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Combining Ability and Gene Action Controlling Chocolate Spot Resistance and Yield Traits in Faba Bean (*Vicia faba* L.)

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ABSTRACT
Chocolate spot disease devastatingly impacts faba bean growth and productivity. Thenceforth, genetic study of chocolate spot resistance and yield traits is crucial to conceive appropriate strategies for breeding and sustaining faba bean production particularly under abrupt climate change and a fast-growing global population. The current study was performed to identify promising resistant and high-yielding progenies, to study the mode of inheritance for chocolate spot resistance and yield traits using half-diallel mating design, and to investigate the association between seed yield and its attributes traits under conditions of chocolate spot disease. Two resistant (Nubaria-1 and Sakha-1) and two susceptible (Tribe-White and Camolina) parents previously characterized were used to generate six F_1 hybrids which were selfed to produce F_2 progenies. The parents and their F_1 and F_2 were evaluated at hot-spot location for chocolate spot disease. Significant variation was detected for chocolate spot resistance and yield traits among the evaluated parents and their cross combinations in both generations. The general (GCA) and specific (SCA) combining ability effects were highly significant for chocolate spot severity and yield traits in both generations. From the results, it is noteworthy that the cross combinations of P_1(Nubaria-1)×P_2(Sakha-1), P_1×P_4(Camolina) and P_2×P_3(Tribe-white) displayed the highest seed yield per plant in the F_1 generation (155.66, 199.96, and 147.96 g respectively) as well as the F_2 generation (172.36, 123.06, and 119.80 g respectively) simultaneously with high resistance to chocolate spot. Consequently, these crosses could be promising combinations for increasing seed yield, and resistance to chocolate spot in breeding programs of faba bean. The additive gene effect was predominant for chocolate spot resistance, plant height, days to flowering, number of branches per plant and 100-seed weight in both generations. Accordingly, selection could be effective to improve these traits in early generations. By contrast, the non-additive gene effects were preponderant for seed yield per plant, number of seeds per plant and number of pods per plant. This suggests the importance of transgressive segregation for improving these traits through breeding programs. While selection for improving these traits could be less effective in the segregated generations which should be postponed to advanced generations. A strong positive association was identified between seed yield per plant and each of number of branches per plant, 100-seed weight, plant height, days to flowering, number of pods per plant and number of seeds per plant. This signifies their significance as vital attributes for indirect selection, especially in the early generations due to their ease of evaluation in comparison with seed yield. On the contrary, linear regression analysis revealed a steeply inverse relationship between seed yield and chocolate spot disease in both generations.

Keywords: *Vicia faba*, Chocolate spot, Heterosis, Heritability, Cluster analysis, Principal components, Linear regression

1. Introduction

Faba bean (*Vicia faba* L.) is a globally essential pulse crop (Karkanis et al. 2018; Desoky et al. 2021). It is an important source of protein, dietary fibers, carbohydrates, and micronutrients for humans as well as livestock. Besides, it improves soil properties and contributes to sustainable agriculture through atmospheric nitrogen fixation (van Berkum et al. 1995; Duc 1997; Youseif et al. 2017). The gap between consumption and faba bean production is increasing due to population growth, particularly in developing countries. Accordingly, productivity and the cultivated area should be increased to limit this gap (Zohry & Ouda 2017; Mansour et al. 2021a).

Chocolate spot disease that caused by *Botrytis fabae* threatens faba bean production worldwide, through damaging its foliage and constraining photosynthetic activity (Duc 1997; Beyene et al. 2016). Severe epidemics can destructively reduce faba bean yield by over 60% (Deneke 2018). Furthermore, infected plants produce seeds with reddish-brown discoloration which reduces their market value (Kaur et al. 2018). Subsequently, developing resistant and high-yielding genotypes is a crucial goal for improving faba bean productivity alongside agricultural practices particularly under the current fast-growing global population.

The success of plant breeding programs depends principally on a better understanding genetic basis of the important economic traits (Gracia et al. 2012; Abaza et al. 2020; Kamara et al. 2021). Therefore, it is required to provide sufficient information on the inheritance nature and heritability of the important characters. Diallel mating system is a powerful biometric approach to assess the effects of general combining ability (GCA) and specific combining ability (SCA) as well as assess the gene action involved in different traits in faba bean. It also aids in the knowledge of heterotic patterns of progeny at the earlier stage of crossing programs (Şimşek & Ceyhan 2017; Salem et al. 2020; Kamara et al. 2021).

Seed yield is the most important trait, but it is a complex trait for genetic improvement (Shi et al. 2009; Ceyhan & Şimşek 2021). In this context, several yield attributes as number of seeds, number of pods, and seed weight could be exploited as indirect indices for improving seed yield (Desoky et al. 2020; Mansour et al. 2021). Consequently, it is essential to determine the interrelationship among seed yield and its attributes under chocolate spot disease conditions.

The present study aimed at identifying promising hybrids that could be exploited for improving chocolate spot resistance and productivity in faba bean, determining the type of gene action controlling chocolate spot resistance and yield traits in faba bean, and investigating the association between seed yield and its attributes traits under conditions of chocolate spot disease.

