

## Genetic effects on morphological and yield traits in cotton (*Gossypium hirsutum* L.)

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### Abstract

The nature and magnitude of genetic effects on morpho-yield traits were studied in a  $6 \times 6$   $F_1$  and  $F_2$  diallel cross in upland cotton. An additive-dominance model was adequate for most of the traits except plant height and seed cotton yield, where the model was partially adequate. Genetic parameters were estimated following Hayman's and Mather's model. Additive effects controlled lint percentage and monopodia in both generations, and plant height and sympodia in  $F_2$ . Non-additive inheritance with over-dominance controlled yield in both generations, and plant height and sympodia in  $F_1$ . Most traits presented an unequal proportion of positive (U) and negative (V) alleles in the loci ( $H_2 < H_1$ ) and an asymmetrical distribution of genes in the parents ( $H_2/4H_1 < 0.25$  and F different to zero). The value of  $H_2/4H_1$  was lower than maximum value (0.25) for all of traits, which arises when  $U = V = 0.5$  over all loci. The proportion  $\sqrt{4DH_1 + F} / \sqrt{4DH_1 - F}$  confirmed by half of the traits that dominant alleles were in excess as compared to recessive alleles. Dominance effects ( $h^2$ ) for most of the traits suggested that substantial contribution of dominance was not due to heterogeneity of loci in these parameters. Broad and narrow sense heritabilities were high for most of the traits. Correlation coefficient between the  $W_r + V_r$  and mid parental ( $y$ ) indicated that dominant genes were responsible for increased sympodia, lint % and yield, and recessive genes increased monopodia and plant height. Genetic gain was encouraging for most traits. Cultivar CIM-1100 was identified by genetic advancement as a promising parental cultivar to cross combinations.

**Additional key words:** additive-dominance model; additive and dominance effects; D,  $H_1$  &  $H_2$  genetic components of variance; seed cotton yield; upland cotton.

### Resumen

#### Efectos genéticos en caracteres morfológicos y de rendimiento en algodón (*Gossypium hirsutum* L.)

Se estudió la naturaleza y la magnitud de los efectos genéticos sobre los caracteres morfo-productivos en un cruce dialélico  $F_1$  y  $F_2$  de  $6 \times 6$  en algodón tipo upland. Para la mayoría de los caracteres, excepto altura de planta y rendimiento de semilla, fue adecuado un modelo aditivo-dominante. Se estimaron los parámetros genéticos según Hayman y Mather. Los efectos aditivos controlaron el porcentaje de pelusa y los monopodios en ambas generaciones, y la altura de la planta y los simpodios en la  $F_2$ . La herencia no aditiva con superdominancia controló el rendimiento en ambas generaciones y la altura de planta y los simpodios en la  $F_1$ . La mayoría de los caracteres presentaron una proporción desigual de alelos positivos (U) y negativos (V) en los loci ( $H_2 < H_1$ ) y una distribución asimétrica de los genes en los parentales ( $H_2/4H_1 < 0,25$  y  $F \neq 0$ ). El valor de  $H_2/4H_1$  estuvo por debajo del valor máximo (0,25) para todos los caracteres, lo que surge cuando  $U = V = 0,5$  en todos los loci. La proporción  $\sqrt{4DH_1 + F} / \sqrt{4DH_1 - F}$  confirmó, para la mitad de los caracteres, que había un exceso de alelos dominantes respecto a los recesivos. Los efectos de dominancia ( $h^2$ ) para la mayoría de los caracteres sugieren que la contribución sustancial de la dominancia no se debió a la heterogeneidad de los loci en estos parámetros. Las heredabilidades en sentido amplio y estricto fueron altas para la mayoría de los caracteres. El coeficiente de correlación entre  $W_r + V_r$  y los medios parentales ( $y$ ) indicó que los genes dominantes fueron los responsables del aumento de simpodios, el % de pelusa y el rendimiento, y los genes recesivos del aumento de monopodios y altura de la planta. La ganancia genética fue fundamental para la mayoría de los caracteres. Se identificó el cv. CIM-1100 mediante el avance genético como un cultivar parental promisorio para combinaciones cruzadas.

**Palabras clave adicionales:** algodón Upland; componentes genéticos de varianza D,  $H_1$  y  $H_2$ ; efectos aditivos y dominantes; modelo aditivo-dominante; rendimiento de la semilla de algodón.

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## Introduction

Plant breeders have great interest in quantitative genetics as most of the traits such as seed cotton and lint yields and fiber quality are polygenic. Quantitative traits have constant variation in a population and can be altered significantly by the environment (Ragsdale, 2003; Khan *et al.*, 2009c). Crop development requires the ability to identify and select high performing genotypes in a population. Some difficulties can result when breeders make selections for improvements in quantitative traits (Khan, 2003; Ragsdale and Smith, 2007). For identification of superior genotypes, the genetic variation is required in the breeding population. However, this is usually also a problem with crossing of individuals with broad genetic base for creation of genetic variation followed by selection. Another reason is that quantitative traits are controlled by many genes, and finding a genotype with desirable genes at all loci is difficult. To overcome this issue, it is better to make selections collectively on the basis of parental cultivar performance for the targeted traits and then proceed to make crosses. Sometimes, the expression of one trait (one gene) is often modified by the expression of other characters (other genes). In addition, genes linkage blocks are difficult to break up. And finally, variation in the natural environment can mislead breeders, thus environmental effects should be minimized through selection of locations, sampling procedures, and replicated screening of breeding material to control experimental errors. The polygenic traits are highly influenced by the environment (Khan, 2003; Yuan *et al.*, 2005; Percy *et al.*, 2006; Khan *et al.*, 2009b). Many researchers have found difficult to solve these genetic problems using simple genetic models, where few genetic parameters are used to describe complex situations (Godoy and Palomo, 1999; Khan *et al.*, 2009c).

Diallel analyses can be a dependable and effective technique for identification and selection of superior genotypes, and to understand gene action involved in different characteristics. To introduce genetic variability, diallel crossing techniques have been widely utilized by breeders (Basal and Turgut, 2005; Basal *et al.*, 2009; Khan *et al.*, 2009a,c). Consequently, the use of genotypes with desirable genetic components of variance is a prerequisite for synthesis of physiologically efficient and genetically superior genotypes showing

promise for increased production per unit area under a given set of environments (Khan *et al.*, 2009a). To achieve these objectives using quantitative genetics, workers have advocated a comprehensive study of assumptions of additive-dominance model (through different scaling tests), genetic mechanism and genetic components of variation which control the various plant characters in parents and their cross combinations under various environmental conditions (Hayman, 1954; Mather and Jinks, 1982; Tang *et al.*, 1993, 1996; McCarty *et al.*, 1996, 2004a,b; Hussain *et al.*, 1999; Khan, 2003; Ragsdale, 2003; Lukonge, 2005; Mei *et al.*, 2006; Wu *et al.*, 2006; Esmail, 2007; Lukonge *et al.*, 2007; Khan *et al.*, 2007, 2009a,c; Aguado *et al.*, 2008; Ali *et al.*, 2008; Ali and Awan, 2009; Basal *et al.*, 2009; Gamal *et al.*, 2009).

