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Diallel analysis and inbreeding depression in agronomic and technological traits of cotton genotypes

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ABSTRACT: Cotton provides about 90% of the world textile fiber, and is one of the crops of greater industrial relevance. The objectives of this study were to estimate the inbreeding depression and the genetic effects involved in the control of the agronomic and fiber quality traits in F_1 and F_2 generations and to identify promising hybrids for obtaining superior cotton genotypes. Two cultivars of upland cotton and two moco (Brazilian endemic) cotton were crossed using a half-diallel scheme. The following traits were evaluated: percentage of fibers and weight of one boll, fiber length, fiber uniformity, short fiber index, fiber strength, and micronaire

index. The additive genetic effects are predominant in the evaluated agronomic and fiber quality traits. Cultivar FM 966 is the most suitable parent to compose crossing blocks for the improvement of cotton agronomic and fiber quality traits. The hybrids FM 966 × CNPA 7MH and FM 966 × BRS 286 are the most promising for obtaining segregating populations aiming to select superior genotypes. Inbreeding depression is more pronounced in the agronomic traits than in the fiber quality traits.

Key words: *Gossypium hirsutum* L. r. *latifolium* Hutch, *Gossypium hirsutum* L. r. *marie galante* Hutch, combining ability, parents selection.

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INTRODUCTION

Cotton (*Gossypium hirsutum* L.) provides about 90% of the world textile fiber, and is one of the crops of greater industrial relevance. It is cultivated in more than 30 million hectares, in more than 90 countries in the temperate, subtropical and tropical region in the world (Panni et al. 2012). Brazil is the fifth largest cotton lint producer in the world, with production of 1.3 million tons (CONAB 2016); however, the mean yield ($1.4 \text{ t} \cdot \text{ha}^{-1}$) is considered low. Therefore, the main objective of breeders is to develop cotton cultivars with high yield and quality of fiber for processing in the textile industry.

One of the most important steps in a breeding program is the choice of parents. The efficient choice of the parents and the selection of the best hybrid combinations increase the chances of obtaining a successful breeding program (Queiroz et al. 2017). The diallel scheme is a genetic design developed by Griffing (1956) that enables the breeder to know information regarding the behavior of the parents between each other, denominated general combining ability (GCA), which is attributed to genes with additive effects; and specific combining ability (SCA), which is attributed to non-additive effects of their hybrid combinations.

Several studies (Baloch et al. 1999; Hassan et al. 2000; Chinchane et al. 2002; Yuan et al. 2002; Tuteja et al. 2003; Khan et al. 2007; 2009; Aguiar et al. 2007; Hague et al. 2008; Bechere et al. 2016) have demonstrated that additive genetic effects are predominant in the control of most agronomic and fiber quality traits of cotton plant. However, in countries such as China and India, hybrid vigor in cotton has been explored to improve yield and quality of fiber (Khan et al. 2007). Nevertheless, the F_1 hybrids used in these countries have high inbreeding depression over the advance of generations, which prevents their use in breeding methods aimed at using pure lines (Soomor and Kalhoro 2000).

Inbreeding depression is caused by an increase in individual's homozygosity. There are two distinct ways in which the increase in homozygosity may decrease adaptability: increase in the homozygosity of partially recessive mutations, and increase in homozygosity of alleles in loci where there is heterozygote advantage. Shull (1908) demonstrated that inbred lines presented vigor and high yield in the F_1 generation when crossed; and Falconer (1987) evidenced that, with the increase in homozygosity by selfing, vigor and yield reduced by 50% for each generation, due to inbreeding depression.

Heterosis and inbreeding depression are opposing attributes, and traits that have high heterosis due to dominant allelic factors, proportionally present high inbreeding depression, due to fixation of allelic genes with increasing in homozygosity. Several authors (Meredith Jr. 1979; Soomor and Kalhoro 2000; Khan et al. 2007; 2009; Liang et al. 2015; Esmail 2016; Zhang et al. 2016) have reported higher inbreeding depression in cotton for agronomic traits than for fiber quality traits. Therefore, this study aimed to estimate the inbreeding depression and the genetic effects involved in the control of the agronomic and fiber quality traits in F_1 and F_2 generations, and to identify promising hybrids for obtaining superior genotypes by using two parents of *G. hirsutum* L. r. marie galante Hutch, and two parents of *G. hirsutum* L.r. latifolium Hutch.