2. Material and Methods

2.1. Parental genotypes and crossing

Four diverse faba bean genotypes were chosen based on their resistance to chocolate spot, genetic diversity, growth habit, and yielding ability from preliminary trials. The selected parents included two cultivars resistant to chocolate spot (Nubaria-1and Sakha-1) and two susceptible genotypes (Tribe-White and Camolina) obtained from the national gene bank and genetic resources of Egypt. The description of used parents is presented in Table 1. During the growing season of 2016-2017, the selected parents were grown at Giza Agricultural Research Station, Agricultural Research Center (30° 01' N, 31° 12' E). Half-diallel mating design excluding reciprocal (4×4) was applied to generate 6 F1 hybrids. During the next growing season of 2017-2018, the F1 hybrids were selfed to produce F2 seeds and simultaneously the parents were crossed again to secure adequate F1 seeds.

Table 1- Description of the used parental faba bean genotypes

Genotype	*Origin*	*Pedigree*	*Botanical group*	*Reaction to Botrytis fabae*
Nubaria-1	Egypt	Single plant selection form Giza Blanka	Large	Resistant
Sakha-1	Egypt	716/724/83 × 620/ 283/8	Medium	Resistant
Tribe-White	Sudan	Individual selection	Medium	Susceptible
Camolina	Spain	Imported from Spain	Small	Susceptible

2.2. Experimental sites and agronomic practices

The parental genotypes, F1 and their corresponding F2 progenies were evaluated during the growing season of 2018-2019 at Nubaria Agricultural Research Station, Agricultural Research Center, Egypt (30° 49' N, 30° 01' E). The experimental site soil is classified as sandy loam soil throughout the profile (72.11% sand, 8.52% silt 19.37% clay) with pH 8.31 and electrical conductivity 1.95 dS/m. Nubaria is considered a hot-spot for chocolate spot disease in Egypt. Randomized Complete Block Design in three replications was applied for each generation. Each plot comprised of six rows with 3-m long and 0.60-m distance between rows and 0.2-m among plants with two seeds in each hill. The sowing date was carried out in the optimum time for faba bean growing in the region which is the end of October. Potassium and phosphorus were added before sowing at a rate of 95 kg K/ha as potassium sulfate (48% K_2SO_4) and 32 kg P/ha as superphosphate (15.5% P_2O_5). Nitrogen fertilizer was added once at sowing as a basal dose with a rate of 45 kg N/ha as ammonium sulfates (21% N). Surface irrigation was applied as the commonly used system in the region.

2.3. Measured traits

The scale outlined by Bernier et al. (1993) was used to score the degrees of chocolate spot disease (Table 2). Days to flowering was determined as number of days from planting to 50 percent of the plants in each plot have open flowers. Plant height (cm) was recorded from the soil surface to the top of the branch at physiological maturity in each plot from readings of ten plants. Likewise, number of pods number per plant was estimated in each plot and 100-seed weight was recorded from the weight of two sets of 100 seeds.

Table 2- Used scale for chocolate spot disease (Botrytis fabae)

Scale	*Description*	*Grade*
1	No disease symptom or very small specks	Highly resistance
3	Few small discrete lesions	Resistance
5	Some coalesced lesions with some defoliation	Moderately resistance
7	Large coalesced sporulating lesions, some dead plants, 50% defoliation	Susceptible
9	Extensive lesions leaves, severe defoliation, stems and pods, stem girding, heavy sporulating, blackening and death of more than 80% of plant	Highly susceptible

2.4. Statistical analysis

The analysis of variance (ANOVA) was applied for all recorded data using R statistical software version 3.6.1. Combining ability analysis was performed according to Griffing's method 2 model 1 (Griffing, 1956). The genetic components and related genetic parameters were estimated as suggested by Hayman (1954). Heritability values in the narrow and broad sense were determined according to Mather & Jinks (1971). The hierarchical cluster analysis was employed to group the assessed genotypes and the principal component analysis (PCA) was utilized to assess their relationships among the evaluated traits utilizing R statistical software version 3.6.1.

3. Results and Discussion

3.1. Analysis of variance

The analysis of variance disclosed highly significant differences among evaluated genotypes in both generations for all assessed traits (Table 3). Besides, the GCA and SCA effects were highly significant for all studied traits except number of pods per plant in F2. These findings indicate wide genetic variability among used parents and their progenies for all evaluated variables. In the light of that, similarly high genetic variability for yield traits and resistance to chocolate spot was disclosed in faba bean by Rhaïem et al. (2002); Abo-Hegazy et al. (2012); Beyene et al. (2016); Tekalign et al. (2017); Beyene et al. (2018) and Lee et al. (2020). They depicted genetic variations are valuable for developing new genotypes with high-yielding and resistance to chocolate spot.

