

Research Paper

## Study of gene effects for seed yield and anti-nutritional components in cowpea [*Vigna unguiculata* (L.) Walp]

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### ABSTRACT

The present study investigated gene effects for seed yield, its quality and anti-nutritional traits through generation mean analysis of two diverse crosses of cowpea (CL 367 × C 88, CL 400 × BL 1), parents and their segregating generations ( $F_2$ ,  $BC_1$  and  $BC_2$ ). The significant values for scaling tests (A, B, C, and D) were reported in the traits such as seed yield, crude protein percent, anthocyanins and anti-nutritional components such as total phenols, flavonoids, tannins, and saponins content in the case of May and July sowing. The results indicated the presence of epistatic interactions, and the six-parameter model was best suited to explore these properties. The magnitude of the dominance gene effect (h) was greater than the additive gene effect (d) in the traits studied. The epistatic interactions viz; additive × additive, additive × dominance, and dominance × dominance, were significant for most of the traits in two crosses. The duplicate type of epistasis was observed for the traits due to opposite signs of (h) and (l) gene effects. These results suggested that recurrent selection and selection in later generations could be the best option to exploit both additive and non-additive gene effects.

**Key words:** Anti-nutritional components, Generation mean analysis, Gene effects, Cowpea, Seed yield

### INTRODUCTION

Cowpea is an annual, dicotyledonous leguminous crop that belongs to the family *Fabaceae*. This crop is grown throughout the world and is highly adapted to the areas receiving low rainfall and having high-temperature conditions. Cowpea is grown for green pods, vegetables, dry seeds, green manure, and as a forage crop. The capability of the crop to grow in various soil conditions, higher protein content, resistance to drought, suitability for intercropping and improved soil fertility make it a major economic crop in many underdeveloped countries throughout the world. It is a major crop for human consumption in many African countries (Shirisha *et al.* 2024)

Cowpea grains are a big source of proteins, vitamins, and essential minerals for human nutrition in many countries (Sreerama *et al.* 2012). However, its wide consumption is limited by the presence of indigestible oligosaccharides and some anti-nutritional factors such as tannins, phytase, and digestive enzyme inhibitors (Heke 2014). These are mostly derived from the secondary metabolism of plants and adversely affect the nutritive value

of food (Martins *et al.* 2011). They interfere with the bioavailability of minerals and the digestibility of essential nutrients. (Nassourou *et al.* 2020). It is therefore necessary to reduce these inhibitors to make the nutrients bioavailable to the body.

Elimination of these anti-nutrient substances by soaking, dehulling, fermentation, and cooking (Adekanmi *et al.* 2009) requires extra energy for households and causes a reduction of some nutrients by leaching (Goyal *et al.* 2023). Some of the anti-nutrients are thermostable, and their destruction by some processes is difficult. Therefore, selection of cowpea cultivars with low concentration of these elements may be the simplest and most effective method for improving the nutritional value and acceptability of cowpea (Nassourou *et al.* 2020). Therefore, the study of genetic variability and heritability for these quality traits is essential for initiating any breeding programme.

Information regarding the gene effects controlling these quality and anti-nutritional traits can be obtained through several methods like diallel analysis, line × tester analysis, but out of these methods, generation mean analysis provides more information about various gene interactions

by attempting a few controlled hybridization operations. Generation mean analysis allows the partitioning of genetic effects into additive, dominance, and epistatic components, which are crucial for understanding the inheritance of traits (Ola *et al.* 2024). Epistasis, which is the interaction between genes influencing a phenotype, can significantly impact various selection procedures. It affects the response to selection by modifying the effects of alleles, influencing genetic variation, and potentially leading to complex evolutionary outcomes. Only a few studies for the evaluation of the above-mentioned seed quality and anti-nutrition traits in cowpea have been initiated in the recent past (Upadhaya *et al.* 2011, Goyal *et al.* 2023). The current investigation was conducted to determine the gene action for various traits through generation mean analysis and to predict suitable breeding methods for cowpea improvement.

