

## **Original Research Article**

# **Generation mean analysis for estimating gene action, heterosis and inbreeding depression in yield and foliar disease resistance in three faba bean (*Vicia faba* L.) crosses**

### ABSTRACT

This study was conducted at the Sakha Agricultural Research Station farm over three growing seasons (2019/20, 2020/21, and 2021/22) to introduce new faba bean genotypes possessing high yield potential and increased resistance to foliar diseases. The research involved six populations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$ , and  $BC_2$ ) from three crosses (Cross-1: Santamora x Foal SbaiLabiade, Cross-2: Santamora x Misr 3, and Cross-3: Cairo 4 x Misr 3), analyzed using a randomized complete block design with three replications. Generation mean analysis revealed significant mid and better parent heterosis for most traits, indicating over-dominance. Inbreeding depression manifested negatively for chocolate spot and rust diseases but positively for seed count and seed yield per plant across all crosses. Non-allelic interactions were present for all traits, and dominance gene effects were more influential than additive gene effects for most traits. Mean performance analysis showed that  $F_1$  populations had lower disease reactions, but higher yields compared to the better parent, while  $F_2$  populations displayed greater genetic variability due to segregation. Heterosis was significant for yield and its components across all crosses but less beneficial for disease resistance. Inbreeding depression was significant and negative for disease reactions but positive for yield traits. The study found high broad-sense heritability for all traits, suggesting potential for phenotypic selection. Narrow-sense heritability values were moderate for qualitative traits and lower for quantitative traits. Genetic advance under selection indicated the highest gains were associated with moderate heritability values. Significant non-allelic interactions suggested the need for specific breeding strategies, with dominance gene effects more pronounced than additive effects. These findings support the feasibility of selecting high-yielding, disease-resistant faba bean genotypes through targeted breeding methods, aligning with previous research on the genetic inheritance of these traits.

Keywords: Faba bean, foliar disease resistance, generation mean analysis, genetic resources.

### INTRODUCTION

Faba bean is a crucial legume crop in Egypt, valued for its high nutritional content as a protein source and its role in enhancing soil fertility through nitrogen fixation. It is commonly used in crop rotation systems. The crop is partially self-pollinated and exhibits both heterosis and inbreeding depression [1]. During the 2020/21 season, Egypt faba bean cultivation covered approximately 120,000 feddan, producing around 281,000 tons with an average yield of 10 ardab per feddan (1 ardab = 155 kg), meeting about 41% of the country's consumption needs.

Comment [L1]: Reference

Understanding gene action is vital for breeders to plan effective breeding programs. Using generation mean analysis on multiple populations can provide essential genetic insights. Foliar diseases like chocolate spot and rust significantly impact faba bean crops globally, with susceptible varieties experiencing losses exceeding 55% [2]. To address these challenges, breeders use various biometrical techniques to enhance breeding procedures, tackling both biotic and abiotic stresses. These techniques help assess the genetic effects on quantitative traits, thereby optimizing crop yield potential.

Hybrid vigor for seed yield is linked to heterotic effects on yield and its components. In faba bean, these effects are particularly notable in the F<sub>1</sub> generation, especially among widely divergent parents [3, 4]. Inbreeding depression reduces autofertility and yield in the absence of pollinators and diminishes yield due to the loss of hybrid vigor. Poulsen (1979) reported that inbreeding depression can reduce yield by approximately 11%.

This study aimed to explore the genetic factors influencing yield and disease resistance in three faba bean crosses. The goal was to identify traits with higher heritability for targeted breeding efforts, focusing on gene action, heterosis, inbreeding depression, and the expected and predicted genetic advances for resistance to foliar diseases, yield, and its components.

Comment [L2]: Few lines on validity of Generation mean analysis must be included

## MATERIALS AND METHODS

This study, conducted over three seasons (2019/20, 2020/21, and 2021/22) at the Sakha Agricultural Research Station, aimed to identify new faba bean genotypes with high yield and resistance to chocolate spot and rust diseases. The research focused on estimating heterosis, inbreeding depression, and the inheritance of yield and its components using generation mean analysis for three faba bean crosses. Table 1 provides details on the parental genotypes, including their name, origin, botanical group, and special remarks.

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Table 1: Name, origin, botanical group, and special remarks of the parental genotypes.

| Genotypes          | Original | Botanical group | Special remarks   |
|--------------------|----------|-----------------|---|
| Santamora          | Spain    | Major           | Medium flowering and maturity, high-yielding ability and resistance to foliar diseases  |
| Foul SbaiLabiade   | Morocco  | Major           | Medium flowering and maturity, high-yielding ability and resistance to foliar diseases  |
| Misr 3 and Cairo 4 | Egypt    | Equina          | This varieties exhibits early flowering and maturity, along with tolerance to Orobanche and moderate resistance to foliar diseases. |

