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Genetics of lodging resistance in chickpea (*Cicer arietinum* L)

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Abstract Lodging (stem bending) is a serious problem causing severe yield reduction, poor grain filling, lower harvest index and deterioration in grain quality of chickpea in environments characterized by favorable temperatures and soil moisture conditions. Breeding for lodging resistance is also required to improving adaptation to better agronomy for achieving a breakthrough in its productivity and stability of production. However, no information is available on genetics of lodging resistance in chickpea. The objectives were to (i) characterize the newly identified lodging resistant germplasm FLIP07-183C for important plant characteristics and (ii) study the inheritance of lodging resistance in an inter-varietal cross between lodging susceptible high yielding desi cultivar Pusa 362 and the newly identified lodging resistant kabuli germplasm FLIP07-183C. FLIP07-183C was a tall, erect, late flowering genotype with semi-determinate stem growth habit and large seeds. It contained higher lignin content than the lodging susceptible cultivar, Pusa 362. Lodging resistance was found to be dominant over susceptibility. The segregation patterns in F_2 and F_3 of the cross Pusa 362 × FLIP07-183C showed that two dominant non-allelic genes with duplicate gene action controlled lodging resistance in FLIP07-183C. The two non-allelic duplicate dominant genes for lodging resistance in FLIP07-183C are designated as *Sb1/sb1 and Sb2/sb2*. The homozygous recessive for both alleles (*sb1sb1sb2sb2*) produced a lodging susceptible phenotype. The utilization of genes identified for lodging resistance has the major impact on chickpea breeding for better adaptation to cool climate, high fertility and irrigated environments.

Keywords Chickpea · Stem bending · Lodging resistance · Lignin · Inheritance

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Introduction

Chickpea (*Cicer arietinum* L.), a crop rich in protein, minerals and vitamins is the second most important food legume being cultivated in more than 65 countries worldwide (FAO 2018) and therefore contribute significantly to alleviate the problems associated with malnutrition and hidden hunger. It is cultivated on an area of 17.81 million hectares with a production of 17.19 million tonnes, contributing about 18%–19% to total pulses production globally.

Chickpea is important because it provides food for humans as well as feed for livestock. Chickpea being a staple diet component, supplies carbohydrate and protein to the predominantly vegetarian population in India and considered to be a health food in western countries (Abbo et al. 2005). India is the largest producer of chickpea with a share of about 66% (11.38 million tonnes) of its global production (FAO 2018). In India, chickpea is cultivated in a wide range of agro-ecological regions that can be broadly classified as short (Peninsular India), medium (central India) and long (northern Indian plains and hills) duration environments (Hegde et al. 2016). Intensive breeding efforts in the past has been successful in reducing chickpea crop duration and improving resistance to biotic stresses particularly soil borne disease like Fusarium wilt. But, a significant breakthrough in its yield has not been possible so far as compared to the green revolution crops which broke the yield plateau of wheat and rice. During the last 55–60 years, the average yield of chickpea in India has marginally increased from 0.674 t/ha in 1961 to 0.956 t/ha in 2018 compared to its competing crops such as wheat and mustard (FAO 2018). Expanding irrigation facilities in the northern Indo-Gangetic plains, availability of input responsive high yielding varieties of wheat and later rapeseed mustard, has shifted the chickpea producing areas of the northern Indian plains and the crop has thus descended to non-traditional less productive central and southern India (Ali and Gupta 2012). Another important reason for withdrawal of chickpea cultivation from the fertile Indo-Gangetic plains is the non-availability of lodging resistant chickpea varieties that can withstand and are responsive to better agronomic management in terms of higher doses of fertilizers and irrigation (Hegde et al. 2016). The previous studies have shown that chickpea has high yield potential under favorable environmental and agronomic conditions. For example, two light irrigations, one at branching and the other at pod initiation significantly increased the seed yield (Prasad 2011). The better agronomic practices like appropriate date of sowing, balanced nutrient management, and improved irrigation regime are the important strategies for improving chickpea productivity and its yield maximization. However, due to its indeterminate nature, whenever chickpea crop is sown early and under irrigated high fertility conditions, it accumulates high vegetative biomass resulting in complete lodging which is a serious problem causing severe yield reduction, poor grain filling, poor harvest index and deterioration in grain quality. Lodging also affects the suitability of the crop to both manual and machine harvesting. This makes chickpea production economically less competitive and unattractive to farmers particularly in the northern Indo-Gangetic plains characterized by somewhat favorable temperature and soil moisture conditions due to cool winter and intermittent rainfall during the crop season. Therefore, lodging is considered a major constraint for increasing chickpea yields under favorable agronomic management conditions. It results in destruction of normal canopy structure leading to reduced photosynthetic ability, dry matter production, increased disease pressure, reduced harvest efficiency and ultimately seed yield (McPhee and Muehlbauer 1999; Chen et al. 2011). The extent of loss depends on the timing and the severity of the lodging which is a highly complex trait influenced by both the genotype and the environment.

