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Integration of Extra-Large-Seeded and Double-Podded Traits in Chickpea (*Cicer arietinum* L.)

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Abstract: A large seed size in the kabuli chickpea (*Cicer arietinum* L.) is important in the market not only due to its high price but also for its superior seedling vigor. The double-podded chickpea has a considerable yield and stability advantage over the single-podded chickpea. The study aimed at (i) integrating extra-large-seeded and double-podded traits in the kabuli chickpea, (ii) increasing variation by transgressive segregations and (iii) estimating the heritability of the 100-seed weight along with important agro-morphological traits in F_2 and F_3 populations. For these objectives, the large-seeded chickpea, Sierra, having a single pod and unifoliolate leaves, was crossed with the small-seeded CA 2969, having double pods and imparipinnate leaves. The inheritance pattern of the extra-large-seeded trait was polygenically controlled by partial dominant alleles. Transgressive segregations were found for all agro-morphological traits. Some progeny with 100-seed weights of ≥55 g and two pods had larger seed sizes than those of the best parents. As outputs of the epistatic effect of the double-podded gene in certain genetic backgrounds, three or more flowers or pods were found in some progeny. Progeny having imparipinnate leaves or two or more pods should be considered in breeding, since they had higher numbers of pods and seeds per plant and seed yields than their counterparts.

Keywords: *Cicer arietinum*; intraspecific crosses; transgressive segregations; large seed; double pod

1. Introduction

The domesticated chickpea, *Cicer arietinum* L., is not only an important food legume but is also one of the most important crops on the basis of drought resistance [1–3]. It is used as a cash crop in trade, having a high level of protein in its seeds, a rotation crop due to its ability to fix atmospheric nitrogen to soil, and a cover crop in sustainable agriculture [4–6]. Globally, it has the widest sowing area among cool season food legumes, with a 17.8 million ha cultivation area in 2018 [7].

The domesticated chickpea is well-defined in two classes as "*macrosperma*" or "kabuli" and "*microsperma*" or "desi" according to the pigmentation of the plant, the flower and the seed size, shape and color. The plants in the former class do not possess pigment on the vegetative green parts and flowers, and these plants generally produce larger cream and whitish-cream seeds. On the other hand, the plants of the latter class possess pigments with purple-pink and pinkish-blue flowers, and these generally produce smaller seeds with an angular and rough appearance with different colors including brown, black and green [8,9]. Seed size and color are important criteria in the market [10]. The seed size in chickpeas is referred to as the single seed weight [11,12], 100-seed weight [13] and scale of the sieve size in mm [14,15]. In "kabuli" chickpeas, three distinct seed shapes have been recognized—ram-headed, owl-headed and pea-shaped [16]—and chickpeas with ram-head-shaped seeds generally have the largest seed size, as high as 60 g ≥ per 100-seed weight [17,18]. Seed size in chickpeas is not only governed by genetic factors but also affected by environment [9,12,19], generally having a high heritability [9,20]. Farmers (producers) prefer to produce large-seeded chickpeas due to consumer preference, since a larger seed size commands a higher price in regional and international markets [21–23]. In addition to a higher price, a large seed size confers an advantage during germination, higher seedling vigor, allowing deeper sowing than that of small seeds in order to escape drought [24]. Large seed size has therefore been considered to be a noteworthy trait in breeding programs [12]. To investigate the genetics of large seed size, several studies have been carried out from the 1950s to date [13,25–29]. The inheritance of seed size was determined as monogenic, digenic and polygenic [12,13,29–33]. Seed size in chickpeas was mapped using recombinant inbred lines (RILs) and some quantitative trait loci (QTL), and candidate genes were located in LG1, LG2, LG4, LG5, LG6, LG7 and LG8 [32,34–37].