MATERIALS AND METHODS

Parental Material

Two cultivars of upland cotton (*G. hirsutum* L. r. latifolium Hutch: FM966 and BRS 286) and two moco (Brazilian endemic) cotton (*G. hirsutum* L. r. marie galante Hutch: CNPA 5M and CNPA 7MH) were crossed in half-diallel without parents or reciprocal crosses. The choice of the parents was due to their divergence in mean percentage of fibers and fiber strength. Cultivars FM966 and BRS 286 have percentage of fibers above 40%, and fiber strength above $30 \text{ gf} \cdot \text{tex}^{-1}$, whose measurements were taken in the experiment. CNPA 5M was selected for earliness. CNPA 7mH is derivative from CNPA 5M by a cross with *G. hirsutum* L r. latifolium Hutch., thus they are related.

Obtainment of the F_1 and F_2 Hybrids

To carry out the cross of the parents were sown in a greenhouse, in 5 m rows, from January to July of 2014. Crosses were carried out at flowering. About 50% of the seeds of the F_1 hybrids were sown in the same soil, at flowering they were self-pollinated, and consequently the F_2 seeds were obtained.

Two experiments were carried out in August 2015 (one with seeds of the F_1 generation, and another with seeds of the F_2 generation, in the experimental area of Embrapa Cotton, in the municipality of Patos (lat $7^{\circ}00'04.4''$ S, long $37^{\circ}18'47.0''$ W, 245 m above sea level), in the state of

Paraíba, Brazil. The weather is classified as Aw according to Koppen classification (hot and humid with summer-fall rains, and rainfall of approximately 700 mm). Sowing of each experiment occurred on the same day in soil classified as Luvisol Chromic Orthic, medium texture gravelly loam.

Experimental Design and Evaluated Traits

Each experimental unit consisted of a 5 m row, spaced 1.0 m from the adjacent, with 25 plants in each row. At harvest, five plants were randomly collected in each plot, in both experiments. The agronomic traits evaluated were percentage of fibers (PF, %) and weight of one boll (P1C, g). Fiber samples were analyzed for HVI, and the following fiber quality traits were obtained by roller ginning: fiber length (UHM, mm), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR, KN m·kg⁻¹), and micronaire index (MIC).

Statistical Analysis

After detecting homogeneity of variances within each F₁ and F₂ trials, analysis of variance was carried out for both generations splitting the treatments source, in order to verify the significance of the F₁ vs. F₂ contrast to estimate the presence or absence of inbreeding depression. Treatments mean were clustered by the Scott and Knott test at 5% probability.

Subsequently, data were subjected to diallel analysis of each generation separately, by calculating the general (GCA) and specific combining ability (SCA), according to the Griffing's method 4 (Griffing 1956), as well as the quadratic component of these parameters (Eq. 1):

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + e_{ij} \quad (1)$$

where: Y_{ij} is the mean value of the hybrid combination ($i \neq j$); μ is the general mean; g_i and g_j are the effects of the general combining ability of the i^{th} and j^{th} genotypes, respectively; s_{ij} is the effect of the specific combining ability for crosses between parents i and j ; and e_{ij} is the effect of the mean error associated with the ij observation with $\sim \text{NID}(0, \sigma^2)$.

Inbreeding depression was calculated as percentage decrease (d) of the trait in F₂ in relation to F₁, by using the Eq. 2:

$$d = [(F_2 - F_1)/F_1] \times 100 \quad (2)$$

where: F₁ is the mean of the hybrid in the diallel scheme; F₂ is the mean of the F₂ generation after selfing. The significance of the GCA, SCA and inbreeding depression estimates was verified by t-test at 5% probability. All analyses were carried out using the Genes software (Cruz 2013).