Reactions to foliar diseases were recorded in mid-February for chocolate spot and mid-March for rust, using a grading system from 1 to 9, where 1-4 indicates resistance, 5-6 moderate resistance, and 7-9 high susceptibility, based on the disease scales suggested by Bernier et al. (1993). In the 2019/20 season, four parental genotypes were crossed in wire cages to produce three crosses: Cross-1 (Santamora x Foul SbaiLabiade), Cross-2 (Santamora x Misr 3), and Cross-3 (Cairo 4 x Misr 3). In the 2020/21 season, hybrid seeds from these crosses were sown to produce F<sub>1</sub> plants, which were then selfed to generate the F<sub>2</sub> generation. Each F<sub>1</sub> was also backcrossed to its parents to produce BC<sub>1</sub> and BC<sub>2</sub> seeds, and additional F<sub>1</sub> seeds were obtained by crossing the parents again. In the 2021/22 season, six populations (P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub>, and BC<sub>2</sub>) from the three crosses were planted in a randomized complete block design with three replications. Plot sizes varied: four ridges for P<sub>1</sub>, P<sub>2</sub>, and F<sub>1</sub>; nine ridges for BC<sub>1</sub> and BC<sub>2</sub>; and 20 ridges for F<sub>2</sub>. Each ridge was three meters long and 60 cm wide, with hills spaced 20 cm apart and one seed per hill. The studied traits included flowering date, chocolate spot disease reaction, rust disease reaction, plant height, number of branches per plant, number of pods per plant, number of seeds per plant, 100-seed weight (g), and seed yield per plant (g). Data were collected from 30 plants for P<sub>1</sub>, P<sub>2</sub>, and F<sub>1</sub>; 250 plants for F<sub>2</sub>; and 120 plants for each of BC<sub>1</sub> and BC<sub>2</sub> in each cross.

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Statistical and genetic analysis:

The mean ( $\bar{x}$ ), variances ( $S^2$ ), and variance of the mean ( $S^2m$ ) were calculated for each population ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $BC_1$ ,  $BC_2$ , and  $F_2$ ) to assess the presence of non-allelic interactions. A scaling test, as outlined by [5] and [6], was employed. Generation mean analysis was conducted following [7]. Heritability estimates were computed in both broad (H) and narrow ( $h^2$ ) senses according to [8] and [9], respectively. The expected genetic advance from selection (Ga) was calculated using the formula proposed by [10], and the predicted genetic advance from selection was expressed as a percentage of the  $F_2$  mean (Ga%) according to [11]. Potence ratio estimates were determined following [12].

Comment [L5]: Name the workers

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**Heterosis was expressed as the deviation of  $F_1$  from the mid-parent and better parent as follows:**

$$\text{Heterosis over mid-parent (MP) \%} = \frac{\bar{F}_1 - \bar{M} P}{\bar{M} P} \times 100$$

$$\text{Heterosis over better-parent (BP) \%} = \frac{\bar{F}_1 - \bar{B} P}{\bar{B} P} \times 100$$

**Inbreeding depression:**

$$I. D \% = \frac{\bar{F}_1 - \bar{F}_2}{\bar{F}_1} \times 100$$

To test the significance of inbreeding depression (ID), the variance deviation was calculated as:

$$\text{Variance of (ID) deviation} = V\bar{F}_1 + V\bar{F}_2$$

## RESULTS AND DISCUSSION

Mean performance:

The mean performance and variance of traits in six populations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$ , and  $BC_2$ ) from the first cross are presented in **Table 2**. The  $F_1$  population showed lower mean values for chocolate spot and rust disease reactions compared to the better parent but had higher plant height, number of pods per plant, number of seeds per plant, seed weight per plant, and 100-seed weight. The  $F_1$  number of branches per plant was intermediate. The  $F_2$  population exhibited lower mean values for all traits compared to  $F_1$ , except for chocolate spot and rust disease reactions. Mean values of  $BC_1$  and  $BC_2$  populations varied relative to  $F_1$  and  $F_2$ . Similar trends were observed in **Tables 3 and 4** for crosses 2 and 3, with higher disease reactions. In cross-2,  $F_1$  mean values were lower than the better parent for plant height, number of branches per plant, and 100-seed weight. In cross-3,  $F_1$  values were lower for the number of branches per plant, number of seeds per plant, and 100-seed weight. Genetic variability in the  $F_2$  population was significantly larger than in  $P_1$ ,  $P_2$ , and  $F_1$  for all traits, likely due to genetic segregation.

Table 2. Mean performance ( $\bar{X}$ ), variance ( $S^2$ ) and variance of mean ( $S^2\bar{x}$ ) of  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$  populations of Cross-1 (SantamoraxFoal Sbailabiade) for all studied traits.

| Trait                  | Statistical Parameter | $P_1$ | $P_2$ | $F_1$ | $F_2$ | $BC_1$ | $BC_2$ |
|------------------------|-----------------------|-------|-------|-------|-------|--------|--------|
| Flowering date (day)   | $\bar{X}$             | 67.80 | 68.83 | 69.27 | 49.66 | 61.52  | 48.81  |
|                        | $S^2$                 | 2.44  | 3.45  | 1.03  | 41.93 | 32.56  | 34.29  |
|                        | $S^2\bar{x}$          | 0.08  | 0.12  | 0.03  | 0.14  | 0.31   | 0.33   |
| Chocolate spot disease | $\bar{X}$             | 3.30  | 3.02  | 1.83  | 4.14  | 4.04   | 4.02   |

