning	0	1	47	125	2	2.73	0.48	17.64	
	RILSB	Sichuan	0	6	58	105	11	2.67	0.64	24.01	−1.73
		Liaoning	1	4	56	98	21	2.74	0.71	25.87	

Note: * and ** represent significant at $P<0.05$ and $P<0.01$ levels, respectively.

The same tendency was found in RILSB, but the changes of seed setting rate and thousand-grain weight did not reach the significant level in RILSB. There was no significant difference on grains per panicle in two populations under different environments. Such a difference of yield structure resulted in significantly higher yield of RIILA and RILSB in Liaoning than in Sichuan.

RILSA and RILSB could be divided into four types, *indica*, *indicalinous*, *japonicalinous* and *japonica*. It can be seen from Fig. 2 that the panicle number in different types was higher in Liaoning than in Sichuan. There existed no significant difference among the different types under different environments. The seed setting rate showed an *indica* < *indicalinous* < *japonicalinous* < *japonica* tendency and was higher in Liaoning than in Sichuan, the same tendency was found in RILSA and RILSB. The 1000-grain weight was *indica* < *indicalinous* < *japonicalinous* < *japonica*, which was little affected by environments. The yield showed an obvious trend as *indica* < *indicalinous* < *japonicalinous* < *japonica* in RILSB, with no significant difference in different types in RILSA. However, the yields of both *japonica* and *japonicalinous* types, were all significantly higher than *indica* and *indicalinous* types. The same tendency was found that the yield in Liaoning was higher than that in Sichuan.

3.3 Relationship between subspecies characteristics and economic traits under different ecological environments

The relationship between Cheng's index and yield showed a significantly positive correlation in RILSB under different ecological environments (Table 2). The same tendency was showed in RILSA in Sichuan, but it did not reach the significant level in Liaoning. Both in Sichuan and in Liaoning, the relationship between Cheng's index, seed setting rate and thousand-grain weight all showed significantly positive correlations in RILSA and RILSB. As a whole, the relationship between subspecies characteristics and most of economic traits showed a significantly positive correlation.

4 Discussion

Rice growth is closely related to its environment. The yield potential expression depends on the utilization of local ecological environment (Zhou and Lu, 2005). During the past years, Chinese researchers paid more attention to the study on the relationship between environments and economic traits, and proposed the principle of introducing cultivars from different region and the concept of shuttle breeding, but fewer studies were put on the changes and their relationship between subspecies characteristics and economic traits on cultivars under different ecological environments. The phenomenon was determined by the cultivated pattern that *indica* was grown in southern China and *japonica* was grown in northern China. *Indica* grows in low latitude and low altitude areas, which is tolerant to wet, hot and intense-light (Chinese Academy of Agriculture Science, 1984), while *japonica* grows in high latitude and high altitude areas, which is tolerant to drought, chilling temperature and weak light. The past studies mainly focused on intrasubspecies because