Like large seed size, the double-podded trait in chickpea is a significant trait for increasing yield [20,38–41] and seed yield stability [42,43]. It was first described in a mutant desi chickpea in the 1930s and was determined to be governed by a single recessive gene "*s*" or "*sfl*" [9,44]. QTLs were identified on LG 4 and LG 6 [45–49]. For the integration of the gene conferring the double-podded trait, interspecific and intraspecific crosses in chickpeas were made [40,42,43,48,49] and transgressive segregations were reported for quantitative traits [20,41,50]. Progeny in segregated populations having higher or lower values than their parents are transgressive segregations [51]. Some example studies on the "kabuli" chickpea have not only been conducted to increase seed size [52,53] but also integrated with resistance to ascochyta blight, caused by *Ascochyta rabiei* (Pass.) Labr. [54]. Thus, some improved cultivars have been described [55–62]. None of these studies have reported the integration of a large seed size and the double-podded trait. Therefore, the present study aims (i) to integrate extra-large-seeded and double-podded traits in the "kabuli" chickpea, (ii) to increase variation by transgressive segregations in intraspecific crosses and (iii) to estimate the heritability of 100-seed weight along with important agro-morphological traits.

2. Materials and Methods

2.1. Parents in Intraspecific Crosses

The female parent Sierra (PI 631078) is an extra-large-seeded "kabuli" chickpea improved by USDA-ARS in cooperation with the Washington Agricultural Research Center, Pullman, WA based on a large seed size and resistance to ascochyta blight. Sierra was derived from F_8 of a three-way cross, "Dwelley"//FLIP 85-58C/Spanish or Mexican White, and released according to pedigree breeding in 2004. Its prominent plant traits were reported to be a plant height of 53 cm, branching at the base, a simple or unifoliolate leaf, a single flower per axil and a 100-seed weight of 61.4 g [55]. The pollen donor parent CA 2969 (PI632396) is also a "kabuli" chickpea developed by CIFA, Cordoba, Spain since it has a good resistance to ascochyta blight. It was selected from [CA 2156/JG 62 (PI 439821)]//ILC 3279 (PI 471915). CA 2156, JG 62 (ICC 5149) and ILC 3279 are large-seeded, double pods and resistant to ascochyta blight, respectively. CA 2969 possesses imparipinnate or fern-like (normal) leaves, double pods per axil and a seed weight of 30.1 g per 100 seeds [63]. The leaves and flowers of Sierra and CA 2969 are shown in Figure 1.

Figure 1. Morphological traits of parents, Sierra (single-podded and unifoliolate leaf, left side) and CA 2969 (double-podded and imparipinnate leaf, right side).

As reported by Auckland and van der Maesen [64], flowers of the female Sierra were emasculated at early morning and then pollinations were done using flowers of the pollen donor CA 2969 within one hour at the campus of Akdeniz University, Antalya, Turkey (30°38′ E, 36°53′ N, 51 m above sea level). F_1, F_2 and F_3 plants were grown as single plant progeny and individually harvested in 2017, 2018 and 2019, respectively. The present study consists of F_1 progeny and F_2 and F_3 populations.

2.2. Agronomic Applications

Parents and progeny were planted in rows spaced 50 cm apart with a within-row plant spacing of 10 cm. The parent plants were grown as four replicates (about 40 plants), while F_1, F_2 and F_3 progeny were grown as progeny rows in the same field. F_1 progeny and the F_2 population were grown under rainfed conditions, while drip irrigation was used for the F_3 population. Weeds were controlled by hand during the seedling and before the flowering stages. No input such as fertilization was used.

2.3. Soil Properties

Soil in the experimental area was sampled between 0 and 30 cm and then analyzed to determine the experimental soil traits. Some plant nutrition elements were found to be at a sufficient level, while organic matter and nitrogen were determined to be at low levels. Like organic matter and nitrogen, iron and zinc levels were considered to be possibly deficient due to high pH. The soil texture was loam, with a $CaCO_3$ content of 26.5%, whereas the pH was high, at 7.69.

2.4. Weather Conditions

When the growing periods of F_1, F_2 and F_3 were considered, from February to July, the total precipitation in 2017, 2018 and 2019 was recorded as 405.7 mm, 545.1 mm and 653.1 mm, respectively. The extreme maximum temperatures during the flowering stage, when the F_1, F_2 and F_3 progeny were grown, were 33.9, 32.4 and 31.9 °C, respectively, whereas during the pod formation stage, they were 44.8, 38.9 and 39.7 °C, respectively (Table S1). Due to the sudden increase in extreme temperature (38.9 °C) during the pod setting (Table S1), a considerable number of progeny produced empty pods.