Morphological traits like sympodia are very important in cotton plant because sympodia are positively correlated with yield and manage the seed cotton yield. The present study makes use of the additive-dominance model of genetic analysis. We used D (additive effects) and H (dominance effects) genetic components of variation and heritability (broad and narrow sense) to study the gene action involved in the inheritance of morpho-yield traits and to understand the genetic potential of parents and their diallel hybrids. Before diallel analyses, we used data check with validity tests with three scaling tests (regression analysis, arrays analysis of variance and  $t^2$  test) for different morphological and yield traits in a  $6 \times 6$   $F_1$  and  $F_2$  diallel cross of upland cotton.

## Material and methods

### Genetic material

Breeding material was comprised of six *Gossypium hirsutum* genotypes and their 30  $F_1$  and  $F_2$  hybrids generated through  $6 \times 6$  complete diallel crossing. The parental cultivars (CIM-109, CIM-240, CIM-1100, FH-682, BH-36 and CRIS-9) have a broad genetic base and varied by date of release, pedigree, seed cotton yield and fiber yields as well as fiber quality traits.

### Experimental design and field procedures

The study was conducted at the Agricultural Research Institute, Dera Ismail Khan, Pakistan over three years

Abbreviations used: b (regression coefficient), RCB (randomized complete block), SS (sum of squares),  $W_r + V_r$  and  $W_r - V_r$  (arrays analysis of variance),  $\bar{X}$  (population mean).

(2007-2009). Dera Ismail Khan, Pakistan, lies between 31°, 50' North latitude and 70°, 50' East longitude. Experiments were comprised of a crossing block, F<sub>1</sub> and F<sub>2</sub> populations of upland cotton. The six diverse genotypes of upland cotton were hand sown during May, 2007, in a non-replicated crossing block. Plots consisted of five rows, each 27 m in length, with plant and row spacings of 60 and 100 cm, to facilitate hand emasculature and crossing. All the cultivars were crossed in a complete diallel fashion. The F<sub>1</sub> population of a 6 × 6 complete diallel cross with six parents was hand sown during May, 2008, and all the traits were studied and allowed to self and advance the generation to have seeds for the F<sub>2</sub> crop. During crop season 2009, the experiment had 30 F<sub>1</sub> and F<sub>2</sub> hybrids along with parents, hand sown using a randomized complete block (RCB) design. The F<sub>1</sub> genotypes were planted in a single row measuring 3.30 m (having 12 plants of each F<sub>1</sub> population per replication) with three replications. In F<sub>2</sub>s, the plant population was increased and each F<sub>2</sub> population/genotype was planted in four rows with row length of 6.60 m (having 96 plants of each F<sub>2</sub> population per replication) with four replications. The plant and row spacings were 30 and 75 cm, respectively. All recommended cultural practices and inputs including fertilizer, hoeing, irrigation and pest control were applied similarly for all entries. The crop was grown under uniform conditions to minimize environmental variability to the maximum possible extent. All the crops were harvested during November-December every year and ginning was done with eight saw-gins.

### Trait measurement and statistical analyses

Data were recorded for plant height (cm), monopodia per plant (vegetative branches) and sympodia per plant (fruiting branches), lint % and seed cotton yield per plant (g). The mean data were subjected to analysis of variance (ANOVA) according to Steel and Torrie (1980) to test the null hypothesis of no differences among various F<sub>1</sub>s as well as F<sub>2</sub> hybrids population and their parental cultivars.

### Diallel analyses

The genetic analyses used Hayman's diallel approach (1954) and Mather's concept of D and H genetic components of variation for additive and dominance varian-

ces, respectively (D used for additive variance instead of A, and H<sub>1</sub> and H<sub>2</sub> for dominance components of variance instead of D). The same technique has also been described by Mather and Jinks (1982). The F<sub>1</sub> genetic components of variation were estimated. For F<sub>2</sub> genetic components of variance, the formulas were modified as suggested by Verhalen and Murray (1969), Verhalen *et al.* (1971) and Singh and Chaudhary (1985).

### Diallel analysis assumptions and tests of adequacy

The validity of information from a group of genotypes obtained from the diallel method is based on the following assumptions: a) diploid segregation of chromosomes, b) homozygosity of parents, c) absence of reciprocal effects, d) absence of epistasis, e) no multiple allelism, and f) independent distribution of genes among parents.

To fulfill the assumptions such as absence of epistasis, no multiple allelism and independent assortment of genes, the data were tested through three scaling tests (regression analysis, arrays analysis of variance  $W_r + V_r$  and  $W_r - V_r$  and  $t^2$  test) to evaluate the adequacy of the additive-dominance model for the data. According to Mather and Jinks (1982) the regression coefficient is expected to be significantly different from zero and not from unity. Failure of this test means the presence of epistasis. If non-allelic interaction is present,  $W_r + V_r$  must change from array to array. Similarly, if there is epistasis,  $W_r - V_r$  will vary between arrays. Non-significant values of a  $t^2$  test confirm the presence of no nonallelic interaction and signify that genes are independent in their action for random association in genotypes. Failure of these three tests completely invalidates the additive-dominance model. However, if even one meets the assumptions, then the additive-dominance model is considered to be partially adequate.

### Estimation of genetic components

The genetic components of variation, their ratio along with standard error and correlation coefficient were estimated as follows:

— D: additive genetic variance;  $F_1 = [D = V_{o1} - E$  ( $V_{o1}$  = Variance of the parents)],  $F_2 = V_{o2} - E$  ( $V_{o2}$  =  $V_{o1} - E$ ), where E is the expected environmental component of variation.

—  $H_1$ : dominance variance [ $H_1 = \text{Volo} - 4\text{Wolo}_1 + 4\text{V}_1\text{L}_1 - (3n-2)\text{E}/n$ , ( $\text{Wolo}$  = Mean covariance between the parents and the arrays)], where  $\text{V}_1\text{L}_1$  is mean variance of arrays, and  $n$  is number of parental cultivars.

—  $H_2$ :  $H_1 [1 - (u-v)^2]$ , where  $u$  and  $v$  are the proportions of positive and negative genes, in the parents.

—  $F$ : mean of  $\text{Fr}$  values over arrays =  $2\text{Volo} - 4\text{Wolo}_1 - 2(n-2)\text{E}/n$ , where  $\text{Fr}$  is the covariance of additive and dominance effects in a single array.  $F$  is positive where dominant genes are more frequent than recessive.

—  $h^2$ :  $4(\text{ML}_1 - \text{MLo})^2 - 4(n-1)\text{E}/n^2$ ; dominance effect (as algebraic sum over all loci in heterozygous phase in all crosses). When frequency of dominant and recessive alleles is equal, then  $H_1 = H_2 = h^2$ . Significance of  $h^2$  confirms that dominance is unidirectional.

