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 F1 and F2 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 F1 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 F1 and F2 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 (H1;H2) and an asymmetrical distribution of genes in the parental cultivars (H2;4H1 < 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 F1 and F2 progenies had the best performance for majority of traits. The CIM-1100 F1 populations revealed a ratio of 3:1 (CLCuV resistant:diseased plants) due to monogenic dominant nature of CLCuV resistance.

Keywords: Additive-dominance model; additive vs. dominance genetic components; broad and narrow sense heritability; diallel analysis; F1 and F2 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; H1 & H2 dominance variance; H1/2 (H1 [1-(u-v)²]) [u = positive genes, v negative genes]; h² dominance effect; \( \sqrt{H1/2} \) average degree of dominance; H2/4H1 proportion of genes with positive and negative effects in the parents; \( \sqrt{4DH1}+F/\sqrt{4DH1} \) 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). Affectected 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 F1 hybrids between highly susceptible (S-12) and highly resistant (LRA-5166) cotton cultivars were found to be virus free, and their F2 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., 2009c; Aguado et al., 2006, 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 F₁ and F₂ 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 F₁ and F₂ populations and parental cultivars

Analysis of variance revealed significant (p<0.01) differences among F₁ and F₂ 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 F₂ generation, the 10 F₂ 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 F₂ 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 F₂ generation (Table 3), CLCuV incidence showed some variation due to segregation in seven CIM-1100 F₁ 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 F₁ population exhibited the lowest level of CLCuV disease, with mild (2-8%), medium (3-9%), and severe (4-12%) symptoms. The CIM-1100 F₂ 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 F₁, and 49 to 64 days among F₂ populations (Table 4). The minimum days to flowering (52 days) were recorded in cv. CIM-240, closely followed by seven F₁ populations (54 to 56 days). Maximum days to flowering (68 days) were for parental cultivar CIM-1100 and F₁ hybrid FH-682 × CIM-240. In the F₂ generation, the fewest days to flowering (49 days) were recorded for CIM-240 × CIM-109 followed by seven other F₂ 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, F₁ and F₂ populations, respectively (Table 4). Equal bolls per plant (average = 53) were recorded in CIM-1100 F₁ 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 F₂ 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 × CIM-1100 (37), CIM-1100 × 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, F₁ and F₂ populations, respectively (Table 4). Highest and equal yield was recorded in F₂ 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 F₂ 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 F₂ hybrid CIM-240 × FH-682 (64 g). Overall, the CIM-1100 F₁ and F₂ 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, F₁, and F₂ populations varied from 4.0 to 5.8 g, 3.9 to 5.8 g and 3.8 to 5.2 g, respectively (Table 4). The highest lint index was recorded for F₂ 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).

<table>
<thead>
<tr>
<th>CLCuV Reaction</th>
<th>CLCuV Symptoms</th>
<th>CLCuV Rating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resistant</td>
<td>No CLCuV symptoms</td>
<td>0</td>
</tr>
<tr>
<td>Mild</td>
<td>Leaf veins thickening of small groups</td>
<td>1</td>
</tr>
<tr>
<td>Medium</td>
<td>Leaf full veins thickening</td>
<td>2</td>
</tr>
<tr>
<td>Severe</td>
<td>Leaf curling, enation and plant stunting</td>
<td>3</td>
</tr>
</tbody>
</table>

Table 2. Mean squares for various variables of 6 × 6 F1 and F2 diallel cross in upland cotton.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Genotypes mean squares</th>
<th>CV %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F1s</td>
<td>F2s</td>
</tr>
<tr>
<td>CLCuV resistant plants (%)</td>
<td>2831.34**</td>
<td>845.11**</td>
</tr>
<tr>
<td>CLCuV diseased plants (%)</td>
<td>2830.60**</td>
<td>845.11**</td>
</tr>
<tr>
<td>Days to flowering</td>
<td>49.08**</td>
<td>80.64**</td>
</tr>
<tr>
<td>Bolls per plant</td>
<td>261.82**</td>
<td>83.14**</td>
</tr>
<tr>
<td>Seed cotton yield per plant</td>
<td>4472.99**</td>
<td>1343.96**</td>
</tr>
<tr>
<td>Lint index</td>
<td>0.89**</td>
<td>0.51**</td>
</tr>
<tr>
<td>Lint %</td>
<td>4.77**</td>
<td>4.56**</td>
</tr>
</tbody>
</table>