2.5. Data Collection

The days to first flowering and days to 50% flowering were recorded as phenological traits, whereas the plant height, first pod height, number of main stems, pods and seeds per plant, seed yield per plant, seed weight or seed size, number of pods per axil (as single or double pods) and leaf shape (as fern-like or unifoliolate leaves) were recorded as agro-morphological traits of each parent and progeny. The seed size in the present study as hereafter referred to is the 100-seed weight, determined by using following formula [13,33]:

100-seed weight (g) = [Total seed weight per plant (g)/Total number of seeds per plant] × 100

2.6. Data Analyses

All the agro-morphological data were analyzed to determine descriptive statistics using the MINITAB 17 software [65]. Transgressive segregations, the progeny with higher or lower values than those of their parents in the F_2 and F_3 populations, were determined using minimum and maximum values of the F_2 and F_3 populations. Besides, progeny in the F_2 and F_3 populations were divided into four classes to compare agro-morphological traits, as (i) imparipinnate leaf and single-podded, (ii) imparipinnate leaf and double-podded, (iii) unifoliolate leaf and sing-podded and (iv) unifoliolate leaf and double-podded.

Narrow-sense heritability (h^2) in the F_2 population was estimated using progeny–parent regression according to Poehlman and Sleper [66]:

$$h^2 = b,$$

$$b = \sum (X - \overline{X}) \left(Y - \overline{Y}\right) / \sum \left(X - \overline{X}\right)^2,$$

where b is the regression coefficient, and X, Y, $\overline{X}$ and $\overline{Y}$ are the values and means for the progeny and parents, respectively.

The chi-square test (χ^2) [67] was used to test the goodness of fit to the expected 9:3:3:1 ratio of segregation in the F_2 populations:

$$\chi^2 = \frac{(O - E)^2}{E},$$

where O and E are the observed and expected values, respectively.

3. Results

3.1. F_1 Progeny and F_2 and F_3 Populations

In F_1, negative selection was applied for untrue hybrids according to dominant morphological traits such as a single pod per axil and imparipinnate leaf shape. Hence, progeny with unifoliolate leaves due to selfing such as the female Sierra were discarded from rows in 2017. The true F_1 had imparipinnate leaves and produced single flowers and pods per axil. Fifty-one F_1 progeny were produced from intraspecific crosses between Sierra and CA 2969 in 2017. Each F_1 progeny had about 18 seeds per plant. Thus, a total 915 progeny were sown in F_2 in 2018. F_1 plants were single-podded with imparipinnate leaves, while F_2 plants segregated as imparipinnate leaves and a single-podded, imparipinnate leaves and double-podded, unifoliolate leaves and single-podded, and unifoliolate leaves and double-podded. The segregation was found to be a good fit to a 9:3:3:1 ratio (Table 1).

Table 1. Inheritance of the leaf shape (imparipinnate vs. unifoliolate) and number of pods per axil (single vs. double) in F_2 population derived from intraspecific crosses between Sierra and CA 2969.

Phenotype of F_{1s}	F_2			χ^2	p
	Phenotype of F_2 Population	Observed	Expected		
Imparipinnate leaf and single pod	Imparipinnate leaf and single pod	475	9:3:3:1	8.25	0.50–0.10
	Imparipinnate leaf and double pods	181			
	Unifoliolate leaf and single pod	189			
	Unifoliolate leaf and double pods	70			

3.2. Transgressive Segregations

According to data analyses to determine descriptive statistics in the F_2 and F_3 populations, transgressive segregations were found for all the agro-morphological traits, including 100-seed weight (Tables 2 and 3). The minimum and maximum values of the days to the first flowering of the F_2 population were found to be 45 days and 66 days, respectively, whereas the days to 50% flowering in the F_2 population ranged from 45 days to 75 days, respectively (Table 2). The days to the first flowering and days to 50% flowering of Sierra and CA 2969 were 48 and 50 days and 50 and 52 days, respectively. The plant height of the F_2 population varied from 17 cm to 59 cm, whereas the plant heights of Sierra and CA 2969 were 41 cm and 34.3 cm, respectively. The mean first pod height in the F_2 population was 31.7 cm, whereas it was 21 cm for Sierra and 19.7 cm for CA 2969. The mean number of main stems per plant in the F_2 population was 2.3, while it was 2.7 in Sierra and 2.3 in CA 2969. The number of pods per plant in the F_2 population ranged from 1 to 25, whereas the number of pods per plant was 5.2 in Sierra and 3 in CA 2969. The number of seeds per plant in the F_2 population ranged from 1 to 24, whereas the means of this trait were 4.2 in Sierra and 11.7 in CA 2969. The seed yield per plant was recorded as 0.1–7 g in the F_2 population, but it was 1.8 in Sierra and 3.7 in CA 2969. As for the 100-seed weight, this ranged from 9.5 g to 69 g in the F_2 population, while the 100-seed weights of Sierra and CA 2969 were 49.9 g and 31 g, respectively (Table 2).