## MATERIALS AND METHODS

### Breeding material

The present research was conducted in the experimental area of Forage, Millet and Nutrition Section, Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana. The analysis of biochemical parameters was carried out in the field and forage evaluation laboratory of the Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana. Two different sets of crosses viz., CL 367 × C 88 and CL 400 × BL 1 were grown in the field conditions along with their parents and segregating generations ( $F_2$ ,  $BC_1$  and  $BC_2$ ). The crosses were attempted using diverse parents (Table 1) during August 2022 to get  $F_1$  seeds and the final evaluation trial was sown along with segregating generations on two different dates of sowing. The first sowing of the crop was done in the month of May (Summer 2024) and the second sowing was done in July (Kharif 2024). Data were recorded for various traits viz, seed yield (g/plant), crude protein percent, anthocyanins (mg/g), total phenols (mg/g), flavonoids (mg/g), tannins (mg/g) and saponins (mg/g) content.

**Table 1.** Description of Parents used in crossing

| Crosses                        | Parents | Description                               |
|--------------------------------|---------|-------------------------------------------|
| Cross I (CL 367 × CL367 C88)   |         | Small round creamish white seeds          |
|                                | C 88    | Bold seeded having chocolate brown colour |
| Cross II (CL 400 × CL 400 BL1) |         | Bold seeded having dark grey seed colour  |
|                                | BL 1    | Medium sized dark red seeds               |

### Experimental design

The experimental plant material was sown during the months of May and July. The parental lines and their respective  $F_1$  crosses were grown in two row plots, and the backcross and  $F_2$  populations were grown in 15 row plots, each of 3 m in length. The plant material was replicated thrice in a randomized block design (RBD). The non-experimental rows were planted around the experimental rows to avoid the border rows effect. The crop was raised as per the recommendation in the Package of Practices for Kharif crops by Punjab Agricultural University, Ludhiana. The data were collected from 10 random plants of parental lines,  $F_1$ , and 125 plants of the  $F_2$  generation and 20 plants were selected from backcross generations for analysis. Ripe pods from selected plants of each cross were harvested separately. Pods were sun-dried and seeds were removed after drying. The traits recorded were seed yield (g/plant), crude protein percent, anthocyanins (mg/g), anti-nutritional components such as total phenols (mg/g), flavonoids (mg/g), tannins (mg/g) and saponins (mg/g) content. Seed yield was measured for each plant separately and seeds were removed from pods after drying. The Crude Protein Percent was determined using Kjeldahl digestion procedure as described by AOAC (2005). The estimation of anthocyanins was done by the method described by Rabino *et al.* (1977). The anti-nutritional components were estimated by grinding 500 g seed sample for analysis. The extraction and estimation of total phenols was done by the method described by Swain and Hills (1959) while tannins were estimated by the method given by Sadasivan and Manickam (1992). The method used for the estimation of flavonoids was given by Chang *et al.* (2002) whereas saponins were estimated by the method described by Fenwick and Oakenfull (1983).

### Statistical analysis

The collected data were subjected to test the equality of means of different generations of a cross. The generation mean analysis was performed using Mather and Jinks (1971) method. A, B, and C scaling test (Mather 1949) and the least square method (Hayman 1960) were tested for adequacy of the additive-dominance model by t-test at 5% and 1% level of significance by computing the variance of generation means. When any scale deviates from zero, the additive-dominance model was considered as inadequate due to the presence of non-allelic interactions and a parameter model was used, given by Mather and Jinks (1971). The

significance of the genetic effect was tested using a t-test at 5% and 1% levels of significance. Broad-sense heritability ( $h^2$ ) and narrow-sense heritability ( $h_n^2$ ) were calculated using back backcross method (Mather and Jinks 1982)

## RESULTS AND DISCUSSION

In the present study, six generations of cowpea were used to collect data on seed yield and antinutritional components linked with the seed coat. The information from parental lines,  $F_1$ , segregating generation  $F_2$ , and backcrosses ( $BC_1$  and  $BC_2$ ) of crosses namely: cross I (CL 367  $\times$  C 88) and cross II (CL 400  $\times$  BL 1), were examined to estimate the components of generation means, and the results obtained were explained further below.