** = Significant at p < 0.01 and p < 0.05

× CIM-1100 and CRIS-9 × CIM-1100 ranging from 5.4 to 5.5 g in F1 generation. The CIM-1100 F1 hybrid CRIS-9 × CIM-1100 (5.2 g) had the highest lint index, followed by CIM-240 x CIM-1100 and its reciprocal with 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 F1 and F2 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, F1 and F2 populations, respectively (Table 4). Maximum and equal lint % was observed in F1 hybrid BH-36 × CIM-1100 (36.9%) and its reciprocal (36.8%) followed by 10 other F1 populations (four derivatives of CIM-1100) and two parental lines ranging from 35.6 to 36.6%. The six F1 hybrids showed lowest lint % ranging from 32.8 to 33.8%. In the F2 generation, the highest lint % was exhibited by CIM-1100 × CRIS-9 (36.1%), followed by nine other F2 populations (five progenies of CIM-1100) varying from 35.0 to 35.5%. The lowest lint % was produced by F1 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 F2 generation averaged a minimum of 55 days, which were less than equivalent days (60) took by parental cultivars and F1 hybrids. In case of bolls per plant and seed cotton yield, the F1 hybrids had the highest number of bolls per plant (36) and seed cotton yield (112 g), followed by F2 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 F1 hybrids (4.9 g, 35.1%) compared to F2 hybrids (4.5 g, 34.4%) and parental cultivars (4.6 g, 34.5%). Due to inbreeding depression during segregation, the F2 populations showed some decrease relative to F1 hybrids; however, F2 populations still performed better than parental cultivars for earliness and yield traits. Overall, the F1 and F2 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 t² 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 F1 and F2 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 t² 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 F1 and F2, populations respectively. In these traits, the analysis of variance of arrays was non-significant; however, the regression coefficient and t² 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 (H1, H2), dominance effect (h²), and environmental component of variation (E) were significant, while covariance of additive and dominance effects (F) was non-significant in the F1 generation (Table 6). Environmental variation played a large role in phenotypic appearance of CLCuV resistant plants % in the F1 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 h² (695.40). Additive control of this trait was confirmed by the ratio of $\sqrt{ADH1+D/F/ADH1-F}$ (0.35). For percent CLCuV resistant plants in the F2 generation, the additive component was highly significant, whereas H1, H2, F, h², and E 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 h² (11.22). Data suggest an unbalanced distribution of positive and negative genes, due to unequal values of H1 and H2 as confirmed by ratios of H2/4H1 (0.15, 0.17) in both generations. High narrow (0.86, 0.89) and broad sense (0.97, 0.99) heritabilities in F1 and F2 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 F1 and F2 diallel cross in upland cotton.

