GENETIC ANALYSIS OF MODE OF INHERITANCE OF SEED YIELD AND ITS COMPONENTS IN TROPICAL SOYBEAN GENOTYPES

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ABSTRACT

The decision related to efficient breeding methods depends largely on the understanding of the type of gene action controlling the expression of the characters to be selected. The objective of this study was to estimate the gene action controlling yield and components in soybean (Glycine max L. Merrill). The study involved six basic soybean generations (P₁, P₂, F₁, F₂, BC₁ and BC₂) of two crosses, i.e. cross I (TGx1987-62F × TGx1830-20E) and cross II (TGx1987-10F × TGx1740-2F), at the Research farm of the International Institute for Tropical Agriculture, IITA, Ibadan. Data were subjected to generation mean analysis to determine gene actions and interactions, using Hayman model. The results obtained from the individual scaling test A, B, C indicated that the simple additive-dominance model was inadequate to reveal the inheritance of the gene governing most traits. Non-allelic gene interaction was crucial in the inheritance of most studied traits. The Hayman six-parameter genetic model demonstrated that the signs of [h] and [l] were contrasting for most of the traits; suggesting duplicate epistasis. In fact, the effect of dominance was important and significant in the genetic control of most of the traits studied. Therefore, improvement of soybean seed yield and its related characters need intensive selection and should be delayed until later generations.

Key Words: Additive, dominance, epistasis, gene action

RÉSUMÉ

La décision relative aux méthodes de sélection efficaces dépend en grande partie de la compréhension du type d’action des gènes contrôlant l’expression des caractères à sélectionner. L’objectif de cette étude était d’estimer l’action des gènes contrôlant le rendement et les composants du soja (Glycine max L. Merrill). L’étude portait sur six générations de base de soja (P₁, P₂, F₁, F₂, BC₁ et BC₂) de deux croisements, à savoir le croisement I (TGx1987-62F × TGx1830-20E) et le croisement II (TGx1987-10F × TGx1740-2F), à la ferme de recherche de l’Institut international d’agriculture tropicale, IITA, Ibadan. Les données ont été soumises à une analyse moyenne de génération pour déterminer les actions et les
interactions des gènes, à l’aide du modèle Hayman. Les résultats obtenus à partir du test de mise à l’échelle individuelle A, B, C ont indiqué que le modèle simple de dominance additive était insuffisant pour révéler l’héritabilité du gène régissant la plupart des traits. L’interaction des gènes non alléliques était cruciale dans l’héritabilité des traits les plus étudiés. Le modèle génétique à six paramètres de Hayman a démontré que les signes de [h] et [l] étaient contrastés pour la plupart des traits ; suggérant une épistasie en double. En fait, l’effet de dominance était important et significatif dans le contrôle génétique de la plupart des traits étudiés. Par conséquent, l’amélioration du rendement en graines de soja et de ses caractéristiques associées nécessite une sélection intensive et doit être reportée aux générations suivantes.

Mots Clés : Additif, dominance, épistasie, action génique

INTRODUCTION

Soybean (Glycine max L. Merrill) is one of the world’s important oil crops, which is a popular raw material for livestock feeds, human food and industrial oil products. Nigeria is the second-largest soybean producer in sub-Saharan Africa, producing up to 679,000 metric tonnes in 2016 (FAOSTAT, 2016). Soybean production in Nigeria covers the tenth largest arable land area, mainly in Benue, Oyo and Kogi states.

To improve the performance of any crop, information on genetic diversity and relationships among breeding materials is essential. Knowledge about genetic diversity can also be effectively used in gene-bank management like tagging of germplasm, identification and/or elimination of duplicates in the gene stock; and establishment of core collections (Dwivedi et al., 2001).

In order to exploit the existing genetic diversity present in the breeding materials efficiently, and to plan for an efficient selection programme, the breeder needs basic information regarding the inheritance of grain yield and its components. Adoption of suitable breeding methods for improvement of any crop mainly depends on the nature of gene action involved in the expression of the traits. To decide on suitable breeding strategies for improvement of yield and yield contributing characters, information regarding gene action involved in control of inheritance of these characters is of immense significance to plant breeders.