Lodging refers to permanent displacement of above ground plant parts from their vertical stance either due to stem lodging (stem bending or stems breakage) or may be by the failure of root-soil anchorage system called root lodging (Berry et al. 2003). Stem breaking is prevalent mostly in cereals due to stiff culm strength whereas stem bending is a problem in pulses due to low stem stiffness and strength. Root lodging is actually considered when a plant is tilted $> 30^0$ from an upright position (Bruce et al. 2001). Lodging is a complex trait related to several intrinsic crop characteristics and extrinsic environmental factors like wind, rain and insect infestation which makes replication of breeding results difficult (Larsson et al. 2017). Lignin is found to be one of the chemical components present in basal internodes of stem responsible for culm rigidity and significantly influences stem breaking resistance in cereals (Pinthus 1973). However, no such information is available in chickpea.

The modification of plant architecture improves adaptation of crops to different environments and increases the seed yield and its stability (Huyghe 1998). A change in plant architecture by introduction of dwarfing genes resulted in a dramatic increase in yields of wheat and rice cultivars known as the 'Green Revolution' (Peng et al. 1999). A change in chickpea plant architecture is therefore needed to improve its adaptation to better agronomy for achieving a

breakthrough in its productivity and stability of production. The information on sources of genes for lodging resistance and an understanding of their inheritance required to breed chickpea cultivars resistant to lodging is lacking in chickpea. A thorough understanding of the sources of genotypic variation for lodging resistance, plant morphological and biochemical traits associated with lodging resistance and inheritance pattern helps in planning an effective breeding and selection strategy for designing a lodging resistant plant type in chickpea. The present investigation in chickpea is to characterize a newly identified lodging resistant germplasm for important plant characteristics and study the inheritance of lodging resistance in an inter-varietal cross between a lodging susceptible high yielding cultivar and the newly identified lodging resistant germplasm. Utilization of gene (s) for lodging resistance in the genetic restructuring of plant type is expected to result in chickpea plants with more rigid stems, ability to withstand accumulation of greater biomass, improvement in harvest index and seed yield.

Materials and methods

Morphology of FLIP07-183C, a lodging (stem bending) resistant genotype.

A lodging (stem bending) resistant genotype was noticed in one of the station trials during winter season of 2014–15. In this year more than 300 mm rainfall was received during the chickpea crop season (November to March). As a result, all other breeding lines and control varieties under evaluation during the season except FLIP 07-183C (Fig. 1), lodged due to excessive rainfall and soil moisture that resulted in excessive growth and accumulation of vegetative biomass. A single tall and erect plant resistant to lodging was harvested separately to grow in the next season. There was no segregation for plant height, erect plant type and lodging within the progeny of the selected lodging resistant plant and it was maintained through selfing. The lodging resistant genotype, FLIP07-183C was characterized for some of the plant and seed characters according to IBPGR, ICRISAT, ICARDA (1993) during the winter season of 2017–18. It was also characterized for the basal stem lignin content by using acetyl bromide method (Morieravilar et al. 2014).

Genetics of lodging resistance in FLIP07-183C

The inheritance of lodging resistance was studied in a cross between Pusa 362 (lodging susceptible) x FLIP07-183C (lodging resistant). The Pusa 362 is a high yielding commercial cultivar released for general cultivation in the North Western Plains Zone (northern Indo-Gangetic Plain) characterized by cool long winter. The lodging susceptible genotype, Pusa 362 was crossed as female to the lodging resistant genotype FLIP07-183C to obtain F_1 seeds. The three F_1 plants, after confirming their true hybridity based on flower colour, seed size, shape and colour and phenology were advanced to F_2 by self-fertilization. Thus obtained F_2 seeds were used for the inheritance study.