<table>
<thead>
<tr>
<th>F1, F2 hybrids and parental cultivars</th>
<th>F1 generation</th>
<th>F2 generation</th>
<th>Classified CLCuV F1 diseased plants (%)</th>
<th>Classified CLCuV F2 diseased plants (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CLCuV DP (%)</td>
<td>CLCuV RP (%)</td>
<td>CLCuV DP (%)</td>
<td>CLCuV RP (%)</td>
<td>Mild (%)</td>
</tr>
<tr>
<td>CIM-109 × CIM-240</td>
<td>46</td>
<td>54</td>
<td>72</td>
<td>28</td>
</tr>
<tr>
<td>CIM-109 × CIM-1100</td>
<td>100</td>
<td>0</td>
<td>91</td>
<td>9</td>
</tr>
<tr>
<td>CIM-109 × FH-682</td>
<td>53</td>
<td>47</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td>CIM-109 × BH-36</td>
<td>53</td>
<td>47</td>
<td>77</td>
<td>23</td>
</tr>
<tr>
<td>CIM-109 × CRIS-9</td>
<td>64</td>
<td>36</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>CIM-240 × CIM-109</td>
<td>53</td>
<td>47</td>
<td>72</td>
<td>28</td>
</tr>
<tr>
<td>CIM-240 × CIM-1100</td>
<td>100</td>
<td>0</td>
<td>85</td>
<td>15</td>
</tr>
<tr>
<td>CIM-240 × FH-682</td>
<td>31</td>
<td>69</td>
<td>66</td>
<td>34</td>
</tr>
<tr>
<td>CIM-240 × BH-36</td>
<td>38</td>
<td>62</td>
<td>31</td>
<td>69</td>
</tr>
<tr>
<td>CIM-240 × CRIS-9</td>
<td>47</td>
<td>53</td>
<td>56</td>
<td>44</td>
</tr>
<tr>
<td>CIM-1100 × CIM-109</td>
<td>100</td>
<td>0</td>
<td>88</td>
<td>12</td>
</tr>
<tr>
<td>CIM-1100 × CIM-240</td>
<td>100</td>
<td>0</td>
<td>78</td>
<td>22</td>
</tr>
<tr>
<td>CIM-1100 × FH-682</td>
<td>100</td>
<td>0</td>
<td>77</td>
<td>23</td>
</tr>
<tr>
<td>CIM-1100 × BH-36</td>
<td>100</td>
<td>0</td>
<td>88</td>
<td>12</td>
</tr>
<tr>
<td>CIM-1100 × CRIS-9</td>
<td>100</td>
<td>0</td>
<td>84</td>
<td>16</td>
</tr>
<tr>
<td>FH-682 × CIM-109</td>
<td>44</td>
<td>56</td>
<td>73</td>
<td>27</td>
</tr>
<tr>
<td>FH-682 × CIM-240</td>
<td>41</td>
<td>59</td>
<td>61</td>
<td>39</td>
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<tr>
<td>FH-682 × CIM-1100</td>
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<td>78</td>
<td>22</td>
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<tr>
<td>FH-682 × BH-36</td>
<td>55</td>
<td>45</td>
<td>55</td>
<td>45</td>
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<tr>
<td>FH-682 × CRIS-9</td>
<td>41</td>
<td>59</td>
<td>65</td>
<td>35</td>
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<td>BH-36 × CIM-109</td>
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<tr>
<td>BH-36 × CIM-240</td>
<td>24</td>
<td>76</td>
<td>57</td>
<td>43</td>
</tr>
<tr>
<td>BH-36 × CIM-1100</td>
<td>100</td>
<td>0</td>
<td>89</td>
<td>11</td>
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<td>83</td>
<td>17</td>
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<tr>
<td>CRIS-9 × FH-682</td>
<td>19</td>
<td>81</td>
<td>59</td>
<td>41</td>
</tr>
<tr>
<td>CRIS-9 × BH-36</td>
<td>29</td>
<td>71</td>
<td>57</td>
<td>43</td>
</tr>
</tbody>
</table>

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 |

**LSD0.05**

16.32 8.23

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

Under selection was 64.36% and 32.61%, equivalent to percent values of 112.64% and 46.64% in F1 and F2 generations, respectively. Significant negative correlation coefficient (r = -0.957, r = -0.802) between Wr+Vr and parental means (y) in F1 and F2 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 F1 generation, components of variance other than F (D, H1, H2, h2, 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 h2 (715.64), which was authenticated by the ratio of √(4DH1+ F) / √(4DH1− F) (0.43). For percent disease among F2 CLCuV plants, the D was highly significant, while H1, H2, F, h2, and E2 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 h2 (16.12). Uneven values of H1 and H2 indicated irregular allocation of positive and negative genes as confirmed by the ratios of H1/H4H4 i.e. 0.16, 0.17 in F1 and F2 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 F1 and F2 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 F1 and with maximum ratio of resistant plants in the F2 generation after segregation. For days to flowering, the D and H2, H2 genetic components of variance