—  $E$ : expected environmental component of variation;

$$E = \left[ \frac{\text{Error SS} + \text{Reps. SS}}{\text{d.f.}} \right] / \text{Number of replications}$$

where  $\text{SS}$  is the sum of squares.

From these estimates, the following genetic ratios were determined:

—  $F_1 = \sqrt{H_1/D}$ ,  $F_2 = \sqrt{1/4 H_1/D}$ : denotes the «average degree of dominance», if the value of this ratio is zero, there is no dominance; if value is equal to 1 then there is complete dominance; if it is greater than zero but less than unity (1), there is partial dominance; and if it is greater than 1, it denotes over-dominance.

—  $H_2/4H_1$ : denotes the «proportion of genes with positive and negative effects in the parents», and if the ratio is equal to 0.25, indicates symmetrical distribution of positive and negative genes.

—  $F_1 \sqrt{4\text{DH}_1 + F} / \sqrt{4\text{DH}_1 - F}$  and  $F_2 =$

$$1/4 \sqrt{4\text{DH}_1 + 1/2 F} / 1/4 \sqrt{4\text{DH}_1 - 1/2 F} :$$

denotes the «proportion of dominant and recessive genes in the parents»: If the ratio is 1, the dominant and recessive genes in the parents are in equal proportion; if it is less than 1, it indicates an excess of recessive genes; but being greater than 1, it indicates excess of dominant genes.

—  $h^2/H_2$ : denotes the «number of gene groups/genes, which control the character and exhibit dominance».

— Correlation coefficient: negative value of correlation coefficient ( $r$ ) indicates dominant genes, while if its value is positive then recessive genes are responsible for the phenotypic expression of the trait.

Correlation coefficient ( $r$ ) =

$$= \frac{\sum XY - \frac{(\sum X)(\sum Y)}{n}}{\sqrt{\frac{(\sum X^2) - (\sum X)^2}{n} \times \frac{(\sum Y^2) - (\sum Y)^2}{n}}}$$

## Heritability

The narrow sense heritability ( $h^2$ ) in  $F_1$  generation was calculated for each character according to Mather and Jinks (1982):

$$\begin{aligned} F_1 \text{ narrow sense heritability } (h^2) &= \\ &= \frac{(\frac{1}{2})D + (\frac{1}{2})H_1 - (\frac{1}{2})H_2 - (\frac{1}{2})F}{(\frac{1}{2})D + (\frac{1}{2})H_1 - (\frac{1}{4})H_2 - (\frac{1}{2})F + E} \end{aligned}$$

The narrow sense heritability ( $h^2$ ) in  $F_2$  generation was calculated for each character according to Verhalen and Murray (1969).

$F_2$  narrow sense heritability ( $h^2$ ) =

$$= \frac{(\frac{1}{4})}{(\frac{1}{4})D + (\frac{1}{16})H_1 - (\frac{1}{8})F + E}$$

where  $D$  = variation due to additive effect;  $H_1$  = component of variation due to dominance effect of genes;  $H_2 = H_1 [1 - (u-v)^2]$  [ $u$  = positive and  $v$  = negative genes];  $F$  = mean of « $\text{Fr}$ » over the arrays; and  $E$  = expected environmental component of variation.

## Genetic advance

When broad sense heritability ( $H^2$ ) estimates are available, progress from selection can be predicted for any breeding system, since expected gain (genetic advance) is a function of heritability. Therefore, such guided selection produces genetic advance. This change is of great interest to plant breeders, since it changes the population mean. The broad ( $H^2$ ) heritability in  $F_1$ s and  $F_2$ s was calculated for each character according to Hayman (1954), Verhalen and Murray (1969) and Mather and Jinks (1982). The magnitude of genetic advance from selection for a character in a cross under 5% selection intensity ( $K = 2.063$ ) and genetic advance as a

percent of the sample mean was calculated for each character in  $F_1$  and  $F_2$  generations according to Breese (1972).

$$F_1 \text{ and } F_2 \text{ broad sense heritability (H}^2\text{)} = \frac{\sigma^2_g}{\sigma^2_{ph}}$$

$$\text{Genetic advance} = K\sqrt{\sigma^2_{ph}} \cdot h_{(bs)}^2$$

$$\text{Genetic advance \%} = \frac{G.A}{\bar{X}} \times 100$$

$$\text{Genetic variance } (\sigma^2_g) = \frac{MSG - MSE}{r}$$

$$\text{Phenotypic variance } (\sigma^2_{ph}) = \frac{MSG}{r}$$

where MSG = genetic mean square of ANOVA; MSE = phenotypic (error) mean squares of ANOVA; r = number of replications;  $\bar{X}$  = population mean;  $\sigma^2_{ph}$  = standard deviation of phenotypic variation.

## Results

The analysis of variance manifested significant differences ( $p \leq 0.01$ ) among the  $F_1$  and  $F_2$  hybrids and their parental means for all the traits (Table 1).

### Parental differences and $F_1$ s performance

According to genetic potential, in the  $F_1$  generation the plant height varied from 105 to 155 cm among the

**Table 1.** Mean squares for 6 × 6  $F_1$  and  $F_2$  diallel cross of upland cotton

Variables	$F_1/F_2$	Genotypes mean squares <sup>1</sup>	CV % <sup>2</sup>
Plant height	$F_1$	1,095.637**	9.83
	$F_2$	392.399**	4.43
Monopodia	$F_1$	0.977**	14.44
	$F_2$	1.259**	8.86
Sympodia	$F_1$	34.337**	8.24
	$F_2$	13.276**	10.45
Lint %	$F_1$	4.773**	2.47
	$F_2$	4.560**	1.55
Seed cotton yield	$F_1$	4,472.994**	4.70
	$F_2$	1,343.963**	6.20

<sup>1</sup> \*\* Significant at  $p \leq 0.01$ . <sup>2</sup> CV: coefficient of variation.

parents and 117 to 187 cm among the hybrids (Table 2). The highest and statistically equal plant height of 168 to 187 cm was exhibited by the six  $F_1$  hybrids and reciprocals of cv CIM-1100 (CIM-1100 × FH-682, CIM-109 × CIM-1100, CIM-1100 × BH-36 and its reciprocal, CIM-1100 × CRIS-9 and its reciprocal). The shortest plants were recorded in cv CIM-240 (105 cm) and its crosses as a maternal parent with CIM-109 (117 cm) and CRIS-9 (119 cm). In the  $F_2$  generation the plant height varied from 116 cm (BH-36 × CRIS-9) to 161 cm (FH-682 × BH-36) among the hybrids. The highest and statistically equal plant height of 160 to 161 cm was exhibited by  $F_2$  hybrids CIM-1100 × BH-36 and FH-682 × BH-36, respectively, while the hybrid BH-36 × CRIS-9 (116 cm) exhibited the shortest plants.