### Mean performance

The mean performance of different generations for various traits in both crosses is given in Table 2 for May and July sowing of the crop. The range of mean values for May sowing was less compared to the July sowing of the crop. The seed yield in cowpea ranged from 12.6 g to 18.5 g for May sowing and 15.3 g to 21.2 g for July sowing of the crop. The crude protein percent in the present research varied from 19.7% to 23.5% for May sowing and 20.8% to 24.5% for July sowing of the crop. The anthocyanin concentration ranged from 0.62 mg/g to 1.98 mg/g for May and the 0.70 mg/g to 2.00 mg/g for July crop sowing. The total phenols concentration in the seed ranged from 0.97 mg/g to 2.2 mg/g for May sowing and 1.0 mg/g to 2.2 mg/g for July sowing. The flavonoid concentration in the seed ranged from 0.36 mg/g to 0.82 mg/g for May and 0.38 mg/g to

0.93 mg/g for July sowing. The tannin concentration in the seed ranged from 0.67 mg/g to 1.42 mg/g for May and from 0.73 mg/g to 1.47 mg/g for July sowing. The saponin content in the seed ranged from 2.69 mg/g to 6.05 mg/g for May and from 2.76 mg/g to 6.14 mg/g for July sowing crop. The date of sowing can significantly affect the levels of antinutrients in cowpeas. Generally, delayed sowing can lead to an increase in antinutrient content, such as tannins and phytic acid, while early sowing may be more beneficial for reducing these compounds. Delayed sowing can cause a reduction in the vegetative stage, leading to early flowering and a decrease in dry matter accumulation (Prasanthi *et al.* 2023), ultimately resulting in increased levels of antinutrients like tannins and phytic acid (Shaheen *et al.* 2019)

The mean values for seed yield of  $F_1$  and  $F_2$  were less than the parental lines in both crosses. Singh *et al.* (2016) reported similar observations for mean performance. The mean performance observed for tannins, total phenols, and flavonoids content agreed with the results of a previous investigation by Nassourou *et al.* (2020) while working on anti-nutrient components in cowpea seeds.

### Generation mean analysis

The relative number of fixable and non-fixable gene effects is the most important aspect in determining the success of any breeding operation in almost all crops. Breeders must establish unbiased estimates of additive and dominance gene effects to apply this information in diverse crop improvement programmes to produce superior varieties (Mather and Jinks 1971). The current study attempted to

**Table 2.** Mean performance of Cross I (CL 367  $\times$  C 88) and Cross II (CL 400  $\times$  BL 1) at different dates of sowing (May and July) for various traits