1958
were significant, while F₁, h², and E were non-significant in F₁ generation (Table 6). The additive component was smaller than dominance components and the average degree of dominance (√H₁/Đ = 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 h² (-1.33); this was confirmed by the ratio of \( \frac{\sqrt{4DH₁} + F}{\sqrt{4DH₁} - F} \) (1.91). In the F₂ generation, D was highly significant, whereas H₁, H₂, F, h², and E₂ components of variance were non-significant (Table 6). Average degree of dominance (√H₁/Đ = 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 h² (45.30), and these results were confirmed by the ratio of \( \frac{\sqrt{4DH₁} + F}{\sqrt{4DH₁} - F} \) (2.85) as well. In both generations, unequal values of H₁ and H₂ indicated uneven allocation of positive and negative genes as confirmed by ratios of H₁/4H₂ (0.20, 0.21). Medium narrow (0.45, 0.77) and high broad sense (0.85, 0.94) heritabilities in F₁ and F₂ generations, respectively, indicated that most genetic variation was controlled by non-additive gene effects. In the F₁ generation, the genetic advance under selection was 8.04 days, while its value as percent of the population mean was 13.49%. In the F₂ generation, the corresponding values were 9.33 days and 16.63%, respectively. The nonsignificant positive correlation between Wr+Vr and parental means in F₁ (r = 0.399) and F₂ (r = 0.781) generations indicate that parental cultivars with recessive genes were responsible for earliness. Genetic components of variance for F₁ bolls per plant revealed that D, H₁, H₂, and h² 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 h² (76.31). In case of F₂ 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 H₁ and H₂ indicated an asymmetric distribution of positive and negative genes as confirmed by H₁/4H₂ ratios in both generations. In F₁ and F₂ populations, the

