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Diallel analysis of cotton leaf curl virus (CLCuV) disease, earliness, yield and fiber traits under CLCuV infestation in upland cotton

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Abstract

Genetic effects of CLCuV, earliness, yield, and lint traits were studied in a 6 × 6 F_1 and F_2 diallel populations of upland cotton. Hayman and Mather's genetic model (D and H) was used to determine the genetic mechanism and mode of inheritance for selected variables. The breeding material comprised one CLCuV tolerant (CIM-1100) and five CLCuV susceptible cotton cultivars (CIM-109, CIM-240, CIM-1100, FH-682, BH-36, CRIS-9), crossed in a 6 × 6 diallel fashion to generate thirty F_1 hybrids. An additive-dominance model was adequate for lint %, CLCuV resistant and affected plants, and partially adequate for bolls plant^{-1} and yield in both generations. However, the data were adequate for lint index and earliness in F_1 and F_2 populations, respectively, and partially fit in their respective generations. Additive effects controlled all the traits except bolls plant^{-1} and yield that proscribed non-additively in both generations. Most of the traits showed 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 parental cultivars ($H_2/4H_1 < 0.25$). Dominance effects suggested that substantial contribution of dominance was not due to heterogeneity of the loci in these parameters. Broad and narrow sense heritabilities were high for most of the traits. Dominant genes in CIM-1100 were reliable for increased CLCuV resistance, and its F_1 and F_2 progenies had the best performance for majority of traits. The CIM-1100 F_2 populations revealed a ratio of 3:1 (CLCuV resistant:diseased plants) due to monogenic dominant nature of CLCuV resistance.

Keyword: Additive-dominance model; additive vs. dominance genetic components; broad and narrow sense heritability; diallel analysis; F_1 and F_2 diallel crosses; genetic gain; *Gossypium hirsutum* L.
Abbreviations: CLCuBV_Burewala-CLCuV; CLCuMV_Multan-CLCuV; CLCuV_cotton leaf curl virus; D_additive genetic variance; E_environmental component of variation; F_mean of Fr values over arrays; H_1 & H_2_dominance variance; H_2 _(H_1 [1-(u-v)^2] [u = positive genes, v_negative genes); h^2_dominance effect; $\sqrt{H_1}/D$_average degree of dominance; $H_2/4H_1$_proportion of genes with positive and negative effects in the parents; $\sqrt{4DH_1}+F/\sqrt{4DH_1}-F$_proportion of dominant and recessive genes in the parental lines.

Introduction

Pakistan's economy is highly dependent on production of upland cotton, with 1815 textile and ginning units supported by millions of farmers, traders, and laborers earning livelihoods directly or indirectly from this crop (Tariq and Chaudhry, 2003; Khan and Hassan, 2011). Cotton leaf curl geminivirus (CLCuV) is a disease of cotton caused by a whitefly (*Bemisia tabaci* L.)-transmitted virus belonging to the genus Begomovirus (family Geminiviridae), Gemini virus subgroup III (Briddon et al., 2000). In Pakistan, CLCuV was first reported in 1967 near Multan, east of the Chenab River (Hussain and Ali, 1975; Mahmood et al., 2003, Mahmood, 2004). Affected cotton plants exhibit a wide range of symptoms such as stunted growth, small boll size, leaf curling / cupping, late maturity, and poor yield. In severe form, CLCuV affected plants may develop leaf-like outgrowths (enations) from the veins on the underside of leaves (Siddig, 1968; Farooq et al., 2011, 2013). During the last two decades, CLCuV has become a severe problem, imposing huge losses to cotton crop productivity in Pakistan (Farooq et al., 2011). By 1993-94, the cotton most commercial cultivars had become susceptible to CLCuV and cotton production seemed impossible in the Punjab, Pakistan until CLCuV-resistant cultivars were released (Tariq and Chaudhry, 2003). In 2001-2002, the commercial cotton cultivars resistant to Multan-CLCuV (CLCuMV) become susceptible to Burewala-CLCuV (CLCuBV), a new race of CLCuMV. Even the parental genetic stock from which new cotton cultivars were bred showed susceptibility to CLCuBV (Mahmood et al., 2003; Farooq et al., 2011, 2013). More recent study found that although cultivated genotypes were susceptible to CLCuBV, sources of resistance were observed in the wild genotypes of *G. hirsutum* L., *G. arboreum* L., *G. anomalum* L., *G. herbaceum* L. and *G. thurberi* L. (Akhtar et al., 2010). CLCuV disease is qualitative and controlled by single dominant gene or closely linked genes in cotton (Siddig, 1968). There has been some controversy about inheritance of CLCuV resistance among cotton breeders; however, it is controlled by single dominant gene and can be transferred to other cotton cultivar through backcrossing (Ali, 1997, 1999). The concept of polygenic inheritance of CLCuV disease was changed to a single dominant gene (with minor modifier genes) in cotton (Ahuja et al., 2006; Aslam et al., 2000). The F_1 hybrids between highly susceptible (S-12) and highly resistant (LRA-5166) cotton cultivars were found to be virus free, and their F_2 segregating population was close to a ratio of 3:1 (CLCuV resistant : diseased plants). This revealed the presence of a single dominant gene for the inheritance of resistance against CLCuV disease (Mahmood, 2004; Rehman et al., 2005). However, ambiguity prevails whether the CLCuV is controlled by dominant or recessive

genes which may be monogenic or polygenic (Farooq et al., 2011, 2013). Morphological, yields (seed and lint and contributing traits), and fiber quality traits are polygenic and quantitatively inherited in nature. Most cotton breeders realize difficulties in making genetic improvement by using simple genetic models, wherein few genetic features are used to illustrate mutable situations (Godoy and Palomo, 1999; Khan et al., 2009a; Khan and Hassan, 2011). Therefore, the quantitative traits in cotton are difficult to investigate because a) their demonstration is altered by environmental instability; b) yield is a complex characteristic resulting from various morpho-yield traits that are controlled by many genes with inconsistent effects (Yuan et al., 2005; Khan et al., 2009c); c) the expression of an individual gene is often masked and modified by other genes; d) linkage barriers are difficult to overcome; and e) the best genotype for a given environment may require genes from diverse sources to have broad genetic base (Ragsdale and Smith, 2007; Khan et al., 2009d, e; Batool and Khan, 2012). However, positive direct and indirect impacts of yield contributing traits on seed cotton and lint yields with high heritability are an indication that selection for these traits might be effective to enhance seed cotton yield even under severe CLCuV conditions (Farooq et al., 2013). Biometrical models using certain principal assumptions have been used to describe and analyze genetic variability. Diallel analysis, widely used by breeders for upland cotton (Basal and Turgut, 2005; Mei et al., 2006; Wu et al., 2006), is an effective tool to acquire specific information about superior genotypes and their cross combinations, understand the gene action involved in various traits, and to determine the performance of segregating populations. Several reviews have indicated that quantitative inheritance can help explain a considerable amount of useful genetic variability in cotton (Mather and Jinks, 1982; Ragsdale and Smith, 2007). Diallel analysis provides thorough knowledge about the inheritance pattern of polygenic economic traits, which is a pre-requisite for cotton improvement (Khan et al. 2007; Batool and Khan, 2012). Understanding quantitative genetics requires an ample study of diallel assumptions, additive-dominance models (through various scaling tests), genetic mechanisms, and genetic components of variation (additive vs. non-additive) (Esmail, 2007; Khan et al., 2009e; Aguado et al., 2008, 2010). These genetic attributes control the various variables in different cotton populations under diverse environmental conditions (Ali and Awan, 2009; Gamal et al., 2009). The objectives of this study were 1) to evaluate the genetic potential of 6 × 6 F_1 and F_2 diallel populations, 2) to appraise assumptions of the additive-dominance model for design and data adequacy, and 3) to determine the genetic mechanism and mode of inheritance of CLCuV disease resistance / susceptibility, earliness, bolls per plant, seed cotton yield and lint traits under CLCuV infestation in upland cotton.

