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Heterosis and Gene Action of Boll Weight and Lint Percentage in High Quality Fiber Property Varieties in Upland Cotton*

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Abstract　Twenty F_1 combinations crossed among 5 varieties and strains different in fiber properties according to complete diallel crossing design were used to evaluate the heterosis and gene action of boll weight and lint percentage in high quality fiber property varieties in Upland Cotton in 1998~1999 for two year successively at Nanjing. It was indicated that there existed small interactions with the environmental factors without maternal effects and the additive gene effect was in chief, attaining to 51.2% and 65.4% respectively for boll weight and lint percentage. The dominant effect was also in higher rate, 32.6% and 16.8% respectively. The population mean heterosis of boll weight and lint percentage over the mid-parental mean were relatively prominent 13.3% and 3.5% respectively in extreme significance. However, boll weight showed no significantly surpassing parental F_1 heterosis over the better parent based on population mean (2.0%); while the lint percentage expressed significant negative heterosis value (-2.1%). The gene actions were in conformity with the heterosis expression. It was shown clearly that the F_1 combinations crossed between parents with similar performances had relatively high dominant effects and significant positive F_1 surpassing parental heterosis (F_1 heterosis over the better parent); while no F_1 combination crossed between the parents with prominent mutual difference surpassed the higher parent in yield components, which indicated that among those parents with less difference and close relationships, there still existed sufficient genetic variation or certain mechanism for creating variation and achieving greater advances in breeding. Correlation analyses also indicated that there still existed severely undesirable negative correlation between yield and fiber properties as well as the difficulties for their simultaneous improvements.

Key words　Upland cotton; High quality fiber property; Boll weight; Lint percentage; Inheritance; Heterosis
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陆地棉优异纤维品系的铃重和衣分的遗传及杂种优势分析

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摘　要　利用5个具有不同纤维品质性状的品种(系)配制完全双列杂交组合20个，通过亲本和F_1的2年随机区组试验发现产量性状的铃重和衣分与环境的互作效应小，不存在母体效应，并以加性遗传效应为主，分别占表型方差的51.2%和65.4%；显性遗传效应所占的比率也较高，分别为32.6%和16.8%。铃重和衣分的群体平均优势较大，分别为13.3%和3.5%，达到了极显著；铃重的超亲优势为2.0%，不显著；衣分为显著的负值(-2.1%)。遗传分析与杂种优势结果一致。具体表现在产量性状上，亲本相当配制的组合杂合显性较高，其超亲优势正向显著，而极值亲本(差异较大)所

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配组合没有超过高亲的。这表明亲本差异小、亲源关系较近的亲本中仍然存在足够的遗传变异或某种机制以创造变异使育种取得更大的进展。相关分析表明了仍然存在严重的品质与产量的负相关，遗传改良的难度较大。

关键词 陆地棉；优质纤维；铃重；衣分；遗传；杂种优势

Up to date, the yield increase in ordinary cotton varieties seems not very prominent, whereas hybrid cotton showed rather promising potential for yield increasing[1~5], especially the commercial cultivation of transgenic *Bt* insect-resistant hybrid cotton promoted the utilization of cotton heterosis to a new stage[6].

In the wake of successes in breeding large amount of materials with excellent fiber quality[7], to realize the genetic speciality of these materials and the potentiality of their hybrid vigor may be conducive to enforcing the tactics for breeding desirable varieties and hybrid combinations. In this research, complete diallel-crossing combinations among Upland cotton varieties with different fiber strength were analyzed to realize the inheritance of the high quality fiber properties and the potentiality for improving yield and fiber properties simultaneously. It was found that the boll weight and lint percentage of these parents were all diversified from each other, besides, the inheritance and heterosis for these two characters were significantly different from those of fiber properties. In this paper, the results of studying the boll weight and lint percentage of these materials were discussed more emphatically.