The minimum and maximum values of the days to the first flowering of the F_3 population were between 36 and 75 days, whereas the days to 50% flowering ranged from 38 days to 82 days (Table 3). The plant height varied from 19 cm to 68 cm, whereas the plant heights of Sierra and CA 2969 were 52.3 cm and 42.7 cm, respectively. The first pod height ranged from 13 cm to 46 cm, whereas it was 31.3 cm for Sierra and 33.3 cm for CA 2969. The number of main stems ranged from 1 to 6, whereas it was found to be 2.3 in both Sierra and CA 2969. The number of pods per plant varied from 1 to 254, whereas it was 36.7 in Sierra and 42.7 in CA 2969. The number of seeds per plant ranged from 1 to 267, whereas the means of this trait were 32.7 in Sierra and 50.7 in CA 2969. The seed yield per plant was between 0.1 and 79 g, but it was 15.2 g in Sierra and 13.9 g in CA 2969. As the seed size in the F_3 population, the 100-seed weight ranged from 7 g to 64 g, while it was 46.9 g in Sierra and 27.4 g in CA 2969 (Table 3).

Table 2. Means ± standard errors, ranges and narrow sense heritability for agro-morphological traits in F_2 derived from intraspecific crosses between Sierra (single-podded and unifoliolate leaf) and CA 2969 (double-podded and imparipinnate leaf).

Traits	Sierra	CA 2969	Imparipinnate Leaf		Unifoliolate Leaf		F_2 Population		h^2
			Single Pod	Double Pods	Single Pod	Double Pods			
	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	Range	
Days to first flowering (days)	48.0 ± 0.97	50.0 ± 0.90	41.0 ± 0.29	41.5 ± 0.50	41.3 ± 0.47	40.8 ± 0.70	41.2 ± 0.21	45–66	0.80
Days to 50% flowering (days)	50.0 ± 0.97	52.0 ± 0.90	47.6 ± 0.29	47.8 ± 0.50	48.1 ± 0.46	47.5 ± 0.77	47.8 ± 0.24	45–75	0.80
Plant height (cm)	41.0 ± 0.97	34.3 ± 1.17	37.7 ± 0.31	37.6 ± 0.50	38.9 ± 0.43	41.7 ± 0.70	38.9 ± 0.21	17–59	0.43
First pod height (cm)	21.0 ± 0.73	19.7 ± 2.35	30.5 ± 0.32	30.2 ± 0.44	32.2 ± 0.49	34.0 ± 0.85	31.7 ± 0.23	11–58	0.65
Main stems per plant (No.)	2.7 ± 0.49	2.3 ± 0.21	2.0 ± 0.04	2.1 ± 0.06	2.4 ± 0.07	2.7 ± 0.15	2.3 ± 0.03	1–7	0.38
Pods per plant (No.)	5.2 ± 1.30	3.0 ± 2.54	3.6 ± 0.16	4.5 ± 0.30	3.6 ± 0.28	4.5 ± 0.55	4.1 ± 0.11	1–25	0.49
Seeds per plant (No.)	4.2 ± 1.08	11.7 ± 1.96	3.5 ± 0.14	4.2 ± 0.28	3.3 ± 0.22	4.2 ± 0.44	3.8 ± 0.11	1–24	0.66
Seed yield (g)	1.8 ± 0.56	3.7 ± 0.72	1.3 ± 0.05	1.5 ± 0.10	1.3 ± 0.10	1.5 ± 0.16	1.4 ± 0.04	0.1–6.9	0.60
100-seed weight (g)	49.9 ± 1.61	31.0 ± 1.26	37.2 ± 0.54	35.2 ± 0.76	37.3 ± 1.70	36.0 ± 0.9	36.4 ± 0.36	9.5–69.0	0.45

Table 3. Means ± standard errors and ranges for agro-morphological traits in F_3 derived from intraspecific crosses between Sierra (single-podded and unifoliolate leaf) and CA 2969 (double-podded and imparipinnate leaf).