Results

Mean performance of F_1 and F_2 populations and parental cultivars

Analysis of variance revealed significant ($p \leq 0.01$) differences among F_1 and F_2 populations and their parental cultivars means for all measured traits (Table 2), indicating significant genetic variability among the populations. The CLCuV tolerant cultivar CIM-1100 had 100% CLCuV resistant plants (Table 3), while for other cultivars, the highest percentages of CLCuV resistant plants were recorded in CIM-109 (57%), followed by FH-682 (55%), CRIS-9 (49%), CIM-240 (48%) and BH-36 (31%). The CLCuV diseased plants % in FH-682, CRIS-9, CIM-109, CIM-240 and BH-36 ranged from 51 to 69% with mild (10-26%), medium (13-33%) and severe (6-18%) symptoms. Cultivar BH-36 was highly susceptible to CLCuV, with 69% CLCuV diseased plants and mild (26%) to severe (10%) symptoms on plants. However, severe CLCuV infestation was found for cultivars FH-682 (18%), CIM-240 (14%), CIM-109 (9%), BH-36 (10%), and CRIS-9 (6%). In the F_1 generation, the 10 F_1 progenies of CIM-1100 had 100% CLCuV resistant plants; no small vein thickening was observed on the leaves, which confirmed the monogenic dominant nature of CLCuV resistance. However, 15 F_1 hybrids of five other cultivars were severely affected by CLCuV (53 to 81%), had mild (13-39%), medium (12-42%), and severe (3-16%) damage. In the F_2 generation (Table 3), CLCuV incidence showed some variation due to segregation in seven CIM-1100 F_2 populations (CRIS-9 × CIM-1100, CIM-240 × CIM-1100, CIM-1100 × CIM-109, CIM-1100 × BH-36, CIM-1100 × CRIS-9, BH-36 × CIM-1100, CIM-109 × CIM-1100), and CLCuV resistant plants ranged from 83 to 91%. The CIM-1100 F_2 population exhibited the lowest level of CLCuV disease, with mild (2-8%), medium (3-9%), and severe (4-12%) symptoms. The CIM-1100 F_2 populations had a ratio of 3:1 CLCuV resistant:diseased plants, which supports the hypothesis that CLCuV resistance is controlled by a single dominant gene. For earliness, days to flowering varied from 52 to 68 days among parental cultivars, 54 to 68 for F_1, and 49 to 64 days among F_2 populations (Table 4). The minimum days to flowering (52 days) were recorded in cv. CIM-240, closely followed by seven F_1 populations (54 to 56 days). Maximum days to flowering (68 days) were for parental cultivar CIM-1100 and F_1 hybrid FH-682 × CIM-240. In the F_2 generation, the fewest days to flowering (49 days) were recorded for CIM-240 × CIM-109 followed by seven other F_2 populations (50 to 52 days). All other genotypes showed medium days to flowering. Bolls per plant varied from 20 to 39, 20 to 53 and 25 to 44 among parental cultivars, F_1 and F_2 populations, respectively (Table 4). Equal bolls per plant (average = 53) were recorded in CIM-1100 F_1 hybrids i.e. CRIS-9 × CIM-1100, CIM-1100 × CIM-109 and its reciprocals, BH-36 × CIM-1100, and CIM-1100 × CRIS-9. However, in F_2 populations the boll number was highest in CIM-1100 × FH-682 (44) followed by CIM-1100 progenies as paternal parent i.e. FH-682 × CIM-1100 (40), CRIS-9 × CIM-1100 (39), CIM-109 × CIM-1100 (37) and as maternal parent CIM-1100 × CRIS-9 (39), CIM-1100 × CIM-109 (38) and CIM-1100 × BH-36 (38). Cultivar CIM-240 (20.00) and its crosses with CIM-1100 (20), BH-36 (22), CIM-109 (27) and FH-682 (23) and its reciprocal (26) produced the fewest bolls per plant. Seed cotton yield per plant ranged from 54 to 95 g, 59 to 189 g and 64 to 138 g among parental cultivars, F_1, and F_2 populations, respectively (Table 4). Highest and equal yield was recorded in F_1 hybrids that had CIM-1100 as a parent, i.e. CRIS-9 × CIM-1100 (189 g), BH-36 × CIM-1100 (184 g) and CIM-1100 × CIM-109 (181 g). In the F_2 generation, the CIM-1100 hybrids were promising for seed cotton yield, including CIM-1100 × FH-682 (138 g) followed by FH-682 × CIM-1100 (123 g), CIM-1100 × CRIS-9 (122 g), and CRIS-9 × CIM-1100 (120 g). However, the lowest seed cotton yield was measured for F_2 hybrid CIM-240 × FH-682 (64 g). Overall, the CIM-1100 F_1 and F_2 hybrids showed the best genetic potential, suggesting that base material could be developed in early segregating populations. For lint index, mean values for the parent cultivars, F_1, and F_2 populations varied from 4.0 to 5.4 g, 3.9 to 5.8 g and 3.8 to 5.2 g, respectively (Table 4). The highest lint index was recorded for F_1 hybrid CIM-240 × CIM-1100 (5.8 g), followed by CIM-1100 progenies i.e. CIM-109 × CIM-1100, CIM-1100 × FH-682 and their reciprocals, CIM-1100 × CIM-240, BH-36

Table 1. Cotton leaf curl virus (CLCuV) reaction, symptoms and rating (Siddig, 1968; Mahmood et al., 2003; Akhtar et al., 2010).

CLCuV Reaction	CLCuV Symptoms	CLCuV Rating
Resistant	No CLCuV symptoms	0
Mild	Leaf veins thickening of small groups	1
Medium	Leaf full veins thickening	2
Severe	Leaf curling, enation and plant stunting	3

Table 2. Mean squares for various variables of 6 × 6 F_1 and F_2 diallel cross in upland cotton.

Variables	Genotypes mean squares		CV %	
	F_1s	F_2s	F_1s	F_2s
CLCuV resistant plants (%)	2831.34**	845.11**	17.54	4.27
CLCuV diseased plants (%)	2830.60**	845.11**	11.79	8.65
Days to flowering	49.08**	80.64**	4.59	3.82
Bolls per plant	261.82**	83.14**	5.52	7.50
Seed cotton yield per plant	4472.99**	1343.96**	4.70	6.20
Lint index	0.89**	0.51**	3.95	4.73
Lint %	4.77**	4.56**	2.47	1.55

**, * = Significant at $p \leq 0.01$ and $p \leq 0.05$

× CIM-1100 and CRIS-9 × CIM-1100 ranging from 5.4 to 5.5 g in F_1 generation. The CIM-1100 F_2 hybrid CRIS-9 × CIM-1100 (5.2 g) had the highest lint index, followed by CIM-240 x 1100 and its reciprocal with at par lint index (5.1 g). The cross BH-36 × CRIS-9 showed the least lint index of 3.9 and 3.8 g in F_1 and F_2 generations, respectively. In parental cultivars, cv. CIM-1100 (5.4 g) showed maximum while cv. BH-36 (4.0 g) was observed with least lint index. Lint percentage varied from 32.5 to 36.5%, 32.8 to 36.9% and 32.4 to 36.1% among parental cultivars, F_1, and F_2 populations, respectively (Table 4). Maximum and equal lint % was observed in F_1 hybrid BH-36 × CIM-1100 (36.9%) and its reciprocal (36.8%) followed by 10 other F_1 populations (four derivatives of CIM-1100) and two parental lines ranging from 35.6 to 36.6%. The six F_1 hybrids showed lowest lint % ranging from 32.8 to 33.8%. In the F_2 generation, the highest lint % was exhibited by CIM-1100 × CRIS-9 (36.1%), followed by nine other F_2 populations (five progenies of CIM-1100) varying from 35.0 to 35.5%. The lowest lint % was produced by F_2 hybrid FH-682 × CRIS-9 (32.8%). In parental genotypes, the CIM-1100 (36.5%) and CIM-240 (36.1%) were the leading genotypes for lint %; followed by cultivars CIM-109, BH-36, and CRIS-9, however, lowest lint % was observed in FH-682 (32.5%). Days to flowering for the F_2 generation averaged a minimum of 55 days, which were less than equivalent days (60) took by parental cultivars and F_1 hybrids. In case of bolls per plant and seed cotton yield, the F_1 hybrids had the highest number of bolls per plant (36) and seed cotton yield (112 g), followed by F_2 hybrids (32 bolls per plant; 88 g seed cotton yield) and parental cultivars (31 # and 81 g), respectively. The lint index and lint percentage were highest in the F_1 hybrids (4.9 g, 35.1%) compared to F_2 hybrids (4.5 g, 34.4%) and parental cultivars (4.6 g, 34.5%). Due to inbreeding depression during segregation, the F_2 populations showed some decrease relative to F_1 hybrids; however, F_2 populations still performed better than parental cultivars for earliness and yield traits. Overall, the F_1 and F_2 hybrids of crosses CRIS-9 × CIM-1100, CIM-1100 × CIM-109, and BH-36 × CIM-1100 and their reciprocals, being tolerant to CLCuV, performed best for yield and fiber related traits.

Diallel analysis

Adequacy of the additive-dominance model was verified through three scaling tests (regression analysis, arrays analysis, and t^2 test) (Table 5). The model was adequate for CLCuV resistant and diseased plant % and lint % in both generations. For lint index and days to flowering, the model was adequate at F_1 and F_2 levels, respectively. For the above traits, the regression analysis indicated that the regression coefficient (b) differed significantly from zero and not from 1.0, which fulfills the assumptions of the additive-dominance model. Analysis of variance of arrays (Wr+Vr and Wr-Vr) revealed non-significant differences and an absence of dominance. There was no nonallelic interaction, and the genes were independent in their action for random association. This analysis was confirmed by a non-significant value of the t^2 test and inclined to allelic interaction. However, the model was partially adequate for bolls per plant and seed cotton yield in both generations, and for days to flowering and lint index in F_1 and F_2, populations respectively. In these traits, the analysis of variance of arrays was non-significant; however, the regression coefficient and t^2 test didn't fulfill the assumptions of additive-dominance model and were inclined to inadequacy that made the model partially adequate. For describing the percent of CLCuV resistant plants, the additive (D), dominance components of variance (H_1, H_2), dominance effect (h^2), and environmental component of variation (E) were significant, while covariance of additive and dominance effects (F) was non-significant in the F_1 generation (Table 6). Environmental variation played a large role in phenotypic appearance of CLCuV resistant plants % in the F_1 generation. The additive component was greater than dominance and average degree of dominance (0.91) was also less than 1.0, suggesting additive gene action for inheritance. The negative F value (-728.01) also indicated an excess of recessive genes, with increasing ratio due to the positive and significant value of h^2 (695.40). Additive control of this trait was confirmed by the ratio of $\sqrt{4DH1+F}$ / $\sqrt{4DH1-F}$ (0.35). For percent CLCuV resistant plants in the F_2 generation, the additive component was highly significant, whereas H_1, H_2, F, h^2, and E_2 were nonsignificant (Table 6). The greater additive component than dominance components, and the < 1.0 average degree of dominance (0.31), revealed absence of dominance. The nonsignificant positive F value (105.07) could not confirm the dominant genes with increasing ratio due to positive value of h^2 (11.22). Data suggest an unbalanced distribution of positive and negative genes, due to unequal values of H_1 and H_2 as confirmed by ratios of $H_2/4H_1$ (0.15, 0.17) in both generations. High narrow (0.86, 0.89) and broad sense (0.97, 0.99) heritabilities in F_1 and F_2 generations suggested that in CLCuV resistant plants the prevalence of genetic variation was controlled by additive gene effects. The genetic advance

Table 3. CLCuV incidence effect on plants (%) of 6 × 6 F_1 and F_2 diallel cross in upland cotton.