| Characters    | Crosses | Parent 1 |       | Parent 2 |       | $F_1$ |       | $F_2$ |       | $BC_1$ |       | $BC_2$ |       |
|---------------|---------|----------|-------|----------|-------|-------|-------|-------|-------|--------|-------|--------|-------|
|               |         | May      | July  | May      | July  | May   | July  | May   | July  | May    | July  | May    | July  |
| Seed yield    | CI      | 16.47    | 18.92 | 18.54    | 21.12 | 14.49 | 16.37 | 12.63 | 15.35 | 15.42  | 17.26 | 17.05  | 19.90 |
| (g/plant)     | CII     | 17.99    | 19.50 | 18.55    | 21.25 | 14.28 | 16.07 | 14.40 | 16.97 | 15.50  | 16.90 | 17.00  | 19.02 |
| Crude protein | CI      | 23.18    | 22.83 | 23.48    | 24.13 | 22.08 | 21.73 | 20.67 | 21.30 | 22.90  | 22.54 | 23.85  | 24.50 |
| percent       | CII     | 21.75    | 21.92 | 23.11    | 23.29 | 19.66 | 20.84 | 22.01 | 22.06 | 22.76  | 22.94 | 22.90  | 22.97 |
| Anthocyanins  | CI      | 0.768    | 0.812 | 1.619    | 1.703 | 0.625 | 0.703 | 0.766 | 0.779 | 0.824  | 0.871 | 1.162  | 1.111 |
| (mg/g)        | CII     | 1.450    | 1.486 | 1.929    | 1.924 | 1.607 | 1.609 | 1.779 | 1.780 | 1.776  | 1.776 | 1.980  | 2.002 |
| Total phenols | CI      | 0.965    | 1.021 | 2.115    | 2.177 | 1.270 | 1.304 | 1.272 | 1.280 | 1.110  | 1.174 | 1.425  | 1.479 |
| (mg/g)        | CII     | 1.418    | 1.423 | 2.211    | 2.226 | 1.045 | 1.076 | 1.867 | 1.871 | 1.179  | 1.184 | 1.527  | 1.528 |
| Flavonoids    | CI      | 0.599    | 0.708 | 0.818    | 0.928 | 0.542 | 0.651 | 0.550 | 0.557 | 0.433  | 0.680 | 0.809  | 0.920 |
| (mg/g)        | CII     | 0.690    | 0.717 | 0.528    | 0.530 | 0.362 | 0.385 | 0.463 | 0.467 | 0.505  | 0.505 | 0.581  | 0.583 |
| Tannins       | CI      | 0.766    | 0.794 | 1.407    | 1.452 | 1.096 | 1.122 | 0.668 | 0.734 | 1.171  | 1.198 | 1.282  | 1.295 |
| (mg/g)        | CII     | 1.377    | 1.379 | 1.420    | 1.469 | 1.285 | 1.310 | 1.405 | 1.410 | 1.330  | 1.334 | 1.396  | 1.393 |
| Saponins      | CI      | 3.801    | 3.891 | 6.053    | 6.139 | 3.572 | 3.659 | 3.215 | 3.400 | 3.823  | 3.919 | 4.380  | 4.472 |
| (mg/g)        | CII     | 4.425    | 4.586 | 2.905    | 2.911 | 2.695 | 2.760 | 4.288 | 4.294 | 3.622  | 3.626 | 3.041  | 3.043 |

**Table 3a.** Scaling test for various traits in Cross I (CL 367 × C 88) May and July sowing

| Characters            | A              |                | B              |                | C              |                | D              |                |
|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|                       | May            | July           | May            | July           | May            | July           | May            | July           |
| Seed yield            | 0.120±0.187    | 0.760±0.408    | -1.070±0.202** | -0.310±0.393   | 13.465±0.543** | 11.356±0.669** | -7.208±0.273** | -5.453±0.281** |
| Crude protein percent | -0.543±0.226*  | -0.507±0.216*  | -1.137±0.243** | -1.138±0.243** | 5.133±0.372**  | 5.215±0.366**  | -3.407±0.196** | -3.430±0.191** |
| Anthocyanins          | -0.235±0.014** | -0.229±0.014** | 0.179±0.014**  | 0.182±0.013**  | 0.653±0.043**  | 0.807±0.042**  | -0.354±0.022** | -0.427±0.022** |
| Total phenols         | 0.025±0.017    | -0.023±0.017   | 0.545±0.012**  | 0.523±0.015**  | 0.550±0.053**  | 0.685±0.054**  | 0.010±0.027    | -0.093±0.027** |
| Flavonoids            | 0.276±0.200    | -0.341±0.032** | -0.257±0.042** | -0.423±0.031** | 0.303±0.074**  | 0.710±0.074**  | -0.142±0.107   | -0.737±0.040** |
| Tannins               | -0.480±0.009** | -0.480±0.012** | -0.041±0.009** | -0.015±0.012   | 1.448±0.025**  | 1.555±0.026**  | -0.985±0.013** | -1.025±0.013** |
| Saponins              | -0.274±0.030** | -0.288±0.030** | 0.866±0.024**  | 0.853±0.029**  | 3.441±0.087**  | 3.748±0.090**  | -1.425±0.044** | -1.591±0.046** |