|                                    |               |        |        |        |        |        |        |
|------------------------------------|---------------|--------|--------|--------|--------|--------|--------|
| reaction                           | $S^2$         | 0.04   | 0.03   | 0.04   | 1.29   | 0.95   | 0.88   |
|                                    | $S^2 \bar{X}$ | 0.001  | 0.001  | 0.001  | 0.004  | 0.01   | 0.01   |
| Rust disease reaction              | $\bar{X}$     | 2.30   | 2.00   | 1.13   | 3.46   | 3.03   | 2.76   |
|                                    | $S^2$         | 0.03   | 0.03   | 0.02   | 1.36   | 0.98   | 0.81   |
|                                    | $S^2 \bar{X}$ | 0.001  | 0.001  | 0.001  | 0.005  | 0.01   | 0.01   |
| Plant height                       | $\bar{X}$     | 145.3  | 128.97 | 157.0  | 128.48 | 139.14 | 142.19 |
|                                    | $S^2$         | 4.56   | 4.65   | 5.38   | 101.62 | 85.35  | 86.14  |
|                                    | $S^2 \bar{X}$ | 0.15   | 0.16   | 0.18   | 0.34   | 0.81   | 0.82   |
| No of branches plant <sup>-1</sup> | $\bar{X}$     | 4.83   | 5.07   | 5.63   | 3.23   | 4.78   | 4.12   |
|                                    | $S^2$         | 0.13   | 0.15   | 0.09   | 3.05   | 2.44   | 2.65   |
|                                    | $S^2 \bar{X}$ | 0.004  | 0.01   | 0.003  | 0.01   | 0.02   | 0.03   |
| No of pods plant <sup>-1</sup>     | $\bar{X}$     | 28.83  | 25.47  | 44.77  | 30.52  | 32.28  | 31.61  |
|                                    | $S^2$         | 6.42   | 5.36   | 5.56   | 113.51 | 105.68 | 95.45  |
|                                    | $S^2 \bar{X}$ | 0.21   | 0.18   | 0.19   | 0.38   | 1.01   | 0.91   |
| No of seeds plant <sup>-1</sup>    | $\bar{X}$     | 98.53  | 116.57 | 145.33 | 96.25  | 110.96 | 105.86 |
|                                    | $S^2$         | 7.09   | 8.94   | 11.95  | 207.98 | 197.48 | 178.07 |
|                                    | $S^2 \bar{X}$ | 0.24   | 0.30   | 0.40   | 0.69   | 1.88   | 1.70   |
| Seed yield plant <sup>-1</sup> (g) | $\bar{X}$     | 114.12 | 132.00 | 165.80 | 92.12  | 119.56 | 120.91 |
|                                    | $S^2$         | 6.54   | 9.41   | 11.08  | 203.95 | 182.77 | 171.58 |
|                                    | $S^2 \bar{X}$ | 0.22   | 0.31   | 0.37   | 0.68   | 1.74   | 1.63   |
| 100- seed weight(g)                | $\bar{X}$     | 114.93 | 113.98 | 116.45 | 105.71 | 115.48 | 114.08 |
|                                    | $S^2$         | 9.47   | 7.61   | 8.54   | 156.66 | 133.43 | 136.52 |
|                                    | $S^2 \bar{X}$ | 0.32   | 0.25   | 0.28   | 0.52   | 1.78   | 1.82   |

Table 3. Mean performance ( $\bar{X}$ ), variance ( $S^2$ ) and variance of mean ( $S^2 \bar{X}$ ) of  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$  populations of Cross-2 (Santamora x Misr 3) for all studied traits.

| Trait                           | Statistical Parameter | $P_1$ | $P_2$  | $F_1$  | $F_2$ | $BC_1$ | $BC_2$ |
|---------------------------------|-----------------------|-------|--------|--------|-------|--------|--------|
| Flowering date (day)            | $\bar{X}$             | 68.50 | 63.00  | 65.30  | 56.87 | 66.43  | 65.00  |
|                                 | $S^2$                 | 1.43  | 2.21   | 1.57   | 45.67 | 38.24  | 34.39  |
|                                 | $S^2 \bar{X}$         | 0.05  | 0.07   | 0.05   | 0.15  | 0.36   | 0.33   |
| Chocolate spot disease reaction | $\bar{X}$             | 2.30  | 4.00   | 3.40   | 4.76  | 3.34   | 4.11   |
|                                 | $S^2$                 | 0.02  | 0.01   | 0.01   | 0.56  | 0.43   | 0.46   |
|                                 | $S^2 \bar{X}$         | 0.001 | 0.0003 | 0.0004 | 0.002 | 0.004  | 0.004  |

|  |               |        |        |        |        |        |        |
|--|---------------|--------|--------|--------|--------|--------|--------|
| <b>Rust disease reaction</b>             | $\bar{X}$     | 2.13   | 2.60   | 3.00   | 4.37   | 2.51   | 3.50   |
|  | $S^2$         | 0.02   | 0.01   | 0.01   | 0.64   | 0.53   | 0.42   |
|  | $S^2 \bar{X}$ | 0.001  | 0.0004 | 0.0004 | 0.002  | 0.01   | 0.004  |
| <b>Plant height</b>                      | $\bar{X}$     | 128.83 | 140.00 | 138.50 | 152.38 | 132.38 | 144.82 |
|  | $S^2$         | 8.32   | 6.90   | 8.19   | 172.16 | 133.52 | 148.12 |
|  | $S^2 \bar{X}$ | 0.28   | 0.23   | 0.27   | 0.57   | 1.27   | 1.41   |
| <b>No of branches plant<sup>-1</sup></b> | $\bar{X}$     | 5.90   | 3.63   | 5.30   | 4.73   | 4.92   | 4.04   |
|  | $S^2$         | 0.11   | 0.12   | 0.11   | 3.65   | 3.48   | 2.29   |
|  | $S^2 \bar{X}$ | 0.004  | 0.00   | 0.004  | 0.01   | 0.03   | 0.02   |
| <b>No of pods plant<sup>-1</sup></b>     | $\bar{X}$     | 25.73  | 32.03  | 36.33  | 33.42  | 35.22  | 40.85  |
|  | $S^2$         | 4.96   | 5.76   | 5.40   | 98.25  | 81.95  | 84.52  |
|  | $S^2 \bar{X}$ | 0.17   | 0.19   | 0.18   | 0.33   | 0.78   | 0.80   |
| <b>No of seeds plant<sup>-1</sup></b>    | $\bar{X}$     | 116.57 | 94.13  | 127.15 | 107.62 | 123.93 | 115.39 |
|  | $S^2$         | 7.39   | 5.77   | 6.65   | 105.23 | 93.25  | 88.64  |
|  | $S^2 \bar{X}$ | 0.25   | 0.19   | 0.22   | 0.35   | 0.89   | 0.84   |
| <b>Seed yield plant<sup>-1</sup> (g)</b> | $\bar{X}$     | 136.34 | 63.01  | 148.36 | 105.22 | 127.88 | 116.74 |
|  | $S^2$         | 5.01   | 4.24   | 6.28   | 113.14 | 91.24  | 95.13  |
|  | $S^2 \bar{X}$ | 0.17   | 0.14   | 0.21   | 0.38   | 0.87   | 0.91   |
| <b>100- seed weight(g)</b>               | $\bar{X}$     | 116.69 | 66.80  | 111.65 | 92.87  | 108.74 | 96.43  |
|  | $S^2$         | 3.37   | 5.02   | 4.75   | 149.82 | 129.41 | 123.74 |
|  | $S^2 \bar{X}$ | 0.11   | 0.17   | 0.16   | 0.50   | 1.73   | 1.65   |