**Table 4. Mean performance of cultivars and F₁ and F₂ populations for various traits in upland cotton.**

<table>
<thead>
<tr>
<th>Parental cultivars, F₁ × F₂ hybrids</th>
<th>Days to flowering</th>
<th>Bolls plant⁻¹</th>
<th>Seed cotton yield plant⁻¹ (g)</th>
<th>Lint index (g)</th>
<th>Lint %</th>
</tr>
</thead>
<tbody>
<tr>
<td>CIM-109 × CIM-240</td>
<td>56</td>
<td>50</td>
<td>32</td>
<td>28</td>
<td>102</td>
</tr>
<tr>
<td>CIM-109 × CIM-1100</td>
<td>60</td>
<td>55</td>
<td>52</td>
<td>37</td>
<td>163</td>
</tr>
<tr>
<td>CIM-109 × FH-682</td>
<td>57</td>
<td>52</td>
<td>30</td>
<td>30</td>
<td>75</td>
</tr>
<tr>
<td>CIM-109 × BH-36</td>
<td>64</td>
<td>60</td>
<td>35</td>
<td>32</td>
<td>96</td>
</tr>
<tr>
<td>CIM-109 × CRIS-9</td>
<td>59</td>
<td>54</td>
<td>37</td>
<td>35</td>
<td>90</td>
</tr>
<tr>
<td>CIM-240 × CIM-109</td>
<td>54</td>
<td>49</td>
<td>27</td>
<td>27</td>
<td>74</td>
</tr>
<tr>
<td>CIM-240 × CIM-1100</td>
<td>56</td>
<td>52</td>
<td>45</td>
<td>34</td>
<td>161</td>
</tr>
<tr>
<td>CIM-240 × FH-682</td>
<td>59</td>
<td>55</td>
<td>23</td>
<td>25</td>
<td>76</td>
</tr>
<tr>
<td>CIM-240 × BH-36</td>
<td>56</td>
<td>52</td>
<td>34</td>
<td>28</td>
<td>110</td>
</tr>
<tr>
<td>CIM-240 × CRIS-9</td>
<td>57</td>
<td>53</td>
<td>31</td>
<td>31</td>
<td>80</td>
</tr>
<tr>
<td>CIM-1100 × CIM-109</td>
<td>64</td>
<td>62</td>
<td>53</td>
<td>38</td>
<td>181</td>
</tr>
<tr>
<td>CIM-1100 × CIM-240</td>
<td>57</td>
<td>53</td>
<td>20</td>
<td>32</td>
<td>59</td>
</tr>
<tr>
<td>CIM-1100 × FH-682</td>
<td>62</td>
<td>58</td>
<td>47</td>
<td>44</td>
<td>164</td>
</tr>
<tr>
<td>CIM-1100 × BH-36</td>
<td>60</td>
<td>57</td>
<td>40</td>
<td>38</td>
<td>137</td>
</tr>
<tr>
<td>CIM-1100 × CRIS-9</td>
<td>58</td>
<td>53</td>
<td>51</td>
<td>39</td>
<td>170</td>
</tr>
<tr>
<td>FH-682 × CIM-109</td>
<td>57</td>
<td>52</td>
<td>36</td>
<td>31</td>
<td>115</td>
</tr>
<tr>
<td>FH-682 × CIM-240</td>
<td>68</td>
<td>64</td>
<td>26</td>
<td>29</td>
<td>84</td>
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<tr>
<td>FH-682 × CIM-1100</td>
<td>67</td>
<td>62</td>
<td>43</td>
<td>40</td>
<td>155</td>
</tr>
<tr>
<td>FH-682 × BH-36</td>
<td>66</td>
<td>61</td>
<td>29</td>
<td>26</td>
<td>87</td>
</tr>
<tr>
<td>FH-682 × CRIS-9</td>
<td>59</td>
<td>56</td>
<td>33</td>
<td>29</td>
<td>92</td>
</tr>
<tr>
<td>BH-36 × CIM-109</td>
<td>65</td>
<td>62</td>
<td>29</td>
<td>30</td>
<td>77</td>
</tr>
<tr>
<td>BH-36 × CIM-240</td>
<td>56</td>
<td>51</td>
<td>22</td>
<td>34</td>
<td>59</td>
</tr>
<tr>
<td>BH-36 × CIM-1100</td>
<td>63</td>
<td>58</td>
<td>52</td>
<td>35</td>
<td>184</td>
</tr>
<tr>
<td>BH-36 × FH-682</td>
<td>62</td>
<td>58</td>
<td>29</td>
<td>25</td>
<td>88</td>
</tr>
<tr>
<td>BH-36 × CRIS-9</td>
<td>57</td>
<td>53</td>
<td>39</td>
<td>30</td>
<td>114</td>
</tr>
<tr>
<td>CRIS-9 × CIM-109</td>
<td>55</td>
<td>52</td>
<td>41</td>
<td>34</td>
<td>101</td>
</tr>
<tr>
<td>CRIS-9 × CIM-240</td>
<td>58</td>
<td>53</td>
<td>28</td>
<td>28</td>
<td>76</td>
</tr>
<tr>
<td>CRIS-9 × CIM-1100</td>
<td>63</td>
<td>59</td>
<td>53</td>
<td>39</td>
<td>189</td>
</tr>
<tr>
<td>CRIS-9 × FH-682</td>
<td>56</td>
<td>53</td>
<td>35</td>
<td>31</td>
<td>116</td>
</tr>
<tr>
<td>CRIS-9 × BH-36</td>
<td>58</td>
<td>54</td>
<td>36</td>
<td>35</td>
<td>98</td>
</tr>
</tbody>
</table>

**LSD (P=0.05)**

| F₁ and F₂ hybrid means | 4.400 | 3.182 | 8.197 | 0.309 | 1.406 |

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1959
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 $F_1$ (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 bolts 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 bolts 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 $H_2$/4$H_1$ (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 $H_2$/4$H_1$ (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 $\sqrt{4(DH)} + F$ / $\sqrt{4(DH)} - F$ (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 $H_2$/4$H_1$ (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 $1/\sqrt{4(DH)+F}/\sqrt{4(DH)-F}$ (0.78). In $F_1$s and $F_2$s lint index, the narrow sense (0.87, 0.80) and broad sense heritability

