Penetrance and Expressivity of the Gene for Double Podding in Chickpea

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The double-pod per peduncle trait is known to contribute to increased seed yield in chickpea (*Cicer arietinum* L.). A cross was made between the single-podded variety ICCV 2 and the double-podded variety JG 62 in 1993. Penetrance and expressivity of the gene for double podding was studied in an F_2 population and F_{10} recombinant inbred lines (RILs) of this cross. Homozygous recessive allele of this gene (*ss*) governs the production of double flowers and pods per peduncle. Results indicated that the *s* allele has unstable penetrance and variable expressivity. The penetrance of this allele was 53% for the F_2 and 84.5% for the RILs. The ranges for the expression of this trait among the penetrant F_2 individuals and the penetrant RILs were 1.1–14.8% and 0.1–33.0%. These were 8.3–30.8% for early sown and 17.1–68.7% for the late sown double-podded parent JG 62. Thus it appears that the allele shows greater penetrance and enhanced expressivity under soil moisture stress. In the F_2 the seed yield advantage of the double-podded over the single-podded plants was 18%, whereas among the RILs it was 7%. The increased number of pods and seeds contributed to the higher yield. However, there was a slight decrease in seed size of the double-podded genotypes. An increase in the size of seed may have a role in the decreased penetrance and expressivity of this allele among the double-podded segregants of the ICCV 2 × JG 62 chickpea cross.

Most of the 17,250 (1999 count) world chickpea (*Cicer arietinum* L.) germplasm accessions maintained at the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) have only one flower and one pod at each peduncle, but there are some which bear two flowers and two (double) pods per peduncle (Pundir et al. 1988). A recessive gene *s* or *sfl* is reported to govern the double-podded trait (Ahmad 1964; D'Cruz and Tendulkar 1970; Khan and Akhtar 1934; Patil 1966; Singh and van Rheenen 1989, 1994). Precise allelic tests have not been conducted, but it appears that the same locus was involved in the genetic materials used in the different studies (Muehlbauer and Singh 1987). This observation is supported by the absence of segregation for single and double pods within F_2 populations of JG 62 and each of the five most predominant double-podded lines of chickpea used at ICRISAT (Kumar J, unpublished data).

The double-podded trait enhances seed yield under certain environments. (Singh and van Rheenen 1989, 1994). These studies do not quantify the seed yield advantage attributed to the *s* allele. Sheldrake et al. (1978) removed the second flower in double-flowered genotypes. They concluded that the double-podded character conferred a yield advantage of 6–11%. However, their study could not provide any information on the effect of the *s* allele. Rubio et al. (1998) measured the seed yield of five near-isogenic lines (NILs) for single and double pods that were derived from a cross of JG 62 and CA 2156. They observed no yield differences between the two. However, the allele for double pods had a positive effect on the stability of seed yield over locations and years. Knights (1987) observed a negative effect of this trait on seed yield. Sheldrake et al. (1978) studied five double-podded genotypes and reported that all the genotypes had a similar number of double-podded nodes. However, we have observed that this character is not uniformly expressed in several other double-podded accessions and their segregants that carry the *s* allele in homozygous recessive (Kumar J, unpublished data). Rubio et al. (1998) observed 3–13% expressivity for this allele. Thus the penetrance and expression of the *s* allele appear to vary. We therefore planned an experiment to study the pen-

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etrance and expressivity of this allele and its effect on other traits of chickpea.

Materials and Methods

The materials for this investigation comprised parents, F_1, and F_2 populations, and F_{10}-generation recombinant inbred lines (RILs) of a chickpea mapping population ICCV 2 × JG 62. ICCV 2 is a *kabuli* type, single-podded, medium-bold seeded and fusarium wilt resistant variety and JG 62 is a small-seeded *desi* type, double-podded, and fusarium wilt susceptible variety. The cross was made on a single typical plant of ICCV 2 with pollen from a representative plant of JG 62 at ICRISAT (Patancheru, India) in 1993. The F_1 generation, which showed single-podded nodes, was advanced in an off-season nursery in 1993. Sixty-six F_2 plants derived from a single F_1 plant were advanced through the single-seed descent method (Knott and Kumar 1975) to the F_{10} generation in glasshouses from 1994 to 1997. Two separate experiments were conducted to evaluate the materials.