Table 4. Mean performance ( $\bar{X}$ ), variance ( $S^2$ ) and variance of the mean ( $S^2 \bar{X}$ ) of  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$  populations of cross 3 (Cairo 4 x Misr 3) for all studied traits.

| Trait                                  | Statistical Parameter | $P_1$  | $P_2$  | $F_1$  | $F_2$ | $BC_1$ | $BC_2$ |
|--|-----------------------|--------|--------|--------|-------|--------|--------|
| <b>Flowering date (day)</b>            | $\bar{X}$             | 68.50  | 61.67  | 73.00  | 69.07 | 70.68  | 63.81  |
|  | $S^2$                 | 2.43   | 1.75   | 2.21   | 61.90 | 42.70  | 48.04  |
|  | $S^2 \bar{X}$         | 0.08   | 0.06   | 0.07   | 0.21  | 0.41   | 0.46   |
| <b>Chocolate spot disease reaction</b> | $\bar{X}$             | 2.00   | 4.83   | 3.80   | 3.93  | 3.96   | 4.28   |
|  | $S^2$                 | 0.01   | 0.02   | 0.02   | 0.70  | 0.54   | 0.51   |
|  | $S^2 \bar{X}$         | 0.0004 | 0.0007 | 0.0007 | 0.002 | 0.005  | 0.005  |

|                                    |               |        |        |        |        |        |        |
|------------------------------------|---------------|--------|--------|--------|--------|--------|--------|
| Rust disease reaction              | $\bar{X}$     | 2.17   | 4.17   | 3.65   | 3.44   | 3.11   | 4.08   |
|                                    | $S^2$         | 0.01   | 0.01   | 0.02   | 0.66   | 0.53   | 0.44   |
|                                    | $S^2 \bar{X}$ | 0.0004 | 0.0003 | 0.0007 | 0.002  | 0.01   | 0.004  |
| Plant height (cm)                  | $\bar{X}$     | 128.33 | 133.67 | 140.07 | 147.83 | 132.76 | 134.26 |
|                                    | $S^2$         | 9.89   | 7.13   | 5.69   | 157.33 | 136.22 | 128.74 |
|                                    | $S^2 \bar{X}$ | 0.33   | 0.24   | 0.19   | 0.52   | 1.30   | 1.23   |
| No of branches plant <sup>-1</sup> | $\bar{X}$     | 6.10   | 4.93   | 5.93   | 4.75   | 5.10   | 4.82   |
|                                    | $S^2$         | 0.12   | 0.14   | 0.11   | 3.44   | 2.92   | 3.04   |
|                                    | $S^2 \bar{X}$ | 0.004  | 0.00   | 0.004  | 0.01   | 0.03   | 0.03   |
| No of pods plant <sup>-1</sup>     | $\bar{X}$     | 27.27  | 25.00  | 33.37  | 28.33  | 30.37  | 27.60  |
|                                    | $S^2$         | 5.26   | 4.28   | 5.41   | 92.32  | 79.31  | 73.58  |
|                                    | $S^2 \bar{X}$ | 0.18   | 0.14   | 0.18   | 0.31   | 0.76   | 0.70   |
| No of seeds plant <sup>-1</sup>    | $\bar{X}$     | 117.27 | 87.37  | 115.44 | 107.33 | 111.31 | 94.89  |
|                                    | $S^2$         | 6.55   | 7.03   | 5.42   | 124.97 | 98.41  | 106.14 |
|                                    | $S^2 \bar{X}$ | 0.22   | 0.23   | 0.18   | 0.42   | 0.94   | 1.01   |
| Seed yield plant <sup>-1</sup> (g) | $\bar{X}$     | 138.07 | 59.42  | 140.37 | 95.52  | 106.90 | 71.42  |
|                                    | $S^2$         | 7.62   | 5.98   | 6.40   | 128.77 | 108.45 | 100.44 |
|                                    | $S^2 \bar{X}$ | 0.25   | 0.20   | 0.21   | 0.43   | 1.03   | 0.96   |
| 100- seed weight(g)                | $\bar{X}$     | 117.77 | 68.21  | 105.33 | 96.31  | 111.12 | 89.62  |
|                                    | $S^2$         | 4.89   | 5.43   | 3.98   | 129.17 | 108.89 | 113.22 |
|                                    | $S^2 \bar{X}$ | 0.16   | 0.18   | 0.13   | 0.43   | 1.45   | 1.51   |