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

<table>
<thead>
<tr>
<th>Variables</th>
<th>$F_1$ / $F_2$</th>
<th>$t^2$ test</th>
<th>Regression analysis</th>
<th>Analysis of variance of arrays</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F1</td>
<td>F2</td>
<td></td>
<td>b/S.E. b0, b1 Wr + Vr Wr – Vr</td>
<td></td>
</tr>
<tr>
<td>CLCuV resistant plants</td>
<td>0.006NS</td>
<td>1.550NS</td>
<td>0.981 ±0.079</td>
<td>b0 = 12.481 NS b1 = 0.236NS</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td></td>
<td>0.806 ±0.118</td>
<td></td>
<td></td>
<td>b0 = 6.833 NS b1 = 1.640NS</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td>CLCuV diseased plants</td>
<td>0.006NS</td>
<td>1.550NS</td>
<td>0.981 ±0.079</td>
<td>b0 = 12.481 NS b1 = 0.236NS</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td></td>
<td>0.806 ±0.118</td>
<td></td>
<td></td>
<td>b0 = 6.833 NS b1 = 1.640NS</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td>Days to flowering</td>
<td>0.096NS</td>
<td>1.347NS</td>
<td>0.379 ±0.546</td>
<td>b0 = 0.694 NS b1 = 1.136NS</td>
<td>NS NS Partially adequate</td>
</tr>
<tr>
<td></td>
<td>1.156 ±0.307</td>
<td></td>
<td></td>
<td>b0 = 3.759 NS b1 = -0.506NS</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td>Bolls plant^1</td>
<td>3.379NS</td>
<td>8.878^</td>
<td>0.323 ±0.200</td>
<td>b0 = 1.615 NS b1 = 3.384^</td>
<td>NS NS Partially adequate</td>
</tr>
<tr>
<td>Seed cotton yield plant^1</td>
<td>35.665^{**}</td>
<td>71.306^{**}</td>
<td>0.045 ±0.081</td>
<td>b0 = 0.555 NS b1 = 6.374^{**}</td>
<td>NS NS Partially adequate</td>
</tr>
<tr>
<td>Lint index</td>
<td>0.210NS</td>
<td>0.128NS</td>
<td>0.947 ±0.081</td>
<td>b0 = 1.163 NS b1 = 0.649^</td>
<td>NS NS Adequate</td>
</tr>
<tr>
<td>Lint %</td>
<td>2.754NS</td>
<td>0.001NS</td>
<td>1.250 ±0.238</td>
<td>b0 = 5.261 NS b1 = -1.053NS</td>
<td>NS NS Adequate</td>
</tr>
</tbody>
</table>

**NS, ** = Significant at p<0.01 and p<0.05. NS = Non-significant.
Table 6. Genetic components of variance for various traits in 6 × 6 F₁ and F₂ diallel cross in upland cotton.

<table>
<thead>
<tr>
<th>Components of variance</th>
<th>CLCuV resistant plants (%)</th>
<th>CLCuV diseased plants (%)</th>
<th>Days to flowering</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F₁</td>
<td>F₂</td>
<td>F₁</td>
</tr>
<tr>
<td>D</td>
<td>827.57*</td>
<td>±37.34</td>
<td>342.82***</td>
</tr>
<tr>
<td>H₁</td>
<td>684.94*</td>
<td>±94.80</td>
<td>163.78</td>
</tr>
<tr>
<td>H₂</td>
<td>402.13*</td>
<td>±64.69</td>
<td>112.22</td>
</tr>
<tr>
<td>F</td>
<td>-728.01</td>
<td>±91.23</td>
<td>105.07</td>
</tr>
<tr>
<td>h²</td>
<td>±65.96</td>
<td>±112.20</td>
<td>715.64*</td>
</tr>
<tr>
<td>E</td>
<td>55.09*</td>
<td>±14.12</td>
<td>16.25</td>
</tr>
<tr>
<td>F₁: ³DH₁/F₁</td>
<td>0.91</td>
<td>±0.31</td>
<td>0.31</td>
</tr>
<tr>
<td>F₂: ³DH₁/F₁</td>
<td>0.15</td>
<td>±0.17</td>
<td>0.17</td>
</tr>
<tr>
<td>F₁: ³DH₁/F₂</td>
<td>0.35</td>
<td>±2.30</td>
<td>0.43</td>
</tr>
<tr>
<td>F₂: ³DH₁/F₂</td>
<td>1.73</td>
<td>±1.00</td>
<td>1.51</td>
</tr>
<tr>
<td>Heritability (h₂)</td>
<td>0.86</td>
<td>±0.89</td>
<td>0.87</td>
</tr>
<tr>
<td>Genetic advance</td>
<td>64.36%</td>
<td>32.61%</td>
<td>63.31%</td>
</tr>
<tr>
<td>n(Wr+Vr/VP)</td>
<td>-0.957**</td>
<td>±0.802**</td>
<td>0.957**</td>
</tr>
</tbody>
</table>