Table 3-Mean squares of ANOVA and combining ability effects for evaluated traits for F1 and F2 populations

Source of Variance	*df*	*Chocolate spot*	*Days to flowering*	*Plant height*	*No. of branches/ plant*	*No. of pods/ plant*	*No. of seeds/ plant*	*100-seed weight*	*Seed yield/ plant*
F1 generation									
Genotype	9	6.71**	143.2**	369.1**	12.67**	2152**	14374**	2971**	6865**
GCA	3	16.41**	285.6**	908.4**	28.77**	1497**	8709**	8223**	10248**
SCA	6	1.86*	72.00**	99.51	4.62**	2479**	17205**	345.0**	5172**
Parent (P)	3	15.66**	351.4**	537.9**	34.21**	33.62	1228	4493**	11338**
Cross (C)	5	1.48*	40.2*	269.3**	1.97**	2460**	15914**	2653**	2292*
P vs C	1	5.98**	33.37	361.8*	1.55	6966**	46109**	0.12	16310**
Replication	2	0.18	20.25	9.32	0.65	107.1	639.7	65.78	77.69
Error	18	0.47	9.64	51.84	0.36	139.7	580.8	45.82	609.5
Total	29	2.39	51.82	147.4	4.20	761.9	4865	955.1	2514
F2 generation									
Genotype	9	7.52**	136.6**	565.0**	13.82**	512.0*	3022**	2851**	6070**
GCA	3	21.75**	370.5**	1321**	32.79**	509.4	1869	7761**	13548**
SCA	6	0. 93	19.59	187.1*	4.35**	513.3	3597**	395.4**	2331**
Parent (P)	3	15.66**	351.4**	537.9**	34.21**	33.62	1228	4493**	11338**
Cross (C)	5	4.13**	31.04*	643.6**	3.93**	762.9*	4016**	2398**	4122**
P vs C	1	0.07	19.93	253.5	2.11	693.1	3435*	191.2	4.61
Replication	2	0.95	9.47	44.32	0.23	26.14	642.2	52.16	238.6
Error	18	0.35	8.83	58.62	0.70	249.0	748.2	62.09	302.1
Total	29	2.62	48.53	214.8	4.75	315.3	1446	926. 9	2088

* and **: indicate significant at P≤0.05 and P≤0.01, respectively

3.2. Performance of used parents and their F1 and F2 progenies

The evaluated parents and their F1 and F2 progenies displayed a wide significant variation for chocolate spot resistance and agronomic traits (Table 4). The parental genotypes Nubaria-1 and Sakha-1 recorded the lowest severity of chocolate spot compared with Camolina and Tribe-white (Table 4). In addition, Nubaria-1 exhibited the latest flowering and highest values of plant height, number of seeds per plant, number of branches per plant, 100-seed weight, and seed yield per plant. While Camolina displayed earliest flowering and produced the highest number of pods per plant. On the contrary, Tribe-white recorded the lowest values of seed yield per plant and all attributed traits. In the F1 generation, the hybrid P1×P2 followed by "P1×P4" and "P2×P3" displayed the lowest severity of chocolate spot. Besides, the hybrids "P1×P2" and "P3×P4" recorded the earliest flowering followed by "P2×P4" and "P1×P4". Furthermore, the hybrids "P1×P4" and "P2×P4" followed by "P1×P2" and "P2×P3" possessed the highest seed yield per plant and its components. On the contrary, "P3×P4" and "P2×P4" recorded the highest severity of chocolate spot. Besides, "P1×P3" and "P3×P4" recorded the lowest seed yield per plant and its attributed traits. Concerning F2 progenies, the cross "P1×P2" followed by "P2×P3" and "P1×P4" recorded the lowest severity of chocolate spot and displayed superiority for seed yield per plant as well as its attributes. On the contrary, "P3×P4", "P2×P4" and "P1×P3" displayed the highest susceptible values for chocolate spot and lowest seed yield per plant and its attributes.

Table 4- Mean performance for chocolate spot resistance and yield traits of the evaluated parents, F1 and F2 progenies

Genotypes	*Chocolate spot*	*Days to flowering*	*Plant height (cm)*	*No. of branches/ plant*	*No. of pods/ plant*	*No. of seeds/ plant*	*100-seed weight (g)*	*Seed yield/ plant*
F1 generation								
Nubaria-1 (P1)	1.30	63.66	130.80	10.80	44.50	152.33	129.30	187.16
Sakha-1 (P2)	1.87	42.93	112.20	4.50	42.33	131.73	100.36	132.70
Tribe-white (P3)	5.63	42.56	102.63	3.10	38.73	104.03	55.20	56.73
Camolina (P4)	5.40	40.80	102.17	5.10	46.56	137.80	47.30	64.93
P1×P2	1.86	41.90	125.80	6.53	40.73	119.00	137.20	155.66
P1×P3	2.73	51.83	127.47	5.63	44.33	132.13	93.26	129.00
P1×P4	2.20	44.96	126.10	7.56	82.46	250.86	78.10	199.96
P2×P3	2.30	46.63	119.13	5.90	67.46	205.20	71.83	147.96
P2×P4	2.86	44.63	111.90	6.96	98.50	295.83	62.53	181.20
P3×P4	3.86	42.06	103.83	5.53	111.36	265.96	54.53	134.06
LSD 0.05	1.18	3.33	5.35	1.03	9.27	35.34	7.61	30.35
F2 generation								
P1×P2	1.73	50.20	131.66	6.90	47.40	147.30	132.13	172.36
P1×P3	3.53	47.00	122.20	4.20	25.46	83.13	76.40	62.60
P1×P4	3.53	48.63	132.43	6.56	53.86	175.73	76.40	123.06
P2×P3	3.40	42.93	116.63	4.46	55.86	173.13	70.46	119.80
P2×P4	4.50	42.86	111.06	4.60	73.06	158.90	60.03	95.76
P3×P4	5.20	43.33	93.30	5.36	61.40	181.70	51.90	93.50
LSD 0.05	1.01	4.10	6.13	1.44	8.07	32.92	6.52	29.82