According to mean performance, the monopodia per plant varied from 0.75 to 4.00 among the parents and 0.64 to 1.80 among  $F_1$  hybrids (Table 2). In  $F_1$  hybrids, the lowest and statistically equivalent means for monopodia were manifested by cross combinations CIM-240 × CIM-109 (0.64) and CIM-109 × CRIS-9 (0.67). The maximum monopodia were produced by cv CIM-1100 (4.00) followed by its hybrid CIM-1100 × BH-36 (1.80) and reciprocal (1.64). In  $F_2$  generation, the monopodia ranged from 0.58 (CIM-240 × CIM-109) to 1.50 (CIM-1100 × BH-36) among the hybrids. In  $F_2$ S the same hybrids as mentioned in  $F_1$  (CIM-240 × CIM-109 and CIM-109 × CRIS-9) produced the fewest monopodia (0.57 to 0.60). The parent cv CIM-1100 (4.00) produced maximum monopodia followed by its two derivatives, *i.e.* CIM-1100 × FH-682 (1.50) and CIM-240 × CIM-1100 (1.40).

The sympodia per plant were 16.09 to 21.68 among the parents and 22.33 to 33.00 in  $F_1$  hybrids (Table 2). The maximum sympodia in  $F_1$ s were produced by the hybrid CIM-109 × CIM-1100 (33.00). It was statistically equivalent to three hybrids of CIM-1100 as paternal parent *i.e.* FH-682 × CIM-1100 (31.33), BH-36 × CIM-1100 (30.00) and CIM-240 × CIM-1100 (29.67). All the six parent cultivars manifested the lowest sympodia per plant ranged from 16.09 to 21.68. The sympodia per plant varied from 17.81 (BH-36 × FH-682) to 25.87 (CIM-109 × CIM-1100) among the  $F_2$  hybrids. In  $F_2$  mean values, the maximum sympodia per plant were also exhibited by the same hybrid CIM-109 × CIM-1100 (25.87) as mentioned in  $F_1$ . It was statistically equivalent to CIM-1100, *i.e.* CIM-1100 × CRIS-9 (24.21).

In the  $F_1$  generation, the lint % varied from 32.54 to 36.50% among the parents and 32.84 to 36.92% among



**Table 2.** Mean differences for all the traits in 6 × 6 F<sub>1</sub> and F<sub>2</sub> diallel cross of upland cotton

Parents/Hybrids	Plant height (cm)		Monopodia (#)		Sympodia (#)		Lint (%)		Seed cotton yield (g plant <sup>-1</sup> )	
	F <sub>1</sub>	F <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>
<i>Parent cultivars</i>										
CIM-109	125		0.75		21.54		33.77		94.77	
CIM-240	105		0.80		21.68		36.14		54.31	
CIM-1100	141		4.00		16.09		36.50		87.73	
FH-682	155		0.89		19.35		32.54		89.73	
BH-36S	144		1.13		20.55		33.80		88.06	
CRIS-9	124		1.00		19.87		34.06		71.57	
<i>F<sub>1</sub> and F<sub>2</sub> hybrids</i>										
CIM-109 × CIM-240	141	122	0.70	0.65	25.33	17.89	35.76	34.41	101.89	71.25
CIM-109 × CIM-1100	178	144	1.43	1.30	33.00	25.87	36.60	35.34	162.68	96.55
CIM-109 × FH-682	160	134	0.95	0.85	25.00	20.66	32.84	32.96	74.53	68.25
CIM-109 × BH-36	139	124	1.00	0.90	25.67	19.13	34.35	34.60	95.55	69.75
CIM-109 × CRIS-9	125	127	0.67	0.60	23.67	21.94	34.29	34.18	89.61	87.93
CIM-240 × CIM-109	117	134	0.64	0.58	24.00	20.13	35.95	34.49	74.14	69.78
CIM-240 × CIM-1100	135	140	1.50	1.40	29.67	21.17	35.50	34.81	160.56	101.19
CIM-240 × FH-682	131	136	1.00	0.90	26.33	19.31	34.91	34.31	75.59	63.63
CIM-240 × BH-36	143	124	0.90	0.85	24.00	20.00	36.61	35.14	109.86	74.14
CIM-240 × CRIS-9	119	125	0.80	0.70	24.67	19.75	36.38	34.97	80.43	77.32
CIM-1100 × CIM-109	160	140	1.39	1.20	28.33	20.81	36.61	35.28	180.92	109.42
CIM-1100 × CIM-240	137	123	1.45	1.30	28.67	20.76	34.93	35.82	59.49	88.07
CIM-1100 × FH-682	187	150	1.46	1.20	26.00	21.13	35.35	34.29	164.16	138.10
CIM-1100 × BH-36	176	160	1.80	1.50	26.67	19.30	36.79	35.47	137.16	100.24
CIM-1100 × CRIS-9	171	137	1.49	1.20	27.67	24.21	35.58	34.01	169.98	121.84
FH-682 × CIM-109	151	131	0.75	0.67	27.67	18.88	33.31	33.08	114.80	74.33
FH-682 × CIM-240	141	131	0.98	0.85	25.33	19.69	34.54	32.64	83.83	77.84
FH-682 × CIM-1100	163	144	1.40	1.15	31.33	21.76	36.36	34.20	155.19	122.6
FH-682 × BH-36	157	161	1.20	1.00	26.33	21.00	35.11	33.60	87.49	68.77
FH-682 × CRIS-9	153	136	1.10	0.95	25.67	19.16	33.21	32.36	91.90	73.68
BH-36 × CIM-109	146	145	0.95	0.85	28.00	20.91	33.33	33.81	77.16	63.98
BH-36 × CIM-240	121	140	0.80	0.65	25.33	19.81	35.66	35.13	59.12	91.29
BH-36 × CIM-1100	168	140	1.64	1.30	30.00	21.92	36.92	35.13	183.58	102.53
BH-36 × FH-682	157	135	1.15	0.93	25.67	17.81	33.97	33.82	88.00	71.38
BH-36 × CRIS-9	163	116	1.20	0.97	24.67	21.25	33.47	33.91	113.62	81.64
CRIS-9 × CIM-109	140	125	0.90	0.80	25.00	21.09	34.85	34.87	101.03	93.06
CRIS-9 × CIM-240	132	131	0.88	0.78	22.33	19.24	34.66	34.41	75.92	74.05
CRIS-9 × CIM-1100	170	137	1.50	1.36	27.33	20.31	36.21	36.14	188.81	119.96
CRIS-9 × FH-682	159	139	1.05	0.96	26.00	18.83	33.75	33.38	116.26	81.04
CRIS-9 × BH-36	144	134	0.95	0.85	25.67	18.63	34.84	35.07	97.67	91.55
LSD <sub>(0.05)</sub>	23.45		0.277		3.408		1.406		8.197	

the hybrids (Table 2). Maximum and statistically equal values of lint% were recorded in two derivatives of CIM-1100 in direct (36.92%) and reciprocal cross (36.79%) with BH-36 in F<sub>1</sub> hybrids. They were followed by 10 other hybrids (having four derivatives of CIM-1100), and two parents ranged from 35.58 to 36.61%. The minimum values of lint% were those produced by

three parents (CIM-109, BH-36 & CRIS-9) and seven hybrids ranged from 32.84 to 34.06%. However, the lowest lint % was shown by cv FH-682 (32.54%). In F<sub>2</sub>, the lint % varied from 32.36% (FH-682 × CRIS-9) to 36.14% (CRIS-9 × CIM-1100) among the hybrids. Maximum and statistically equivalent lint% was exhibited by CIM-1100 and its three crosses with

CRIS-9, CIM-240 and BH-36 ranged from 35.47 to 36.38%.