Generation mean analysis (GMA) is a useful procedure for ascertaining gene effects for polygenic traits such as yield; though its merits lies greatly in its ability to estimate epistatic gene effects such as additive × additive [i], additive × dominance [j] and dominance × dominance [l] interactions (Mather and Jinks, 1982). New crop variety improvement requires a thorough understanding of the genetic mechanisms controlling yield and its components (El-Badawy and Mehasen, 2012). In view of these, many researchers have reported the significance of non-additive gene action for grain yield and some other agronomic traits in soybean (Raut et al., 2000; Atungwu et al., 2005; Maloo, 2005). The objective of this study was to estimate the gene action and interaction controlling yield and components in soybean.

MATERIALS AND METHODS

The study was conducted at Institute of Tropical Agriculture (IITA) located at 7°31’ N and 7°54’ E), at Ibadan South-western Nigeria, during 2013-2014. South-western Nigeria has a tropical climate, with bimodal rainfall pattern; with long rains from March to July and a short dry spell in early August, generally known as August break. The second, also known as late rains run from Mid-August to November, with a long dry season from December to March. Four inbred lines, namely TGx1987-62F, TGx1830-20E, TGx1987-10F and TGx1740-2F, were selected from 53 lines based on high yield, seed size and seed colour. Fertiliser NPK
Inheritance study yield in tropical soya bean

Parameters measured included number of days to 50% flowering, plant height at maturity, number of branches per plant at maturity, number of days to maturity, number of pods per plant, number of seeds per pod, pod length, number of pods per node, 100 seed weight and seed yield per plant.

**Pattern of crosses.** Two crosses; namely cross I: P₁ (TGx1987-62F) × P₂ (TGx1830-20E) and cross II: P₁ (TGx1987-10F) × P₂ (TGx1740-2F), were made to produce the F₁ generation (Table 1), in the early cropping season of the year 2013. In the late cropping season of 2013, some of the seeds harvested from the hybrid (F₁) plants, along with their parents, were planted in the field. Some of the F₁ plants were backcrossed to P₁ and P₂ to generate BC₁ and BC₂ progeny in each of the two crosses, respectively. Some F₁ plants were self-pollinated to produce F₂ seeds. F₁ seed obtained in first year were saved and used in field evaluation trial. In this way, six generations, P₁, P₂, F₁, F₂, BC₁ and BC₂, were generated for crosses I and II. All the six generations in the two crosses were grown in a randomised complete block design, with three replications, in the late cropping season of year 2014.

Data analysis. The individual scaling test was used to ascertain the presence or absence of non-allelic interactions (Mather and Jinks, 1982). The A, B and C and their variance were estimated to test the sufficiency of the additive-dominance model in each of the case.

Where:

\[ A = 2 \overline{BC}_1 \overline{F}_1 \overline{F}_1 \]

\[ B = 2 \overline{BC}_2 \overline{F}_2 \overline{F}_2 \]

\[ C = 4 \overline{BC}_1 \overline{BC}_2 \overline{F}_1 \overline{F}_2 \]

The significance of A and B scales were used to indicate the presence of all types of non-allelic gene interactions; while the significance of the C scale indicated [dd] type of epistasis (Singh and Narayanan, 1993).

The data were also subjected to generation mean analysis (GMA) for the estimation of gene effects, using the six-parameter model based on the method of (Hayman, 1958; Jinks and Jones, 1958). Each genetic parameter was estimated as follows:

\[ [m] - \overline{F}_2 \]

\[ [d] = \overline{BC}_1 \overline{BC}_2 \]

\[ [h] = -4 \overline{F}_2 \overline{P}_1 \overline{P}_2 + 2(\overline{BC}_1 + \overline{BC}_2) \]

\[ [l] = 2(\overline{BC}_1 + \overline{BC}_2) + 2\overline{F}_2 \]

\[ [i] = \overline{BC}_1 - \overline{BC}_2 - 0.5(\overline{P}_1 - \overline{P}_2) \]

\[ [j] = \overline{F}_1 + \overline{F}_2 - 2\overline{F}_1 + 4\overline{F}_2 + 4\overline{BC}_1 + 4\overline{BC}_2 \]