F_1, F_2 hybrids and parental cultivars	F_1 generation		F_2 generation		Classified CLCuV F_1 diseased plants (%)			Classified CLCuV F_2 diseased plants (%)		
	CLCuV RP (%)	CLCuV DP (%)	CLCuV RP (%)	CLCuV DP (%)	Mild (%)	Medium (%)	Severe (%)	Mild (%)	Medium (%)	Severe (%)
CIM-109 × CIM-240	46	54	72	28	33	12	9	9	9	10
CIM-109 × CIM-1100	100	0	91	9	0	0	0	2	3	4
CIM-109 × FH-682	53	47	75	25	25	22	0	11	9	5
CIM-109 × BH-36	53	47	77	23	31	13	3	13	5	5
CIM-109 × CRIS-9	64	36	70	30	15	18	3	12	9	9
CIM-240 × CIM-109	53	47	72	28	19	22	6	11	14	3
CIM-240 × CIM-1100	100	0	85	15	0	0	0	4	5	6
CIM-240 × FH-682	31	69	66	34	33	33	3	18	9	7
CIM-240 × BH-36	38	62	31	69	34	25	3	23	32	14
CIM-240 × CRIS-9	47	53	56	44	22	15	16	14	22	8
CIM-1100 × CIM-109	100	0	88	12	0	0	0	5	3	4
CIM-1100 × CIM-240	100	0	78	22	0	0	0	5	5	12
CIM-1100 × FH-682	100	0	77	23	0	0	0	8	7	8
CIM-1100 × BH-36	100	0	88	12	0	0	0	5	3	4
CIM-1100 × CRIS-9	100	0	84	16	0	0	0	5	4	7
FH-682 × CIM-109	44	56	73	27	31	19	6	13	9	5
FH-682 × CIM-240	41	59	61	39	13	31	15	13	19	7
FH-682 × CIM-1100	100	0	78	22	0	0	0	7	9	6
FH-682 × BH-36	55	45	55	45	18	18	9	16	15	14
FH-682 × CRIS-9	41	59	65	35	31	22	6	9	9	17
BH-36 × CIM-109	45	55	65	35	22	23	10	9	10	16
BH-36 × CIM-240	24	76	57	43	28	41	7	14	11	18
BH-36 × CIM-1100	100	0	89	11	0	0	0	4	3	4
BH-36 × FH-682	16	84	64	36	28	38	16	12	11	13
BH-36 × CRIS-9	31	69	60	40	36	27	6	20	5	15
CRIS-9 × CIM-109	31	69	75	25	39	24	6	9	9	7
CRIS-9 × CIM-240	34	66	60	40	39	27	0	18	13	9
CRIS-9 × CIM-1100	100	0	83	17	0	0	0	2	7	8
CRIS-9 × FH-682	19	81	59	41	30	42	9	20	13	8
CRIS-9 × BH-36	29	71	57	43	29	32	10	15	14	14
Parental cultivars										
CIM-109	57	43	-	-	-	-	-	21	13	9
CIM-240	48	52	-	-	-	-	-	15	23	14
CIM-1100	100	0	-	-	-	-	-	0	0	0
FH-682	55	45	-	-	-	-	-	10	17	18
BH-36	31	69	-	-	-	-	-	26	33	10
CRIS-9	49	51	-	-	-	-	-	17	28	6
$LSD_{0.05}$	16.32	8.23	-	-	-	-	-	-	-	-

CLCuV RP (%) = CLCuV resistant plants (%), CLCuV DP (%) = CLCuV diseased plants (%)

under selection was 64.36% and 32.61%, equivalent to percent values of 112.64% and 46.64% in F_1 and F_2 generations, respectively. Significant negative correlation coefficient (r = -0.957, r = -0.802) between Wr+Vr and parental means (y) in F_1 and F_2 generations, respectively, suggested that dominant genes contained by CIM-1100 were reliable for increased CLCuV resistance (due to monogenic dominant nature of CLCuV resistance). Five other cultivars with recessive genes had varying and lower ratios of CLCuV resistant plants. For percent CLCuV diseased plants in F_1 generation, components of variance other than F (D, H_1, H_2, h^2, and E) were significant (Table 6). These results suggest that environmental variation played an important role in phenotypic expression of the CLCuV diseased plant %. The additive component was greater than dominance components, and the average degree of dominance (0.88) was less than 1.0, indicating an absence of dominance. A negative F value (-679.43) also indicated an excess of recessive genes with increasing ratio due to a positive and significant value of h^2 (715.64), which was authenticated by the ratio of $\sqrt{4DH1+F}$ / $\sqrt{4DH1-F}$ (0.43). For percent disease among F_2 CLCuV plants, the D was highly significant, while H_1, H_2, F, h^2, and E_2 were non-significant (Table 6). The additive component was greater than dominance components and the average degree of dominance (0.33) was < 1.0, suggesting the absence of dominance. A positive but nonsignificant value of F (116.83) cannot authenticate the dominant genes with increasing ratio due to the positive value of h^2 (16.12). Uneven values of H_1 and H_2 indicated irregular allocation of positive and negative genes as confirmed by the ratios of $H_2/4H_1$ i.e. 0.16, 0.17 in F_1 and F_2 generations, respectively. In both generations, the narrow (0.87, 0.96) and equivalent broad sense heritabilities (0.99) were high, which indicated that inheritance was controlled by additive genes. The genetic advance values were 6.31% (147.64%) and 30.94% (102.85%) in F_1 and F_2 generations, respectively. Significant positive correlation between Wr+Vr and parental means in both generations (r = 0.957, r = 0.802) indicate that parental genotypes holding recessive genes were the cause of increased CLCuV diseased plants % and the decreased resistant plants %. However, cultivar CIM-1100, with maximum dominant genes, was capable of 100% CLCuV resistant plants in the F_1 and with maximum ratio of resistant plants in the F_2 generation after segregation. For days to flowering, the D and H_1, H_2 genetic components of variance

Table 4. Mean performance of cultivars and F_1 and F_2 populations for various traits in upland cotton.

Parental cultivars, F_1s & F_2s	Days to flowering		Bolls plant^{-1}		Seed cotton yield plant^{-1} (g)		Lint index (g)		Lint %	
CIM-109	58		39		95		4.1		33.8	
CIM-240	52		20		54		5.3		36.1	
CIM-1100	68		30		88		5.4		36.5	
FH-682	57		31		90		4.4		32.5	
BH-36	62		34		88		4.0		33.8	
CRIS-9	60		32		72		4.2		34.1	
Cultivar means	60		31		81		4.6		34.5	
F_1 and F_2 hybrids	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
CIM-109 × CIM-240	56	50	32	28	102	71	5.1	4.5	35.8	34.4
CIM-109 × CIM-1100	60	55	52	37	163	97	5.5	4.7	36.6	35.3
CIM-109 × FH-682	57	52	30	30	75	68	4.3	4.0	32.8	33.0
CIM-109 × BH-36	64	60	35	32	96	70	4.3	4.2	34.4	34.6
CIM-109 × CRIS-9	59	54	37	35	90	88	4.2	4.4	34.3	34.2
CIM-240 × CIM-109	54	49	27	27	74	70	5.2	4.7	36.0	34.5
CIM-240 × CIM-1100	56	52	45	34	161	101	5.8	5.1	35.5	34.8
CIM-240 × FH-682	59	55	23	25	76	64	5.2	4.7	34.9	34.3
CIM-240 × BH-36	56	52	34	28	110	74	5.2	4.8	36.6	35.1
CIM-240 × CRIS-9	57	53	31	31	80	77	5.1	4.6	36.4	35.0
CIM-1100 × CIM-109	64	62	53	38	181	109	5.5	4.7	36.6	35.3
CIM-1100 × CIM-240	57	53	20	32	59	88	5.4	5.1	34.9	35.3
CIM-1100 × FH-682	62	58	47	44	164.	138	5.4	4.8	35.4	34.3
CIM-1100 × BH-36	60	57	40	38	137	100	4.8	4.5	36.8	35.5
CIM-1100 × CRIS-9	58	53	51	39	170	122	4.9	4.7	35.6	34.0
FH-682 × CIM-109	57	52	36	31	115	74	4.5	4.0	33.3	33.1
FH-682 × CIM-240	68	64	26	29	84	78	5.1	4.4	34.5	32.6
FH-682 × CIM-1100	67	62	43	40	155	123	5.5	4.8	36.4	34.2
FH-682 × BH-36	66	61	29	26	87	69	4.6	4.3	35.1	33.6
FH-682 × CRIS-9	59	56	33	29	92	74	4.4	4.1	33.2	32.4
BH-36 × CIM-109	65	62	29	30	77	64	4.1	4.0	33.3	33.8
BH-36 × CIM-240	56	51	22	34	59	91	5.0	4.4	35.7	35.1
BH-36 × CIM-1100	63	58	52	35	184	103	5.5	4.5	36.9	35.1
BH-36 × FH-682	62	58	29	25	88	71	4.3	4.2	34.0	33.8
BH-36 × CRIS-9	57	53	39	30	114	82	3.9	3.8	33.5	33.9
CRIS-9 × CIM-109	55	52	41	34	101	93	4.3	4.5	34.9	34.9
CRIS-9 × CIM-240	58	53	28	28	76	74	5.0	4.6	34.7	34.4
CRIS-9 × CIM-1100	63	59	53	39	189	120	5.5	5.2	36.2	36.1
CRIS-9 × FH-682	56	53	35	31	116	81	4.6	4.1	33.8	33.4
CRIS-9 × BH-36	58	54	36	35	98	92	4.4	4.5	34.8	35.1
F_1 and F_2 hybrid means	60	55	36	32	112	88	4.9	4.5	35.1	34.4
$LSD_{(0.05)}$	4.460		3.182		8.197		0.309		1.406	