The severity of chocolate spot and yield traits were utilized to classify the evaluated genotypes and their cross combinations according to their performance. Using hierarchical clustering the parental genotypes and their crosses were classified into three groups (Figures 1A and 1B). The genotypes included in group (a) displayed the highest severity of chocolate spot; thereupon, they could be considered susceptible genotypes. While the genotypes in group (c) had the lowest values; hence, they could be considered resistant genotypes. In respect of yield traits, the genotypes in group (a) exhibited the highest yield traits; consequently, they could be considered high-yielding genotypes compared to the genotypes in groups b and c. Likewise, Mansour et al. (2020); Gharib et al. (2021); Moustafa et al. (2021a); Mansour et al. (2021b); employed hierarchical clustering to classify the genotypes based on their performance.

From the results of F1 and F2 generations, it is noteworthy that the cross combinations of "P1×P2", "P1×P4" and "P2×P3" displayed constant performance through both generations with high-yielding and resistance to chocolate spot. Consequently, these crosses could be promising combinations for increasing seed yield, and resistance to chocolate spot in faba bean breeding programs. Correspondingly, Beyene et al. (2016) and Tekalign et al. (2017) identified promising cross combinations in faba bean for enhancing resistance to chocolate spot and seed yield attributes.

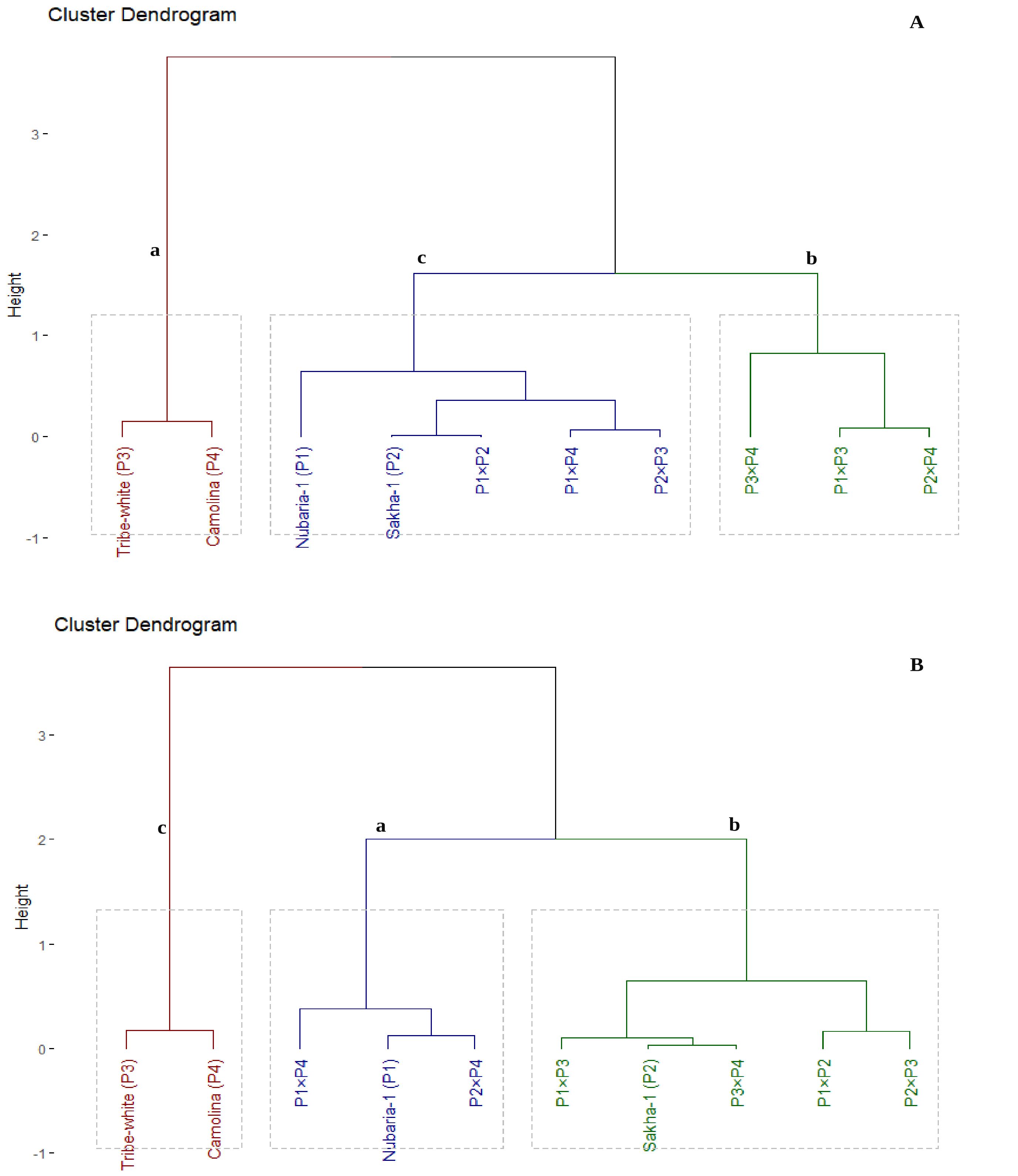

Figure 1- Dendrogram of the phenotypic distances among four faba bean parental genotypes and their six cross combinations based on their performance in chocolate spot disease (A) and seed yield traits (B).