Where:

\[ \overline{P}_1, \overline{P}_2, \overline{F}_1, \overline{F}_2, \overline{BC}_1 \text{ and } \overline{BC}_2 \] are the mean values of P₁, P₂, F₁, F₂, and B₁ and B₂ generations, respectively

**RESULTS**

**Performances of six generations.** The means and standard errors of the six generations in the two crosses for ten traits are presented in Table 2. Generally, the results indicated that means of the F₁’s were greater than either the highest parent or mid-parent value for most of the traits.

A, B, C scaling tests. The results of the A, B and C scaling tests, which authenticated the adequacy of additive-dominance models are presented in Table 3. The non-allelic interaction was found to be involved in the control of genetic variation among the six generations, for almost all the traits. However, the estimates of the A scaling test were significant (P<0.05) for plant height at maturity, number of days to 50% flowering, number of seeds per pod, 100 seed weight and number of primary branches per plant in cross I. On the other hand, days to 50% flowering, plant height at
<table>
<thead>
<tr>
<th>Variety</th>
<th>Pattern of crossing</th>
<th>Source/Origin</th>
<th>Lodging Score</th>
<th>Days to maturity</th>
<th>Seed colour</th>
<th>Yield</th>
</tr>
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<tbody>
<tr>
<td>CROSS I</td>
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</tr>
<tr>
<td>P₁</td>
<td>TGx1987-62F</td>
<td>IITA</td>
<td>Moderate</td>
<td>Early</td>
<td>Yellowish White</td>
<td>Low yield</td>
</tr>
<tr>
<td>P₂</td>
<td>TGx1830-20E</td>
<td>IITA</td>
<td>Moderate</td>
<td>Late</td>
<td>Yellowish White</td>
<td>High yield</td>
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<td>F₁</td>
<td>P₁ × P₂</td>
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<td>F₂</td>
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<td>BC₁</td>
<td>P₁ × F₁</td>
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<tr>
<td>BC₂</td>
<td>P₂ × F₁</td>
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<td>CROSS II</td>
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<tr>
<td>P₁</td>
<td>TGx1987-10F</td>
<td>IITA</td>
<td>Moderate</td>
<td>Early</td>
<td>Yellowish White</td>
<td>Low yield</td>
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<tr>
<td>P₂</td>
<td>TGx1740-2F</td>
<td>IITA</td>
<td>Moderate</td>
<td>Late</td>
<td>Yellow</td>
<td>High yield</td>
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<tr>
<td>F₁</td>
<td>P₁ × P₄</td>
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<td>F₂</td>
<td>F₁ × F₁</td>
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<td>BC₁</td>
<td>P₁ × F₁</td>
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<tr>
<td>BC₂</td>
<td>P₄ × F₁</td>
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</table>