were significant, while F, h^2, and E were non-significant in F_1 generation (Table 6). The additive component was smaller than dominance components and the average degree of dominance ($\sqrt{H_1}/D = 1.13$) was more than 1.0, which showed the presence of dominance. A positive F value (18.56) indicated excess of dominant genes with decreasing ratio due to the negative value of h^2 (-1.33); this was confirmed by the ratio of $\sqrt{4DH1+F}$ / $\sqrt{4DH1-F}$ (1.91). In the F_2 generation, D was highly significant, whereas H_1, H_2, F, h^2, and E_2 components of variance were non-significant (Table 6). Average degree of dominance ($\sqrt{¼H_1}/D = 0.68$) was less than 1.0, which suggested partial dominance. The positive value of F (17.93) indicated an excess of dominant genes with increasing ratio due to positive value of h^2 (45.30), and these results were confirmed by the ratio of $¼\sqrt{4DH_1}+F/¼\sqrt{4DH_1}-F$ (2.85) as well. In both generations, unequal values of H_1 and H_2 indicated uneven allocation of positive and negative genes as confirmed by ratios of $H_2/4H_1$ (0.20, 0.21). Medium narrow (0.45, 0.77) and high broad sense (0.85, 0.94) heritabilities in F_1 and F_2 generations, respectively, indicated that most genetic variation was controlled by non-additive gene effects. In the F_1 generation, the genetic advance under selection was 8.04 days, while its value as percent of the population mean was 13.49%. In the F_2 generation, the corresponding values were 9.33 days and 16.63%, respectively. The nonsignificant positive correlation between Wr+Vr and parental means in F_1 (r = 0.399) and F_2 (r = 0.781) generations indicate that parental cultivars with recessive genes were responsible for earliness. Genetic components of variance for F_1 bolls per plant revealed that D, H_1, H_2, and h^2 were significant while F and E were not (Table 7). The additive component was smaller than both dominance components and the average degree of dominance was > 1.0 (2.19) indicating a high level of dominance of the loci affecting bolls per plant. A non-additive type of gene action with dominant genes in increasing position was confirmed by the significant positive value of h^2 (76.31). In case of F_2 bolls per plant, all the components of variance were nonsignificant (Table 7). Dominance components were greater than the additive component, and mean degree of dominance (2.07) was >1.0, indicating non-additive gene action with over-dominance. Unequal values of H_1 and H_2 indicated an asymmetric distribution of positive and negative genes as confirmed by $H_2/4H_1$ ratios in both generations. In F_1 and F_2 populations, the

Table 5. Additive-dominance model for various traits in 6 × 6 F_1 and F_2 diallel cross in upland cotton.

Variables	F_1 / F_2	t^2 test	Regression analysis (t value of b)		Analysis of variance of arrays		Remarks
			b/S.E	b0, b1	Wr + Vr	Wr – Vr	
CLCuV resistant plants (%)	F_1	0.006^{NS}	0.981 ±0.079	b0 = 12.481^{**} b1 = 0.236^{NS}	NS	NS	Adequate
	F_2	1.550^{NS}	0.806 ±0.118	b0 = 6.833^{**} b1 = 1.640^{NS}	NS	NS	Adequate
CLCuV diseased plants (%)	F_1	0.006^{NS}	0.981 ±0.079	b0 = 12.481^{**} b1 = 0.236^{NS}	NS	NS	Adequate
	F_2	1.550^{NS}	0.806 ±0.118	b0 = 6.833^{**} b1 = 1.640^{NS}	NS	NS	Adequate
Days to flowering	F_1	0.096^{NS}	0.379 ±0.546	b0 = 0.694^{NS} b1 = 1.136^{NS}	NS	NS	Partially adequate
	F_2	1.347^{NS}	1.156 ±0.307	b0 = 3.759^{*} b1 = -0.506^{NS}	NS	NS	Adequate
Bolls plant^{-1}	F_1	3.379^{NS}	0.323 ±0.200	b0 = 1.615^{NS} b1 = 3.384^{*}	NS	NS	Partially adequate
	F_2	8.878^{*}	0.030 ±0152	b0 = 0.200^{NS} b1 = 6.374^{**}	NS	NS	Partially adequate
Seed cotton yield plant^{-1}	F_1	35.665^{**}	0.045 ±0.081	b0 = 0.555^{NS} b1 = 11.739^{**}	NS	NS	Partially adequate
	F_2	71.306^{**}	-0.029 ±0.058	b0 = -0.493^{NS} b1 = 17.629^{**}	NS	NS	Partially adequate
Lint index	F_1	0.219^{NS}	0.947 ±0.081	b0 = 11.634^{**} b1 = 0.648^{NS}	NS	NS	Adequate
	F_2	0.125^{NS}	0.698 ±0.280	b0 = 2.491^{NS} b1 = 1.077^{NS}	NS	NS	Partially adequate
Lint %	F_1	2.754^{NS}	1.250 ±0.238	b0 = 5.261^{**} b1 = -1.053^{NS}	NS	NS	Adequate
	F_2	0.001^{NS}	0.937 ±0.166	b0 = 5.656^{**} b1 = 0.381^{NS}	NS	NS	Adequate

**, * = Significant at *p≤0.01 and p≤0.05*, NS = Non-significant.

negative and positive values of F (-0.91, 3.91, respectively) suggested that additive and dominant genes were equally frequent and in increasing position. The narrow sense heritability was medium in F_1 plants (0.66) and low in F_2 plants (0.16), whereas broad sense heritability was high in both generations (0.99, 0.93) suggesting that inheritance in bolls per plant was mainly governed by dominant genes. The genetic advance was 19.17 # (54.17%) in the F_1 generation, and 9.52 # and 29.72% in the F_2 generation. Correlation coefficient (r = 0.308, r = -0.025) between Wr+Vr and parental means indicated that parental lines with recessive and dominant genes were responsible for increased bolls per plant in F_1 and F_2 generations, respectively. For seed cotton yield, H_1, H_2, and h^2 were significant while other components were non-significant in the F_1 generation (Table 7). Dominance components were greater than the additive component and average degree of dominance was > 1.0 (3.98), suggesting dominance gene action. A non-significant negative value of F (-205.14) suggests no excess of recessive genes with increasing position because of the significant positive value of h^2 (2723.00). In the F_2 generation, all the components of variance (D, H_1, H_2, F, h^2, and E_2) were non-significant for seed cotton yield (Table 7). Dominance components again prevailed, as the average degree of dominance was 2.76, suggesting dominance type of gene action. Non-significant positive value of F (14.48) indicated an excess of dominant genes with increasing position due to a positive value of h^2 (23.15). In both generations, H_1 was greater than H_2, indicating an unbalanced distribution of positive and negative genes as confirmed by the ratios of $H_2/4H_1$ (0.16, 0.16). Medium and low narrow sense (0.59, 0.11) and high broad sense heritability (0.99, 0.98) values in F_1 and F_2 generations, respectively, indicated that genetic effects of seed cotton yield were controlled by dominant genes in both generations. In F_1 and F_2 plants, the genetic advance values were 78.46 g (73.23%) and 37.76 g (43.83%), respectively. Correlation (r = 0.328, r = -0.229) between Wr+Vr and parental means revealed that parental cultivars with recessive and dominant genes were responsible for increased seed cotton yield in F_1 and F_2 generations, respectively. For the F_1 lint index, the additive, dominance and h^2 components of variance were significant, whereas F and E were nonsignificant (Table 7). The additive component was greater than dominance components and the average degree of dominance (0.65) was <1.0, suggesting an absence of dominance. Unequal values of H_1 and H_2 indicated asymmetric distribution of positive and negative genes, which was confirmed by the ratio of $H_2/4H_1$ (0.22). A negative value of F (-0.19) indicated an excess of recessive genes in increasing position due to a significant positive value of h^2 (0.26), which was confirmed by the ratio of $\sqrt{4DH1+F}\ /\ \sqrt{4DH1-F}$ (0.41). In the F_2 generation, the additive component was highly significant while other all components (H_1, H_2, F, h^2, and E_2) were nonsignificant for lint index (Table 7). The additive component was greater than dominance components and the mean degree of dominance (0.19) was less than unity that suggested an absence of dominance. Equal values H_1 and H_2 indicated a balanced arrangement of positive and negative genes as confirmed by the ratio $H_2/4H_1$ (0.25). A negative value of F (-0.01) indicated an excess of recessive genes with decreasing position due to negative value of h^2 (-0.005). Additive gene action with partial dominance was confirmed by the ratio of $\frac{1}{4}\sqrt{4DH_1+\frac{1}{2}F)}\ /\ \frac{1}{4}\sqrt{4DH_1-\frac{1}{2}F)}$ (0.78). In F_1s and F_2s lint index, the narrow sense (0.87, 0.80) and broad sense heritability

Table 6. Genetic components of variance for various traits in 6 × 6 F_1 and F_2 diallel cross in upland cotton.