In the  $F_1$  generation the seed cotton yield per plant varied from 54.31 to 94.77 g among the parents and 59.12 to 188.81 g among the hybrids (Table 2). The highest and statistically equivalent seed cotton yield was recorded in  $F_1$  hybrids CRIS-9  $\times$  CIM-1100 (188.81 g), BH-36  $\times$  CIM-1100 (183.58 g) and CIM-1100  $\times$  CIM-109 (180.92 g). These were followed by second top scoring hybrids, *i.e.* CIM-1100  $\times$  CRIS-9 (169.98 g), CIM-1100  $\times$  FH-682 (164.16 g), CIM-109  $\times$  CIM-1100 (162.68 g), CIM-240  $\times$  CIM-1100 (160.56 g) and FH-682  $\times$  CIM-1100 (155.19 g). In the  $F_2$  generation the seed cotton varied from 63.63 g (CIM-240  $\times$  FH-682) to 138.10 g (CIM-1100  $\times$  FH-682) among the hybrids. The highest seed cotton yield of 138.10 g was obtained in  $F_2$  hybrid CIM-1100  $\times$  FH-682 and was followed by three other derivatives of CIM-1100, *i.e.* FH-682  $\times$  CIM-1100 (122.60 g), CIM-1100  $\times$  CRIS-9 (121.84 g) and CRIS-9  $\times$  CIM-1100 (119.96 g). The lowest seed cotton yield was recorded in hybrid CIM-240  $\times$  FH-682 (63.63 g). The hybrids of

CIM-1100 have the maximum yield which may be utilized in the segregating generations to evolve the cultivars with good yield potential.

### Diallel analysis

The adequacy of additive-dominance model was tested through three scaling tests (regression analysis, arrays analysis and  $t^2$  test). The model was adequate for monopodia and lint % in both generations and for sympodia in  $F_2$  only. This shows that for the above traits, the regression analysis indicated that the regression coefficient (b) differed significantly from zero and not from unity (Table 3) which fulfills the assumptions of the Hayman-Jinks additive-dominance model. The analysis of variance of arrays revealed that  $W_r + V_r$  and  $W_r - V_r$  were non-significant (Tables 2). This indicated an absence of dominance with no nonallelic interaction and the genes were independent in their action for random association. These results were also confirmed by a non-significant value for the  $t^2$  test (Table 3).

**Table 3.** Scaling tests of adequacy of additive-dominance model ( $t^2$  test, regression analysis and arrays analysis of variance) for a  $6 \times 6$   $F_1$  and  $F_2$  diallel cross of upland cotton

Variables	$F_1/F_2$	$t^2$ test	Regression analysis (t value of b)		Analysis of variance of arrays		Conclusions
			b/S.E	b0, b1	$W_r + V_r$	$W_r - V_r$	
Plant height	$F_1$	3.563 <sup>NS</sup>	0.392 $\pm$ 0.187	b0 = 2.098 <sup>NS</sup> b1 = 3.248*	NS	NS	Model is partially adequate due to regression analysis
	$F_2$	4.373 <sup>NS</sup>	0.328 $\pm$ 0.182	b0 = 1.804 <sup>NS</sup> b1 = 3.697*	NS	NS	Model is partially adequate due to regression analysis
Monopodia	$F_1$	0.132 <sup>NS</sup>	1.010 $\pm$ 0.034	b0 = 29.744** b1 = -0.293 <sup>NS</sup>	NS	NS	Model is adequate shown by all the three tests
	$F_2$	0.249 <sup>NS</sup>	0.978 $\pm$ 0.037	b0 = 26.253** b1 = 0.580 <sup>NS</sup>	NS	NS	Model is adequate shown by all the three tests
Sympodia	$F_1$	7.993*	0.650 $\pm$ 0.096	b0 = 6.795** b1 = 3.659*	NS	NS	Model is partially adequate due to regression and «t»
	$F_2$	0.000 <sup>NS</sup>	0.874 $\pm$ 0.243	b0 = 3.600* b1 = 0.519 <sup>NS</sup>	NS	NS	Model is adequate shown by all the three tests
Lint %	$F_1$	2.754 <sup>NS</sup>	1.250 $\pm$ 0.238	b0 = 5.261** b1 = -1.053 <sup>NS</sup>	NS	NS	Model is adequate shown by all the three tests
	$F_2$	0.001 <sup>NS</sup>	0.937 $\pm$ 0.166	b0 = 5.656** b1 = 0.381 <sup>NS</sup>	NS	NS	Model is adequate shown by all the three tests
Seed cotton yield	$F_1$	35.665**	0.045 $\pm$ 0.081	b0 = 0.555 <sup>NS</sup> b1 = 11.739**	NS	NS	Model is partially adequate due to regression and «t»
	$F_2$	71.306**	-0.029 $\pm$ 0.058	b0 = -0.493 <sup>NS</sup> b1 = 17.629**	NS	NS	Model is partially adequate due to regression and «t».

\*, \*\*: Significant at  $p \leq 0.05$  and  $p \leq 0.01$ , respectively. NS: non-significant.

Hence, the model was adequate as confirmed by all the three scaling tests. However, the additive-dominance model was found to be partially adequate for plant height and seed cotton yield in both generations and for sympodia in  $F_1$  (Table 3). In these cases, the regression coefficient (b) and  $t^2$  test were inclined to inadequacy of the model; hence, the model became partially adequate due to the two later scaling tests for these traits.

The genetic components of variance in  $F_1$  for plant height revealed that additive (D), dominance ( $H_1$ ,  $H_2$ ),  $h^2$  and environmental variation (E) were significant, while F value was non-significant (Table 4). The dominance component ( $H_1$ ) was greater than D and the average degree of dominance at each loci ( $\sqrt{H_1/D} = 1.11$ ) was more than unity, confirming a high level of dominance of the loci affecting this trait. But it was not confirmed by the value of equation  $=\sqrt{4DH_1+F}/\sqrt{4DH_1-F}$  (0.46), which means that the recessive genes were more frequent than dominant genes and were in increasing position also due to positive value of  $h^2$ . The contradiction appeared in components of variation may be due to residual heterozygosity in the parents. However, the value of  $H_1$  was greater than  $H_2$ , indicating that positive and negative genes were asymmetrical in the parents as confirmed by the values of  $H_2/4H_1$  (0.20). In the case of plant height in the  $F_2$ ,

D was significant, while  $H_1$ ,  $H_2$ , F,  $h^2$  and  $E_2$  were found to be non-significant (Table 4). Mean degree of dominance ( $\sqrt{1/4 H_1/D} = 0.43$ ) was less than unity, indicating the presence of partial dominance. Asymmetric values of  $H_1$  and  $H_2$ , indicating irregular distribution of positive and negative genes as also observed in the value of  $H_2/4H_1$  (0.18). The F with non-significant negative value ( $-32.64$ ) revealed that recessive genes were more frequent with decreasing position due to negative value of  $h^2$  ( $-2.80$ ). The recessive gene effects were also revealed by the value of  $1/4\sqrt{4DH_1+1/2F}/1/4\sqrt{4DH_1-1/2F}$  (0.29).