*In F₁, the parameter value is significant when it exceeds 1.96 after dividing it with its standard error.

Table 7. Genetic components of variance for various traits in 6 × 6 F₁ and F₂ diallel cross in upland cotton.

<table>
<thead>
<tr>
<th>Components of variance</th>
<th>Bolls plant¹</th>
<th>Seed cotton yield plant¹</th>
<th>Lint index</th>
<th>Lint %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F₁</td>
<td>F₂</td>
<td>F₁</td>
<td>F₂</td>
</tr>
<tr>
<td>D</td>
<td>37.87*</td>
<td>±14.98</td>
<td>3.65</td>
<td>±7.66</td>
</tr>
<tr>
<td>H₁</td>
<td>182.34*</td>
<td>±38.02</td>
<td>62.37</td>
<td>±77.68</td>
</tr>
<tr>
<td>H₂</td>
<td>110.59*</td>
<td>±33.96</td>
<td>39.80</td>
<td>±69.39</td>
</tr>
<tr>
<td>F</td>
<td>-0.91</td>
<td>±35.69</td>
<td>3.91</td>
<td>±37.20</td>
</tr>
<tr>
<td>h²</td>
<td>76.31*</td>
<td>±22.84</td>
<td>8.56</td>
<td>±46.71</td>
</tr>
<tr>
<td>E</td>
<td>1.33</td>
<td>±5.66</td>
<td>1.43</td>
<td>±2.92</td>
</tr>
<tr>
<td>F₁: ³DH₁/D</td>
<td>2.19</td>
<td>±2.9</td>
<td>2.07</td>
<td>±3.98</td>
</tr>
<tr>
<td>F₂: ³DH₁/D</td>
<td>0.15</td>
<td>±0.16</td>
<td>0.16</td>
<td>±0.16</td>
</tr>
<tr>
<td>F₁: ³DH₁/F₂</td>
<td>0.99</td>
<td>±1.70</td>
<td>0.79</td>
<td>±1.17</td>
</tr>
<tr>
<td>F₂: ³DH₁/F₂</td>
<td>0.69</td>
<td>±0.22</td>
<td>1.18</td>
<td>±0.03</td>
</tr>
<tr>
<td>Heritability (h²)</td>
<td>0.66</td>
<td>±0.16</td>
<td>0.59</td>
<td>±0.11</td>
</tr>
<tr>
<td>Genetic advance</td>
<td>19.17 (54.17%)</td>
<td>±9.52 (29.22%)</td>
<td>78.46 g (73.23%)</td>
<td>±7.05 (43.83%)</td>
</tr>
<tr>
<td>n(Wr+Vr/VP)</td>
<td>0.308</td>
<td>±0.023</td>
<td>0.328</td>
<td>±0.229</td>
</tr>
</tbody>
</table>

¹In F₁, the parameter value is significant when it exceeds 1.96 after dividing it with its standard error.