Components of variance	CLCuV resistant plants (%)		CLCuV diseased plants (%)		Days to flowering	
	F_1	F_2	F_1	F_2	F_1	F_2
D	827.57* ±37.34	432.82** ±28.21	864.01* ±37.34	441.64** ±28.21	26.22* ±4.59	27.55** ±3.53
H_1	684.94* ±94.80	163.78 ±286.07	746.10* ±94.80	187.31 ±286.07	33.64* ±11.67	50.48 ±35.84
H_2	402.13* ±84.69	112.22 ±255.55	475.00* ±84.69	129.87 ±255.55	26.54* ±10.42	43.40 ±32.02
F	-728.01 ±91.23	105.07 ±136.97	-679.43 ±91.23	116.83 ±136.97	18.56 ±11.23	17.93 ±17.16
h^2	695.40* ±56.96	11.22 ±172.00	715.64* ±56.96	16.12 ±172.00	-1.33 ±7.01	45.30 ±21.55
E	55.09* ±14.12	16.25 ±10.75	18.66* ±14.11	7.43 ±10.75	2.48 ±1.74	1.15 ±1.35
F_1: $\sqrt{4DH_1/D}$ F_2: $\sqrt{1/4DH_1/D}$	0.91	0.31	0.88	0.33	1.13	0.68
$H_2/4H_1$	0.15	0.17	0.16	0.17	0.20	0.21
F_1: $\sqrt{4DH1+F}/\sqrt{4DH1-F}$ F_2: $\frac{1}{4}\sqrt{4DH_1+F)}/\frac{1}{4}\sqrt{4DH_1-F)}$	0.35	2.30	0.43	2.37	1.91	2.85
h^2/H_2	1.73	0.10	1.51	0.12	-0.05	1.04
Heritability (h^2)	0.86	0.89	0.87	0.96	0.45	0.77
Heritability (H^2)	0.97	0.99	0.99	0.99	0.85	0.94
Genetic advance	64.36% (112.64%)	32.61% (46.64%)	63.31% (147.64%)	30.94% (102.85%)	8.04 days (13.49%)	9.33 days (16.63%)
r(Wr+Vr/VP)	-0.957**	-0.802*	0.957**	0.802*	0.399	0.781

*In F_1, the parameter value is significant when it exceeds 1.96 after dividing it with its standard error.
*In F_2, the parameter value is tested by "t" test at n-2 df after dividing it with its standard error.

Table 7. Genetic components of variance for various traits in 6 × 6 F_1 and F_2 diallel cross in upland cotton.

Components of variance	Bolls plant^{-1}		Seed cotton yield plant^{-1}		Lint index		Lint %	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
D	37.87* ±14.98	3.65 ±7.66	224.11 ±311.30	34.36 ±132.54	0.35* ± 0.02	0.21** ± 0.01	2.11* ±0.27	2.88** ±0.005
H_1	182.34* ± 38.02	62.37 ±77.68	3543.07* ±790.26	1043.46 ±1343.95	0.15* ± 0.04	0.03 ± 0.08	1.49* ±0.70	0.43 ±0.69
H_2	110.39* ±33.96	39.80 ±69.39	2309.48* ±705.96	667.58 ±1200.57	0.13* ± 0.04	0.03 ± 0.07	1.53* ±0.62	0.27 ±0.62
F	-0.91 ±36.59	3.91 ±37.20	-205.14 ±760.51	14.48 ±643.50	-0.19 ± 0.04	-0.01 ± 0.04	-0.19 ±0.67	1.02* ±0.33
h^2	76.31* ±22.84	8.56 ±46.71	2723.00* ±474.80	23.15 ±808.06	0.26* ± 0.02	-0.005 ± 0.05	0.93* ±0.42	0.25 ±0.42
E	1.33 ±5.66	1.43 ±2.92	8.33 ±117.66	7.22 ±50.52	0.01 ± 0.006	0.01 ± 0.003	0.25* ±0.10	0.08 ±0.03
F_1: $\sqrt{4DH_1/D}$ F_2: $\sqrt{1/4DH_1/D}$	2.19	2.07	3.98	2.76	0.65	0.19	0.84	0.19
$H_2/4H_1$	0.15	0.16	0.16	0.16	0.22	0.25	0.26	0.16
F_1: $\sqrt{4DH1+F}/\sqrt{4DH1-F}$ F_2: $\frac{1}{4}\sqrt{4DH_1+F)}/\frac{1}{4}\sqrt{4DH_1-F)}$	0.99	1.70	0.79	1.17	0.41	0.78	0.90	2.70
h^2/H_2	0.69	0.22	1.18	0.03	2.00	-0.17	0.61	0.93
Heritability (h^2)	0.66	0.16	0.59	0.11	0.87	0.80	0.64	0.99
Heritability (H^2)	0.99	0.93	0.99	0.98	0.96	0.91	0.84	0.94
Genetic advance	19.17 # (54.17%)	9.52 # (29.72%)	78.46 g (73.23%)	37.76 g (43.83%)	1.11 g (23.01%)	0.75 g (16.72%)	2.48% (7.09%)	2.25% (6.55%)
r(Wr+Vr/VP)	0.308	-0.025	0.328	-0.229	-0.974**	-0.384	-0.903*	-0.738

*In F_1, the parameter value is significant when it exceeds 1.96 after dividing it with its standard error.
*In F_2, the parameter value is tested by "t" test at n-2 df after dividing it with its standard error.

(0.96, 0.91) were high, revealed that genetic inheritance was controlled by both additive and non-additive genes. Genetic advance values were 1.11 g (23.01%) and 0.75 g (16.72%) in F_1s and F_2s, respectively. A significant negative correlation coefficient (r = -0.974, r = -0.384) between Wr+Vr and parental means suggested that parental lines with dominant genes were responsible for increased lint index in both generations. For the F_1 lint %, analysis of genetic variation showed that except for F, all genetic components (D, H_1, H_2 and h^2, and E) were significant (Table 7). The additive component was higher than dominance components, with a value of < 1.0 for average degree of dominance (0.84), suggesting absence of over-dominance. The ratio $H_2/4H_1$ (0.26) was close to 0.25, which confirmed the equal values of H_1 (1.49) and H_2 (1.53), indicating symmetrical distribution of positive and negative genes. A negative value of F (-0.19) indicated an excess of recessive genes with increasing position due to a significant positive value of h^2 (0.93). Additive control of the trait was confirmed by the ratio of $\sqrt{4DH1+F}$ / $\sqrt{4DH1-F}$ (0.90). For the F_2 lint %, the D and F components were highly significant and significant, respectively, while other components of variance were non-significant (Table 7). The additive component again exceeded dominance components and the average degree of dominance was 0.19. This indicates additive gene action with partial dominance with increasing position due to a significant positive value of h^2 (0.93). Uneven values of H_1 (0.43) and H_2 (0.27) indicated an unbalanced distribution of positive and negative genes, as was also observed in the ratio of $H_2/4H_1$ (0.16). For the F_1 lint %, medium narrow sense (0.64) and high broad sense heritability (0.84) values were observed, while for F_2 the narrow sense (0.99) and broad sense heritability (0.94) values were high, indicating that both additive and non-additive genes were responsible for inheritance of lint % in the F_1 and F_2 generations. Genetic gain values in F_1 and F_2 generations were 2.48% (7.09%) and 2.25% (6.55%), respectively. A significant negative correlation (r = -0.903; r = -0.738) between Wr+Vr and parental means suggests that parental cultivars with dominant genes were responsible for increased lint % in F_1 and F_2 generations, respectively.