The two parents, their F_1 and F_2 plants were grown in an un-replicated trial in the 2017–18 post-rainy seasons. The spacing provided was 45 cm between rows and 20 cm between plants in a row. The crop was

Fig. 1 Field view of Pusa 362 (lodging susceptible, left) and FLIP07-183C (lodging resistant, right) chickpea

provided a basal fertilizer dose of 20 kg N and 40 kg P_2O_5/ha. The crop was provided irrigation after 45 days of sowing. The pod borer (*Helicoverpa armigera*) was effectively controlled by spraying 0.2 per cent Spinosad at 30, 45 and 60 days after sowing. The observation on lodging resistance was recorded at maturity stage in parents and all plants individually in the F_2 population. Each of the plants in parents, F_1 and F_2 was observed for stem bending on individual plant basis at maturity stage and classified them as lodging resistant and susceptible. Two distinct phenotypes could be observed in F_2 of lodging susceptible × lodging resistant cross. The expected values corresponding to the observed values for resistant to susceptible was calculated based on the assumed Mendelian ratio. The deviations of these were subjected to the chi-square ($\chi 2$) test to determine the goodness of fit. All the 383 F_2 plants phenotyped for lodging were harvested individually and advanced to F_3. However, 40 out of 383 plants harvested did not produce enough seeds, might be because of lodging in few of them or due to unknown genotypic and environmental factors, and hence not included for confirmation of segregation pattern in F_3.

The inheritance pattern observed for lodging in F_2 was confirmed in F_3 during the post-rainy season of 2018–19. Out of 343 single plant progenies sown, the germination was poor in 28 progenies and therefore only 315 progenies were considered for phenotyping. Each $F_{2:3}$ progeny comprised of 25–30 plants. The crop production and protection practices remained the same as those in the previous season. In both the seasons, segregating populations (F_2 in 2017–18 and F_3 in 2018–19) were grown under similar high fertility field conditions favorable for lodging and hence did not affect the classification of segregates into lodging susceptible and resistant classes. Each progeny was observed for lodging resistance and susceptibility on individual plant basis at maturity stage, classified them as segregating or non-segregating for lodging and subjected the data to the chi-square test to determine the goodness of fit.

Results

Plant morphology of lodging resistant chickpea genotype, FLIP07-183C

The lodging resistant chickpea genotype, FLIP07-183C was characterized for important plant and stems traits; stem growth habit, days to flowering and maturity, pod and seed traits and grain yield. The characteristic features of Pusa 362 (Parent1) and FLIP07-183C (Parent2) used in the inheritance study on lodging resistance are listed in the Table 1. The newly identified lodging resistant genotype FLIP07-183C is a tall (81.0 cm) and erect large seeded kabuli type with semi-determinate stem growth habit and higher lignin content (145.2 mg/g). It has greater canopy width (45.3 cm), stem diameter (6.7 mm), compressed stem thickness (6.0 mm) and inter-nodal length (3.1 cm) compared to the lodging susceptible parent, Pusa 362 (P1) used in the inheritance study. FLIP07-183C is large seeded (38.1 g per 100 seeds) compared to Pusa 362 (23.2 g per 100 seeds). However, it produces lesser number of pods per plant (61.0), seeds per pod (1.1) and seeds per plant (79.2) compared to Pusa 362. FLIP07-183C is a kabuli type in which plant and stem parts are devoid of Anthocyanin pigmentation. It has light green foliage and the leaf type is multi-pinnate which is like that of Pusa 362. However, FLIP07-183C is relatively late in days to 50 per cent flowering (90–95 days) and days to maturity (145–150 days).

Genetics of lodging resistance in FLIP07-183C

The inheritance of lodging resistance was studied in a cross involving lodging susceptible (Pusa 362) and lodging resistant (FLIP07-183C) genotypes. All the F_1 plants of the cross were lodging resistant. The F_2 plants of the cross Pusa 362 × FLIP07-183C segregated into 350 lodging resistant: 33 lodging susceptible plants (Table 2). These numbers are in good fit with the ratio of 15 Resistant: 1 Susceptible ($\chi 2$ value 3.66, $P = 0.05$–0.1).