Experiment 1

This experiment consisted of the two parents and the F_2 generation. Two rows each of ICCV 2 and JG 62 and 10 rows of the F_2 generation were planted on a deep vertisol on conserved soil moisture on 15 October 1997. The rows were 4 m long, placed 60 cm apart, with 10 cm between plants. Nonexperimental chickpea material was planted all around to provide normal competition. Cultural operations were carried out as necessary and the crop was fully protected from *Helicoverpa* pod borer. Data on plant height (cm), number of primary and secondary branches, number of single and double pods, number of seeds per pod, total number of seeds per plant, 100-seed weight, and seed yield were recorded on 20 competitive random plants for each parent and 120 F_2 plants (derived from two F_1 plants) at physiological maturity.

Experiment 2

The 66 RILs and two parents were planted in an incomplete block design with three replications on 3 November 1997. The plot size was 1 row, 4 m long, 60 cm apart, with 20 cm between plants within a row. The experimental conditions were as described above. The same data characteristics as in experiment 1 were recorded on five competitive random plants for each replication. The means of the five plants were used for analysis.

Table 1. Mean, standard deviation (SD), range, and coefficients of variation (CV) for expressivity of the gene for double-podding in JG 62 and penetrant segregants of F_2 and RILs of ICCV 2 × JG 62 chickpea cross

Experiment	Generation	Expressivity (%)			
		Mean	SD	Range	CV (%)
1	F_2	5.8	4.55	1.1–14.8	78.57
	JG 62[a]	16.1	6.31	8.3–30.8	39.28
2	RILs	8.2	9.57	0.1–33.0	116.80
	JG 62	40.9	16.45	17.1–68.7	40.24

[a] The other parent ICCV 2 is single podded.

The penetrance was calculated using the following formula:

[(Observed number of double-podded plants/RILs)/(Expected number of double-podded plants/RILs)] × 100.

Chi-square tests were performed to know the probability limits at 1 df while explaining penetrance. Expressivity was calculated by the following formula:

[(Number of double-podded nodes) ÷ (Number of double-podded nodes + number of single-podded nodes)] × 100 or

[(Number of double-podded nodes) ÷ (Number of pods − number of double-podded nodes)] × 100.

The seed size and seed yield of the RILs were also measured in a nonreplicated experiment during 1998–1999. The experiment was planted on 18 November. Other experimental details were similar to those mentioned for experiment 2.

Results and Discussion

In this study 25% of the F_2 plants and 50% of the RILs are expected to be double podded. Significant deviation from this would indicate a lack of penetrance. A monogenic segregation for this trait was obtained only for the RILs in the present experiment ($P < .01$ in experiment 2). The penetrance for F_2 was 53% ($\chi^2 = 8.71$; $.01 > P > .001$) and for the RILs it was 84.5% ($\chi^2 = 1.52$; $.25 > P > .20$). JG 62 recorded 100% penetrance in both experiments 1 and 2.

The mean expressivities of the allele *s* in the double-podded parent JG 62 were 16.1% for experiment 1 and 40.9% for experiment 2. These were 5.8% and 8.2% for the penetrant F_2 plants (experiment 1) and for the RILs (experiment 2) (Table 1). Thus it appears that both varying environmental conditions and different genetic backgrounds affect the expression of the *s* allele.

The allele governing the production of double pods is the same in JG 62 double-podded F_2 plants as well as the double-podded RILs of the cross ICCV 2 × JG 62. The ranges for the expressivities of this trait for JG 62 and penetrant F_2 plants (experiment 1) were 8.3–30.8% and 1.1–14.8% (Table 1). Similarly the ranges for JG 62 and penetrant RILs were 17.1–68.7% and 0.1–33.0%. It appears that JG 62 has a favorable genetic background for high expression of this trait. In comparison incomplete penetrance and variable expressivity of this allele in F_2 and the RILs may be due to their different genetic backgrounds. ICCV 2 may have contributed unfavorable nuclear and/or cytoplasmic genes as modifiers or as suppressors.

The difference in the expressivity of the *s* allele between JG 62 in the two planting dates may be caused by the lower moisture stress faced by the early sown rather than the late sown crop. The former received 53 mm of rain after emergence. The latter was exposed to a greater degree of heat and soil moisture stress, especially during the flowering and podding period. Thus it appears that there are substantial environmental effects on the expression of this trait. Sheldrake et al. (1978) also observed variable expressivity for this trait in their experiments grown in three different environments. In the present study the CVs (%) and the errors associated with the means for expressivity of the *s* allele were much lower for JG 62 than those for either the penetrant F_2 plants or for the penetrant RILs. These observations indicate that the background genetic constitutions play a role in the expressivity of the *s* allele. JG 62 expresses the double-poddedness much better than any segregants studied from its cross with ICCV 2. However, it is likely that if larger populations of F_2 and RILs are studied, segregants with a higher number of double pods may be obtained.