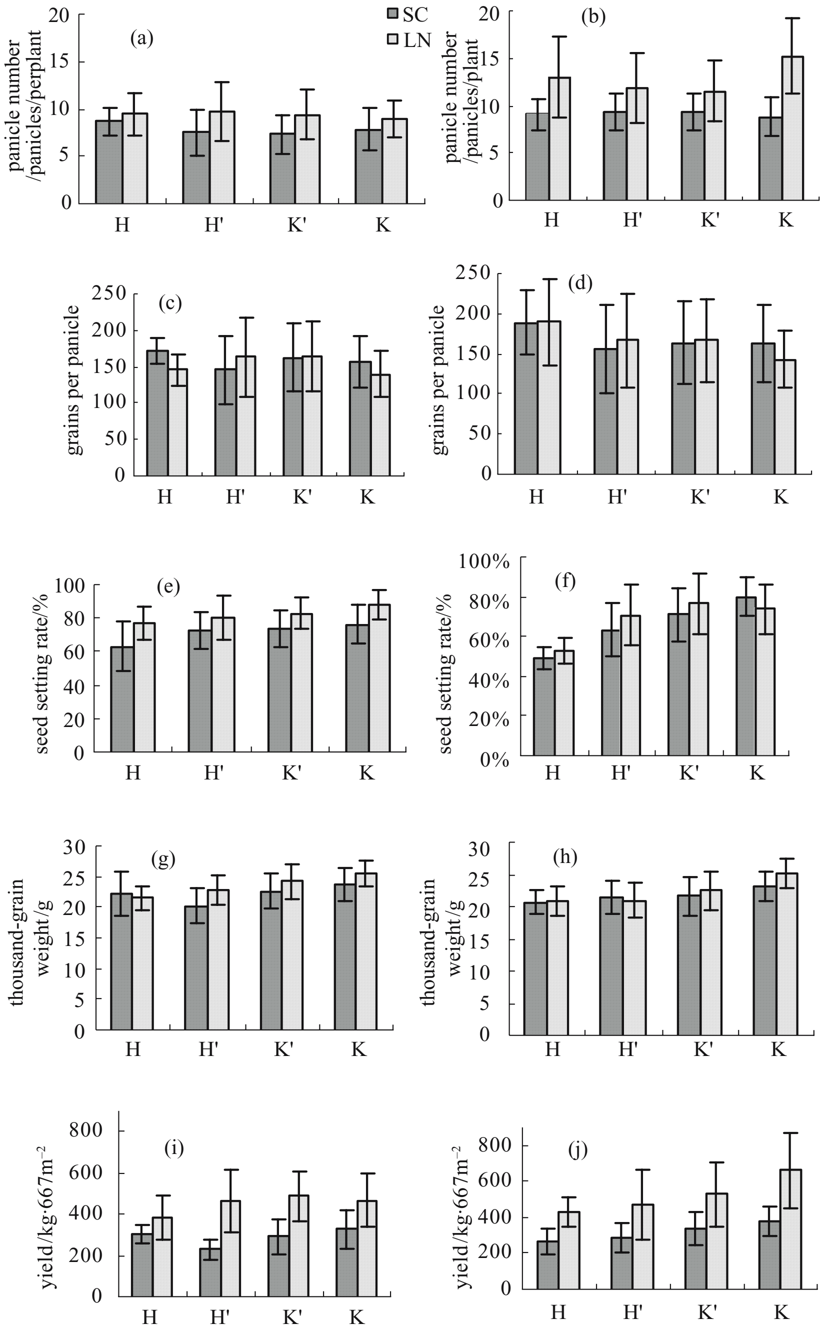

Fig. 2 Changes of economic traits between different subspecies types under different ecological environments. Note: (a) stands for the panicle number of RILSA; (b) for the panicle number of RILSB; (c) for the grains per panicle of RILSA; (d) for the grains per panicle of RILSB; (e) for the seed setting rate of RILSA; (f) for the seed setting rate of RILSB; (g) for the thousand-grain weight of RILSA; (h) for the thousand-grain weight of RILSB; (i) for the yield of RILSA; (j) for the yield of RILSB; and SC, LN, H, H′, K′ and K represent Sichuan, Liaoning, *indica*, *indicalinous*, *japonicalinous* and *japonica*, respectively.

of no combination between *indica* and *japonica*, which resulted from natural selection and artificial selection for long. Since the beginning of the breeding through the crossing between *indica* and *japonica* in 1950 by Yang and Zhao (1959), the consanguinity between *indica* and *japonica* has been infiltrated and fused. A large amount of cultivars were bred successfully through the cross between *indica* and *japonica*, whose position is more and more important in rice production. As mentioned above, analyzed by the conventional characters for classification or the other characters that proved to be different between *indica* and *japonica*, the cultivars deriving from the cross between *indica* and *japonica* in northern China did not combine the subspecies characteristics. In contrast, they remained the *japonica* characteristics

Table 2 Relationship between subspecies characteristics and economic traits under different ecological environments