\*, \*\* significant at 5% and 1%

**Table 3b.** Scaling test for various traits in Cross II (CL 400 × BL 1) May and July sowing

| Characters            | A              |                | B              |                | C              |                | D              |                |
|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|                       | May            | July           | May            | July           | May            | July           | May            | July           |
| Seed yield            | 1.440±0.200**  | 1.770±0.424**  | 0.125±0.204    | -0.730±0.423   | 9.928±0.536**  | 5.002±0.710**  | -3.929±0.260** | -1.981±0.266** |
| Crude protein percent | -3.115±0.327** | -3.115±0.297** | -2.030±0.298** | -1.820±0.323** | -1.843±0.434** | -1.353±0.439** | -1.651±0.242** | -1.791±0.242** |
| Anthocyanins          | -0.464±0.013** | -0.459±0.013** | -0.047±0.013** | -0.474±0.013** | -0.493±0.038** | -0.496±0.038** | -0.221±0.019** | -0.218±0.019** |
| Total phenols         | 0.136±0.013**  | 0.132±0.013**  | 0.244±0.013**  | 0.245±0.014**  | -1.677±0.035** | -1.683±0.036** | 1.028±0.018**  | 1.030±0.018**  |
| Flavonoids            | 0.076±0.024**  | 0.091±0.028**  | -0.251±0.030** | -0.250±0.031** | 0.147±0.175    | 0.150±0.178    | -0.161±0.087   | -0.154±0.089   |
| Tannins               | 0.017±0.008*   | 0.021±0.007**  | -0.018±0.007*  | -0.008±0.009   | -0.180±0.020** | -0.173±0.020** | 0.090±0.010**  | 0.093±0.010**  |
| Saponins              | 0.094±0.028**  | 0.093±0.028**  | -0.419±0.026** | -0.414±0.026** | -4.178±0.097** | -4.161±0.097** | 1.927±0.048**  | 1.920±0.048**  |

\*, \*\* significant at 5% and 1%

**Table 4a:** Estimation of gene effects for seed yield and anti-nutritional components in Cross I (May sowing)

| Characters            | m              | d              | h              | i              | j              | l               | Interaction |
|-----------------------|----------------|----------------|----------------|----------------|----------------|-----------------|-------------|
| Seed yield            | 12.631±0.126** | -1.630±0.108** | 11.400±0.556** | 14.415±0.547** | -1.190±0.250** | -15.365±0.694** | Duplicate   |
| Crude protein percent | 20.677±0.071** | -0.945±0.134** | 5.063±0.410**  | 6.813±0.392**  | -0.595±0.302*  | -8.493±0.653**  | Duplicate   |
| Anthocyanins          | 0.766±0.010**  | -0.239±0.008** | 0.140±0.044**  | 0.708±0.043**  | 0.414±0.017**  | -0.764±0.053**  | Duplicate   |
| Total phenols         | 1.272±0.013**  | -0.315±0.009** | -0.300±0.054** | -0.020±0.054   | 0.520±0.019**  | 0.590±0.063**   | Duplicate   |
| Flavonoids            | 0.550±0.017**  | -0.376±0.102** | 0.118±0.215    | 0.284±0.214    | -0.532±0.203*  | -0.265±0.413    | Duplicate   |
| Tannins               | 0.668±0.006**  | -0.111±0.005** | 1.968±0.026**  | 1.969±0.025**  | 0.439±0.012**  | -2.491±0.033**  | Duplicate   |
| Saponins              | 3.215±0.021**  | -0.556±0.016** | 1.495±0.090**  | 2.850±0.089**  | 1.140±0.035**  | -2.259±0.107**  | Duplicate   |