Discussion

CIM-1100 was tolerant to CLCuV, whereas cultivars CIM-109, FH-682, and CRIS-9 were medium tolerant / susceptible. However, the CIM-1100 crosses with these cultivars (in addition to BH-36) produced promising F_1 and F_2 hybrids with desired genetic potential for CLCuV resistance and high yielding ability. The cultivars BH-36 and CIM-240 proved to be highly susceptible to CLCuV. Involvement of CIM-1100 in most of the F_1 and F_2 hybrids resulted in the synthesis of superior genotypes for most of the traits, and simple selection in top performing hybrids can generate promising population in segregating generations (Khan et al., 2007; Khan et al., 2009a). The F_1 hybrid mean values were higher than values for F_2 plants, though F_2 plants exceeded their parental cultivars, however, for earliness the F_2 populations were the leading. The promising populations (CRIS-9 × CIM-1100, CIM-1100 × CIM-109, and BH-36 × CIM-1100) and their reciprocals were tolerant to CLCuV in F_1 and F_2 generations, and showed remarkable performance for all the traits. Therefore, these populations could be screened for hybrid cotton production at F_1 and F_2 levels because of non-additive control, however, due to desirable narrow sense heritability; the base material can also be developed through intensive selection in early segregating populations. The F_1 and F_2 populations, along with parental lines, revealed significant variability by showing significant differences for all traits. Based on genetic potential, cv. CIM-1100 F_1 and F_2 progenies performed better for studied traits, which could be used to create promising base lines / cultivars. However, the F_1 and F_2 populations included five other cultivars (CIM-109, CIM-240, FH-682, BH-36, and CRIS-9) that did not show reliable performance as compared to CIM-1100 hybrids for CLCuV resistance, earliness, bolls per plant, seed cotton yield, and lint related traits. Cultivar CIM-1100 was the leading general combiner in combination with other cultivars (BH-36, CIM-240, FH-682, and CRIS-9) and their hybrids, which showed high mean performance for yield related traits (Khan et al., 2007, 2009d). Based on transgressive segregation, heritability with appreciable genetic gain, the selection made in CIM-1100 F_2 populations surpassed the standard cultivar CIM-446 for various traits (Khan et al., 2009e). The upland cotton cultivars (CIM-499, CIM-473, CIM-496, CIM-506) had higher genetic variability and space for improvement in seed yield and its attributes (Khan et al., 2009b; 2010a, b). Greater genetic variability indicated variable performance of the F_1 and F_2 populations and their parental lines for yield and lint traits and their vital role in managing seed cotton yield (Aguiar et al., 2007; Khan, 2011). In these studies, days to flowering was used as a measure of earliness. Overall, the F_2 populations took minimum days to flowering, and the parental cultivars and F_1 hybrids were similar for days to flowering. This is a sign of improvement in earliness in the F_2 generation, and through intensive selection, the population with early maturity could be sorted out in the early segregating generations. In past studies, days to first flowering and boll opening (Gody, 1994; Godoy and Palomo, 1999), node for first fruiting branch (Gody, 1994; Babar et al., 2002; Baloch and Baloch, 2004) and earliness index (Iqbal et al., 2003; Rauf et al., 2005) were used as effective selection criterion for the assessment of earliness in combination with seed cotton yield used for comparison among upland genotypes. The analysis showed that the additive-dominance model was adequate for most of the traits except bolls per plant and seed cotton yield, for which the model was partially adequate in both generations. Genetic mechanism in diallel crosses of *G. hirsutum* L. showed that the additive-dominance model was adequate for most of the traits in F_1 and F_2 generations (Khan et al., 2007, 2009c; Aguado et al., 2010; Hussain et al., 2012). Differences between Wr and Vr indicated that an additive-dominance model was adequate for yield and its components in upland cotton (Aguado et al., 2008; Khan and Hassan, 2011). Lack of significant variations in the Wr-Vr arrays for seed cotton yield, lint %, and lint yield suggested that assumptions of diallel analysis were valid in cotton (Godoy and Palomo, 1999). However, some studies relating to the nature of gene action revealed that an additive-dominance model was partially adequate for majority traits in upland cotton (Ali and Awan, 2009; Batool and Khan, 2012), and all the traits were partially fit for an additive dominance genetic model in cotton (Ahmad et al., 2003a, b; Abbas et al., 2008). Our results revealed no epistasis with a lack of dominance and showed that genes were independent in their action with random association among the parental cultivars. Nevertheless, epistasis was observed in the inheritance of boll weight in upland cotton (Sohu et al., 2010). The CLCuV tolerant cv. CIM-1100 F_1 progenies were fully resistant to CLCuV and confirmed that a single dominant gene was responsible for CLCuV disease resistance. In previous studies, the CLCuV disease resistance was controlled by a single dominant gene or closely linked genes in cotton (Siddig, 1968). Genes responsible for CLCuV resistance were, in general, dominant to their alleles responsible for CLCuV susceptibility (Hussain

et al., 2012). Our results revealed that after segregation, the CIM-1100 F_2 populations had a ratio of 3:1 (CLCuV resistant : diseased plants) due to monogenic dominant nature of CLCuV disease resistance. In previous studies, the same ratio was shown by F_2 populations, indicating that a single dominant gene controlled the CLCuV resistance in cotton (Aslam et al., 2000; Mahmood, 2004). Significant negative correlation between Wr+Vr and parental means suggested that dominant genes contained by CIM-1100 were reliable for increased CLCuV resistance in F_1 and F_2 generations. The percent of CLCuV diseased plants was controlled by additive gene action and has a significant positive correlation coefficient in Wr+Vr/VP in F_1 and F_2 populations. This indicates that cultivars (except CIM-1100) with maximum recessive genes were responsible for increased CLCuV diseased plants %. Previous findings showed that dominant genes controlled CLCuV resistance with varied categories of CLCuV incidence observed in various cotton populations (Aslam and Gilani, 2000), which supported the present investigations. The parental genetic stock (from which new cotton cultivars were bread) had shown susceptibility to new strain of virus known as CLCuBV in Pakistan (Mahmood et al., 2003; Tariq and Chaudhry, 2003). However, some new sources of resistance were observed in the wild genotypes of five species (*G. hirsutum, G. arboreum, G. anomalum, G. herbaceum, G. thurberi*), which can be used for development of CLCuBV resistant cultivars (Akhtar et al., 2010). Therefore, breeders should search for CLCuV resistant genes in old land races, cultivars, and wild genotypes of some species, because host plant resistance is the only way for the crop to escape from CLCuV disease. Earliness is an important parameter, and the additive and dominance components of variance revealed that days to flowering were controlled by dominant genes in the F_1 and by additive genes in the F_2 generation. Hence, through intensive selection, the genotypes for early squaring and boll opening could be obtained in early segregating generations, and the late maturity could be handled easily in hybrid cotton production. In past studies, the additive type of gene action with partial dominance governed the earliness in upland cotton (Godoy and Palomo, 1999; Iqbal et al., 2003; Rauf et al., 2005; Song et al., 2005) and our results are in agreement. However, non-additive gene action was responsible for earliness in *G. hirsutum* L. (Basal and Turgut, 2005; Sohu et al., 2010). The two indicators (days to first flowering, node number of first sympodial branch) were more reliable and efficient while predicting the earliness in upland cotton (Panhwar et al., 2002). The contradictory findings might be due to different breeding material used under varied environmental conditions. Bolls per plant is an important yield component, which was governed by non-additive gene action. Selection in promising hybrids can be used in hybrid cotton production for increased bolls per plant. Broad sense heritability values were high in both generations; however, the narrow sense heritability values were medium in F_1 and extremely low in F_2 generation, indicating that non-additive type of gene action was more substantial in inheritance of bolls per plant. Moreover, selection in top performing hybrids can be studied in segregating generations because cultivars with recessive and dominant genes were responsible for increased bolls per plant in F_1 and F_2 generations, respectively. Bolls per plant were non-additively controlled and contributed maximum dominance effects in upland cotton (Ahmad et al., 2000; Mei et al., 2006; Khan et al., 2009a, c; Batool and Khan, 2012), and were in quite corroboration with present results. However, additive gene action for the inheritance of bolls number was observed in upland cotton (Khan et al., 2007). Such contradictory findings could be attributed to genotypic and environmental variations involved in various studies. Seed cotton yield is an important and complex trait and, according to components of variance and correlation, seed cotton yield was controlled by non-additive gene effects with over-dominance. Through intensive selections, the promising populations can be identified for use in hybrid cotton to enhance the seed cotton yield. Predominance of non-additive gene action for seed cotton yield indicating that F_1 hybrids should have an advantage as compared to pure lines for yield and its components in *G. hirsutum* L. (Basal and Turgut, 2005; Esmail, 2007; Aguado et al., 2008; Batool and Khan, 2012). However, additive genetic control for seed cotton yield and major yield contributng traits was reported in upland cotton (Wu et al., 2006; Khan et al., 2007; Abbas et al., 2008; Gamal et al., 2009). Lint index was controlled by additive genes in both generations and there is a greater possibility of selecting desirable genotypes for lint index in early segregating generations. Involvement of additive genetic effects in the phenotypic expression of lint index was observed in upland cotton (Nadeem and Azhar, 2004; Mei et al., 2006; Ali and Awan, 2009; Khan et al., 2007, 2009a) and supported the present results. However, some have suggested that non-additive gene action was responsible for the inheritance of lint index (Ahmad et al.. 2003b; Chandio et al., 2003; Mehetre et al., 2004; Basal and Turgut, 2005; Song et al., 2005; Khan et al., 2009d). A significant negative correlation coefficient between Wr+Vr and parental means, indicates that parental cultivars with dominant genes were responsible for increased lint index in both generations. Such variation with respect to phenotypic manifestation of the trait might be due to different genotypes used under diverse agro-climatic conditions. Lint % was controlled by additive gene action as indicated by genetic components of variance in both generations. Therefore, improvement can be made to lint % through simple selection in early segregating populations. However, the cultivars with dominant genes were responsible for increased lint % in both generations due partial dominance. In previous findings, it was also reported that inheritance of lint % was controlled by additive gene action (Ahmad et al., 2003a; Yuan et al., 2005; Aguiar et al., 2007; Ali and Awan, 2009; Khan and Hassan, 2011), and were in corroboration with present results. However, non-additive gene action with over-dominance was found responsible for management of lint % (Godoy and Palomo, 1999; Iqbal et al., 2003; Gamal et al., 2009). The narrow sense heritability was smaller than broad sense in both generations indicating that additive variance was not too much responsive than other components of variance for yield. However, selection in promising populations could be studied in segregating generations because the cultivars with recessive genes were responsible for increased seed cotton yield. Additive genetic effects and reasonable narrow sense heritability suggested that breeding might be progressive for genetic improvement in seed cotton yield and its attributes (Abbas et al., 2008; Khan et al., 2009a, d, e). The discrepancies with respect of phenotypic manifestation of this complex parameter might be due to different cultivars used under diverse environmental conditions. Data on genetic evidence for various variables of upland cotton in F_1 and F_2 populations suggest a change in the allelic gene action; however, most of the times it might be due to genes interaction. These differences could be attributed to the changes in the genetic material and environmental conditions under which the experiments were conducted. Therefore, one can argued that environments are different and they affect the genetic architecture of crop plants, particularly in space and time. Therefore, while

breeding new crop cultivars, the breeder should not lose sight of different environmental conditions under which a cultivar is being developed, and for those areas where it is going to be cultivated. That is why comprehensive information on the environment and its effect on different genotypes under a particular condition are essential before synthesis of a new genotype for commercial exploitation.