P = Parent, F₁ = First Filial generation, F₂ = Second Filial generation, B₁ = Backcross 1 and B₂ = Backcross
<table>
<thead>
<tr>
<th></th>
<th>Days to 50% flowering</th>
<th>Height at maturity</th>
<th>Days to plant maturity</th>
<th>Pods/plant</th>
<th>Seeds/pod</th>
<th>Hundred seed weight</th>
<th>Primary branches/plant</th>
<th>Pods/node</th>
<th>Pod length</th>
<th>Yield/plant</th>
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<tr>
<td><strong>P&lt;sub&gt;1&lt;/sub&gt;</strong></td>
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<tr>
<td>I</td>
<td>43.30±0.15</td>
<td>33.87±1.17</td>
<td>94.87±0.21</td>
<td>71.03±2.45</td>
<td>2.87±0.06</td>
<td>14.99±0.16</td>
<td>4.93±0.16</td>
<td>2.60±0.09</td>
<td>3.50±0.11</td>
<td>19.90±0.71</td>
</tr>
<tr>
<td>II</td>
<td>45.04±0.10</td>
<td>44.19±1.39</td>
<td>99.56±0.25</td>
<td>43.00±2.98</td>
<td>2.57±0.09</td>
<td>15.39±0.1</td>
<td>4.62±0.16</td>
<td>2.48±0.10</td>
<td>3.93±0.12</td>
<td>18.39±0.33</td>
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<tr>
<td>I</td>
<td>50.13±0.08</td>
<td>30.13±0.92</td>
<td>110.4±0.25</td>
<td>50.47±2.06</td>
<td>2.70±0.08</td>
<td>12.48±0.15</td>
<td>4.67±0.22</td>
<td>2.40±0.11</td>
<td>3.17±0.08</td>
<td>14.89±0.71</td>
</tr>
<tr>
<td>II</td>
<td>50.80±0.24</td>
<td>38.46±0.83</td>
<td>114.05±0.36</td>
<td>39.89±2.73</td>
<td>2.57±0.10</td>
<td>12.61±0.1</td>
<td>2.50±0.16</td>
<td>2.18±0.07</td>
<td>3.50±0.08</td>
<td>16.22±0.30</td>
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<td><strong>F&lt;sub&gt;1&lt;/sub&gt;</strong></td>
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<tr>
<td>I</td>
<td>45.03±0.11</td>
<td>35.95±1.37</td>
<td>100.87±0.21</td>
<td>69.53±2.76</td>
<td>2.90±0.06</td>
<td>16.20±0.53</td>
<td>5.67±0.18</td>
<td>3.10±0.06</td>
<td>3.81±0.03</td>
<td>22.84±0.83</td>
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<tr>
<td>II</td>
<td>44.14±0.16</td>
<td>52.60±0.91</td>
<td>95.53±0.34</td>
<td>58.69±3.95</td>
<td>2.93±0.05</td>
<td>16.14±0.67</td>
<td>3.76±0.18</td>
<td>2.34±0.09</td>
<td>3.96±0.05</td>
<td>20.17±0.77</td>
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<td><strong>F&lt;sub&gt;2&lt;/sub&gt;</strong></td>
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<tr>
<td>I</td>
<td>47.37±0.37</td>
<td>28.87±0.88</td>
<td>103.24±0.76</td>
<td>50.54±3.18</td>
<td>2.48±0.05</td>
<td>13.57±0.43</td>
<td>3.38±0.20</td>
<td>2.69±0.08</td>
<td>3.44±0.06</td>
<td>15.81±0.75</td>
</tr>
<tr>
<td>II</td>
<td>48.26±0.30</td>
<td>53.05±1.27</td>
<td>102.08±0.68</td>
<td>57.98±3.15</td>
<td>2.64±0.05</td>
<td>12.83±0.25</td>
<td>4.28±0.18</td>
<td>2.62±0.07</td>
<td>3.78±0.06</td>
<td>16.17±0.57</td>
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<td><strong>Bc&lt;sub&gt;1&lt;/sub&gt;</strong></td>
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<tr>
<td>I</td>
<td>48.75±0.38</td>
<td>36.87±1.51</td>
<td>103.94±1.30</td>
<td>69.58±5.19</td>
<td>2.62±0.07</td>
<td>12.18±0.30</td>
<td>5.25±0.22</td>
<td>2.83±0.11</td>
<td>3.43±0.06</td>
<td>20.28±1.43</td>
</tr>
<tr>
<td>II</td>
<td>48.08±0.36</td>
<td>44.87±2.38</td>
<td>107.55±0.89</td>
<td>60.96±4.08</td>
<td>2.66±0.06</td>
<td>13.83±0.32</td>
<td>4.53±0.33</td>
<td>2.55±0.10</td>
<td>3.87±0.06</td>
<td>17.97±1.06</td>
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<td><strong>Bc&lt;sub&gt;2&lt;/sub&gt;</strong></td>
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<tr>
<td>I</td>
<td>45.65±0.96</td>
<td>25.42±1.29</td>
<td>103.92±0.93</td>
<td>44.25±3.28</td>
<td>2.34±0.07</td>
<td>11.61±0.30</td>
<td>3.73±0.25</td>
<td>2.43±0.13</td>
<td>3.39±0.07</td>
<td>16.61±0.85</td>
</tr>
<tr>
<td>II</td>
<td>47.93±0.44</td>
<td>44.12±1.59</td>
<td>101.83±0.99</td>
<td>57.35±4.64</td>
<td>2.48±0.08</td>
<td>12.88±0.23</td>
<td>4.49±0.21</td>
<td>2.33±0.08</td>
<td>3.71±0.07</td>
<td>16.33±0.72</td>
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</tbody>
</table>