3.3. General (GCA) and specific (GCA) combining ability effects

The GCA effects of parental genotypes revealed that Nubaria-1 and Sakha-1 expressed highly significant negative GCA for chocolate spot severity which indicates that they could be considered as good combiners for resistance of this disease (Table 5). Likewise, Sakha-1 and Camolina displayed highly significant negative GCA effects (desirable) for days to flowering which indicates that they could be considered as good combiners for earliness. Moreover, Nubaria-1 is a good combiner for plant height, 100-seed weight, number of branches per plant, and seed yield per plant. Similarly, Sakha-1 showed a positive and significant effect for 100-seed weight and seed yield per plant. Furthermore, Camolina had positive GCA for number of pods per plant and number of seeds per plant. Generally, the parental genotypes Nubaria-1 and Sakha-1 had highly significant desirable GCA effects for most assessed traits while Camolina for certain yield attributes. Subsequently, the valuable alleles of these genotypes could be considered good sources for improving yield traits and resistance to chocolate spot in faba bean breeding programs.

Table 5- General combining ability effects of the used parents for all evaluated traits

Parent	*Chocolate spot*	*Days to Flowering*	*Plant height*	*No. of branches/ plant*	*No. of pods/ plant*	*No. of Seeds/ plant*	*100-seed /plant*	*Seed yield/ plant*
Nubaria-1 (P1)	-0.94**	5.84**	9.99**	1.75**	-8.66**	-15.13**	25.39**	27.38**
Sakha-1 (P2)	-0.71**	-1.99**	0.04	-0.41**	-2.85	-2.33	9.58**	9.26*
Tribe-white (P3)	0.86**	-0.89	-4.22*	-1.25**	-1.31	-14.35**	-14.13**	-28.37**
Camolina (P4)	0.79**	-2.96**	-5.81**	-0.09	12.83**	31.80**	-20.84**	-8.27
LSD 0.05	0.29	1.33	3.08	0.25	5.06	6.33	2.90	5.58
LSD 0.01	0.403	1.82	4.23	0.35	6.94	9.16	3.97	7.50

* and **: indicate significant at P≤0.05 and P≤0.01, respectively

The estimates of SCA effects in F1 generation displayed significant negative effects for chocolate spot disease (desirable for resistance) by "P1×P2", "P1×P4" and "P2×P3" (Table 6). Additionally, the cross combinations "P1×P2", "P1×P4", "P2×P4" and "P3×P4" displayed significant negative SCA effects for days to flowering (desirable for earliness). Moreover, positive and significant SCA effects were assigned for "P1×P2", "P1×P4", "P2×P3" and "P2×P4" for seed yield per plant and certain of its attributes. In F2 generation, significant negative effects for chocolate spot disease were displayed by "P1×P2" and "P2×P3". Furthermore, positive, and significant SCA effects were recorded by "P1×P2", and "P2×P3" for seed yield per plant and certain of its components. These cross combinations were derived from parental genotypes with good×good or good×poor general combiners. It could be concluded that the three cross combinations of "P1×P2" and "P2×P3" possessed constant behavior in both generations, accordingly, they are promising for resistance to chocolate spot as well as seed yield and most of its attributes in breeding programs of faba bean. These findings are in consonance with previous studies that elucidated significant GCA and SCA effects for resistance to chocolate spot as well as seed yield and its components in faba bean as Alghamdi (2009); Ghareeb & Helal (2014) and Beyene et al. (2016) and El-Hosary (2020) and in bean as reported by Ceyhan et al. (2014), Ceyhan & Şimşek (2021) and Kepildek & Ceyhan (2021).

Table 6- Specific combining ability effects of F1 and F2 progenies for studied traits

Cross	*Chocolate Spot*	*Days to flowering*	*Plant height*	*No. of branches/plant*	*No. of pods/plant*	*No. of seeds/plant*	*100-seed weight*	*Seed yield/plant*
F1 generation								
P1×P2	-0.51*	-8.40**	0.43	-0.98**	-9.45*	-43.03**	19.26**	19.91*
P1×P3	-0.19	0.68	5.49*	-1.03**	-7.42	-17.88	0.96	-8.95
P1×P4	-0.65*	-4.12**	5.71*	0.26	16.60**	54.70**	-9.41**	41.92**
P2×P3	-0.85**	3.32**	7.11*	1.39**	9.94*	42.38**	-6.58*	28.14**
P2×P4	0.21	-3.38**	-1.47	1.29**	26.83**	86.87**	-9.17**	41.27**
P3×P4	0.78**	-4.29**	-2.34	-0.70**	38.15**	69.02**	-6.54*	-31.76**
F2 generation								
P1×P2	-0.31*	1.31	3.40	0.09	-0.56	-1.41	17.62**	15.33*
P1×P3	0.14	3.93**	1.66	-2.02**	-14.58*	-46.62**	12.42**	-50.45**
P1×P4	0.03	1.97	11.27**	0.73*	3.61	21.66*	8.04*	1.21
P2×P3	-0.32*	-0.55	6.78*	-0.63	8.28	38.05**	-4.99	19.93**
P2×P4	0.67**	-0.81	-0.59	-0.32	15.27*	0.50	-11.05**	-12.91
P3×P4	0.30	-1.86	-9.45**	1.23**	10.40	38.43**	-6.52*	-18.81**