Heterosis and inbreeding depression:

**Table 5** presents percentages of heterosis, inbreeding depression, and potency ratios for traits in the three crosses. Cross-1 exhibited significant negative mid and better parent heterosis for chocolate spot and rust disease reactions, indicating over-dominance ( $P > +1$ ). Positive over-dominance heterosis was also noted for plant height, number of branches, pods, seeds, and seed weight per plant. Cross-2 showed significant positive mid and better parent heterosis for a number of pods, seeds per plant, and seed yield per plant due to over-dominance ( $P > +1$ ). In Cross-3, significant positive heterosis over mid and better parents was observed for plant height, number of pods, and seed per plant, indicating over-dominance. However, no heterosis benefit was seen for chocolate spot and rust diseases. Positive mid-parent heterosis for the number of branches, number of seeds per plant, and 100-seed weight indicated partial dominance ( $P < +1$ ). Negative better parent heterosis was unfavorable for breeding. Inbreeding depression, calculated as the percent deviation of  $F_2$  from  $F_1$ , showed significant negative values for chocolate spot and rust disease reactions in Cross-1, and positive values for several branches, pods, seeds, and seed weight per plant. Cross-2 had significant negative inbreeding depression for disease reactions and positive values for several seeds and seed weight per plant. Cross-3 showed significant negative inbreeding depression for chocolate spot disease reaction and positive values for several branches per plant and seed weight per plant. Overall, significant negative inbreeding depression was observed for chocolate spot and rust diseases across all crosses, while positive inbreeding depression was noted for yield traits.

Comment [L9]: What is P?

Table 5. Heterosis over mid-parent (M.P) and better parent (B.P), potency ratio (P) and inbreeding depression (ID) for the studied traits in three faba bean crosses.

| Trait  | M.P % | P | B.P% | ID % |
|--|-------|---|------|------|
| <b>Cross-1 (Santamora x Foal Sbai labiade)</b> |       |   |      |      |

|                                     |          |       |          |           |
|-------------------------------------|----------|-------|----------|-----------|
| Flowering date (days)               | 1.39**   | 1.84  | 2.16**   | 28.30**   |
| Chocolate spot disease reaction     | -41.95** | -9.35 | -39.23** | -125.64** |
| Rust disease reaction               | -47.29** | -6.78 | -43.33** | -205.59** |
| Plant height                        | 14.49**  | 2.43  | 8.05**   | 18.16     |
| No of branches plant <sup>-1</sup>  | 13.80**  | 5.86  | 11.18**  | 42.66**   |
| No of pods plant <sup>-1</sup>      | 64.89**  | 10.47 | 55.26**  | 31.83**   |
| No of seeds plant <sup>-1</sup>     | 35.13**  | 4.19  | 24.68**  | 33.78**   |
| Seed yield plant <sup>-1</sup> (g)  | 34.74**  | 4.78  | 25.61**  | 44.44**   |
| 100-seed weight(g)                  | 1.74**   | 4.20  | 1.32     | 9.22      |
| <b>Cross-2 (SantamoraxMisr 3)</b>   |          |       |          |           |
| Flowering date (days)               | -0.68*   | -0.16 | 3.65**   | 12.91     |
| Chocolate spot disease reaction     | 7.94**   | 0.45  | 47.83**  | -40.00**  |
| Rust disease reaction               | 27.11**  | 2.71  | 40.63**  | -45.78**  |
| Plant height                        | 3.04**   | 0.73  | -1.07    | -10.02    |
| No of branches plant <sup>-1</sup>  | 11.19**  | 0.47  | -10.17** | 10.75**   |
| No of pods plant <sup>-1</sup>      | 25.78**  | 2.36  | 13.41**  | 8.01      |
| No of seeds plant <sup>-1</sup>     | 20.69**  | 1.94  | 9.08**   | 15.36     |
| Seed yield plant <sup>-1</sup> (g)  | 48.84**  | 1.33  | 8.81**   | 29.08**   |
| 100-seed weight(g)                  | 21.70**  | 0.80  | -4.32**  | 16.82     |
| <b>Cross-3 (Cairo 4 x Misr 3)</b>   |          |       |          |           |
| Flowering date (day)                | 12.16**  | 2.32  | 18.38**  | 5.38      |
| Chocolate spot disease reaction     | 11.22**  | 0.27  | 90.00**  | -3.42**   |
| Rust disease reaction               | 15.26**  | 0.48  | 68.46**  | 5.75**    |
| Plant height                        | 6.92**   | 3.40  | 4.78**   | -5.54     |
| No of branches plant <sup>-1</sup>  | 7.55**   | 0.71  | -2.73**  | 20.00**   |
| No of pods plant <sup>-1</sup>      | 27.69**  | 6.39  | 22.38**  | 15.10     |
| No of seeds plant <sup>-1</sup>     | 12.83**  | 0.88  | -1.56*   | 7.03      |
| Seed weight plant <sup>-1</sup> (g) | 42.15**  | 1.06  | 1.67*    | 31.95**   |
| 100-seed weight(g)                  | 13.28**  | 0.50  | -10.56** | 8.56      |

\* and \*\*refer to significance at 0.05 and 0.01 levels of probability, respectively.