trait	region	population	panicle number	grains per panicle	seed setting rate	thousand-grain weight	biomass	economic coefficient	yield
glume pubescence	Liaoning	RILSA	0.037	–0.138	0.074	0.209**	0.095	–0.118	0.038
		RILSB	0.027	–0.047	0.081	0.012	0.134	–0.020	0.089
	Sichuan	RILSA	0.011	–0.147	0.285**	0.207**			0.172*
		RILSB	–0.087	0.076	0.309**	0.045			0.300**
phenol reaction	Liaoning	RILSA	–0.145	0.194*	0.135	0.249**	0.038	0.284**	0.175*
		RILSB	0.024	0.056	0.062	0.232**	0.067	0.181*	0.174*
	Sichuan	RILSA	–0.214**	0.152	0.060	0.227**			0.092
		RILSB	–0.147	0.220**	0.086	0.217**			0.255**
length of 1st & 2nd rachis	Liaoning	RILSA	–0.218**	0.104	0.136	0.065	–0.103	0.046	–0.020
		RILSB	0.035	0.024	0.313**	0.215**	0.331**	0.041	0.330**
	Sichuan	RILSA	–0.041	0.034	0.217**	0.026			0.087
		RILSB	–0.105	0.073	0.357**	0.016			0.307**
glume color at heading time	Liaoning	RILSA	0.171*	–0.222**	0.146	0.232**	0.034	0.043	0.106
		RILSB	0.049	–0.127	0.218**	0.205**	–0.006	0.193**	0.135
	Sichuan	RILSA	0.227**	–0.147	–0.025	0.104			0.155
		RILSB	0.034	–0.294**	0.393**	0.167*			0.092
leaf pubescence	Liaoning	RILSA	0.116	–0.321**	0.114	0.108	–0.124	–0.130	–0.133
		RILSB	0.044	–0.223**	0.241**	0.125	–0.010	–0.039	0.039
	Sichuan	RILSA	–0.056	–0.081	0.209**	0.067			0.021
		RILSB	–0.024	–0.182*	0.152	0.077			–0.060
length/width ratio of spikelets	Liaoning	RILSA	–0.012	0.022	–0.032	0.159*	0.017	0.022	0.022
		RILSB	0.053	0.100	–0.115	0.328**	0.032	0.284**	0.089
	Sichuan	RILSA	0.064	–0.055	–0.017	0.055			0.033
		RILSB	–0.003	0.079	0.047	0.355**			0.134
cheng's index	Liaoning	RILSA	–0.043	–0.128	0.210**	0.324**	–0.043	0.033	0.032
		RILSB	0.079	–0.072	0.298**	0.381**	0.213**	0.199**	0.316**
	Sichuan	RILSA	0.001	–0.074	0.238**	0.220**			0.189*
		RILSB	–0.124	–0.010	0.494**	0.274**			0.375**

Note: * and ** stand for significant at $P<5\%$ and $P<1\%$ probability levels, respectively; n for RILSA was 175, and n for RILSB was 180.

(Xu et al., 1996; Chen et al., 2003; Xu et al., 2003a), which suggested that subspecies characteristics were correlated with ecological adaptability or intersubspecies reproductive isolation to a certain degree. The results in this paper showed RILs derived from the cross between *indica* and *japonica* were *japonicalinous* without artificial selection as a whole. Further studies indicated that RILs showed obvious continuous normal distribution, and a lot of lines belonged to the mid-type, though they were *japonicalinous*. Therefore, the cultivars belonging to different types could be bred theoretically. It was not enough to explain the above phenomenon. At the same time, there was no genetic polarization in the two populations.

There is no inevitable correlation between subspecies characteristics and economic traits macroscopically, because that there are a large amount of high yield cultivars either *indica* in southern China or *japonica* in northern China, which subspecies types are diversiform. As far as a certain population is concerned, the significant correlation may be represented between subspecies characteristics and economic traits. The results in this paper showed that subspecies characteristics and economic traits were significantly and positively correlated, and the yields of the two populations were all higher in *japonica* than in *indica* both in Sichuan and in Liaoning. Although there is little important effect of the relationship on natural selection, when human selects, the *japonica* or *japonicalinous* lines with good economic traits and high yield should be selected consequentially. On the contrary, *indica* or *indicalinous* should be eliminated. Consequently, in Liaoning region, though no artificial selection focused on subspecies characteristics, the selection focusing on economic traits could indirectly result in the fact that all cultivars bred from the cross between *indica* and *japonica* would remain *japonica* or *japonicalinous* subspecies characteristics. The cultivating patterns of *indica* grown in southern China and *japonica* in northern China will last for long. By this token, they are restricted by local environment, though the breeding method by the cross between *indica* and *japonica* is widely used. Because the ecological adaptability for crop is a long and gradually changed course, the feature of yield structure in different subspecies is different (Peng and Li, 1990; He et al., 1993), and the interaction between cultivars and environments has significant differences (Peng, 1991), some conclusions wait to be verified by more experiments with more years, more regions and more populations.