* and **: indicate significant at P≤0.05 and P≤0.01, respectively

3.4. Components of genetic variation and heritability

The additive component (D) was significant for chocolate spot disease, plant height, days to flowering, number of branches per plant, 100-seed weight and seed yield per plant in F1 and F2 generations (Table 7). These results disclosed that the additive effect was involved in the inheritance of these characters in both generations. Moreover, the dominance components H1 and H2 were significant for all traits in F1 except for chocolate spot disease and 100-seed weight while for chocolate spot disease in F2. The obtained results revealed the importance of both additive and dominant components in the expression of the evaluated traits. While the magnitude of additive component (D) was higher than the dominance component (H1) for all evaluated traits except number of seeds per plant, number of pods per plant, and seed yield per plant in F1 which was confirmed by the average degree of dominance (H1/D)0.5 which was higher than unity for these traits. This indicates that the non-additive gene effects were preponderant for the aforementioned traits while the additive gene effect is more important in controlling chocolate spot resistance, plant height, days to flowering, number of branches per plant and 100-seed weight. This suggests the importance of transgressive segregation for improving seed yield per plant, number of seeds per plant, and number of pods per plant through the breeding program. On the other hand, selection for these traits could be less efficient in the segregated generations which should be postponed to advanced generations. While, selection could be more effective for chocolate spot resistance, plant height, days to flowering, 100-seed weight and number of branches per plant in segregated generations. This was also confirmed by the heritability values in the narrow and broad sense. These findings concur with Ceyhan et al. (2008); Farag & Afiah (2012); Obiadalla-Ali et al. (2013); Ceyhan et al. (2014); Ghareeb & Helal (2014) and El-Hosary (2020) who disclosed that the non-additive gene action was crucial in the expression and regulating seed yield, number of pods per plant and number of seeds per plant.

Table 7- Components of genetic variance for evaluated traits

Genetic component	*Chocolate spot*	*Days to flowering*	*Plant height*	*No. of branches/plant*	*No. of pods/plant*	*No. of seeds/plant*	*100-seed weight*	*Seed yield/plant*
F1 generation								
D	5.07*	113.6**	163.4**	11.27**	-34.26	213.84	1482*	3594**
H1	1.72	92.07*	68.25**	6.38**	2829**	20090**	435.1	5410**
H2	1.47	70.56*	64.09**	4.39*	2198**	15748**	398.6	4494**
F	2.43	92.49*	-46.94	8.75**	-92.40	475.3	-481.1	2740**
E	0.15	3.57	15.86**	0.13	45.47	195. 6	15.94	185.5*
(H1/D)0.5	0.58	0.90	0.63	0.75	5.34	9.69	0.54	1.23
h 2 (ns)	0.74	0.50	0.76	0.65	0.37	0.33	0.90	0.40
H2 (bs)	0.92	0.92	0.88	0.96	0.95	0.97	0.99	0.92
F2 generation								
D	5.08**	114.2**	160.2**	11.18**	-64.36	163.5	1477**	3681**
H1	0.21	19.49*	192.3*	5.46*	500.9**	4133*	468.6*	2982*
H2	0.19	13.68*	166.9*	4.35*	349.4**	3550*	453.6*	2667*
F	0.50	54.08**	-167.2	6.77**	-102.4	215.9	-344.6	1297
E	0.14	2.96*	19.06	0.22	75.57*	245.9	20.37	98.58
(H1/D)0.5	0.20	0.41	1.10	0.70	2.78	5.03	0.56	0.90
h 2 (ns)	0.92	0.84	0.74	0.68	0.37	0.19	0.87	0.64
H2 (bs)	0.94	0.92	0.92	0.95	0.71	0.82	0.98	0.95

* and ** indicate significant at $P \leq 0.05$ and $P \leq 0.01$, respectively

3.5. Interrelationship among traits

Adequate understanding of the association between seed yield and its attributes is essential for identifying selection criteria that could be employed to improve faba bean productivity through breeding programs. Principal components (PCs) analysis is an efficient tool to assess the relationship among traits (Moustafa et al. 2021b; El-Sanatawy et al. 2021). The first two PCs showed most of the variability, about 86.31% (59.97% and 26.34% by PC1 and PC2, in the same order). Consequently, the two PCs were used to construct the PC-biplot (Figure 2). In the PC-biplot, the characters are represented by close vectors to each other signify robust positive relationships while those that were situated almost inverse (at 180°) demonstrate an extremely negative relationship. Consequently, a strong positive association was proven between seed yield per plant and each of 100-seed weight, number of branches per plant, days to flowering, plant height, number of seeds per plant and number of pods per plant. On the contrary, seed yield and all its attributes had a strong negative association with chocolate spot severity. The detected strong association between seed yield and these traits suggests their significance as vital attributes for indirect selection, especially in the early generations due to their ease of evaluation in comparison with seed yield. Similarly, a strong positive relationship between seed yield and its attributes was proved by Alan and Geren (2007); Abo-Hegazy et al. (2012); Abo-Mostafa et al. (2014); Sharifi (2014); Tekalign et al. (2017) and Elshafei et al. (2019).