1 Materials and Methods

1.1 Material

Five varieties or strains, TM-1 (TM-1), PD6992 (PD69), MD51ne (MD51), HS427-10 (HS42) and 7235 different in fiber strength from each other (Table 1) were used. 7235 was supplied by Industrial Crop Institute, Jiangsu Academy of Agricultural Sciences and was further pedigree-selected after being introduced in our laboratory. TM-1, PD6992, MD51ne, and HS427-10 were all supplied by Dr. Kohel in the Southern Plain Agricultural Research Center, College Station, Texas USA. The genes relevant to the excellent fibers in the parental materials used were different from each other. Twenty combinations were produced according to the complete diallel-crossing model in the Wild Cotton Planting Garden of Cotton Research Institute (CRI), CAAS, in Hainan province in the winter 1997 and were planted at the Jiangpu Cotton Breeding Station, Nanjing Agricultural University (NAU) in the summer 1998. For scientific analyses the cross combinations were divided into different types as: high×high (H×H), high×low (H×L), and low×low (L×L) according to fiber strength. The parents were all self-pollinated for keeping their genetic purity.

1.2 Experimental method

Five parents and 20 F_1 combinations were planted in Jiangpu Cotton Breeding Station of NAU in 1998 and 1999 in randomized blocks with 3 replications, double rows in a plot, each row as long as 5 m, 0.8 m apart between two adjoining rows, and 15 plants in each row. Seeds were sown in the nursery on April 15 and April 11, and the seedlings transplanted to the experimental field on May 13 and May 17 in 1998 and 1999. Other field manipulations were same as those exercised in the commercial fields. The climatic conditions were normal in 1998, but with more rainy days and lower temperature during later developmental stage in 1999, which caused adverse influences on the fiber development. The 50 normally opened bolls were picked for assaying the boll weight (grams of seed cotton per boll), lint percentage and fiber property characters.

1.3 Statistical method

The average values per plant were used as units for Statistical analyses. The additive-dominance-maternal genetic model (ADM) and additive-dominance genetic model (AD) were analyzed by MINQUE (1) method[8~9] for estimating variance and covariance as well as for further calculating the ratios of genetic variance (Vg) over phenotypic

Table 1 The fiber properties of five parents

Parents	Fiber strength (cN/tex)		Micronaire		Fiber length (mm)		Uniformity (%)		Elongation (%)	
	1998	1999	1998	1999	1998	1999	1998	1999	1998	1999
TM-1	20.77	20.83	5.13	4.53	30.33	30.37	49.30	48.20	5.97	5.33
PD6992	23.63	23.57	4.77	3.83	33.43	32.97	47.00	45.87	5.27	5.23
MD51ne	21.80	20.07	4.90	4.00	30.93	30.23	49.07	46.00	5.83	5.23
HS427-10	26.20	25.80	4.90	4.57	31.97	33.10	49.17	48.77	5.07	4.30
7235	28.50	29.50	4.13	3.70	34.03	35.50	45.77	46.70	5.13	4.20

variance (Vp). The adjusted unbiased prediction method (AUP)[8] was adopted to estimate the genetic effects, genotypic values, heterosis over the mid-parents or better parent (BP) based on population mean. The Jackknife re-sampling method[10] was used to calculate the standard errors of the estimated values for t-test to assay the significance of differences among properties. The methods for calculating heterosis were as follows:

Heterosis over mid-parent based on population mean (mid-parent population mean heterosis):

$$H_{pm}(F_1) = (F_1 - MP)/\mu;$$

Heterosis over better parent based on population mean (surpassing parental heterosis):

$$H_{pb}(F_1) = (F_1 - BP)/\mu;$$

In above formulas, F_1 was represented as F_1 genotypic value, MP as the average of both parent's genotypic values; BP as the better parents genotypic value, and μ as the arithmetic mean of all the parents and F_1s in the diallel-crossing.