Scaling test:

Generation mean analysis, a quantitative biometrical method, is used to measure the phenotypic performance of quantitative traits across various breeding generations. It helps breeders evaluate the potential for heterosis exploitation or pedigree selection [13, 14]. The significance of at least one scale indicates non-allelic interactions, which can be estimated using a six-parameter model like the Gamble procedure. If all scales are insignificant, a simple additive-dominance model is suitable for estimating genetic components of variance. Table 6 data show that at least one scale (A, B, C, or D) was significant for all traits in the three crosses.

Type of gene action:

Breeding program success relies on genetic variability in breeding materials. If the additive genetic variance is predominant, the selection is more effective; if the non-additive variance is more

significant, an inbred-hybrid program may be better [15]. The analysis provided estimates for six model parameters: (m), (a), (d), (aa), (ad), and (dd) based on [7]. The estimated mean effects (m) were highly significant for all traits in all crosses (Table 6), indicating quantitative inheritance. Dominant gene effects were significantly higher than additive effects for most traits, except for number of branches per plant in cross-2 and the number of seeds per plant and seed weight in cross-3, where additive genes had a higher impact. Additive effects can be overshadowed by significant dominant estimates when there is a high dispersion of alleles between parents [16]. Dominant effects being larger than additive effects suggest that dominant gene effects play a major role in genetic variance, requiring intensive selection in later generations. Large dominance effects may also explain the significantly better parent heterosis values observed. These conclusions align with findings by many researchers [17, 18, 19, 20, 21, 22]. Table 6 shows significant additive (a) and dominant (d) genetic variance in cross-1 for flowering date, number of branches, and seed weight per plant; in cross-2 for number of seeds, seed weight per plant, and 100-seed weight; and in cross-3 for number of pods, seed weight per plant, and 100-seed weight. This indicates both additive and dominance in different proportions were involved in trait inheritance. These results are consistent with those reported by [18, 22, 23].

Comment [L10]: PLEASE NAME THEM

Negative values for main effects (a) or (d) or non-allelic interactions (aa, ad, dd) might indicate that alleles responsible for low trait values were over-dominant over those controlling high values. Table 6 data indicate that the aa epistatic effect was more important and higher in magnitude than dd for traits like plant height, number of branches, seeds, seed weight per plant, and 100-seed weight in cross-1; flowering date, number of pods, seeds, seed weight per plant, and 100-seed weight in cross-2; and chocolate spot and rust disease reactions, number of pods, seed weight per plant, and 100-seed weight in cross-3. Other traits in all crosses had significant and greater dd effects. Traits more affected by aa suggest selection in early segregating generations, while those more affected by dd benefit from delayed selection to later generations. These results are consistent with [18].

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Additive x dominance epistatic gene action was significant and either positive or negative for traits in the three crosses, indicating dominance towards increasing or decreasing, respectively. [24] noted that a high (ad) epistatic effect for traits like flowering date, number of seeds, and seed weight per plant in cross-1 and flowering date in cross-3 might suggest delaying selection and inter-mating segregates followed by pedigree selection. Negative (ad) interaction in some crosses for some traits may suggest gene dispersion in parents. Gene action effects where dominance (d) and dominance x dominance (dd) were similar for traits like flowering date, chocolate spot and rust disease reactions, number of pods and seeds per plant in cross-1, and flowering date, number of branches per plant, and seed weight per plant in cross-3, suggest complementary epistatic genes. This indicates considerable heterosis potential for these traits, confirming Table 5 results. [18] obtained similar results. Similar d and aa gene effects for most traits in all crosses might indicate no complementary non-allelic interaction in genetic control.

Table 6. Scaling test and types of gene actions for the studied traits in the three faba bean crosses.

| Trait                                      | Scaling test |         |          |          | Types of gene action |         |         |         |          |          |
|--|--------------|---------|----------|----------|----------------------|---------|---------|---------|----------|----------|
|  | A            | B       | C        | D        | m                    | a       | d       | aa      | ad       | dd       |
| <b>Cross-1 (Santamora x Foyal labiade)</b> |              |         |          |          |                      |         |         |         |          |          |
| Flowering date                             | -14.02**     | 40.48** | -76.51** | 11.007** | 49.66**              | 12.71** | 22.96** | 22.01** | 13.23**  | 32.49**  |
| Chocolate spot                             | 2.94**       | 3.19**  | 6.56**   | 0.216    | 4.14**               | 0.02    | -1.76** | -0.43   | -0.12    | -5.70**  |
| Rust disease                               | 2.62**       | 2.39**  | 7.29**   | 1.136**  | 3.46**               | 0.27*   | -3.29** | -2.27** | 0.12     | -2.74**  |
| plant height(cm)                           | -24.01**     | -1.59   | -74.33** | 24.367** | 128.5**              | -3.05*  | 68.60** | 48.73** | -11.21** | -23.13** |
| No of branches plant                       | -0.90**      | -2.45** | -8.25**  | 2.445**  | 3.23**               | 0.66**  | 5.57**  | 4.89**  | 0.77**   | -1.53    |