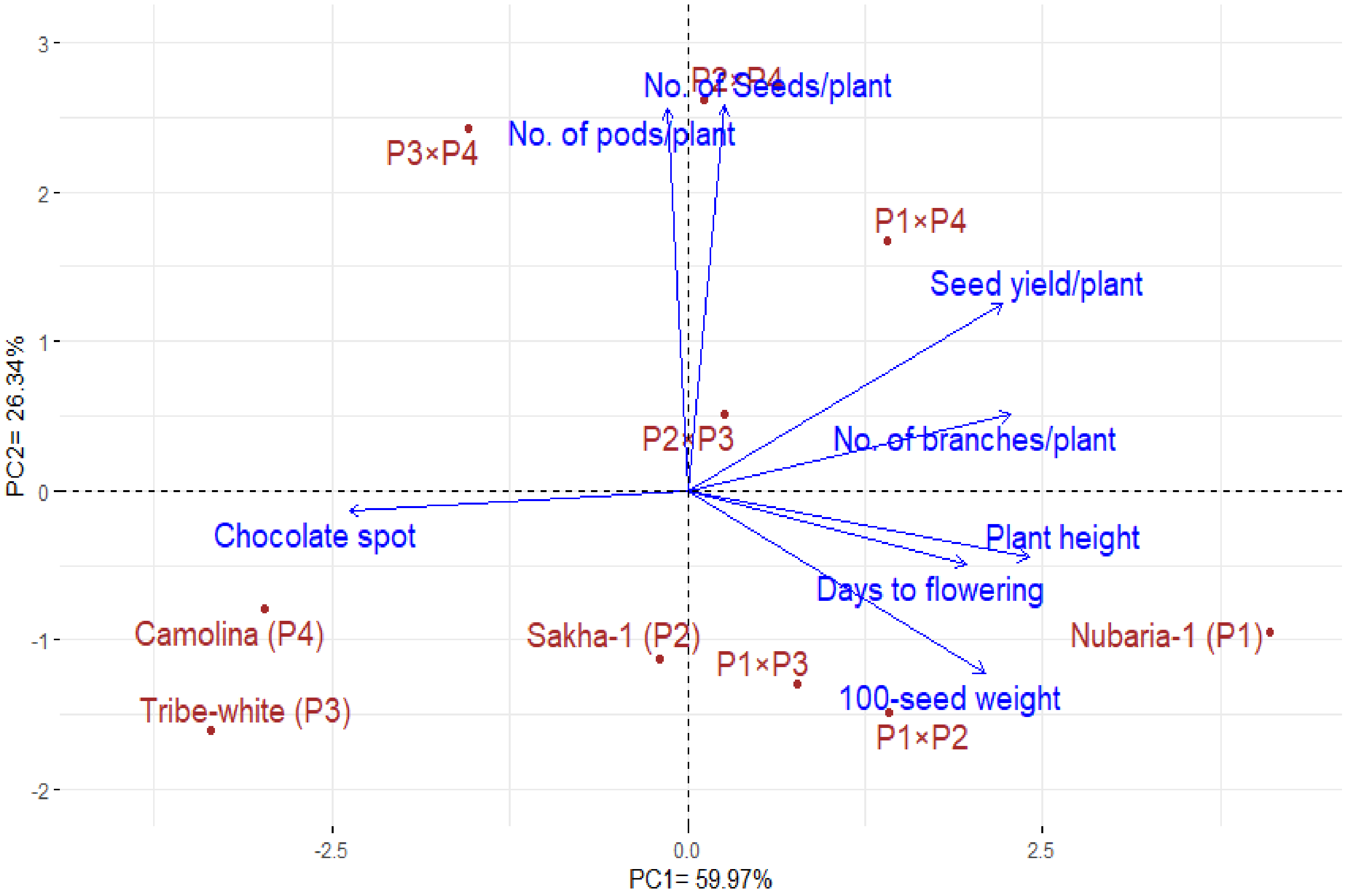

Figure 2- Biplot of PCA for the evaluated parental genotypes and their cross combinations to explore the association among the studied traits

3.6. Seed yield response to chocolate spot severity

The response of seed yield of faba bean to chocolate spot severity was determined in the early generations F1 and F2 (Fig. 3). The seed yield per plant as a dependent variable was regressed upon the incidence of chocolate spot through linear regression analysis. It was found a strong linear inverse relationship between seed yield and chocolate spot severity with a high negative slope in both generations. Hence, seed yield in both generations decreased steeply with increasing chocolate spot severity. The regression equations in both generations could be useful to predict yield loss and response to chocolate spot severity. There was yield loss of 25.56 and 21.65 g per plant in response to increasing each unit of chocolate spot disease in both generations F1 and F2, respectively. In this context, Sahar et al. (2011); Tolessa et al. (2015); Haile et al. (2016); Kora et al. (2017) demonstrated highly negative regression between seed yield and chocolate spot severity in faba bean.