The segregation pattern observed in F_2 was confirmed by studying the breeding behavior of 315 F_3 families of Pusa 362 × FLIP07-183C and details of segregating and non-segregating progenies for lodging are given in the Table 3. The F_3 segregation data showed that 26 lodging susceptible plants selected in

Table 1 Origin and important characteristics of chickpea genotypes, Pusa 362 (P_1) and FLIP07-183C (P_2) used in the inheritance study of lodging resistance

Character	Pusa 362 (P_1)	FLIP 07-183C (P_2)
Origin	ICAR-IARI, New Delhi	ICARDA
Lodging (stem bending)	Susceptible	Resistant
Seed type	Desi	Kabuli
Plant pigmentation	Anthocyanin present	Anthocyanin absent
Leaf type	Normal	Normal
Seed shape	Angular	Owl head
Flower colour	Pink	White
Testa texture	Rough	Smooth
Testa colour	Yellow	White
Plant growth habit	Semi-erect	Erect
Stem growth habit	Indeterminate	Semi-determinate
Plant Height (cm)	56.0	81.0
Branch Number	13.0	12.0
Canopy width (cm)	43.0	45.0
Stem diameter (mm)	5.4	6.7
Compressed stem thickness (mm)	4.7	6.0
Internodal Length (cm)	2.4	3.1
Lignin (mg/g)	68.9	145.2
Days to 50% flowering (days)	75–80	90–95
Days to maturity(days)	135–140	145–150
Number of pods/plant	112.0	61.0
Number of seeds per pod	1.4	1.1
Number of seeds per plant	103.5	79.2
100-seed weight (g)	23.2	38.1
Seed yield(kg/ha)	1252	1302

Table 2 Segregation for lodging in F_2 of a chickpea cross involving lodging susceptible (P1) and resistant (P2) parents and fit to the expected ratio of 15 resistant to 1 susceptible using Chi Square

Cross	Total plants	Observed		Expected		Ratio tested	χ^2value	*p* value
		LR	LS	LR	LS			
Pusa 362(P1) x FLIP 07-183C (P2)								
Pusa 362 (P_1)	10	0	10					
FLIP 07-183C (P_2)	10	10	0					
F_1	10	10	0					
F_2	383	350	33	359.0625	23.9375	15:1	3.66	0.05–0.1

LR Lodging resistant; *LS* Lodging susceptible

F_2 bred true in F_3 and the observation is in good fit with the expected ratio of 0 segregating: 1 non-segregating ($\chi 2$ value 0.00, $P = 1.00$). Of the progenies of lodging resistant plants (289), 103 were non-segregating while 186 segregated into lodging resistant and susceptible plants. The proportion of non-segregating and segregating progenies observed in F_3 of lodging resistant plants are in good fit with the expected ratio of 3 segregating: 5 non-segregating ($\chi 2$ value 0.43, $P = 0.5–0.6$).

Table 3 Segregation for lodging in F_3 of a chickpea cross involving lodging susceptible (P1) and resistant (P2) parents

Cross	Phenotypic class	No. of progeny	Observed		Expected		Ratio tested	χ^2 value	*p* value
			S	NS	S	NS			
Pusa 362(P1) x FLIP07-183C (P2)	LR	289	103	186	108.375	180.625	3:5	0.43	0.5–0.6
	LS	26	0	26	0	26	0:1	0.00	1.0

LR Lodging resistant; *LS* Lodging susceptible; *S* Segregating; *NS* Non-segregating

Discussion

There has been no report on genetics of lodging resistance in chickpea. The inheritance of lodging resistance was studied in a cross involving Pusa 362 (lodging susceptible) x FLIP07-183C (lodging resistant) parents. Pusa 362 is a high yielding desi variety developed at the ICAR-IARI, New Delhi adapted to the North Western Indo-Gangetic Plains. FLIP07-183C is a tall and erect, large seeded kabuli genotype newly identified as highly resistant to lodging. The genetic control and inheritance of lodging resistance in FLIP07-183C is yet to be understood.

All the F_1 plants of the cross obtained between Pusa 362 (lodging susceptible) x FLIP07-183C (lodging resistant) were lodging resistant indicating that gene (s) governing lodging resistance in FLIP07-183C was dominant over that of lodging susceptibility. No information is available on genetics of lodging resistance in chickpea. However, Lee et al. (1996) in soybean identified a dominant *Dt1* locus which explained ~ 56.4% of the total phenotypic variation for lodging. The same genomic region was also identified to control lodging in soybean that explained 45% of total variation (Mansur et al. 1993). In contrast, Cruz et al. (2005) in wheat reported the presence of one or two major genes for lodging resistance and observed the partial dominance of lodging susceptibility over the resistant types.