2 Results

2.1 The variance analysis of boll weight and lint percentage

The boll weight and lint percentage of parents and F_1 combinations in the diallel-crossing design experiment for 1998 and 1999 were listed in Table 2. Except the PD69, (7235 × PD69) F_1, (TM-1 × MD51) F_1, the boll weight of other parents and F_1 combinations in 1999 was heavier by 0.43 g on average than those in 1998 at extremely significant level (t-test, $P = 2.07 \times 10^{-8}$). The boll weight of TM-1, PD-69 and MD51 was relatively heavier, 5.92g, 5.71 g and 5.88 g, respectively; while that of HS42 and 7235 was relatively lighter, 4.01 g and 4.12 g, respectively. Ten F_1 combinations obviously surpassed the better parent in boll weight, showing prominent surpassing parental heterosis. The lint percentages of all the parents and F_1s in 1999 were lower than in 1998 by 2.42% on the average at extremely significant difference level (t-test, $P = 1.6 \times 10^{-13}$). Among 5 parents, HS42 had the highest lint percentage, 38%; while those of 7235 and PD69 were the next 33.16% and 32.98%, respectively; those of TM-1 and MD-51 were relatively low, 31.26% and 30.67% respectively. The lint percentages of most F_1 combinations were approximate to those of the higher valued parent. F_1s from the reciprocal crosses showed small difference both in boll weight and lint percentage.

According to the results analyzed by ADM and AD genetic model[9], the residual variances of boll weight and lint percentage were 11.8% and 15.5% respectively, the interaction variances of the additive and dominance effect with environmental factors were very small, only 0.3%～2.7%, which indicated that both boll weight and lint percentage were mainly controlled by genetic factors. Both boll weight and lint percentage showed no maternal effects, but additive genetic effect was in chief, amounting to 51.2% and 65.4%, respectively. Both boll weight and lint percentage showed, however, relatively high dominance effects at 32.6% and 16.8% respectively, both at extremely significant level by T-test (Table 3). In general, both boll weight and lint percentage, same as fiber strength and length showed high heritability and additive genetic effects in the main and less interaction with environmental

Table 2 The boll weight and lint percentage of parents and 20 F_1 combinations

	Parent	TM1^{b}		PD69^{b}		MD51^{b}		HS42^{b}		7235^{b}	
		1998	1999	1998	1999	1998	1999	1998	1999	1998	1999
Boll	TM1^{a}	5.77	6.07	6.10	6.83	5.70	5.58	5.57	5.87	5.37	5.99
weight	PD69^{a}	6.17	6.67	5.77	5.65	6.10	6.68	5.10	5.76	4.93	5.54
(g)	MD51^{a}	5.73	6.34	6.13	6.84	5.87	5.90	5.73	6.26	5.47	5.99
	HS42^{a}	5.70	6.43	5.37	5.48	5.77	6.23	3.60	4.43	4.53	5.14
	7235^{a}	5.50	5.92	5.50	5.49	5.67	5.93	4.57	4.92	3.83	4.40
Lint	TM1^{a}	32.17	30.36	33.63	31.18	32.51	31.43	34.63	32.99	35.07	32.44
percentage	PD69^{a}	33.69	30.70	34.84	31.12	33.64	30.50	39.08	37.13	37.15	34.55
(%)	MD51^{a}	31.90	31.07	34.25	31.63	31.89	29.45	35.48	33.17	35.16	32.88
	HS42^{a}	35.03	32.80	38.09	37.78	35.46	32.04	39.09	36.91	38.80	36.13
	7235^{a}	34.59	30.94	36.75	33.68	33.98	31.64	39.02	35.96	34.49	31.82

Note: a-maternal parent; b-paternal parent

Table 3 The ratios between estimated variance and phenotypic variance for boll weight and lint percentage

Character	V_A/V_P	V_D/V_P	V_{AE}/V_P	V_{DE}/V_P	V_M/V_P^a	V_{ME}/V_P^a	Residual
Boll weight (g)	0.512± 0.053**	0.326± 0.045**	0.017± 0.005*	0.027± 0.013*	0.003± 0.002	0.034± 0.019	0.118± 0.032**
Lint percentage, (%)	0.654± 0.046**	0.168± 0.038**	0.003± 0.001*	0.020± 0.013	0.036± 0.026	0	0.155± 0.038**