RESULTS AND DISCUSSION

Diallel and Joint Analysis of Variance

There were significant differences among the twelve treatments for all traits, except for UNIF and SFI (Table 1). These results indicate the presence of genetic variability between treatments, and the possibility of selecting superior genotypes with the advance of segregating generations. With the exception of MIC, the F₁ vs. F₂ contrast was significant for all the evaluated traits, which reveals differences between the means of the F₁ and F₂ generations, indicating the presence of inbreeding depression.

Table 1. Joint analysis of variance (mean squares) of the traits percentage of fibers (PF), weight of one boll (P1C), fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in six cotton crosses, in the F₁ and F₂ generations.

SV	DF	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
Blocks	2	11.15	0.08	0.09	0.45	0.08	2.25	0.13
Treatments	11	41.40**	3.24**	2.41**	0.77 ^{ns}	0.16 ^{ns}	63.94**	0.44**
F1	5	16.16**	2.22**	2.42**	0.33 ^{ns}	0.06 ^{ns}	9.61 ^{ns}	0.14 ^{ns}
F2	5	43.16**	3.69**	1.21 ^{ns}	0.35 ^{ns}	0.13 ^{ns}	103.45**	0.82**
F1 vs F2	1	158.76**	6.08**	8.31**	5.06**	0.78*	137.82**	0.08 ^{ns}
Residue	22	2.64	0.33**	0.58	0.57	0.11	6.18	0.05
CV (%)		4.60	10.42	2.47	0.87	5.36	22.95	4.90

^{ns}, * and ** = not significant, significant at 5 and 1% probability by the F test, respectively; SV = source of variation; DF = degrees of freedom; CV = coefficient of variation.

The coefficient of experimental variation ranged from 0.87% (short fiber index) to 10.42% (mean weight of one boll), revealing high experimental precision, according to Pimentel-Gomes and Garcia (2002). Results in similar magnitudes were observed in other studies that used diallel cross in cotton crops (Khan et al. 2007; 2009; Aguiar et al. 2007; Hague et al. 2008).

With the exception of UNIF in the F_1 , there was significant general combining ability (GCA) for all traits in the F_1 and F_2 generations (Table 2). Specific combining ability (SCA) was significant, considering both generations, only for percentage of fibers and fiber strength, which are some of the most important traits in cotton. The other variables had significant SCA only for a given generation (F_1 or F_2). These results indicate that there are additive genetic effects involved in the control of all traits evaluated, and that there are non-additive genetic effects for percentage of fibers and fiber strength, regardless of the generation.

The quadratic components associated with additive effects (Φ_{gc}) were superior to non-additive effects in the genetic control of all traits in both generations, except for the percentage of fibers in the F_2 generation. These results indicate that breeders should use genotypes with higher GCA to obtain the segregating populations for selection, since the additive genetic effect is only directly fixable. Similar results were observed in other studies that used diallel crosses in upland cotton (Baloch et al. 1999; Hassan et al. 2000; Chinchane et al. 2002; Yuan et al. 2002; Tuteja et al. 2003; Khan et al. 2007; 2009; Aguiar et al. 2007; Hague et al. 2008).

Despite the quadratic components associated with non-additive effects (Φ_{sc}) for STR in the F_1 generation and MIC in the F_2 generation be higher than the additive effects (Φ_{gc}), non-additive effects were null or close to zero for most traits. However, there was pronounced non-additive effect for the percentage of fibers in the F_2 generation ($\Phi_{sc} = 20.98$), which shows that the hybrid vigor, due to differences in genetic compositions of the parents used, can be explored to increment this trait. Muthu et al. (2005), Ahuja and Dhayal (2007) and Khan et al. (2009) also observed non-additive effects involved in the control of this trait.

Combining Ability

Cultivars FM 966 and BRS 286 presented higher GCA for the agronomic traits (percentage of fiber and weight of one boll) in both generations (Table 3). This result was expected, since these cultivars have high yield and good quality of fiber, had been the targets of intense selection, and consequently have high frequency of favorable alleles. Results indicate that these cultivars should be included in crossing blocks when the goal of the breeding program is the increase of the main agronomic traits of cotton plants.