Material and methods

Breeding material and field procedure

Studies were conducted during 2008-2010 at The University of Agriculture, Peshawar, Pakistan. Peshawar lies between 34°, 02′ North latitude and 71°, 37′ East longitude. The breeding material composed of one CLCuV tolerant (CIM-1100) and five CLCuV susceptible upland cotton cultivars (CIM-109, CIM-240, CIM-1100, FH-682, BH-36, CRIS-9) had a broad genetic base by parentage, morpho-yield, and fiber quality traits. During 2008, the parental genotypes were crossed in a complete diallel fashion to generate 6 × 6 F_1 diallel populations with the aim to transfer the CLCuV resistance, and to develop the base population through intensive selection in segregating generations. During 2009, some seeds of F_1 populations were hand sown and allowed to self to advance the generation and to have seeds for the F_2 crop. During 2010, 30 F_1 and F_2 populations and their parental cultivars were hand sown using a randomized complete block (RCB) design. The F_1 genotypes were planted in two rows measuring 5.0 m long (with 34 plants of each F_1 hybrid/replication) with three replications. In the F_2 crop, the plant population was increased and each F_2 hybrid was planted in four rows with row length of 5.0 m (68 plants of each F_2 hybrid/replication) with three replications. Plant- and row-spacing were 30 and 75 cm, respectively. Recommended cultural practices, inputs, and plant protection measures were applied equally to all populations. On an individual plant basis, two hand pickings were made during the month of November, and ginning was done with eight saw gins.

Trait measurement and statistical analyses

According to CLCuV incidence, all the plants of the F_1, F_2 populations and parental plants were divided into two groups i.e. CLCuV resistant and CLCuV diseased plants %. However, as per severity of the CLCuV, the diseased plants were further classified into three groups with some modifications i.e. mild, medium and severe (Siddig, 1968; Mahmood et al., 2003; Akhtar et al., 2010) (Table 1). In each population and replication, ten plants were randomly selected, and data were recorded on earliness (days to flowering), bolls per plant (#), seed cotton yield per plant (g), lint index (g), and lint (%). The mean data for all the traits were subjected to analysis of variance to test the null hypothesis of no differences among various F_1 as well as F_2 hybrids and their parental cultivars (Steel et al., 1997). Mean values for each variable were further separated and compared by using the least significant difference (LSD) test at 5% level of probability.

Diallel analysis

Hayman's diallel approach (1954a, b) and Mather's concept of D and H genetic components of variation for additive and dominance variances, respectively (D used for additive variance instead of A, and H_1 and H_2 for dominance components of variance instead of D) were used for genetic analysis (Mather and Jinks, 1982).

Assumptions of diallel analysis and tests of adequacy

In diallel analysis, the information legitimacy from a group of genotypes is based on the following six assumptions: a) diploid segregation of chromosomes, b) homozygosity of the parental genotypes, c) absence of reciprocal effects, d) absence of epistasis, e) no multiple allelism, and f) independent assortment of genes among parental cultivars. Regarding these assumptions underlying the additive-dominance model, it is stated that *Gossypium hirsutum* L. is an amphiploid between the two unrelated species that had the genomes A and D (Kimber, 1961). In the gene pool, cotton cultivars maintained at different Cotton Research Institutes and selfed every year. Therefore, the parental cultivars of the crossing program were assumed to be homozygous for all the traits. The entries in the off diagonal cells of the diallel table were replaced by their means of direct and reciprocal crosses prior to analysis for removing the reciprocal differences. To fulfill the remaining three assumptions (absence of epistasis, no multiple allelism, and independent assortment of genes), the data were evaluated through three scaling tests (regression analysis, arrays analysis of variance Wr+Vr and Wr–Vr, and t^2 test) to determine the adequacy of the additive-dominance model. 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, then Wr+Vr must vary from array to array. Similarly, if there is epistasis, Wr–Vr will vary between arrays. Non-significant values of a t^2 test confirm the presence of no non-allelic interaction and signify that genes are independent in their action for random association in the 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 partially adequate.

Estimation of genetic components

The F_1 genetic components of variation were estimated according Hayman (1954a, b), while for F_2 genetic components of variance, Hayman's formulas were modified as suggested by Verhalen and Murray (1969) and Verhalen *et al.* (1971). The following components of variation i.e. D (additive genetic variance), H_1, H_2 (dominance components of variance), F (F is the mean of Fr values over arrays, while Fr is the covariance of additive and dominance effects in a single array), h^2 (dominance effect), E (environmental component of variation) and their various ratios, heritability (broad vs. narrow sense) and correlation coefficient between Wr+Vr and parental means (y) were estimated in F_1 and F_2 generations (Singh and Chaudhary, 1985). The magnitude of genetic advance from selection for a trait under 5% selection intensity (K = 2.063) and genetic advance as a percent of the population mean was calculated for each variable in F_1 and F_2 generations (Breese, 1972).

Conclusion

Additive gene effects were substantial and desirable narrow/broad sense heritabilities were obtained for most measured traits. Therefore, early-generation selection and pure-line breeding should be successful. The CIM-1100 F_2 populations confirm the ratio of 3:1 (CLCuV resistant:diseased

plants) due to the monogenic dominant nature of CLCuV resistance. Cultivar CIM-1100 was identified as being potentially a good donor parent for hybridization owing to CLCuV resistance and improved character expression for majority traits. In addition, CIM-1100 F_1 and F_2 hybrids could be reconstituted to work better as base material for hybrid cotton production.

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References

Abbas A, Ali MA, Khan TM (2008) Studies on gene effects of seed cotton yield and its attributes in five American cotton cultivars. J Agric Soc Sci 4(4): 147-152.

Aguado A, Santos BDL, Blanco C, Romero F (2008) Study of gene effects for cotton yield and verticillium wilt tolerance in cotton plant (*G. hirsutum* L.). Field Crop Res 107: 78-86.

Aguado A, Santos BDL, Gamane D, Moral LFGD, Romero F (2010) Gene effects for cotton-fiber traits in cotton plant (*G. hirsutum* L.) under verticillium conditions. Field Crop Res 116(3): 209-217.

Aguiar PAD, Penna JCV, Freire EC, Melo LC (2007) Diallel analysis of upland cotton cultivars. Crop Breed Appl Biotechnol 7: 353-359.

Ahmad S, Iqbal MZ, Ahmad S, Sadiq MA, Khan NI (2003a) Genetic analysis of morphological characteristics and seed oil content of cotton (*G. hirsutum* L). J Biol Sci 3: 396-405.

Ahmad S, Iqbal MZ, Hussain A, Sadiq MA, Jabbar A (2003b) Gene action and heritability studies in cotton (*G. hirsutum* L.). J Biol Sci 3: 443-450.

Ahmad S, Khan TM, Khan AM (2000) Genetic studies of some important quantitative characters in *G. hirsutum* L. Int J Agric Biol 2(1-2): 121-124.

Ahuja SL Monga D, Dhayal LS (2006) Genetics of resistance to cotton leaf curl disease in *G. hirsutum* L. under field conditions. J Hered 49: 1-5.

Akhtar KP, Haider S, Khan MKR, Ahmad M, Sarwar N, Murtaza MA, Aslam M (2010) Evaluation of *Gossypium* species for resistance to leaf curl Burewala virus. Ann Appl Biol 157: 135-147.

Ali M (1997) Breeding of cotton varieties for resistance to cotton leaf curl Virus. Pak J Phytopathol 9(1): 1-7.

Ali M (1999) Inheritance of cotton leaf curl virus (CLCuV). Paper presented at the ICAC-CCRI Regional Consultation Insecticide Resistance Management in Cotton, June 28 to July 01, 1999, Multan, Pakistan, pp. 257-260.

Ali MA, Awan SI (2009) Inheritance pattern of seed and lint traits in cotton (*G. hirsutum* L.). Int J Agric Biol 11: 44-48.

Aslam M, Gilani AA (2000) Resistance of different cotton varieties to cotton leaf curl virus under field conditions. J Res Sci 11: 42-45.

Aslam M, Jiang C, Wright R, Paterson AH (2000) Identification of molecular markers linked to leaf curl virus disease resistance in cotton. J Sci IR Iran 11(4): 227-280.

Babar SB, Soomro AR, Anjum R, Memon AM, Soomro AW (2002) Two preliminary reliable indicators of earliness in cotton-II. Asian J Plant Sci 1(2): 121-122.