Notes: a-ADM model analysis; V_P-phenotypic variance; V_A-additive variance; V_D-dominance variance; V_{AE}-interaction variance between additive and environmental effects; V_{DE}-interaction variance between dominance and environmental effects; V_M-maternal genetic variance; V_{ME}-interaction variance between maternal and environmental effects; Residual-proportion of the residual variance

*, **-significance at P=0.05 and P=0.01 level respectively.

Table 4 The dominance genetic effect of boll weight and lint percentage

Cross	Boll weight (g)			Lint percentage (%)		
	D	DE1	DE2	D	DE1	DE2
TM1×PD69	0.44±0.11*	-0.02±0.05	0.28±0.12	-0.56±0.30	-0.13±0.16	-1.24±0.96
TM1×MD51	-0.36±0.20	-0.04±0.11	-0.22±0.24	0.40±0.29	-0.31±0.50	1.68±0.63*
TM1×HS42	0.52±0.06**	0.13±0.07	0.19±0.04**	-1.00±0.31*	-0.42±0.33	-0.21±0.27
TM1×7235	0.30±0.06**	0.04±0.06	-0.13±0.21	0.32±0.18	0.35±0.42	-0.42±0.23
PD69×MD51	0.41±0.05**	-0.06±0.03	0.52±0.19*	-0.24±0.23	0.07±0.14	-1.81±1.68
PD69×HS42	0.06±0.08	0.03±0.04	-0.03±0.05	2.40±0.44**	0.24±0.14	2.67±1.09
PD69×7235	0.01±0.07	0.04±0.03	-0.19±0.18	1.23±0.55	0.51±0.55	1.01±0.85
MD51×HS42	0.62±0.06**	0.11±0.09	0.20±0.05*	-0.69±0.26*	0.06±0.21	-1.58±0.68
MD51×7235	0.40±0.10*	0.06±0.09	0.02±0.08	0.77±0.46	-0.36±0.33	1.50±1.02
HS42×7235	0.10±0.04	0.03±0.06	-0.02±0.04	1.32±0.22**	0.70±0.48	0.22±0.36

Note: D-dominance effect; DE1-interaction effect between dominance and environment 1,

DE2-interaction effect between dominance and environment 2

factors, but they were characterized as rather high positive dominant effects for most of F_1s (Table 4) as compared with fiber strength (published elsewhere).

2.2 Heterosis Analysis of Boll Weight and Lint Percentage

From Table 5, boll weight and lint percentage showed relatively high mid-parent population mean heterosis, 13.3% and 3.5% respectively at extremely significant level. Boll weight showed surpassing parental heterosis 2%, at insignificant level; while lint percentage showed negative surpassing parental heterosis at significant level (-2.1%). As regards to the different F_1 combinations, except TM-1×MD51, all the other nine F_1 combinations showed significantly positive mid-parent population mean heterosis for boll weight (8.9%～21.8%), which might be relevant to the highly positive dominant effect (Table 4); three F_1 combinations (TM-1×PD69, PD69×MD51 and HS42×7235) showed significantly positive surpassing parent heterosis for boll weight (11.1%～13.8%); while the difference between both parents of these combinations were all small, the ratios of both parents in each combination were 1.02～1.04. The combination of TM-1 × 7235 showed significantly negative surpassing parental heterosis(-3%) for boll weight, the ratio of boll weights between both parents was 1.44, much higher than that above mentioned.

Six F_1 combinations showed significantly positive mid-parent population mean heterosis for lint percentage (2.5%～8.8%), which might be similarly relevant to the high positive dominance effects (Table 5). Three F_1 combinations showed surpassing parental heterosis. The surpassing parental heterosis of TM-1 × HS42 and MD51 × HS42 were with significantly negative values -13.7% and -13.1%, respectively; while PD69 ×7235. Showed significantly positive value 7.8%.