50.DF = Number of days to 50% flowering, PHTMAT = Plant height at maturity, NDPLTM = Number of days to plant maturity, NPD.PLT = Number of pods per plant, NS.PD = Number of seeds per pod, 100.SW = Weight of 100 seeds, NPB.PLT = Number of primary branches, NPD.ND = Number of pods per node, PDLGT = Pod length, and YIELD.PLT = Yield per plant
TABLE 3. Estimates of the genetic effects for weighted least square analysis of generation means for different soya bean agronomic traits for cross I and II

<table>
<thead>
<tr>
<th>Trait</th>
<th>Cross</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>m [d]</th>
<th>[e] [h]</th>
<th>[i] [j]</th>
<th>[l] [m]</th>
<th>Epistasis</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF50%</td>
<td>I</td>
<td>9.17±0.78**</td>
<td>-3.86±1.92**</td>
<td>6.98±0.73**</td>
<td>27.94±1.80**</td>
<td>5.99±1.48**</td>
<td>2.27±0.99**</td>
<td>-0.68±2.55</td>
<td>13.03±2.07**</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>6.98±0.73**</td>
<td>6.98±1.44**</td>
<td>9.17±1.88**</td>
<td>47.40±2.53**</td>
<td>-3.42±0.09**</td>
<td>2.08±4.39</td>
<td>-1.02±1.79</td>
<td>6.00±1.13**</td>
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<tr>
<td></td>
<td>II</td>
<td>7.05±3.42**</td>
<td>-2.82±4.92</td>
<td>24.35±5.65**</td>
<td>75.55±2.71**</td>
<td>-2.87±0.81**</td>
<td>67.04±20.15**</td>
<td>-34.22±7.67**</td>
<td>7.23±5.95**</td>
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<tr>
<td>NDPLMT</td>
<td>I</td>
<td>15.04±2.62**</td>
<td>-3.43±1.88**</td>
<td>5.95±3.07**</td>
<td>21.17±11.36*</td>
<td>5.66±1.40</td>
<td>18.47±3.21*</td>
<td>-17.27±7.09**</td>
<td>D</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>20.01±2.08**</td>
<td>-5.92±3.59**</td>
<td>3.65±3.49</td>
<td>23.70±10.45**</td>
<td>10.44±4.27**</td>
<td>25.95±7.72**</td>
<td>-24.53±6.36**</td>
<td>D</td>
</tr>
<tr>
<td>NPD.PL T</td>
<td>I</td>
<td>-1.40±11.01</td>
<td>-31.5±14.11**</td>
<td>35.25±17.65**</td>
<td>10.28±1.60**</td>
<td>26.88±44.94</td>
<td>25.5±17.18*</td>
<td>30.1±12.68*</td>
<td>7.4±28.31</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>20.23±9.54**</td>
<td>16.12±10.45*</td>
<td>31.65±15.18**</td>
<td>15.60±2.02**</td>
<td>63.00±45.10*</td>
<td>4.70±17.45</td>
<td>0.14±12.99</td>
<td>-4.05±29.00*</td>
</tr>
<tr>
<td>NS.PD</td>
<td>I</td>
<td>-0.53±0.16**</td>
<td>-0.92±0.18**</td>
<td>-1.45±0.26**</td>
<td>2.79±0.29**</td>
<td>0.09±0.05</td>
<td>-1.59±0.75**</td>
<td>0.00±0.29</td>
<td>0.39±0.22</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>-0.18±0.17</td>
<td>-0.54±0.19**</td>
<td>-0.44±0.26**</td>
<td>2.85±0.30**</td>
<td>0.00±0.67</td>
<td>-0.92±0.79</td>
<td>-0.28±0.30</td>