To quantify the effect of the *s* allele on seed yield and seed size, a comparison was made between the single- and double-podded F_2 plants (Figure 1) and between single- and double-podded RILs (Figure 2). The mean seed yield of the double-podded F_2 plants was about 18% more than that of the single-podded plants. The double-podded RILs outyielded the single-podded RILs by 7%. The traits that contributed to these increases are total number of pods

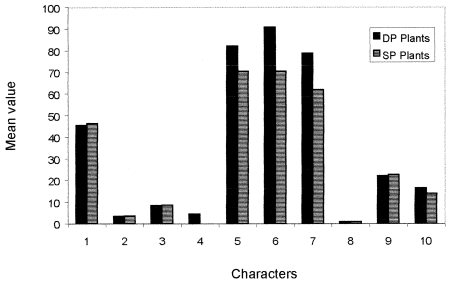

Figure 1. Comparison of characters between single- and double-podded F_2 plants of ICCV 2 × JG 62 chickpea cross. DP = double-podded, SP = single-podded; 1 = plant height (cm); 2 = number of primary branches; 3 = number of secondary branches; 4 = number of double-podded nodes; 5 = number of single-podded nodes; 6 = number of pods; 7 = number of seeds; 8 = number of seeds per pod; 9 = 100-seed weight (g); 10 = seed yield (g).

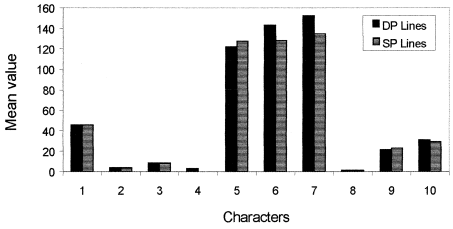

Figure 2. Comparison of characters between single- and double-podded RILs of ICCV 2 × JG 62 chickpea cross. DP = double-podded, SP = single-podded; 1 = plant height (cm); 2 = number of primary branches; 3 = number of secondary branches; 4 = number of double-podded nodes; 5 = number of single-podded nodes; 6 = number of pods; 7 = number of seeds; 8 = number of seeds per pod; 9 = 100-seed weight (g); 10 = seed yield (g).

and seeds. These two traits, along with seed size, are known as components of yield (Rao et al. 1994). As expected, the double-podded F_2 plants and the RILs produced slightly smaller seed size than their respective single-podded segregants. The means for the other traits measured did not differ for single- and double-podded F_2s or RILs. One reason for the low expressivity of the *s* allele in this cross may be the increased seed size contributed by ICCV 2, so that most segregants had larger seed size than JG 62. It appears that there is a competition between the sinks of large seed size and double-poddedness. Knights (1987) reported slightly smaller seed size for the double-podded segregants in two of his three experiments. However, Rubio et al. (1998) did not observe differences for the seed size of single- and double-podded NILs in their study. One reason for this difference could be the low sample size used by them.

The results of this study indicate that the *s* allele shows unstable penetrance and variable expressivity. None of the double-podded segregants showed as many double pods as JG 62. This suggests that JG 62 has a complex favorable genetic background for the expression of this trait, which was not captured in the relatively small populations studied in this investigation. JG 62, and some other chickpea accessions that show better expression of the *s* allele, are highly susceptible to fusarium wilt, a serious yield reducer of this crop (Kumar and Haware 1983). Fortunately one of the two recessive genes (h_1h_1) which complement to impart resistance to race 1 of fusarium wilt segregates independently of the *s* allele (Singh et al. 1988).

The *s* allele ensures a small seed yield advantage and its yield stability over the allele for single pods. These results support the previous findings of Sheldrake et al. (1978), who observed a 6–11% advantage of the double-podded trait at ICRISAT. Knights (1987), who found a negative effect of the allele for double podding on seed yield, probably had nonadapted material in his studies.

It can be concluded that the *s* allele exhibits unstable penetrance and variable expressivity. The studies by Rubio et al. (1998) also support this conclusion. It appears that penetrance and expressivity of this allele can be stabilized by incorporating it in an appropriate genetic background. It produces higher seed yield in the soil moisture stress conditions under which chickpea is generally grown in areas of its adaptation. Therefore small but significant advantage to the seed yield and its stability is already benefiting the crop. Further studies are needed to determine detailed reasons for unstable penetrance and variable expressivity of this allele so that stable double-podded and fusarium wilt resistant genotypes can be developed.

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