On the other hand, the cultivar CNPA 7MH had the highest GCA for the fiber length and fiber uniformity, and negative values for short fiber index in both generations, as well as positive values for weight of one boll in both generations, and high estimates for fiber strength and micronaire index in the F_2 generation. These results suggest that this cultivar can be used as a parent of segregating

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Table 2. Diallel analysis (mean squares) of the traits percentage of fibers (PF), weight of one boll (P1C), fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in six cotton crosses, in the F_1 and F_2 generations.

SV	DF	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
F_1								
GCA	3	24.77**	3.49**	4.00**	0.32 ^{ns}	0.10*	11.37**	0.19*
SCA	2	3.20**	0.33**	0.07 ^{ns}	0.33 ^{ns}	0.00 ^{ns}	6.86**	0.06 ^{ns}
Φ_{gc}	---	3.87	0.55	0.59	0.00	0.01	1.77	0.02
Φ_{sc}	---	0.55	0.04	0.00	0.00	0.00	1.96	0.00
F_2								
GCA	3	28.88**	6.12**	1.88**	0.53**	0.20**	155.13**	0.81**
SCA	2	64.49**	0.01 ^{ns}	0.20 ^{ns}	0.08 ^{ns}	0.02 ^{ns}	25.69**	0.81**
Φ_{gc}	---	4.55	0.97	0.26	0.04	0.02	23.93	0.13
Φ_{sc}	---	20.98	0.00	0.00	0.00	0.00	4.71	0.25

ns, * and ** = not significant, significant at 5 and 1% probability by the F test, respectively; SV = source of variation; DF = degrees of freedom; Φ_{gc} = quadratic component associated with GCA; Φ_{sc} = quadratic component associated with SCA.

populations when the goal of the breeding program is to improve the main fiber quality traits of the cotton plant.

Estimates of SCA were significant in both generations only for percentage of fiber and fiber strength. Table 4 shows that the hybrids FM 966 × CNPA 7MH and BRS 286 × CNPA 5M had the highest estimates of SCA in the F_1 generation, both presenting significant estimates for percentage of fiber, weight of one boll and fiber strength. However, in the F_2 generation, the highest values were

obtained by the hybrids FM 966 × BRS 286 and CNPA 7MH × CNPA 5M. Khan et al. (2009) reported that the decrease in the mean of the best hybrids from the F_1 generation to the F_2 generation is due to inbreeding depression and segregation. Coyle and Smith (1997), Soomor and Kalhor (2000), Khan et al. (2007) and Tigga et al. (2017) observed that the F_1 hybrids with high heterosis were also those associated with high inbreeding depression.

Table 3. Estimates of general combining ability (GCA) between the parents for the traits percentage of fibers (PF), weight of one boll (P1C), fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in four cotton genotypes, in the F_1 and F_2 generations.

GCA	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
F₁							
FM966	0.53*	0.47*	-0.05	0.18	0.00	0.62*	-0.14
CNPA 7MH	-2.10*	0.525*	1.07*	0.21	-0.10	-0.06	-0.04
BRS 286	2.58*	0.11	-0.11	-0.20	0.18	-0.41	-0.07
CNPA 5M	-1.02*	-1.11*	-0.91*	-0.20	-0.08	-0.16	0.26
F₂							
FM966	2.55*	0.77*	0.10	0.31	-0.18	1.93*	0.27
CNPA 7MH	-0.78	0.51*	0.71*	0.04	-0.12	0.67*	-0.15
BRS 286	0.78	0.19	-0.61*	-0.41	0.21	-1.72*	0.33
CNPA 5M	-2.61*	-1.47*	-0.20	0.06	0.09	-0.88*	-0.45

* = Values statistically different from zero by t-test at 5% probability.

Table 4. Estimates of specific combining ability (SCA) among parents for the traits percentage of fibers (PF), weight of one boll (P1C), fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in six cotton crosses, in the F_1 and F_2 generations.