In the 4 F_1 combinations among which the boll weight or lint percentage all showed significantly positive surpassing parental heterosis, the parental values in each combination were mutually corresponding, the ratios between two parent in each combination were in the range of 1.01～1.04, these combinations consisted of such types as H ×H, L × L, and MH ×MH. However, the combinations with parents with polarized values, *i.e.* both parents had large difference from each other, such as TM1 × 7235 for boll weight, TM1 × HS42 and MD51 × HS42 for lint percentage, the parental ratios in each combinations were larger as 1.22～1.44, the population surpassing parental heterisos were all with extremely significant negative values (Table 6). Therefore, as regards yielding traits, the F_1 combination with both parents mutually corresponding in values showed rather high heterozygous dominance and significantly positive surpassing parental heterosis, whereas no F_1 combination with mutually polarized parents (with large difference in values between them) showed surpassing parental heterosis (with heterosis higher than the better parent).

2.3 The correlations between boll weight, lint percentage and fiber properties

Correlation analyses(Table 7) indicated that boll weight showed extremely significant negative correlation with fiber length and strength, with genotypic correlation coefficients -0.47 and -0.74, respectively, whereas the lint percentage, just on the contrary, showed extremely significant positive correlation with these fiber properties, which

Table 5 Mid-parent population mean heterosis and surpassing parental heterosis of boll weight and lint percentage

Character	Hpm (F_1)				Hpb(F_1)			
	Average	Range	+N	-N	Average	Range	+N	-N
Boll weight(g)	0.133**	-0.007～0.218	9(9)	1	0.02	-0.057～0.138	5(3)	5(1)
Lint percentage(%)	0.035**	-0.028～0.088	8(6)	2	-0.021*	-0.137～0.078	5(1)	5(2)

Note: Hpm (F_1): Average mid-parent population mean heterosis in F_1; Hpb(F_1): surpassing parental heterosis in F_1;
+N: number of combinations with positive heterosis; (): number of combinations attaining to positive and negative heterosis;
-N: number of combinations with negative heterosis

Table 6 The parental difference and dominance effects of combinations with significant heterosis over mid-parent or the better parent based on population mean

Character	Combination	Type	P_1-P_2	P_1/P_2	Dij	Hpm (F_1)	Hpb(F_1)
Boll weight g	TM1×7235	H×L	1.80	1.44	0.30**	0.137**	-0.030*
	PD69×MD51	H×H	0.17	1.03	0.41**	0.133**	0.116**
	TM1×PD69	H×H	0.21	1.04	0.44*	0.131**	0.111**
	HS42×7235	L×L	0.11	1.02	0.10	0.154**	0.138**
Lint percentage%	TM1×HS42	L×H	6.74	1.22	-1.00*	-0.028	-0.137**
	MD51×HS42	L×H	7.33	1.24	-0.69*	-0.010	-0.131**
	PD69×7235	MH×MH	0.18	1.01	1.23	0.079*	0.078*
	TM1×MD51	L×L	0.59	1.02	0.40	0.028	0.017

Dij: dominance effect

Table 7 The correlation between boll weight, lint percentage and fiber properties

Character	Length	Uniformity	Strength	Elongation	Micronaire	Boll weight
Boll weight	-0.39±0.03^{**a}	-0.04±0.09	-0.65±0.04**	0.49±0.06**	0.18±0.07*	-
	-0.47±0.04^{**b}	-0.11±0.12	-0.74±0.05**	0.63±0.07**	0.23±0.09*	-
Lint percentage %	0.43±0.04**	0.21±0.11	0.55±0.04**	-0.49±0.06**	0.17±0.07	-0.53±0.04**
	0.55±0.05**	0.34±0.17	0.65±0.06**	-0.61±0.10**	0.13±0.09	-0.59±0.04**

Note: a-phenotypic correlation; b-genotypic correlation

kept in conformity with the extremely negative correlation heterosis between boll weight and lint percentage (-0.59). In this experiment, we found that boll weight showed significant heterosis expression, which suggested there still existed severely negative correlation between fiber property and yields.