The narrow ( $h^2$ ) and broad sense ( $H^2$ ) heritabilities were 0.67 and 0.81 in  $F_1$ s, while in  $F_2$  the  $h^2$  value was moderate (0.39) with high  $H^2$  (0.91) for plant height (Table 4). The value of  $H^2$  showed the genetic proportion (additive + dominant + interaction) of the total phenotypic variation, while  $h^2$  indicated only the additive proportion. Thus,  $H^2$  estimates eventually are to be greater than  $h^2$  and their relative magnitude explicates the proportion of additive variation within genetic variation. The genetic advance under 5% selection was 37.09, and its value as a percent of the population mean was 25.31%, while in  $F_2$  generation, the values were 20.79 and 15.37%. A negative correlation coefficient ( $r = -0.277$ ) in  $F_1$ s between the  $W_r + V_r$  and mid paren-

**Table 4.** Genetic components of variance for plant height, monopodia and sympodia plant<sup>-1</sup>, lint and seed cotton yield in a 6 × 6  $F_1$  and  $F_2$  diallel cross of upland cotton

Components	Plant height		Monopodia		Sympodia		Lint %		Seed cotton yield	
	$F_1$	$F_2$	$F_1$	$F_2$	$F_1$	$F_2$	$F_1$	$F_2$	$F_1$	$F_2$
D	258.45±49.64*	45.04±14.77*	1.60±0.02*	1.60±0.02**	2.73±2.59	4.21±1.31*	2.11±0.27*	2.88±0.005**	224.11±311.30	34.36±132.54
$H_1$	318.48±126.03*	77.25±149.82	0.61±0.05*	0.83±0.25*	49.55±6.56*	13.65±13.23	1.49±0.70*	0.43±0.69	3,543.07±790.26*	1,043.46±1,343.95
$H_2$	256.27±112.58*	56.98±133.84	0.34±0.05*	0.49±0.22	39.40±5.86*	7.14±11.82	1.53±0.62*	0.27±0.62	2,309.48±705.96*	667.58±1,200.57
F	-211.66±121.28	-32.56±71.74	1.30±0.05*	1.46±0.12**	10.80±6.32	10.64±6.34	-0.19±0.67	1.02±0.33*	-205.14±760.51	14.48±643.50
$h^2$	755.38±75.72*	-2.80±90.08	0.26±0.03*	0.57±0.15*	122.16±3.94*	2.64±7.96	0.93±0.42*	0.25±0.42	2,723.00±474.80*	23.15±808.06
E	67.22±18.76*	8.94±5.64	0.01±0.008	0.002±0.01	1.49±0.98	1.12±0.50	0.25±0.10*	0.08±0.03	8.33±117.66	7.22±50.52
$\sqrt{1H_1/D}$	1.11	0.43	0.62	0.36	4.26	0.81	0.84	0.19	3.98	2.76
$H_2/4H_1$	0.20	0.18	0.14	0.15	0.20	0.13	0.26	0.16	0.16	0.16
$\sqrt{4H_1+F}/\sqrt{4H_1-F}$	0.46	0.29	4.85	-8.49	2.73	-5.96	0.90	2.70	0.79	1.17
$h^2/H_2$	2.95	-0.05	0.76	1.16	3.10	0.37	0.61	0.93	1.18	0.03
Heritability ( $h^2$ )	0.67	0.39	0.75	0.99	0.08	0.62	0.64	0.99	0.59	0.11
Heritability ( $H^2$ )	0.81	0.91	0.97	0.99	0.87	0.66	0.84	0.94	0.99	0.98
Genetic advance	37.09 cm	20.79 cm	1.17	1.14	6.76	3.51	2.48%	2.25%	78.46 g	37.76 g
	(25.31%)	(15.37%)	(99.83%)	(108.67%)	(26.62%)	(17.35%)	(7.09%)	(6.55%)	(73.23%)	(43.83%)
$r(W_r + V_r/VP)$	-0.277	0.706	0.993**	0.990**	-0.942**	-0.975**	-0.903*	-0.738	0.328	-0.229

\* In  $F_1$  parameter value is significant when it exceeds 1.96 after dividing it by its standard error. \* In  $F_2$  parameter value is tested by «t» test at n-2 df after dividing it by its standard error.



tal ( $y$ ) denotes that dominant genes were more responsible for increased plant height (Table 4). However, the positive correlation between  $Wr + Vr$  and parental means indicated that recessive genes were responsible for plant height variation in  $F_{2s}$ , which was confirmed by the results of  $F_1$  generation where dominant genes increased this trait.

All the genetic components of variance ( $D$ ,  $H_1$ ,  $H_2$ ,  $F$  and  $h^2$ ) for  $F_1$  monopodia per plant were significant, while  $E$  was non-significant (Table 4). The additive component was greater than the dominance components and the genetic parameter value ( $\sqrt{H_1/D} = 0.62$ ) being less than 1 indicated an additive type of gene action. This was confirmed by a positive and significant value of  $h^2$  (0.26). An unequal value of  $H_1$  and  $H_2$  indicated asymmetric distribution of positive and negative genes and was confirmed by value of  $H_2/4H_1$  (0.14). In  $F_2$  monopodia, the  $D$  and  $F$  were highly significant;  $H_1$  and  $h^2$  were significant, while  $H_2$  and  $E_2$  were non-significant (Table 4). The  $D$  was also greater than  $H_1$  and  $H_2$  and the average degree of dominance was less than unity, indicating additive type gene action. This was also established by the ratio  $\frac{1}{4}\sqrt{4DH_1 + \frac{1}{2}F} / \frac{1}{4}\sqrt{4DH_1 - \frac{1}{2}F}$  (-8.49) and were in increasing position due to positive value of  $h^2$  (0.52). Unequal values of  $H_1$  and  $H_2$  and the value of formula  $H_2/4H_1$  (0.15) indicated asymmetry in the distribution of positive and negative genes. High values of  $h^2$  (0.75) and  $H^2$  (0.97) were also recorded in  $F_{1s}$ , while in  $F_{2s}$  the values were equivalent (0.99) for monopodia (Table 4). The genetic advance was 1.17 and its value as percent of the population mean was 99.83%, while in  $F_{2s}$  the values for selection response were 1.14 and 108.67%.