The F_2 plants of the cross Pusa 362 (lodging susceptible) x FLIP07-183C (lodging resistant) segregated into 350 lodging resistant: 33 lodging susceptible plants. These numbers are in good fit with the ratio of 15 resistant: 1 susceptible ($\chi 2$ value 3.66, $p = 0.05$—0.1) suggesting that two dominant non-allelic genes with duplicate gene action controlled lodging resistance in FLIP07-183C. The two non-allelic duplicate dominant genes for lodging resistance are designated as *Sb1/sb1 and Sb2/sb2*. The presence of both the alleles in homozygous (*Sb1Sb1Sb2Sb2)* or heterozygous (*Sb1-Sb2-)* or either of the two dominant alleles, *Sb1 and Sb2*, in homozygous (*Sb1Sb1sb2sb2 or sb1sb1Sb2Sb2)* or heterozygous (*Sb1sb1sb2sb2 or sb1sb1Sb2sb2)* condition governed lodging resistance. The presence of recessive alleles at both the loci in homozygous (*sb1sb1sb2sb2)* condition resulted in lodging susceptibility.

The segregation pattern observed in F_2 was confirmed by studying the breeding behavior of 315 F_3 families of the cross Pusa 362 (lodging susceptible) × FLIP07-183C (lodging resistant). The F_3 segregation data showed that 26 lodging susceptible plants selected in F_2 bred true in F_3 and the observation is in good fit with the expected ratio of 0 segregating: 1 non-segregating ($\chi 2$ value 0.00, $p = 1.00$). Of the 289 F_3 progenies of lodging resistant F_2 plants, 103 were non-segregating while 186 segregated into lodging resistant and susceptible plants. The proportion of non-segregating and segregating progenies observed in F_3 of lodging resistant plants are in good fit with the expected ratio of 3 segregating: 5 non-segregating ($\chi 2$ value 0.43, $p = 0.5$–0.6). On the basis of F_2 genotypic ratio of 15 lodging resistant: 1 lodging susceptible, the lodging resistant F_2 plants are expected to belong to 8 genotypic classes (*Sb1Sb1Sb2Sb2, Sb1Sb1Sb2sb2, Sb1Sb1sb2sb2, Sb1sb1Sb2Sb2, Sb1sb1Sb2sb2, Sb1sb1sb2sb2, sb1sb1Sb2Sb2 and sb1sb1Sb2sb2).* Out of these 8 genotypic classes, 3/8 (*Sb1sb1Sb2sb2, Sb1sb1sb2sb2 and sb1sb1Sb2sb2*) are expected to segregate into lodging resistant and lodging susceptible plants in F_3 whereas the remaining 5/8 (*Sb1Sb1Sb2Sb2, Sb1Sb1Sb2sb2, Sb1Sb1sb2sb2, Sb1sb1Sb2Sb2 and sb1sb1Sb2Sb2*) are expected to non-segregate. All the F_2 plants susceptible (*sb1sb1sb2sb2)* to lodging are expected to breed true in F_3. Thus, the segregation pattern observed in F_3 for lodging

resistance and susceptibility confirmed the segregation observed in F_2. No information is available on the number of genes involved and nature of inheritance of lodging resistance in chickpea. In other crops too, information available on the number of genes and nature of gene action involved in the inherence of lodging resistance is limited. In field pea, Kujur (2015) observed duplicate gene action for lodging resistance in some of the crosses studied by using generation mean analysis and Cavalli's joint scaling test. Jezowski (2005) reported that the lodging resistance was governed by 1–5 numbers of genes and additive type of gene action responsible for lodging resistance in barley. Tar 'an et al. (2003) reported two QTL associated with lodging resistance which together explained 58% of the total phenotypic variation in field pea. Watanbe (1997) reported the involvement of limited number of genes controlling lodging resistance in rice. Based on the F_2 and F_3 segregation pattern in the cross Pusa 362 (lodging susceptible) × FLIP07-183C (lodging resistant), the genotype of the newly identified lodging resistant germplasm is designated as *Sb1Sb1Sb2Sb2*. The utilization of the lodging resistant germplasm FLIP07-183C in chickpea breeding to restructure plant type is expected to result in a cultivar with improved adaptation to better agronomy, particularly high fertility and irrigated conditions thereby achieving a breakthrough in its productivity. Kabuli and desi are the two diverse groups belonging to the same species, *Cicer arietinum* L. and therefore there are no barriers in transferring genes for lodging resistance from the newly identified kabuli chickpea to desi types through simple hybridization.

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Author contribution Conceptualization of research (VSH, R); Designing of experiments (VSH, R); Contribution of experimental materials (VSH); Execution of field/lab experiments and data collection (R, VK, VSH); Analysis of data and interpretation (R, VSH, VK, CB, ST, PKJ); Preparation of manuscript (R, VSH).

Declarations

Conflict of interest Authors declare no conflict of interest.

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