**Table 4b.** Estimation of gene effects for seed yield and anti-nutritional components for Cross I (July sowing)

| Characters            | m              | d              | h             | i              | j             | l               | Interaction |
|-----------------------|----------------|----------------|---------------|----------------|---------------|-----------------|-------------|
| Seed yield            | 15.356±0.104** | -1.635±0.190** | 7.256±0.621** | 10.906±0.562** | -1.070±0.470* | -10.456±1.012** | Duplicate   |
| Crude protein percent | 21.306±0.070** | -0.963±0.130** | 5.110±0.399** | 6.860±0.381**  | -0.630±0.294* | -8.505±0.636**  | Duplicate   |
| Anthocyanins          | 0.777±0.010**  | -0.240±0.008** | 0.299±0.044** | 0.855±0.044**  | 0.411±0.018** | -0.902±0.054**  | Duplicate   |
| Total phenols         | 1.280±0.013**  | -0.305±0.009** | -0.110±0.055* | 0.185±0.054**  | 0.547±0.020** | 0.315±0.065**   | Duplicate   |
| Flavonoids            | 0.557±0.017**  | -0.151±0.019** | 1.308±0.081** | 1.475±0.079**  | -0.082±0.041* | -2.239±0.108**  | Duplicate   |
| Tannins               | 0.734±0.006**  | -0.096±0.007** | 2.049±0.027** | 2.050±0.027**  | 0.466±0.015** | -2.545±0.038**  | Duplicate   |
| Saponins              | 3.400±0.021**  | -0.553±0.017** | 1.826±0.093** | 3.182±0.091**  | 1.141±0.039** | -2.616±0.112**  | Duplicate   |

\*, \*\* significant at 5% and 1%

m = mean values; [d] = additive gene effect; [h] = dominance gene effect; [i] = additive × additive gene effect; [j] = additive × dominance gene effect; [l] = dominance × dominance gene effect.

identify and quantify the type and amount of additive [d] and dominance [h] components of gene action, as well as any inter-allelic interactions that may have occurred. The analysis of the generation mean was done for two crosses, viz: Cross I (CL 367 × C 88) and Cross II (CL 400 × BL 1) for various traits.

#### **Cross I (CL 367 × C 88)**

In the case of the cross I (CL 367 × C 88) significant, values for scaling tests (A, B, C and D) were reported in the majority of the traits in the case of May and July sowing (Table 3a). The results indicated the presence of epistatic interactions. As a result, the simple additive-dominance model was insufficient. Therefore, a six-parameter model was best suited to explore these properties.

The mean values [m] were significant and positive for all the traits studied in the case of May and July sowing of the crop (Table 4a & 4b). This indicated differences in the mean value of the generation studied and depicts the quantitative nature of the traits studied. The additive gene effect was significantly negative for all characters under study in the case of May sowing and July sowing. The Dominance gene effect was significantly positive for various characters studied, except total phenols and flavonoids content for May sowing and July sowing data. Total phenol content was significantly negative for both May and July sowing. Additive × Additive gene effect was significantly positive for various characters under study except total phenols and flavonoids content for May sowing, whereas it was positive and significant for all the traits studied for July sowing data. The additive × dominance gene effect was significantly positive for characters such as anthocyanins, phenols, tannins, and saponins for both May sowing and July sowing of the crop. It was significantly negative for crude protein percent, seed yield, and flavonoid content for both May sowing and July sowing. Dominance × Dominance gene effect was significantly positive for total phenols content in May and July sowing of the crop. It was significantly negative for seed yield, crude protein percent, anthocyanins, tannins, and saponins for May sowing and seed yield, crude protein percent, anthocyanins, flavonoids, tannins, and saponins for crop sown in July (Table 4a & 4b).

The sign of dominance gene effect and dominance × dominance gene effect were employed to identify epistasis type governing the trait (Kearsey and Pooni 1996). The dominance and dominance ×

dominance gene effect had opposite signs for all the characters under study in May and July sowing of the crop. This suggests that duplicate epistasis was present. It would restrict the range of variability, slowing down the rate of advancement through trait selection.

#### **Cross II (CL 400 × BL 1)**

In Cross II (CL 400 × BL 1), significant values for scaling tests (A, B, C, and D) were reported in the majority of the traits in the case of May and July sowing (Table 3b). The results indicated the presence of epistatic interactions. As a result, the simple additive-dominance model was insufficient. Therefore, a six-parameter model was best suited to explore these properties.