It sounds reasonable for explaining the results that the filial generations of the cross between *indica* and *japonica* were *japonicalinous* in northern China from the above analyses. Why were the relationships between subspecies characteristics and economic traits similar both in Sichuan and in Liaoning? One possibility was, when the two populations were built without artificial selection. some *indica* and *indicalinous* lines, which were sensitive to long sunlight, with weak tolerance to low temperature, could neither germinate normally in spring nor head normally in northern China. those lines had to be eliminated gradually by natural selection. Those eliminated lines were probably more suitable for the ecological environment in Sichuan than in Liaoning, and those *indica* and *indicalinous* survived were improbably more suitable for the ecological environment in Sichuan than in Liaoning. Another possibility was that the *japonica* and *japonicalinous* lines were more suitable for the ecological environment in Sichuan than in Liaoning. This argumentation needs to be further studied and confirmed. *Indica* and *japonica* belong to different climate-ecology types. The cultivated patterns of *indica* grown in southern China and *japonica* grown in northern China are the results of not only ecological adaptability but also the social factors. For example, the changes of growing area between *indica* and *japonica* in Korea or Taiwan of China in history include the increase and decrease of growing area in *indica-japonica* interlaced zone. It is worth further studying for evaluating the ecological adaptability of *indica* and *japonica* by analyzing the relationship between subspecies characteristics and economic traits in filial generations of the cross between *indica* and *japonica* under different ecological environments.

F_1 deriving from the cross between *indica* and *japonica* is not suitable for analyzing subspecies characteristics because of no segregation of the traits. The genotypes of lower generations such as F_2 and F_3 are hybrid, and their characters are unstable. Moreover seed setting rate changes remarkably, and heterosis is invigorative. some lines can not head and produce seed because of sensitivity to low temperature and long sunlight, and the experimental results can not be repeated. The genotype of RILs, which are higher generations (more than F_6), is pure, with stable characters and continuous normal distribution of the *indica-japonica* differentiation (Chen et al., 2001). Experimental results are representative and can be repeated. Populations from higher generations, such as RILs, are the idea materials to study the effects of ecological environments on subspecies characteristics and economic traits. However, the populations from higher generations tend to show distorted segregation (Chen et al., 2001) because of natural selection and reproductive isolation.

As a morphological marker method, Cheng's index classification method is simple and convenient, consistent with isozyme, RFLP and SSR classification (Wang et al., 1997), widely used by researchers for long. However, it adopts so many quantitative traits and is easy to be influenced by subjective experiences. Along with the rapid development of molecular marker technology since 1980, it has been used widely in rice classification (Qian et al., 1995; Qi et al., 2001; Chen et al., 2002; Wang et al., 2006) and phylogeny (Wang et al., 1996; Nonnatus et al., 2001; Sun et al., 2001; Cai et al., 2006), which is simple, convenient, objective, with no influence by environments. However, the molecular marker method has not become an independent classification system, which depends on the conventional morphological marker method to make verification. *Indica-japonica* differentiation is involved with so many locations, which may distribute in the whole genome, and the blood relationships of cultivars bred from the cross between *indica* and *japonica* are very complex, it is difficult to reflect the difference of the whole genome by several morphological markers or molecular markers. Now we are studying the differentiation patterns between *indica* and *japonica* by combining morphological markers with molecular markers, and tracking the segregation and combination of genetic substance from *indica* and *japonica* parents, to further reveal the genetics, especially to molecular genetic basis in *indica-japonica* differentiation.

5 Conclusion

Two RILs populations, deriving from crossing between *indica* and *japonica* conducted in Liaoning Province, were grown in Liaoning and Sichuan Provinces, respectively. The results showed that both the subspecies and their economic traits changed significantly. The effects of ecological environments on Cheng's index and six subspecies characteristics were different on the basis of populations and characteristics. The distribution of Cheng's index in RILSA was *japonicalinous* in Liaoning and in Sichuan. The distribution of Cheng's index in RILSB approached to normal distribution in Liaoning, but it was *japonicalinous* in Sichuan. As a whole, the two populations were more *japonicalious* in Sichuan than in Liaoning. The panicle number, seed setting rate and thousand-grain weight were decreased significantly in Sichuan. The grains number per panicle showed no significant changes. Significant positive correlation was found between Cheng's index and economic traits, including six subspecies characteristics. It suggested that the main reason that the filial generation of cross between *indica* and *japonica* in northern China showed *japonicanous* subspecies characteristics in northern China is the artificial selection by breeders on economic traits. Our experiment has laid a foundation for further studying the law of *indica-japonica* differentiation and genetics mechanism in filial generations of the cross between *indica* and *japonica* under different ecological environments.

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