The genetic components of variance for  $F_1$  fruiting branches (sympodia) revealed that  $H_1$ ,  $H_2$  and  $h^2$  were significant, while the  $D$ ,  $F$ , and  $E$  were non-significant and dominance components were found greater than additive component (Table 4). The average degree of dominance was also more than unity, showing a dominance type of gene action. However, the  $H_1$  value was greater than  $H_2$ , indicating that positive and negative genes were not equally distributed as confirmed by the value of  $H_2/4H_1$  (0.20). The positive and non-significant value of  $F$  and significant positive value of  $h^2$  revealed that dominant genes were more frequent than recessive and were in increasing position in the parents for  $F_1$  sympodia. These results were confirmed by  $\sqrt{4DH_1 + F} / \sqrt{4DH_1 - F}$

(2.73) ratio. In the  $F_2$  generation, all the components of variance, exceptive the additive, were non-significant for sympodia (Table 4). The average degree of dominance was also less than one, confirming an additive type of gene action. This was also indicated by the ratio of  $\frac{1}{4}\sqrt{4DH_1 + \frac{1}{2}F} / \frac{1}{4}\sqrt{4DH_1 - \frac{1}{2}F}$  (-5.96).

Unequal values of  $H_1$  and  $H_2$  indicated an unbalanced distribution of positive and negative genes, which was confirmed by the value of  $H_2/4H_1$  (0.13). The positive and non-significant value of  $F$  (10.64) and positive value of  $h^2$  (2.64) indicated that the dominant genes were more frequent than recessive genes with increasing position. In the  $F_1$  generation,  $H^2$  and  $h^2$  were 0.87 and 0.08, while in  $F_{2s}$  the heritability values were 0.66 and 0.62 for sympodia, and  $F_{2s}$  showed almost the control of genetic variation by additive type of gene action. The genetic advance was 6.76 and its value as percent was 26.62% in  $F_{1s}$ , while the values were 3.51 and 17.35% in  $F_2$  generation. A significant negative correlation coefficient ( $r = -0.942$ ;  $r = -0.975$ ) was observed between  $Wr + Vr$  and mid parent ( $y$ ). Results indicated that for increased sympodia the dominant genes were responsible in both generations (Table 4).

The analysis of genetic variation showed that except  $F$ , all the genetic components ( $D$ ,  $H_1$ ,  $H_2$  and  $h^2$ ,  $E$ ) were significant for  $F_1$  lint % (Table 4). The additive component was higher than dominance components with the ratio of mean degree of dominance (0.84), which being less than unity also suggested absence of overdominance. The ratio  $H_2/4H_1$  (0.26) was close to 0.25, which confirmed the equal values of  $H_1$  and  $H_2$ , indicating symmetrical distribution of positive and negative genes. The negative value of  $F$  (-0.19) indicated an excess of recessive genes with increasing position due to the positive and significant value of  $h^2$  (0.93). The additive control of the trait was also confirmed by the ratio of  $\sqrt{4DH_1 + F} / \sqrt{4DH_1 - F}$  (0.90). In  $F_2$  lint %, the  $D$  component was highly significant and  $F$  was significant, while other components of variance were non-significant (Table 4). The additive component again exceeded dominance components and the average degree of dominance (0.19) was less than unity revealed additive gene action with partial dominance and also with increasing position due to significant positive value of  $h^2$  (0.93). The uneven values of  $H_1$  and  $H_2$  indicated unbalanced distribution of positive and negative genes as also observed in  $H_2/4H_1$  (0.16) ratio. In  $F_{1s}$  lint %, the medium  $h^2$  (0.64) and high  $H^2$  (0.84) values were observed (Table 4). However, in  $F_{2s}$  high  $h^2$  (0.99)

and  $H^2$  (0.94) values for said trait revealed that majority of the genetic inheritance was controlled by additive genes in  $F_2$  generation. The genetic advance was 2.48 and its percent value was 7.09% in  $F_1$ s, while in  $F_2$ s the values were 2.25 and 6.55% (Table 4).

Regarding genetic components of variance for seed cotton yield, D, F and E were non-significant. This may be due to significance of  $H_1$ ,  $H_2$  and  $h^2$  in  $F_1$  generation (Table 4). Dominance components dominated the additive component. The average degree of dominance was more than unity and suggested a dominance type of gene action. The non-significant negative value of F (-205.14) can not confirm the excess of recessive genes with increasing position due to positive and significant value of  $h^2$ . In  $F_2$ s, all the components of variance (D,  $H_1$ ,  $H_2$ , F,  $h^2$  and  $E_2$ ) were non-significant for seed cotton yield (Table 4). Dominance components again prevailed, as the average degree of dominance was being more than unity suggested dominance type of gene action. The non-significant positive value of F (14.48) indicated the excess of dominant genes with increasing position. The  $H_1$  was found greater than  $H_2$  which revealed the unbalanced distribution of positive and negative genes as also exhibited by the ratios of  $H_2/4H_1$  in both generations. In  $F_1$  generation, medium  $h^2$  (0.59) and high  $H^2$  (0.99) values were found, which indicated that half of the genetic effects were controlled by additive and half by dominant genes in seed cotton yield. In  $F_2$ s, low  $h^2$  (0.11) and high  $H^2$  (0.98) were also observed, which indicated that seed cotton yield was controlled by dominant genes. In  $F_1$ s the genetic advance was 78.46 and its value as percent of the population mean was 73.23%, whereas in  $F_2$ s the values were 37.76 and 43.83%. A positive correlation coefficient ( $r = 0.328$ ) between  $W_r + V_r$  and parental means ( $y$ ) revealed that recessive genes were responsible for increased seed cotton yield (Table 4).

## Discussion

On the basis of genetic potential of the parental lines and promising cross combinations, the derivatives of cv CIM-1100 could be used to create good cultivars. CIM-1100  $F_1$  and  $F_2$  hybrids with CIM-109, CIM-240, FH-682, BH-36 and CRIS-9 performed better for all the traits. But the in-between crosses of the later five cultivars (except CIM-1100) have not shown so much dependable good performance as compared to CIM-1100 hybrids for plant height, sympodia, lint% and

seed cotton yield. Due to significant differences among  $F_1$  and  $F_2$  hybrids along with parents for all the traits, the adequacy of additive-dominance model was tested through three scaling tests. The model was adequate for most of the traits except plant height and seed cotton yield for which the model was partially adequate in both generations. Hussain *et al.* (1999), Khan (2003) and Khan *et al.* (2007) analyzed the genetic mechanism in diallel cross of *G. hirsutum* and found that the Hayman-Jinks additive-dominance model was adequate for most of the traits in both generations. Aguado *et al.* (2008) also mentioned that the differences between  $W_r$  and  $V_r$  indicated that the additive/dominance model was adequate for seed cotton yield and its components. Lack of significant variations in the  $W_r - V_r$  arrays for seed cotton yield, lint% and lint yield suggested that assumptions of diallel analysis were valid (Godoy and Palomo, 1999). Hussain *et al.* (1999), Ahmad *et al.* (2003a,b), Ali *et al.* (2008) and Ali and Awan (2009) studied the nature of gene action and found that the additive-dominance model was partially adequate for majority of the traits. The present results revealed no epistasis with lack of dominance and showing that genes were independent in their action with random association among the parents. Verhalen *et al.* (1971) and Khan *et al.* (2003) also detected no epistasis in diallel studies of cotton.