<td>0.36±0.25</td>
</tr>
<tr>
<td>100.SW</td>
<td>I</td>
<td>-6.83±0.81**</td>
<td>-5.46±0.82**</td>
<td>-5.59±2.02**</td>
<td>20.44±1.91**</td>
<td>1.26±0.11</td>
<td>-23.23±4.31**</td>
<td>-6.7±1.91</td>
<td>-1.37±0.88</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>-3.87±1.04**</td>
<td>-2.99±0.94**</td>
<td>-8.96±2.05**</td>
<td>11.9±1.48**</td>
<td>1.39±0.09</td>
<td>-0.52±2.53</td>
<td>2.1±1.47</td>
<td>-0.88±2.47</td>
</tr>
<tr>
<td>NPB/PL T</td>
<td>I</td>
<td>-0.1±0.50</td>
<td>-2.88±0.57**</td>
<td>-7.42±0.92**</td>
<td>0.36±1.05</td>
<td>0.13±0.13</td>
<td>6.77±2.59**</td>
<td>4.44±1.04</td>
<td>2.78±0.71*</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.68±0.49</td>
<td>2.72±0.71**</td>
<td>2.48±0.85**</td>
<td>0.52±0.19</td>
<td>1.09±0.12</td>
<td>5.44±2.82**</td>
<td>0.92±1.08</td>
<td>-2.04±0.82</td>
</tr>
<tr>
<td>NPD.ND</td>
<td>I</td>
<td>-0.04±0.26</td>
<td>-0.64±0.28**</td>
<td>-0.44±0.37</td>
<td>2.74±0.48**</td>
<td>0.14±0.07</td>
<td>-0.56±1.26</td>
<td>-0.24±0.48</td>
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<tr>
<td></td>
<td>II</td>
<td>0.28±0.24</td>
<td>0.14±0.20</td>
<td>1.14±0.36**</td>
<td>3.05±0.39**</td>
<td>0.15±0.40</td>
<td>-1.01±0.41**</td>
<td>-0.72±0.41</td>
<td>0.14±0.43</td>
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<tr>
<td>PDLGT</td>
<td>I</td>
<td>-0.12±0.15</td>
<td>0.47±0.18**</td>
<td>0.47±0.25</td>
<td>2.96±0.27**</td>
<td>0.34±0.07**</td>
<td>1.09±0.71**</td>
<td>-0.12±0.27</td>
<td>-0.59±0.23</td>
</tr>
<tr>
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<td>II</td>
<td>-0.15±0.16</td>
<td>-0.54±0.18**</td>
<td>-0.22±0.27</td>
<td>3.69±0.29**</td>
<td>0.22±0.07**</td>
<td>0.09±0.73</td>
<td>0.02±0.28</td>
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<tr>
<td>YIELD.PL T</td>
<td>I</td>
<td>-2.18±2.06</td>
<td>-4.51±2.02**</td>
<td>-17.23±3.57**</td>
<td>6.8±4.52</td>
<td>2.51±0.50</td>
<td>19.84±11.79*</td>
<td>10.54±4.49*</td>
<td>2.33±3.48</td>
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<tr>
<td></td>
<td>II</td>
<td>-2.6±1.36*</td>
<td>-3.7±1.76**</td>
<td>-10.27±3.40**</td>
<td>13.3±3.81**</td>
<td>1.09±0.27**</td>
<td>9.61±4.36**</td>
<td>3.92±2.80</td>
<td>1.11±2.63</td>
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</tr>
<tr>
<td>50.DF</td>
<td></td>
<td>Number of days to 50% flowering</td>
<td>PHTMAT = Plant height at maturity</td>
<td>NDPLMT = Number of days to plant maturity</td>
<td>NPD.PL T = Number of pods per plant</td>
<td>NS.PD = Number of seeds per pod</td>
<td>100.SW = Weight of 100 seeds</td>
<td>NPB.PL T = Number of primary branches</td>
<td>NPD.ND = Number of pods per node</td>
</tr>
</tbody>
</table>