GCA	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
F₁							
FM 966 × CNPA 7MH	0.78*	0.27*	-0.12	-0.14	-0.00	3.76*	0.10
FM 966 × BRS 286	-0.67*	-0.14	0.06	0.27*	-0.0	2.6*	-0.10
FM 966 × CNPA 5M	-0.10	-0.12	0.06	-0.13	0.18	-1.14	0.00
BRS 286 × CNPA 7MH	-0.10	-0.12	0.06	-0.13	0.18	-1.14	0.00
CNPA 7MH × CNPA 5M	-0.67*	0.14	0.06	0.27*	-0.02	2.61*	-0.10
BRS 286 × CNPA 5M	0.78*	0.27*	-0.12	-0.14	-0.00	3.76*	0.10
F₂							
FM 966 × CNPA 7MH	-2.80*	0.01	0.10	0.05	0.07	-7.50*	0.26
FM 966 × BRS 286	3.61*	-0.00	0.10	0.07	-0.03	3.73*	-0.42
FM 966 × CNPA 5M	-0.82*	-0.01	-0.21	-0.13	-0.05	3.77*	0.16
BRS 286 × CNPA 7MH	-0.82*	-0.01	-0.21	-0.13	-0.05	3.77*	0.16
CNPA 7MH × CNPA 5M	3.61*	-0.00	0.10	0.07	-0.03	3.73*	-0.42
BRS 286 × CNPA 5M	-2.79*	0.01	0.10	0.05	0.07	-7.50*	0.26

* = Values statistically different from zero by t-test at 5% probability.

Means Grouping Between both Generations

The means of the F_1 and F_2 generations presented no statistical differences for the traits fiber uniformity and short fiber index (Table 5), indicating that no crossing presented significant inbreeding depression for these traits. For the other traits, there was difference between the means of the F_1 and F_2 generations, which indicates that at least one cross expressed inbreeding depression. These results are in accordance with those obtained by Soomor and Kalhoro (2000), Khan et al. (2007; 2009), Lukonge et al. (2008) and Tigga et al. (2017), who reported more pronounced inbreeding depression in agronomic traits of cotton plants.

The means of the hybrids FM 966 × CNPA 7MH and FM 966 × BRS 286 did not statistically differ between the two

generations for most of the traits. Khan et al. (2009) emphasize that the mean of F_1 hybrids are not suitable for predicting the performance in the next generations; however, when analyzed in conjunction with the F_2 generation, it becomes good indicators to identify the most promising segregating populations. Given these considerations, it is clear that these crosses are recommended to select cotton genotypes for both agronomic and fiber quality traits.

Inbreeding Depression

Table 6 shows that the agronomic traits presented greater inbreeding depression, corroborating the results reported by Virusparkshappa et al. (1978), Bertini et al.

Table 5. Mean values of the traits percentage of fibers (PF), weight of one boll (P1C) fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in six cotton crosses, in the F_1 and F_2 generation.

Genotype (Generation)	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
FM 966 × CNPA 7MH (F_1)	36.60 a	7.23 a	32.07 a	87.10 a	5.93 a	348.41 a	4.70 a
FM 966 × BRS 286 (F_1)	39.83 a	6.40 a	31.07 a	87.10 a	6.20 a	338.60 a	4.47 a
FM 966 × CNPA 5M (F_1)	36.80 a	5.20 b	30.27 b	86.70 a	5.97 a	342.52 a	4.90 a
BRS 286 × CNPA 5M (F_1)	39.73 a	5.23 b	30.03 b	86.30 a	6.13 a	337.33 a	5.07 a
BRS 286 × CNPA 7MH (F_1)	37.77 a	6.47 a	32.20 a	86.73 a	6.13 a	333.40 a	4.67 a
CNPA 7MH × CNPA 5M (F_1)	33.60 b	5.23 b	31.40 a	87.13 a	5.83 a	334.39 a	4.90 a
FM 966 × CNPA 7MH (F_2)	33.73 b	6.43 a	31.13 a	86.50 a	6.10 a	344.88 a	5.07 a
FM 966 × BRS 286 (F_2)	38.63 a	6.10 a	29.80 b	86.07 a	6.33 a	332.72 a	4.87 a
FM 966 × CNPA 5M (F_2)	32.30 b	4.43 c	29.90 b	86.33 a	6.20 a	340.95 a	4.67 a
BRS 286 × CNPA 5M (F_2)	32.43 b	3.87 c	29.50 b	85.80 a	6.70 a	293.89 b	4.83 a
BRS 286 × CNPA 7MH (F_2)	34.97 b	5.83 a	30.10 b	85.60 a	6.37 a	320.36 a	5.03 a
CNPA 7MH × CNPA 5M (F_2)	27.07 c	4.17 b	30.83 a	86.27 a	6.27 a	328.50 a	3.67 b
Mean F_1	37.39	5.96	31.17	86.84	6.03	339.09	4.78
Mean F_2	33.19	5.14	30.21	86.09	6.33	326.83	4.69