Traits	Sierra	CA 2969	Imparipinnate Leaf		Unifoliolate Leaf		F_3 Population	
			Single Pod	Double Pods	Single Pod	Double Pods		
	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	$\bar{X} \pm S_{\bar{x}}$	Range
Days to first flowering (days)	48.3 ± 0.08	50.0 ± 0.50	46.1 ± 0.23	46.2 ± 0.19	45.0 ± 0.29	46.4 ± 0.27	46.0 ± 0.12	36–75
Days to 50% flowering (days)	50.3 ± 0.08	52.3 ± 0.42	48.9 ± 0.20	49.2 ± 0.17	47.9 ± 0.23	49.2 ± 0.21	48.9 ± 0.10	38–82
Plant height (cm)	52.3 ± 0.61	42.7 ± 0.08	43.8 ± 0.27	44.5 ± 0.25	48.9 ± 0.42	50.8 ± 0.40	46.3 ± 0.18	19–68
First pod height (cm)	31.3 ± 0.38	33.3 ± 0.79	29.9 ± 0.26	30.7 ± 0.25	31.6 ± 0.41	32.4 ± 0.37	30.9 ± 0.15	13–46
Main stems per plant (No.)	2.3 ± 0.09	2.3 ± 0.08	2.7 ± 0.04	2.8 ± 0.04	2.8 ± 0.05	2.9 ± 0.04	2.8 ± 0.02	1–6
Pods per plant (No.)	36.7 ± 2.05	42.7 ± 2.7	62.7 ± 1.87	69.9 ± 1.85	48.5 ± 1.75	48.8 ± 1.35	59.5 ± 0.96	1–254
Seeds per plant (No.)	32.7 ± 2.02	50.7 ± 2.46	68.0 ± 2.06	77.9 ± 2.09	51.4 ± 1.85	52.3 ± 1.46	64.9 ± 1.07	1–267
Seed yield (g)	15.2 ± 0.86	13.9 ± 0.72	24.3 ± 0.74	26.4 ± 0.69	16.3 ± 0.58	16.3 ± 0.46	21.9 ± 0.37	0.1–79.0
100-seed weight (g)	46.9 ± 0.31	27.4 ± 0.34	42.1 ± 0.38	41.4 ± 0.38	38.9 ± 0.45	38.5 ± 0.41	40.7 ± 0.21	7.0–64.0

3.3. Comparisons of Number of Pods per Node and Leaf Shapes

The numbers of pods, seeds per plant and seed yields were higher in the double-podded progeny than those in the single-podded ones, while the 100-seed weight was higher in the single-podded progeny than that in the double-podded progeny (Tables 2 and 3). Progeny having unifoliolate leaves had higher plant heights, first pod heights and numbers of main stems per plant than those of progeny having imparipinnate leaves (Tables 2 and 3).

3.4. Inheritance of Seed Size and Agro-Morphological Traits

The narrow-sense heritability for the days to first flowering; days to 50% flowering; plant height; first pod height; numbers of main stems, pods and seeds per plant; and seed yield per plant were estimated to be 0.80, 0.80, 0.43, 0.65, 0.38, 0.49, 0.66, and 0.60, respectively (Table 2). The narrow-sense heritability for the 100-seed weight was found to be h^2 = 0.45. The inheritance pattern of the 100-seed weight was found to be polygenic and governed by partial dominant genes in the present population (Figure 2).