50.DF = Number of days to 50% flowering, PHTMAT = Plant height at maturity, NDPLMT = Number of days to plant maturity, NPD.PL T = Number of pods per plant, NS.PD = Number of seeds per pod, 100.SW = Weight of 100 seeds, NPB.PL T = Number of primary branches, NPD.ND = Number of pods per node, PDLGT = Pod length, YIELD.PL T = Yield per plant, D = Duplicate, C = Complementary
maturity, number of days to plant maturity, number of pods per plant, hundred seed weight and yield per plant were significant (P<0.05) in the cross II. The values for B scaling test were significant (P<0.05) for all the traits in cross I, whereas in cross II, number of days to plant maturity, number of pods per plant, number of seeds per pod, hundred seed weight, number of primary branches per plant, pod length and seed yield per plant were significant. Scaling test C values were significant (P<0.05) for all traits studied, except number of days to plant maturity in cross II and pod length in both crosses.

**Gene effects.** The estimates of genetic effects of the six parameters in the two crosses for ten agronomic traits of soybean are presented in Table 3. The mean effects were highly significant for all traits in the two crosses, except for number of primary branches in the two crosses and seed yield per plant in cross I.

Additive effects [d] were significant for days to 50% flowering, plant height at maturity, number of days to plant maturity, 100 seed weight, pod length and seed yield per plant in the two crosses. However, number of pods per plant was significant only in cross I and number of primary branches only in cross II. The additive effect was negative for days to 50% flowering, plant height at maturity and number of days to plant maturity.

The dominance effect [h] was significant in the two crosses for plant height at maturity, number of days to plant maturity, number of primary branches per plant; while other traits were either significant in cross I or II (Table 3). The dominance effect was higher in value than the additive effects in most of the characters.

The additive × additive [i] effects were significant for plant height at maturity and a hundred seed weight in crosses I and II; number of days to plant maturity in cross II and number of pods per plant, number of primary branches per plant and yield per plant in cross I.

The additive × dominance [j] interaction showed high significance for number of days to 50% flowering, plant height at maturity, number of days to plant maturity and number of primary branches per plant in crosses I and II. The number of pods per plant and pod length were also significance in cross I.

The dominance × dominance effect [l] was significant for days to 50% flowering, plant height at maturity, number of pods per plant, and number of primary branches per plant in cross II. Significance was also observed for plant height at maturity, number of days to plant maturity, number of seeds per pod, hundred seed weight and seed yield per plant in crosses I and II.

Most of the signs of the estimates of [l] were the opposite of that of [h] in both crosses, except in plant height at maturity in crosses I and II, number of pods per plant in cross I, pod length in cross II and yield per plant in cross II.

**DISCUSSION**

**A.B.C scaling test.** The different types of gene effects estimated are useful for analysing the gene action controlling seed yields and its component in soybean, this important for planning an effective breeding procedure. During the present study, there was variation among the gene actions between the two crosses, indicating the importance of environment and maternal influence on the expression of the characters (Table 3). The presence or absence of epistasis was revealed by the analysis of generation means, using the scaling test. The non-allelic interaction was found to be operating and predominant in the control of gene action among the six generations for number of days to plant maturity, number of seeds per pod, number of pods per node and pod length indicating that the additive dominance model was not adequate to explain the genetic variation.

**Performances of six generations.** In Table 2, the means of the F$_s$ were higher than either
the highest parent or mid-parent value in the
two crosses for most of the traits studied,
indicating the presence of heterosis and
dominance.

**Gene effects.** Additive effects \([d]\) were
significant for most traits in the two crosses,
suggesting existence of potential for further
improvement of these traits, using a simple
selection procedure. In close agreement with
this study is the report of Agrawal *et al.*
(1999). As presented in the result, the additive
effects estimates was negative for days to
50% flowering, plant height at maturity and
number of days to plant maturity. The negative
or positive signs for additive effects relied
largely on the parent chosen as parent 1
(Edwards *et al.*, 1975; Cukadar-Olmedo and
Miller, 1997).