Baloch MJ, Baloch QB (2004) Plant characters in relation to earliness in cotton (*G. hirsutum* L.). Paper read at the Pak Acad Sci 41(2):103-108.

Basal H, Turgut I (2005) Genetic analysis of yield components and fiber strength in upland cotton (*G. hirsutum* L.). Asian J Plant Sci 4: 293-298.

Batool S, Khan NU (2012) Diallel studies and heritability estimates using Hayman's approach in upland cotton. SABRAO J Breed Genet 44(2): 322-338.

Breese EL (1972) Biometrical Genetics and its Application. Eucarpia Congress, Cambridge, pp. 135-146.

Briddon RW, Mansoor S, Bedford ID, Pinner MS, Markham PG (2000) Clones of cotton leaf curl geminivirus induce symptoms atypical of cotton leaf curl disease. Virus Genes 20(1): 19-26.

Chandio MA, Kalwar MS, Baloch GM (2003) Gene action for some quantitative characters in upland cotton (*G. hirsutum* L.). Pak J Sci Ind Res 46: 295-299.

Esmail RM (2007) Genetic analysis of yield and its contributing traits in two intra specific cotton crosses. J Appl Sci Res 3: 2075-2080.

Farooq A, Farooq J, Mahmood A, Shakeel A, Rehman A, Batool A, Riaz M, Shahid MTH, Mahboob S (2011) An overview of cotton leaf curl virus disease (CLCuD) a serious threat to cotton productivity. Aust J Crop Sci 5(13): 1823-1831.

Farooq J, Anwar M, Riaz M, Mahmood A, Farooq A, Iqbal MS, Iqbal MS (2013) Association and path analysis of earliness, yield and fiber related traits under cotton leaf curl virus (CLCuV) intensive conditions in *G. hirsutum* L. Plant Knowledge J 2(1): 43-50.

Gamal IAM, Abd-El-Halem SHM, Ibrahim EMA (2009) Genetic analysis of yield and its components of Egyptian cotton (*G. barbadense* L.) under divergent environments. Am-Eur J Agric Environ Sci 5: 05-13.

Godoy AS, Palomo GA (1999) Genetic analysis of earliness in upland cotton (*G. hirsutum* L.). I. Morphological and phonological variables. Euphytica 105: 155-160.

Gody S (1994) Comparative study of earliness estimates in cotton (*G. hirsutum* L.). ITEA Production-Vegetal 90(3): 175-185.

Hayman BI (1954a) The theory and analysis of diallel crosses. Genet 39: 789-809.

Hayman BI (1954b) The analysis of variance of diallel cross. Biometrics 10: 235-245.

Hussain T, Ali M (1975) A review of cotton diseases in Pakistan. Pak Cottons 19: 71-86.

Hussain M, Azhar FM, Khan AA, Ali Z (2012) Expression of genes controlling the inheritance of resistance to cotton leaf curl virus disease (CLCuD) in *G. hirsutum* L. a quantitative analysis. Pak J Bot 44(1): 247-254.

Iqbal M, Chang MA, Jabbar A, Iqbal MZ, Hassan M, Islam N (2003) Inheritance of earliness and other characters in upland cotton. J Biol Sci 3: 585-590.

Khan NU (2011) Economic heterosis for morpho-yield traits in F_1 and F_2 diallel crosses of upland cotton. SABRAO J Breed Genet 43(2): 144-164.

Khan NU, Basal H, Hassan G (2010a) Cottonseed oil and yield assessment via economic heterosis and heritability in intra-specific cotton populations. Afr J Biotechnol 9(44): 7418-7428.

Khan NU, Hassan G (2011) Genetic effects on morphological and yield traits in cotton (*G. hirsutum* L.). Span J Agric Res 9(2): 460-472.

Khan NU, Hassan G, Kumbhar MB, Marwat KB, Khan MA, Parveen A, Aiman U, Saeed M (2009a) Combining ability analysis to identify suitable parents for heterosis in seed cotton yield, its components and lint % in upland cotton. Ind Crop Prod 29: 108-115.

Khan NU, Hassan G, Kumbhar MB, Parveen A, Aiman U, Ahmad W, Shah SA, Ahmad S (2007) Gene action of seed traits and its oil content in upland cotton (*G. hirsutum* L.). SABRAO J Breed Genet 39: 17-29.

Khan NU, Hassan G, Marwat KB, Farhatullah, Batool S, Makhdoom K, Khan I, Khan IA, Ahmad W (2009b) Genetic variability and heritability in upland cotton. Pak J Bot 41(4): 1695-1705.

Khan NU, Hassan G, Marwat KB, Farhatullah, Kumbhar MB, Parveen A, Aiman U, Khan MZ, Soomro ZA (2009c) Diallel analysis of some quantitative traits in *G. hirsutum* L. Pak J Bot 41(6): 3009-3022.

Khan NU, Hassan G, Marwat KB, Kumbhar MB, Khan I, Soomro ZA, Baloch MJ, Khan MZ (2009d) Legacy study of cottonseed traits in upland cotton using Griffing's combining ability model. Pak J Bot 41(1): 131-142.

Khan NU, Marwat KB, Hassan G, Farhatullah, Batool S, Makhdoom K, Ahmad W, Khan HU (2010b) Genetic variation and heritability for cottonseed, fiber and oil traits in *G. hirsutum* L. Pak J Bot 42(1): 615-625.

Khan NU, Marwat KB, Hassan G, Kumbhar MB, Farhatullah, Soomro ZA, Khan N, Parveen A, Aiman U (2009e) Study of fiber quality traits in upland cotton using additive dominance model. Pak J Bot 41(3): 1271-1283.

Kimber G (1961) Basis of diploid meiotic behavior of polyploid cotton. Nature 19: 98-100.

Mahmood T, Arshad M, Gill MI, Mahmood HT, Tahir M, Hussain S (2003) Burewala strain of cotton leaf curl virus: A threat to CLCuV cotton resistant varieties. Asian J Plant Sci 2(13): 968-970.

Mahmood Z (2004) Inheritance of cotton leaf curl virus resistance in cotton (*G. hirsutum* L.). J Res (Sci) 15(3): 297-299.

Mather K, Jinks JL (1982) Introduction to Biometrical Genetics. Chapman and Hall Ltd. London.

Mehetre SS, Shinde GC, Rajput HJ, Solunke BD (2004) Genetic studies of seed cotton yield and its components in cotton. Ann Agric Res 4: 529-531.

Mei YJ, Ye ZH, Zhang LL (2006) Genetic analysis for F_1 yield traits with conditional approach in island cotton (*G. barbadense* L.). Acta Genet Sin 33(9): 841-850.

Nadeem K, Azhar FM (2004) Genetic analysis of seed cotton yield and its components in *G. hirsutum* L. Int J Agric Biol 6: 865-868.

Panhwar GN, Soomro AR, Anjum R, Babar SB, Memon AM, Soomro AW (2002) Predicting earliness in cotton during crop development stage-11. Asian J Plant Sci 1: 37-38.

Ragsdale PI, Smith CW (2007). Diallel analysis of within-boll seed yield components. Crop Sci 47(3): 1013-1017.

Rauf S, Shah KN, Afzal I (2005) A genetic study of some earliness related characters in cotton (*G. hirsutum* L.). Caderno de Pesquisa Ser Bio Santa Cruz do Sul 17(1): 81-93.

Rehman M, Hussain D, Malik TA, Zafar Y (2005) Genetics of resistance to cotton leaf curl disease in *G. hirsutum*. Plant Pathol 54: 764-772.

Siddig MA (1968) Genetics of resistance to cotton leaf curl virus in Sakel cotton, *G. barbadense* L. J Agric Sci Camb 70: 99-102.

Singh RK, Chaudhary BD (1985) Diallel Analysis. In: Biometrical Methods in Quantitative Genetic Analysis. Kalyani Publishers Ludhiana, New Delhi. pp. 102-164.

Sohu RS, Kumar T, Gill MS, Gill BS (2010) Genetic analysis for yield and earliness complex in upland cotton (*G. hirsutum* L.). J Cotton Res Dev 24(1): 1-4.

Song MZ, Yu SX, Fan SL, Ruan RH, Huang ZM (2005) Genetic analysis of main agronomic traits in short season upland cotton (*G. hirsutum* L.). Cotton Sci 17(2): 94-98.

Steel RGD, Torrie JH, Dickey DA (1997) Principles and Procedures of Statistics. A biometrical approach. 3rd Ed., McGraw Hill Book Co., New York, USA.

Tariq MA, Chaudhry IM (2003) Cotton crisis in the making? DAWN Newspaper, The Internet Edition (http://archives.dawn.com/2003/05/19/ebr8.htm).

Verhalen LM, Morrison RC, Al-Rawi BA, Fein KC, Murray JC (1971) A diallel analysis of several agronomic traits in upland cotton for various characters of cotton (*G. hirsutum* L.). Crop Sci 11: 92-96.

Verhalen LM, Murray JC (1969) A diallel analysis of several fiber properties traits in upland cotton (*G. hirsutum* L.). Crop Sci 9: 311-315.

Wu J, Jenkins JN, McCarty JC, Wu D (2006) Variance component estimation using the additive, dominance, and additive × additive model when genotypes vary across environments. Crop Sci 46: 174-179.

Yuan YL, Zhang TZ, Guo WZ, Pan JJ, Kohel RJ (2005) Diallel analysis of superior fiber quality properties in selected upland cotton. Acta Genet Sin 32(1): 79-85.