The mean values [m] were significant and positive for all the traits studied in the case of May and July sowing of the crop (Table 5a & 5b). The additive gene effect was significantly negative for various characters under study, except crude protein percent and saponin content in the case of May sowing data. Total saponin content was positive and significant for May and July sowing. The dominance gene effect was significantly positive for characters such as crude protein percent, seed yield, and anthocyanin content for May sowing and crude protein percent, anthocyanin content for July sowing of the crop. The dominance gene effect was significantly negative for total phenols, tannins, and saponins content for May and July sowing. Additive × Additive gene effect was significantly positive for characters such as crude protein percent, seed yield, and anthocyanin content for May and July sowing of the crop. The additive × additive gene effect was significantly negative for total phenols, tannins and saponins content for May and July sowing. The additive × dominance gene effect was significantly positive for total phenols content for May sowing and crude protein percent, and total phenols content for July sowing of the crop. It was significantly negative for seed yield, flavonoids, tannins, and saponins content for May and July sowing. The dominance × dominance gene effect was significantly positive for total phenols, tannins, and saponins content for May and July sowing of the crop. It was significantly negative for seed yield, crude protein percent, anthocyanins, and flavonoids for May and July sowing of crop (Table 5a & 5b).

The dominance and dominance × dominance gene effect had opposite signs for most of the traits for May and July sowing of the crop. This suggests

that duplicate epistasis was present. It would restrict the range of variability, slowing down the rate of advancement through trait selection. High values of broad sense heritability were noted in both the cross combinations (Table 6) for all the traits, suggesting that selection can be an effective tool for improving these traits improvement (Nassourou *et al.* 2020) and these traits are inherited from parents to offspring.

In the present research, the involvement of additive gene effects and predominant non-additive gene effects for most of the traits suggested that the recurrent selection could be used in the breeding programmes to develop superior varieties. The selection should be delayed in later generations due to a higher magnitude of dominance gene effects in most of the traits studied. Nassourou *et al.* (2020) suggested that breeding for tannins, flavonoids, and phenol contents in cowpea seeds would be quite efficient through recurrent selection and

selection in advanced generations. The importance of both additive and non-additive gene effects in the inheritance of seed yield has been reported by Mote *et al.* (2007). Nassourou *et al.* (2020) reported that both additive and predominant non-additive gene effects for the inheritance of flavonoid content, whereas significant epistatic gene action has been reported by (Noubissie *et al.* 2012) for total phenols content in cowpea.

Genetic improvement of the nutritional value of cowpea seed by reducing anti-nutrient levels is possible by exploiting the wide genetic variability and using appropriate breeding techniques. Due to significant epistasis observed, selection for these traits would be most effective at later generations by using the pedigree method and recurrent selection (Santos *et al.* 2012). For the pedigree method, selection would be postponed in  $F_6$  generation and operated in bulk and by single seed or single-pod

**Table 5a.** Estimation of gene effects for seed yield and anti-nutritional components for Cross II (May sowing)

| Characters            | m              | d              | h              | i              | j              | l              | Interaction |
|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------|-------------|
| Seed yield            | 14.405±0.119** | -1.500±0.101** | 3.538±0.533**  | 7.858±0.519**  | -1.440±0.251** | -6.418±0.672** | Duplicate   |
| Crude protein percent | 22.012±0.079** | -0.140±0.182   | 1.534±0.506**  | 3.302±0.483**  | 1.085±0.413**  | -8.447±0.849** | Duplicate   |
| Anthocyanins          | 1.779±0.009**  | -0.228±0.007** | 0.344±0.039**  | 0.442±0.038**  | -0.007±0.016   | -1.378±0.047** | Duplicate   |
| Total phenols         | 1.867±0.008**  | -0.348±0.008** | -2.800±0.037** | -2.056±0.036** | 0.108±0.018**  | 2.435±0.047**  | Duplicate   |
| Flavonoids            | 0.463±0.043**  | -0.076±0.015** | 0.090±0.176    | 0.322±0.175    | -0.327±0.036** | -0.497±0.185** | Duplicate   |
| Tannins               | 1.405±0.005**  | -0.062±0.004** | -0.298±0.021** | -0.180±0.020** | -0.035±0.010** | 0.179±0.026**  | Duplicate   |
| Saponins              | 4.288±0.023**  | 0.581±0.015**  | -4.839±0.098** | -3.853±0.097** | -0.513±0.034** | 3.528±0.113**  | Duplicate   |