Dominance effects were positive and
significant in the two crosses for all traits,
except days to 50% flowering, number of
seeds per pod, number of pods per node in
cross I; hundred seed weight in cross II and
pod length in crosses I and II; indicating the
importance of dominance gene effects in
inheritance of these characters (Table 3). A
negative \([h]\), suggests that the alleles
responsible for the decreasing value of the traits
are dominant over the alleles governing
increasing the value (Cukadar-Olmedo and
Miller, 1997).

The estimates of the dominance gene effect
were higher than the additive gene effect for
almost all the studied traits in the two crosses,
indicating the important role of the dominant
component of gene action within the
inheritance of those traits. The dominance
gene effects being greater in magnitude than
additive effects in the inheritance of soybean
was also reported by Rajput *et al.* (1987) and
Datt *et al.* (2011). The significance of additive
\([d]\) and dominance \([h]\) in the inheritance of
plant height at maturity, number of days to
plant maturity, and yield per plant in the two
crosses, number of primary branches per plant
in cross II and hundred seed weight in cross
I, demonstrated that both types of additive and
dominance effects were involved in the
genetics of these traits. Bhor *et al.* (2014)
reported the significance of both additive and
dominance gene effects in the inheritance of
yield and hundred seed weight in soybean.

The present study showed that apart from
the additive and dominance genetic effects,
epistasis also contributes to genetic variations
for the characters mentioned. Different types
of epistasis effects were found for the
different traits under study; however, their
relative magnitudes varied among traits. In
such a situation, the acceptable breeding
programme is one which will effectively and
simultaneously use the three types of gene
effects. This finding agrees with the results
of Marco Antonio *et al.* (2012) who studied
thirty-two inbred lines and observed that
epistasis is present in yield expression of
soybean. Most of the signs of the estimates
of \([l]\) observed were opposite to that of \([h]\) in
both crosses, indicating existence of duplicate
type epistasis. This type of epistasis generally
impede the improvement of characters through
selection. It also suggests that selection for
improvement should be delayed till after many
generations of selection until a high level of
gene fixation and low level of dominance is
achieved. On the other hand, plant height at
maturity in the first and second crosses,
number pods per plant in cross I and pod
length and yield per plant in cross II revealed
the same signs of \([h]\) and \([l]\) components,
indicating a complimentary type of gene action
for these traits. Thus, immediate selection can
be exploited for these traits for their
improvement. Several researchers (Mehetre
*et al.*, 1998; Rahangdale and Raut, 2002) also
noted that complimentary epistasis was
prevalent for these traits in soybean. The
presence of duplicate epistasis can impede
progress and make it complex to fix genes at
a high level of expression. The predominance
of non-additive gene action in the control of
yield was also reported by several researchers (Kaw and Menon, 1983; Halvankar and Patil, 1993; Sharma and Phul, 1994). Duplicate epistasis involving the inheritance of yield was reported by Rahangdale and Raut (2002). Our findings also illustrated that duplicate epistasis prevailed for most of the studied traits in the two crosses, suggesting that duplicate epistasis was greater and more important for all studied traits. Duplicate epistasis may limit the expression of a trait in early segregating generations. These types of gene effects may be used by crossing the selected segregants and delaying the selections to advanced generations. El-Ameen (2008) also reported duplicate type of epistasis for all characters studied in a few crosses in soybean. In contrast with our results, however, Sherif and Damarany (1992) reported that both complementary and duplicate types of non-allelic gene interaction were present in all traits in soybean.

The expression of genes and their interactions are highly influenced by the environment, thus, genetic by environment interactions can also be put into consideration in future studies. Moreover, several crosses involving different genotypes with different traits can be also be used for estimation of large genetic effect.

CONCLUSION

This study has revealed that mean values of F1 from all crosses of soybean exceeded those of the better parent for most of the yield and its contributing characters, indicating dominance effects. Moreover, these results also suggested the involvement of duplicate epistasis governing the genes controlling seed yield and components in soybean. This further indicates that selection for high yielding genotypes improvement would be complex and should be postponed until after several generations when the effect dominance would have reduced. Further study can be carry out using more than two genotypes.

ACKNOWLEDGEMENT

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REFERENCES