²In F₂, 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 F₁S and F₂S, 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 F₁ lint %, analysis of genetic variation showed that except for F, all genetic components (D, H₁, H₂ and h², 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 H₁/H₂ (0.26) was close to 0.25, which confirmed the equal values of H₁ (1.49) and H₂ (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 h² (0.93). Additive control of the trait was confirmed by the ratio of $\frac{\sqrt{DHI} + F}{\sqrt{DHI} - F}$ (0.90). For the F₂ 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 h² (0.93). Uneven values of H₁ (0.43) and H₂ (0.27) indicated an unbalanced distribution of positive and negative genes, as was also observed in the ratio of H₁/H₂ (0.16). For the F₃ lint %, medium narrow sense (0.64) and high broad sense heritability (0.84) values were observed, while for F₄ 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 F₁ and F₂ generations. Genetic gain values in F₁ and F₂ generations were 2.48% (7.09%) and 2.25% (6.55%), respectively. A significant negative correlation (r = -0.403; r = -0.738) between Wr+Vr and parental means suggests that parental cultivars with dominant genes were responsible for increased lint % in F₁ and F₂ 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 F₁ and F₂ 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 F₁ and F₂ 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 F₁ hybrid mean values were higher than values for F₂ plants, though F₂ plants exceeded their parental cultivars, however, for earliness the F₂ populations were the leading. The promising populations (CRIS-9 × CIM-109, CIM-1100 × CIM-109, and BH-36 × CIM-1100) and their reciprocals were tolerant to CLCuV in F₁ and F₂ generations, and showed remarkable performance for all the traits. Therefore, these populations could be screened for hybrid cotton production at F₁ and F₂ 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 F₁ and F₂ populations, along with parental lines, revealed significant variability by showing significant differences for all traits. Based on genetic potential, cv. CIM-1100 F₁ and F₂ progenies performed better for studied traits, which could be used to create promising base lines / cultivars. However, the F₁ and F₂ 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 F₁ 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 F₁ and F₂ populations and their parental lines for yield and lint traits and their vital role in managing seed cotton yield (Aguir et al., 2007; Khan, 2011). In these studies, days to flowering was used as a measure of earliness. Overall, the F₂ populations took minimum days to flowering, and the parental cultivars and F₁ hybrids were similar for days to flowering. This is a sign of improvement in earliness in the F₂ 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 (Godoy, 1994; Godoy and Palomo, 1999), node for first fruiting branch (Godoy, 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 criteria 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 F₁ and F₂ generations (Khan et al., 2007, 2009c; Aguado et al. 2010; Hussain et al., 2012). The 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; Batooll 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 (Sooh et al., 2010). The CLCuV tolerant cv. CIM-1100 F₁ 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 1962).
et al., 2012). Our results revealed that after segregation, the CIM-1100 F2 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 F2 populations, indicating that a single dominant gene controlled the CLCuV resistance in cotton (Aslam et al., 2000; Mahmood, 2004). Significant negative correlation between Wt+Wt and parental means suggested that dominant genes contained by CIM-1100 were reliable for increased CLCuV resistance in F1 and F2 generations. The percent of CLCuV diseased plants was controlled by additive gene action and has a significant positive correlation coefficient in Wt+Wt/VP in F1 and F2 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 bred) 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. arboresum, 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 F1, and by additive genes in the F2 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. herbaceum L. (Basal and Turgut, 2005; Sohmo 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 F1 and extremely low in F2 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 F1, and F2 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 F2 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 contributing traits was reported in upland cotton (Wu et al., 2006; Khan et al., 2007; Abbasi 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; Mehret et al., 2004; Basal and Turgut, 2005; Song et al., 2005; Khan et al., 2009d). A significant negative correlation coefficient between Wt+Wt 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 corroborated with present results. However, 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 F1 and F2 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 F1 diallel populations with the aim to transfer the CLCuV resistance, and to develop the base population through segregation in segregating generations. During 2009, some seeds of F1 populations were hand sown and allowed to self to advance the generation and to have seeds for the F2 crop. During 2010, 30 F1, and F2 populations and their parental cultivars were hand sown using a randomized complete block (RCB) design. The F1 genotypes were planted in two rows measuring 5.0 m long (with 34 plants of each F1 hybrid/replication) with three replications. In the F2 crop, the plant population was increased and each F2 hybrid was planted in four rows with row length of 5.0 m (68 plants of each F2 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 F1, F2 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 (b), 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 F1 as well as F2 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 H1 and H2 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 r2 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 r2 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 F1 genetic components of variation were estimated according Hayman (1954a, b), while for F2 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), H1, H2 (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), h2 (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 F1 and F2 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 F1 and F2 generations (Breeze, 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 F2 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 F₁ and F₂ hybrids could be reconstituted to work better as base material for hybrid cotton production.

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