Means followed by the same letters in the same column do not differ by the Scott and Knott test at 5% probability.

Table 6. Estimate of mean inbreeding depression (%) of percentage of fibers (PF), weight of one boll (P1C), fiber length (UHM), fiber uniformity (UNIF), short fiber index (SFI), fiber strength (STR), and micronaire index (MIC), evaluated in six cotton crosses, in the F_1 and F_2 generations.

Genotype	PF (%)	P1C (g)	UHM (mm)	UNIF	SFI	STR (KN m·kg ⁻¹)	MIC
FM 966 × CNPA 7MH	-7.83*	-11.06*	-2.91	-0.69	+2.81	-10.10	+7.80*
FM 966 × BRS 286	-3.01*	-4.69*	-4.08	-1.19	+2.15	-17.06	+8.96*
FM 966 × CNPA 5M	-12.23*	-14.74*	-1.21	-0.42	+3.91	-4.71	-4.76
BRS 286 × CNPA 5M	-18.37*	-26.11*	-1.78	-0.58	+9.24*	-126.40*	-4.61
BRS 286 × CNPA 7MH	-7.41*	-9.79*	-6.52*	-1.31	+3.81	-38.44	+7.86*
CNPA 7MH × CNPA 5M	-19.44*	-20.38*	-1.80	-0.99	+7.43*	-17.26	-25.17*
Mean	-11.38	-14.46	-3.05	-0.86	+4.89	-35.69	-1.65

* = Values statistically different from zero by t-test at 5% probability.

(2001), Soomor and Kalhor (2000), Khan et al. (2007), Khan et al. (2009) and Tigga et al. (2017). The hybrids FM 966 × CNPA 7MH and FM 966 × BRS 286 had the lowest estimates of inbreeding depression for most of the traits. Thus, due to the predominance of additive genetic effects, conventional selection methods can be used in these crosses for increments in agronomic and fiber quality traits.

The crosses involving the cultivar CNPA 5M presented high inbreeding depression. This cultivar is derivative from moco (Brazilian endemic) cotton, which presented great mixture (Faria 1940) and variability (Harland 1933). Menezes et al. (2010) found a total of 62 alleles with 3 to 8 polymorphic alleles per locus, and high heterozygosity index in moco (Brazilian endemic) cotton. The natural condition of high heterozygosity index in moco (Brazilian endemic), and therefore in the cultivar CNPA 5M may have contributed to the higher inbreeding depression of their F_2 hybrids with different cultivars, in relation to the other cultivars. Thus, the cross CNPA 7MH × CNPA 5M, involving two related parents with high heterozygosity, showed the highest inbreeding depression rates for most of the traits.

CONCLUSION

The additive genetic effects are predominant in the evaluated agronomic and fiber quality traits. Cultivar FM 966 is the most suitable parent to compose crossing blocks for the improvement of cotton agronomic and fiber quality traits. The hybrids FM 966 × CNPA 7MH and FM 966 × BRS 286 are the most promising for obtaining segregating populations aiming to select superior genotypes. Inbreeding depression is more pronounced in the agronomic traits than in the fiber quality traits.

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