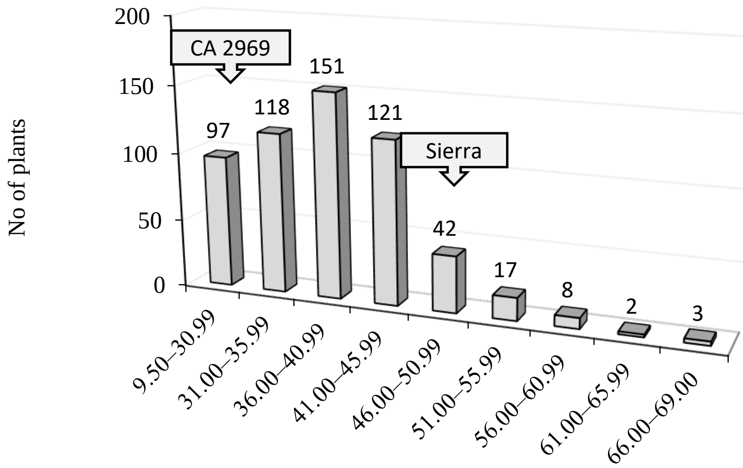

Figure 2. Distribution of F_2 progeny derived from intraspecific crosses between Sierra (single-podded and unifoliolate leaf) and CA 2969 (double-podded and imparipinnate leaf) according to 100-seed weight.

4. Discussion

Agro-morphological traits were negatively affected by drought and heat stress (Table 1), since the progeny from F_1 to F_2 were not only grown under rainfed conditions without using inputs but they were also grown in low-quality organic matter and nitrogen. However, the F_3 progeny had higher yields and more pods and seeds per plant than those of the F_1 and F_2 progeny, due to irrigation (Tables 2 and 3). The domesticated chickpea prefers to grow at temperatures of less than 30 °C [2,8,24], because heat stress may trigger drought stress, which is the major reason for the shedding of flowers.

All the progeny in F_1 had imparipinnate leaves and a single flower or pod per axil as in the male parent CA 2969, indicating that imparipinnate leaves and a single flower or pod per axil were dominant over unifoliolate leaves and double flowers or pods per axil. The F_2 progeny segregated by leaf shape and the number of pods per axil. With a non-significant χ^2 value (χ^2 = 8.25 < p 0.05), the segregation ratio was found to be a good fit to a ratio of 9 (imparipinnate leaf and single-podded):3 (imparipinnate leaf and double-podded):3 (unifoliolate leaf and single-podded):1 (unifoliolate leaf and double-pooded). The inheritance of leaf shape in domesticated chickpeas in the present study was in agreement with the results of studies [9,68–71]. As in the present study, the presence of double pods per axil was governed by a recessive single gene [9,39,40,42]. Once progeny in the F_2 and F_3 populations having two pods per axil are selected for this unique trait, this trait, controlled by a single recessive gene, will not segregate in later generations [9].

Transgressive segregations were found for all the agro-morphological traits (Tables 2 and 3) and the 100-seed weight in F_2 (Figure 2) and F_3 (Figure 3). Among the progeny, 30 progeny in the F_2 population had a higher 100-seed weight than that of the best parent Sierra, which had a 49.9 g one (Figure 2). A total of 131 progeny in the F_3 population had a 100-seed weight higher than 50 g (Table 3). Some of them had produced two pods and extra-large seed sizes as large as 63 g (Figure 3). Transgressive segregations were considered to be derived from the complementary action of genes and the expression of suppressed recessive genes in the parents [20,41,50,51]. As promising progeny, extra-large-seeded progeny with two or three pods per axil were isolated in F_3 (Figures 3 and 4). As outputs of the epistatic effect of the double-podded trait in a different background, three or more flowers or pods per axil were discovered in some progeny (Figure 4).

Figure 3. Seeds of a progeny (with two pods per axil and 63 g per 100 seeds, left side) in F_3 derived from intraspecific crosses between Sierra (single-podded, unifoliolate leaf and 46.9 g per 100 seeds, right side) and CA 2969 (double-podded, imparipinnate leaf and 27.4 g per 100 seeds, middle).

Figure 4. A progeny in F_3 (with three flowers per axil, unifoliolate leaves and large seeds) derived from intraspecific crosses between Sierra (single-podded and unifoliolate leaf) and CA 2969 (double-podded and imparipinnate leaf). Red circles indicate three flowers/pods.