3 Discussion

3.1 The inheritance of boll weight and lint percentage of excellent fiber varieties

Although the five parents used in this research project were significantly different in fiber properties (length, strength and micronaire) and yielding components (boll weight and lint percentage), yet the inheritance patterns of yield component were apparently different from those of fiber properties. Boll weight and lint percentage did not show maternal effect, while additive genetic effects were in chief with rate as high as 51.2% and 65.4%, respectively, which was in conformity with the inheritance of fiber length and strength. However, the rate of dominance genetic effect of boll weight and lint percentage were as high as 32.6% and 16.8%, respectively, while that of strength and length were only 3.8% and 6.0%, respectively, that of micronaire was also as low as 11.5% (published elsewhere). It confirmed our previous result that the inheritance of fiber properties was chiefly controlled by additive effects, less by dominance effects; whereas among yielding components, boll weight and lint percentage were controlled by additive genetic effects in chief and by relatively high dominance effects as well. The interaction effect with the environmental factor was less on both aspects. These results were in accordance with majority results by former researches.

3.2 Heterosis performance of yielding performances under different fiber property backgrounds

Boll weight and lint percentage showed rather prominent mid-parent population mean heterosis, 13.3% and 3.5%, respectively, attaining to extremely positive significant level in most combinations. The surpassing parental heterosis of boll weight was insignificant 2.0%; while that of lint percentage was negative significantly -2.1%. These results of this experiment were also in conformity with those in current researches. In this experiment, boll weight and lint percentage showed significant mid-parent population mean heterosis, while fiber properties showed less mid-parent population mean heterosis, only micronaire showed relatively high value (3.2%). The significance in mid-parent population mean heterosis may keep close relationship with the dominance effect of these traits and was in conformity with the formerly mentioned genetic analytical results.

There existed rather large difference among fiber properties and yielding component among the parental varieties used in this research. The hybrids could be divided into different types of crossing combinations such as high×high, high×low and low×low etc. In 15 F_1s (H×L) with the maximum difference between two parents for yield components and fiber properties, negatively surpassing parental heterosis were produced, in 12 of them the heterosis attained to extremely significant level, which meant that none of the F_1 combinations with significant parental differences gave positive surpassing parental heterosis. Eight F_1 combinations with insignificant difference between two parents (H×H, L×L, and MH×MH) for the fiber properties showed no significant mid-parent population mean and surpassing parental heterosis. However, for boll weight and lint percentage, 5 F_1 combinations with insignificant difference between two parents (H×H, L×L, and MH×MH) showed positive dominance effect, positive mid-parent population mean and surpassing parental heterosis 4 of them attaining to significant or extremely significant levels. These results indicated apparently that F_1 combinations with similar parental values usually produced relatively strong heterosis for yield components. The results were in conformity with those of heterosis expressed in F_2 reported by Tang et al. (1993).

Currently with regard to the relationship between parental diversity and F_1 heterosis Meredith (1998) concluded that parental coefficients and molecular markers could scarcely be utilized in distinguishing the parents of excellent F_1 combinations. The correlation coefficient between genetic distance (calculated from RFLP data) and heterosis was 0.08, while that between parental coefficient and heterosis was also low 0.05 only, all showed very insignificant correlation[18], Van Esbroeck (1998) considered that genetic distance did not contribute much to the varietal improvement, while excellent varieties might be originated from the parents with close relationships[19].

It was indicated by all these researches that among parents with less diversities while with close relationships, there still exist sufficient genetic variation or certain mechanism that may be conductive to creating variation for the advances in breeding. Present QTL researches revealed that among morphologically alike parents do exist large amount of QTL with diversified effects and opposite in direction[20].

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