**Table 5b.** Estimation of gene effects for seed yield and anti-nutritional components for Cross II (July sowing)

| Characters            | m              | d              | h              | i              | j              | l              | Interaction |
|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------|-------------|
| Seed yield            | 16.972±0.101** | -2.125±0.173** | -0.343±0.606   | 3.962±0.531**  | -2.500±0.506** | -2.922±0.992** | Duplicate   |
| Crude protein percent | 22.065±0.085** | -0.035±0.180   | 1.814±0.506**  | 3.582±0.484**  | 1.295±0.409**  | -8.517±0.843** | Duplicate   |
| Anthocyanins          | 1.780±0.009**  | -0.226±0.007** | 0.339±0.038**  | 0.437±0.038**  | -0.014±0.016   | -1.369±0.048** | Duplicate   |
| Total phenols         | 1.871±0.008**  | -0.345±0.008** | -2.809±0.037** | -2.060±0.037** | 0.114±0.017**  | 2.438±0.047**  | Duplicate   |
| Flavonoids            | 0.467±0.044**  | -0.077±0.016** | 0.070±0.179    | 0.309±0.178    | -0.341±0.038** | -0.467±0.189*  | Duplicate   |
| Tannins               | 1.410±0.005**  | -0.059±0.005** | -0.300±0.021** | -0.186±0.021** | -0.030±0.011** | 0.199±0.028**  | Duplicate   |
| Saponins              | 4.294±0.023**  | 0.584±0.015**  | -4.829±0.098** | -3.840±0.097** | -0.508±0.035** | 3.519±0.114**  | Duplicate   |

\*, \*\* significant at 5% and 1%

m = mean values; [d] = additive gene effect; [h] = dominance gene effect; [i] = additive × additive gene effect; [j] = additive × dominance gene effect; [l] = dominance × dominance gene effect.

**Table 6.** Estimation of heritability for seed yield and anti-nutritional components

| Characters            | Cross I (CL 367 x C88)           |      |                                   |      | Cross II (CL 400 x BL1)          |      |                                   |      |
|-----------------------|----------------------------------|------|-----------------------------------|------|----------------------------------|------|-----------------------------------|------|
|                       | $h^2$ (heritability broad sense) |      | $h_n^2$ heritability narrow sense |      | $h^2$ (heritability broad sense) |      | $h_n^2$ heritability narrow sense |      |
|                       | May                              | July | May                               | July | May                              | July | May                               | July |
| Seed yield            | 0.92                             | 0.90 | 0.34                              | 0.38 | 0.88                             | 0.87 | 0.29                              | 0.31 |
| Crude protein percent | 0.91                             | 0.92 | 0.29                              | 0.34 | 0.98                             | 0.94 | 0.21                              | 0.29 |
| Anthocyanins          | 0.97                             | 0.91 | 0.25                              | 0.39 | 0.96                             | 0.95 | 0.18                              | 0.34 |
| Total phenols         | 0.90                             | 0.95 | 0.37                              | 0.36 | 0.94                             | 0.97 | 0.24                              | 0.30 |
| Flavonoids            | 0.89                             | 0.91 | 0.21                              | 0.23 | 0.99                             | 0.98 | 0.14                              | 0.16 |
| Tannins               | 0.98                             | 0.99 | 0.26                              | 0.24 | 0.97                             | 0.95 | 0.16                              | 0.19 |
| Saponins              | 0.94                             | 0.96 | 0.19                              | 0.20 | 0.95                             | 0.98 | 0.18                              | 0.17 |

descent (Nassuorou *et al.* 2020). These methods being laborious, marker-assisted selection would also be utilized for more efficiency.

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