|  |          |         |          |          |          |          |          |          |          |          |
|--|----------|---------|----------|----------|----------|----------|----------|----------|----------|----------|
| No of pods plant <sup>-1</sup>         | -9.05**  | -7.01** | -21.77** | -2.852   | 30.52**  | 0.67     | 23.32**  | 5.70     | -1.02    | 10.36    |
| No of seeds plant <sup>-1</sup>        | -21.94** | 50.19** | -120.8** | 24.328** | 96.25**  | 5.10**   | 86.44**  | 48.66**  | 14.12**  | 23.47**  |
| Seed weight plant <sup>-1</sup><br>(g) | -40.80** | 55.98** | -209.3** | 56.239** | 92.12**  | -1.35    | 155.2**  | 112.5**  | 7.59**   | -15.69   |
| 100-seed weight                        | -0.42    | -2.27   | -38.97** | -18.14** | 105.7**  | 1.40     | 38.27**  | 36.28**  | 0.93     | -33.59** |
| <b>Cross-2 (SantamoraxMisr 3)</b>      |          |         |          |          |          |          |          |          |          |          |
| Flowering date                         | -0.94    | 1.70    | -34.63** | 17.697** | 56.87**  | 1.43     | 34.94**  | 35.39**  | -1.32    | -36.15** |
| Chocolate                              | 0.39**   | 0.83**  | 5.35**   | 2.070**  | 4.76**   | -0.77**  | -2.99**  | -4.14**  | -0.22*   | 2.92**   |
| Rust disease                           | -0.10    | 1.39**  | 6.76**   | 2.737**  | 4.37**   | -0.98**  | -4.84**  | -5.47**  | -0.75**  | 4.19**   |
| plant height(cm)                       | -2.57    | 11.14** | 63.69**  | 27.559** | 152.38** | -12.44** | -51.03** | -55.12** | -6.86**  | 46.55**  |
| No of branches plant <sup>-1</sup>     | -1.36**  | -0.86** | -1.21**  | 0.502    | 4.73**   | 0.88**   | -0.47    | -1.00    | -0.25    | 3.22**   |
| No of pods plant <sup>-1</sup>         | 8.38**   | 13.33** | 3.25     | -9.228** | 33.42**  | -5.63**  | 25.90**  | 18.46**  | -2.48    | -40.16** |
| No of seeds plant <sup>-1</sup>        | 4.15*    | 9.50**  | -34.52** | 24.084** | 107.62** | 8.54**   | 69.97**  | 48.17**  | -2.67*   | -61.82** |
| Seed weight plant <sup>-1</sup><br>(g) | -28.94** | 22.11** | -75.19** | 34.180** | 105.22** | 11.14**  | 117.04** | 68.36**  | -25.53** | -61.53** |
| 100-seed weight                        | -10.86** | 14.41** | -35.30** | 19.43**  | 92.87**  | 12.31**  | 58.77**  | 38.86**  | -12.63** | -42.42** |
| <b>Cross-3 (Cairo 4x Misr 3)</b>       |          |         |          |          |          |          |          |          |          |          |
| Flowering date                         | -0.14    | -7.05** | 0.11     | 3.650**  | 69.07**  | 6.87**   | 0.62     | -7.30**  | 3.45**   | 14.49**  |
| Chocolate                              | 2.12**   | -0.08   | 1.29**   | 0.378**  | 3.93**   | -0.31**  | 1.14**   | 0.76**   | 1.10**   | -2.80**  |
| Rust disease                           | 0.41**   | 0.34*   | 0.13     | -0.310*  | 3.44**   | -0.96**  | 1.10**   | 0.62*    | 0.04     | -1.37**  |
| plant height(cm)                       | -2.88    | -5.21*  | 49.20**  | 28.647** | 147.83** | -1.50    | -48.23** | -57.29** | 1.17     | 65.39**  |
| No of branches plant <sup>-1</sup>     | -1.82**  | -1.23** | -3.91**  | 0.430    | 4.75**   | 0.29     | 1.28*    | 0.86     | -0.30    | 2.19*    |
| No of pods plant <sup>-1</sup>         | 1.11     | -4.17*  | -5.69**  | 1.310    | 28.33**  | 0.77*    | 11.85**  | 6.62     | -0.36    | -11.56   |
| No of seeds plant <sup>-1</sup>        | -10.09** | 13.03** | -6.19*   | 8.460**  | 107.3**  | 16.42**  | -3.80    | -16.92** | 1.47     | 40.03**  |
| Seed weight plant <sup>-1</sup><br>(g) | -64.64** | 56.95** | -96.15** | 12.716** | 95.52**  | 35.48**  | 16.19**  | -25.43** | -3.84**  | 147.01** |
| 100-seed weight                        | -0.86    | 5.70**  | -11.39** | 8.120**  | 96.31**  | 21.50**  | 28.58**  | 16.24**  | -3.28*   | -21.09** |

\* and \*\*refer to not significant and significant at 0.05 and 0.01 levels of probability, respectively.

Heritability and genetic advance from selection:

Heritability estimates based on genetic variance components (a) and (d) are listed in **Table 7**. Broad-sense heritability for all traits ranged from 93.71% in Cross-2 for number of seeds per plant to 98.06% in Cross-1 for rust disease reaction. These high values suggest that superior genotypes for these traits can be identified phenotypically, emphasizing the importance of phenotypic selection [25]. The results also indicate that traits were minimally affected by environmental factors, with most variability due to genetics. [22] reported broad-sense heritability in faba bean ranging from 49.45% to 91.29%.