Plant breeders are mostly interested in short stature cotton plants due to lodging problems in tall plants and the ease of picking shorter plants manually or by machine. The shortest plants were controlled by recessive genes according to correlation coefficient in both generations and the degree of dominance in the  $F_2$  generation. The additive component was significant in both generations, while  $H_1$ ,  $H_2$  were non-significant in the  $F_2$  with high heritability, hence, the plant height of desirable genotypes can be maintained through simple selection. Luckett *et al.* (1989), Ahmad *et al.* (2003a) and Khan *et al.* (2005) also mentioned that analysis of genetic components and parameters indicated that additive effects were more substantial as compared to nonadditive. Hussain *et al.* (1999), McCarty *et al.* (2004a,b) and Wu *et al.* (2006) have also mentioned additive variance. However, Ahmad *et al.* (1997) and Iqbal *et al.* (2005) noticed nonadditive type of gene action. The results in  $F_2$  generation were consistent with the findings of McCarty *et al.* (1996), who also observed additive gene action with partial dominance. The contradictory findings may be due to different factors such as the breeding material used and the climatic con-

ditions under which the experiments were conducted.

The additive component was significant and higher than dominance components in both generations for monopodia, while  $H_1$ ,  $H_2$  were non-significant in  $F_2$ . According to the degree of dominance, and the high ratios of heritability in both generations, we conclude that monopodia were governed by additive gene action. Therefore, the desirable genotypes can be maintained through simple selection in segregating generations. Significant positive correlation coefficients between  $W_r + V_r$  and parental means indicated that parents containing recessive genes were responsible for monopodia in both generations. Ahmad *et al.* (1997, 2003a) found similar results for vegetative branches in upland cotton. McCarty *et al.* (1996) also reported a similar ratio of heritability and genetic advance in both generations. However, the present results are in contradiction with the findings of Khan (2003) and Khan *et al.* (2005), as they found nonadditive gene action in inheritance of monopodia per plant. This exception might be due to different breeding materials and agro-climatic conditions under which the experiments were conducted.

In case of fruiting branches, the additive component was non-significant, while the dominance components were significant. This showed that dominance components were greater than additive component as confirmed by degree of dominance. However, in  $F_2$ s, components of variance—except additive—were non-significant for sympodia and the inheritance turned to additive type of gene action as authenticated by degree of dominance and high heritability and appreciable genetic gain. The sympodia can be improved in desirable genotypes through simple selection in  $F_2$  segregating generation. However, the overdominance in  $F_1$  generation can be used for exploitation of heterosis by selection in promising hybrids which can be used in hybrid cotton production for increased sympodia. McCarty *et al.* (1996) mentioned similar results for sympodia in both generations. The present results are in accordance with the findings of Khan *et al.* (2005) and Iqbal *et al.* (2005) who reported non-additive type of gene action for sympodia per plant. However, Ahmad *et al.* (2003a) and McCarty *et al.* (2004a,b) found that additive type of gene action was responsible for inheritance of this trait. The contradictory findings for the trait might be due to genotypic and environmental differences.

The lint % was controlled by additive gene action in both generations as indicated by significant additive components and higher values than dominance

components in both generations. It was also confirmed by mean degree of dominance and high heritability and genetic gain. At this sense, improvement can be made to lint % through simple selection. Parents with dominant genes were responsible for increased lint % in both generations. The present results are also in line with the findings of Tang *et al.* (1993), McCarty *et al.* (1996, 2004a,b), Hussain *et al.* (1999), Ahmad *et al.* (2003b), Yuan *et al.* (2005), Aguiar *et al.* (2007) and Ali and Awan (2009), who reported additive type of gene action with partial dominance for inheritance of lint%. However, Tang *et al.* (1996), Godoy and Palomo (1999), Basal and Turgut (2005), Iqbal *et al.* (2005), Mei *et al.* (2006), Esmail (2007) and Gamal *et al.* (2009) concluded non-additive type of gene action with over-dominance for lint %. Similar magnitude of heritability and genetic advance were also reported by Tang *et al.* (1996), Godoy and Palomo (1999) and Hussain *et al.* (1999) in both generations.

Seed cotton yield is an important trait and according to genetic components of variance, the dominance components dominated the additive variance and the average degree of dominance also suggested dominance type of gene action in both generations. A negative correlation coefficient (between  $W_r + V_r$  and parental means) in  $F_2$  indicated that the seed cotton yield was controlled by nonadditive gene action with overdominance. Selections in such promising hybrids can be used in hybrid cotton production for increased seed cotton yield. Tang *et al.* (1996), Basal and Turgut (2005), Iqbal *et al.* (2005), Khan *et al.* (2005), Esmail (2007) and Aguado *et al.* (2008) also mentioned that dominant gene effects were higher than additive for yield, because additive variance was found smaller than dominant components and that expression was also confirmed by degree of dominance. However, Luckett *et al.* (1989), Ahmad *et al.* (2003a,b), Aguiar *et al.* (2007) and Gamal *et al.* (2009) mentioned that for seed cotton yield, the additive gene effects were more important under favorable conditions but under stress, the nonadditive effects of the genes were more imperative. But heritability ( $h^2$ ) values were much smaller relative to broad sense heritability in both environments indicating that the additive component was smaller than the other components of variance.

McCarty *et al.* (2004a,b) also reported that additive effects significantly controlled all the agronomic traits. Tang *et al.* (1996) and Khan *et al.* (2005) mentioned that dominance genetic variances were greater than additive for yield and revealed the predominance of

nonadditive gene action for the inheritance of said trait indicating that hybrids should have an advantage for these traits compared to pure lines. However, the results revealed that selection in top promising hybrids having high heterotic effects can also be studied in segregating generations because the cultivars having recessive genes were responsible for increased seed cotton yield. Esmail *et al.* (1999) and Kumaresan *et al.* (2000) also reported high heritability for seed cotton yield. These results confirm the findings of Iqbal *et al.* (2005) who reported overdominance type of gene action for seed cotton yield. However, Tang *et al.* (1993), McCarty *et al.* (1996), Ahmad *et al.* (1997), Godoy and Palomo (1999), Hussain *et al.* (1999), Khan (2003), Lukonge (2005), Wu *et al.* (2006), Aguiar *et al.* (2007), Lukonge *et al.* (2007) and Khan *et al.* (2007) reported additive type of genetic control for seed cotton yield. The discrepancies with respect of phenotypic manifestation of this complex parameter might be due to different cultivars used under different environmental conditions.

As final conclusions, analysis of genetic components and parameters indicated that additive effects were substantial and heritability was high for a majority of traits. Therefore early-generation selection and pure-line breeding should be successful. The genotype CIM-1100 was identified as being potentially a good donor for hybridization owing to improved character expression for most traits. In addition, CIM-1100 hybrids can be reconstituted to work better as base material for hybrid cotton production.

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