Single-podded progeny had larger seed sizes than double-podded progeny, while double-podded progeny had higher seed yields, numbers of pods and numbers of seeds per plant than single-podded progeny (Tables 2 and 3). The triple-flowered trait (sfl^t) in the domestic chickpea is controlled by a single recessive gene. The double-flowered trait (sfl^d) is dominant over the triple-flowered trait, and the dominance relationship of these alleles at the *Sfl* locus was reported to be *Sfl* (single flower) > sfl^d (double flower) > sfl^t (triple flower) [44].

Progeny having imparipinnate leaves had higher seed yields than those of progeny having unifoliolate leaves (Tables 2 and 3). This result was in agreement with the findings of Abbo et al. [72] in chickpeas having compound leaves. Additionally, progeny having imparipinnate leaves attained more pods and seeds per plant and higher 100-seed weights than those of unifoliolate progeny (Tables 2 and 3). The higher seed yields and larger seed sizes of the progeny having imparipinnate leaves may stem from the wider photosynthetic area of the progeny having imparipinnate leaves than their counterparts. Abbo et al. [72] indicated that compound leaf lines of chickpeas attained higher leaf area indices at both low and high sowing densities.

Regarding seed size, the 100-seed weight had one of the smallest values of narrow-sense heritability, at $h^2 = 0.45$, showing that the 100-seed weight was one of the most affected agro-morphological traits by genotype-by-environment or genotype-by-year interactions. When considering the environment, heat and drought stress (Table 1) had the greatest effects on seed size (Tables 2 and 3). In the present study, the inheritance pattern for the 100-seed weight was revealed to be polygenic due to continuous distribution (Figure 2). Most of the progeny in F_2 had higher 100-seed weights than that 100-seed weight of the parent CA 2969 (Figure 2), indicating that partial dominant genes played a crucial role in the inheritance of 100-seed weight. Without reciprocal crosses, it was hard to say, despite the fact that the cytoplasmic effect of the female parent might have dominated the large seed size, since most of the progeny produced heavier seeds than those of the smallest-seeded parent CA 2969 (Figure 2). In the present study, seed size was not divided into classes as small, medium and large according to preference. In inheritance studies on seed size in domesticated chickpeas, inheritance was reported as being monogenic [13], digenic [12,13,32,73] and polygenic [27,29–31,33]. The main reason for these differences stems from the phenotypic preference used by researchers. Although maternal genetic effects were not found on the inheritance of seed size in the domesticated chickpea by Upadhyaya et al. [12], it was suggested that the female parent should have a large seed size to increase seed size in the chickpea [74]. Small seed size in chickpeas was dominant over large seed size and controlled by two genes [32,73]. By contrast, normal seed size was dominant over small seed size [12]. In interspecific reciprocal backcrosses, Ceylan et al. [74] indicated that seed size and yield components could be improved by using the domesticated chickpea as female. As a polygenic trait, seed size was governed by both additive and dominant genes [14,27], as in the present study (Figure 3).

5. Conclusions

In conclusion, the inheritance pattern of the extra-large-seeded trait in the domesticated chickpea was polygenic and controlled by partial dominant alleles or might have been affected by the female parent. Not only the 100-seed weight but also the days to the first flowering, days to 50% flowering, plant height, first pod height, number of pods and seeds per plant and seed yield per plant in the F_2 and F_3 populations were found as transgressive segregations, revealing that the seed size in chickpeas could be improved by crossing suitable parents. Double-podded progeny had higher seed yields and numbers of pods and seeds per plant than those of single-podded ones, while single-podded progeny had larger seed sizes than those of double-podded progeny. Progeny having imparipinnate leaves attained higher seed yields than those of progeny having unifoliolate leaves. Extra-large seeds of ≥55 g and two pods per axil traits were assembled in a considerable number of progeny in F_2 and F_3. With the epistatic effect of the double-podded gene in certain genetic backgrounds, three pods per axil were present in some progeny. Progeny having imparipinnate leaves double or more pods should be considered in breeding programs because these progeny had higher numbers of pods and seeds per plant and seed yields than their counterparts. Extra-large-seeded and double-podded traits can be integrated with intraspecific crossing when suitable "kabuli" chickpeas are crossed.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/10/6/901/s1. Table S1: Monthly rainfall, relative humidity and extreme maximum and minimum temperatures during progeny growing seasons from F_1 to F_3.

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