Narrow-sense heritability values ranged from 19.43% for the number of seeds per plant to 68.37% for rust disease reaction in Cross-1, from 27.15% for number of seeds per plant to 51.56% for rust disease reaction in Cross-2, and from 26.74% for the number of branches per plant to 54.17% for rust disease reaction in Cross-3. Moderate  $h^2$  values (40.57% to 58.14%) were observed for traits like flowering date and chocolate spot and rust disease, which are somewhat qualitative. In contrast, for quantitative traits like plant height, number of branches, pods, seeds, seed weight per plant, and 100-seed weight,  $h^2$  values ranged from 19.43% to 42.09%, considered low. These results are expected as recent genetic material is controlled by non-additive gene effects. [22] reached similar conclusions.

Genetic advance under selection, as shown in **Table 7**, indicated expected genetic advance (Ga) ranged from 1.19 for number of branches per plant to 7.72 g for seed weight in Cross-1, from 0.63 for chocolate spot disease reaction to 9.84 cm for plant height in Cross-2, and from 0.87 for chocolate spot disease reaction to 8.83 g for seed weight in Cross-3. The highest predicted genetic advance (Ga%)

values were coupled with moderate  $h^2$  values across all traits in all crosses. Conversely, low expected (Ga) and predicted (Ga%) advance estimates were associated with low  $h^2$  values for number of seeds per plant, seed weight per plant, and 100-seed weight in all three crosses. Ga% values ranged from 5.05% for plant height to 47.42% for rust disease reaction in Cross-1, from 5.33% for number of seeds per plant to 35.02% for number of branches per plant in Cross-2, and from 5.52% for plant height to 26.39% for rust disease reaction in Cross-3. These results align with [10], who reported that heritability estimates combined with genetic advance upon selection are more valuable for predicting selection effects. These findings support selection in late generations ( $F_4$  and  $F_5$ ) through the bulk method to obtain high-yielding faba bean genotypes with improved disease resistance. These results are consistent with those of [18, 22].

**Table 7. Heritability percentage in broad (H), narrow ( $h^2$ ) senses and expected (Ga) and predicted (Ga %) genetic advance for selection in the three crosses of faba bean for the studied traits.**

| Traits                                      | H     | $h^2$ | Ga       |       |
|---|-------|-------|----------|-------|
|   |       |       | Expected | %     |
| <b>Cross-1(Santamora xFol Sbai labiade)</b> |       |       |          |       |
| Flowering date (days)                       | 95.26 | 40.57 | 5.41     | 10.90 |
| Chocolate spot disease reaction             | 97.09 | 58.14 | 1.36     | 32.88 |
| Rust disease reaction                       | 98.06 | 68.37 | 1.64     | 47.42 |
| Plant height                                | 95.09 | 31.25 | 6.49     | 5.05  |
| No of branches plant <sup>-1</sup>          | 96.23 | 33.11 | 1.19     | 36.88 |
| No of pods plant <sup>-1</sup>              | 94.96 | 22.81 | 5.01     | 16.40 |
| No of seeds plant <sup>-1</sup>             | 95.20 | 19.43 | 5.77     | 6.00  |
| Seed weight plant <sup>-1</sup> (g)         | 95.33 | 26.26 | 7.72     | 8.39  |
| 100-seed weight(g)                          | 94.55 | 27.68 | 7.14     | 6.75  |
| <b>Cross-2 (SantamoraxMisr 3)</b>           |       |       |          |       |
| Flowering date (days)                       | 96.29 | 40.96 | 5.70     | 10.03 |
| Chocolate spot disease reaction             | 97.32 | 41.07 | 0.63     | 13.29 |
| Rust disease reaction                       | 97.77 | 51.56 | 0.85     | 19.43 |
| Plant height                                | 95.41 | 36.41 | 9.84     | 6.46  |
| No of branches plant <sup>-1</sup>          | 96.88 | 42.09 | 1.66     | 35.02 |
| No of pods plant <sup>-1</sup>              | 94.52 | 30.56 | 6.24     | 18.67 |
| No of seeds plant <sup>-1</sup>             | 93.71 | 27.15 | 5.74     | 5.33  |
| Seed weight plant <sup>-1</sup> (g)         | 95.18 | 35.27 | 7.73     | 7.35  |
| 100-seed weight(g)                          | 97.01 | 31.03 | 7.82     | 8.43  |
| <b>Cross-3(Cairo 4x Misr 3)</b>             |       |       |          |       |
| Flowering date (days)                       | 96.53 | 53.41 | 8.66     | 12.53 |
| Chocolate spot disease reaction             | 97.46 | 50.43 | 0.87     | 22.12 |
| Rust disease reaction                       | 97.62 | 54.17 | 0.91     | 26.39 |
| Plant height                                | 95.49 | 31.59 | 8.16     | 5.52  |
| No of branches plant <sup>-1</sup>          | 96.51 | 26.74 | 1.02     | 21.53 |
| No of pods plant <sup>-1</sup>              | 94.49 | 34.39 | 6.81     | 24.03 |
| No of seeds plant <sup>-1</sup>             | 95.11 | 36.32 | 8.36     | 7.79  |
| Seed weight plant <sup>-1</sup> (g)         | 94.87 | 37.78 | 8.83     | 9.25  |
| 100-seed weight(g)                          | 96.46 | 28.05 | 6.57     | 6.82  |

## CONCLUSION

This study successfully introduced high-yielding, disease-resistant faba bean genotypes by analyzing six populations from three crosses over three growing seasons. Significant heterosis and high broad-sense heritability values indicated that phenotypic selection is effective for improving these traits. Dominant gene effects were more influential than additive effects, highlighting the need for intensive selection in later generations. The presence of non-allelic interactions necessitates specific breeding strategies. These findings support the feasibility of developing superior faba bean genotypes through targeted breeding, providing valuable insights for future breeding programs.

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