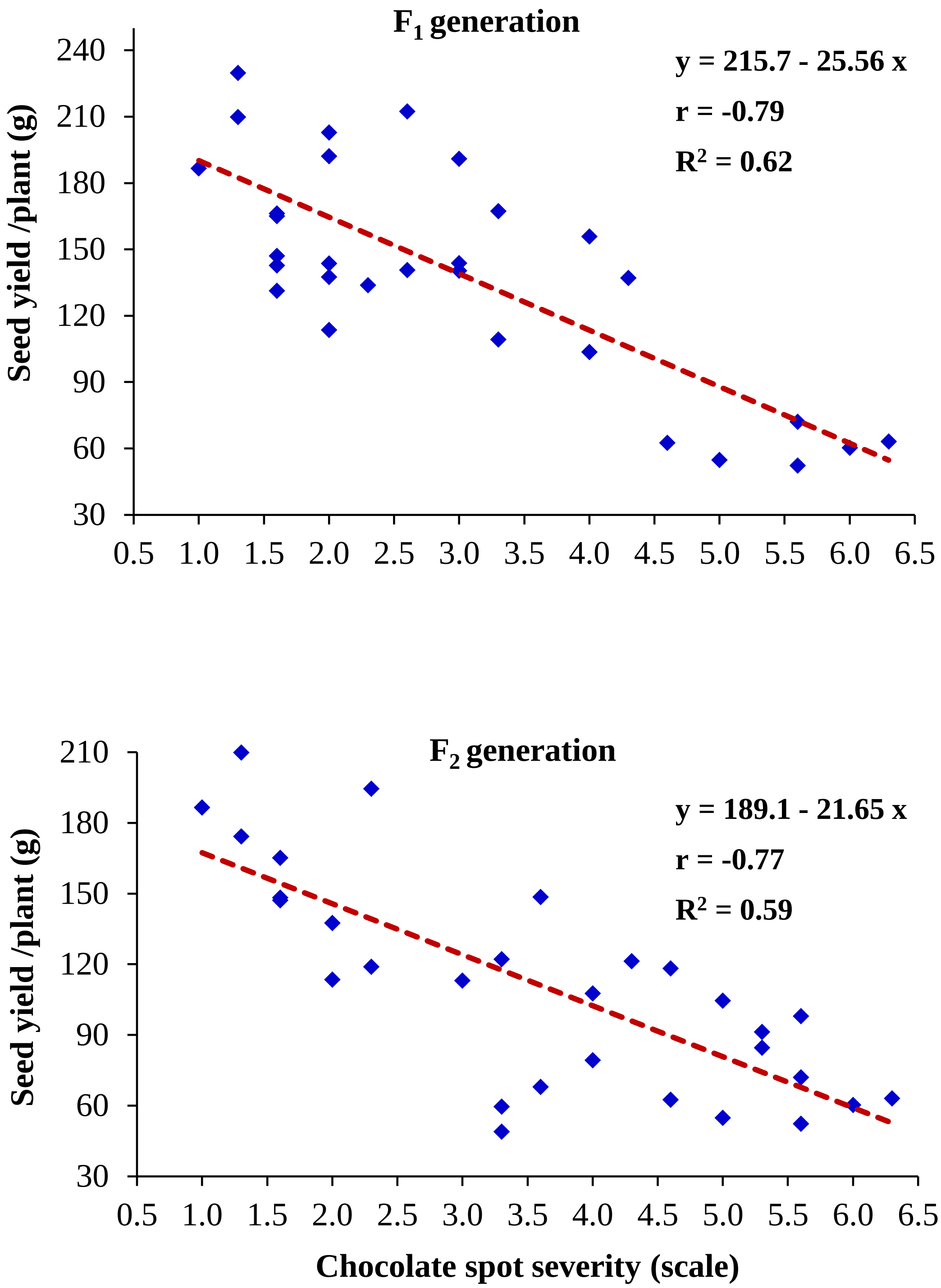

Figure 3- Response of seed yield of faba bean to chocolate spot disease in the F1 and F2 generations

4. Conclusions

Considerably genetic variations were identified among parental genotypes and their F1 and F2 progenies for chocolate spot resistance and assessed yield traits. The cross combinations of "P1(Nubaria-1)×P2(Sakha-1)", "P1(Nubaria-1)×P4(Camolina)" and "P2(Sakha-1)×P3(Tribe-white)" possessed constant performance through both generations with high-yielding and resistance to chocolate spot. Accordingly, these crosses are proposed to be exploited in faba bean breeding as valuable sources of high-yielding and resistance to chocolate spot disease. The additive gene effect was predominant for chocolate spot resistance, plant height, days to flowering, number of branches per plant and 100-seed weight in both generations. The predominance of additive effect for these traits indicates that selection could be efficient for improving them in early generations. On the other hand, the non-additive gene effects were preponderant for seed yield per plant, number of pods per plant and number of seeds per plant. This implies the significance of transgressive segregation and developing hybrids in enhancing these traits through breeding programs. Strong positive association was detected between seed yield per plant and each of number of branches per plant, 100-seed weight, plant height, days to flowering, number of pods per plant and number of seeds per plant. This reflects their importance for indirect selection, especially in the early generations due to their ease of evaluation in comparison with seed yield.

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