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Genetics of semi-determinacy and identification of molecular marker linked to *Dt1* locus in chickpea (*Cicer arietinum* L.)

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Abstract

Chickpea is predominantly an indeterminate (IDT) plant due to which high fertility and irrigation have adverse effect on seed yield. The semi-determinate (SDT) types are relatively early, lodging resistant and found to be similar in their yield potential to that of IDT genotypes. However, the inheritance of SDT stem type is not well understood in chickpea. The present investigation was aimed at studying the genetics of SDT stem type and identifying molecular marker linked to *Dt1* locus through Bulked Segregant Analysis (BSA). The genetics of semi-determinacy was studied in BGD 72 (IDT) x BG 3078-1(SDT) cross in which the genetic constitution of BGD 72 was already known as *Dt1Dt1Dt2Dt2* based on the previous study. The F_1 was IDT indicating the dominance of indeterminacy over semi-determinacy. The segregation in F_2 and F_3 revealed that SDT stem growth in the new-found genotype BG3078-1 was governed by a single dominant gene *Dt2* and its genotype designated as *dt1dt1Dt2Dt2*. The study of polymorphic survey between BGD-72(IDT) and BG 3078-1(SDT) using 581 SSR markers found 50 markers polymorphic. The BSA using 50 polymorphic markers has identified *TA42* and *TR29* as polymorphic between IDT and SDT parents as well as IDT and SDT bulks and hence considered putatively linked to *Dt1* locus governing IDT stem growth in chickpea. The two linked markers were validated in 15 IDT and 15 SDT F_2 plants individually. These two markers were also validated in 3 IDT, 8SDT and 3 DT genotypes. This is the first report on the identification of a molecular marker associated with stem growth habit in chickpea.

Key words: Chickpea, stem growth habit, genetics, gene tagging

Introduction

Chickpea (*Cicer arietinum* L.) belongs to the Leguminosae family, the sub-family Papilionoideae, the tribe Cicereae Alef., and the genus *Cicer* L. There are nine annual and thirty-five perennial species in the genus *Cicer* L. (van der Maesen et al. 2007). Based on morphological characters chickpea is classified into two types, desi and kabuli. The predominant type cultivated is desi occupying about 80-85% of the area and the remaining 15-20% by kabuli chickpea. The genome size of chickpea is ~738Mb with an estimated 28,269 genes (Varshney et al. 2013). Chickpea is an integral part of diet of individuals who cannot afford animal protein or are vegetarian by choice in the developing countries, especially the semi-arid tropics. There is a growing interest for chickpea because of its dietary and nutritional significance.

Based on morphology, flowering plants are classified into IDT (indeterminate), SDT (semi-determinate) and DT (determinate) depending on whether the terminal meristems are reproductive or vegetative. In indeterminates, the terminal meristems at the stem and branch apices remain in a vegetative state during which it controls the production of new nodes with leaves, produce an inflorescence meristem that only generates axillary floral meristems and hence continue to grow in stem length, flower and set pods whenever moisture and temperature conditions are favorable (Bradley et al. 1997; Tiana et al. 2010); plants similar to indeterminate types having elongated flowering branches but terminating with a flower bud or fully opened flower are classified as semi-determinates. In determinates, the terminal meristems eventually converted from a vegetative to a reproductive state, resulting in the production of a

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terminal flower and because of which the vegetative growth stops at flowering or continues for a very short period there after (Bernard 1972; Bradley et al. 1997). Chickpea, the second most important grain legume globally, is predominantly an IDT crop. Hegde (2011) was the first to report the occurrence of a fertile true breeding DT chickpea, BGD 9971, in the segregating generation of an inter-varietal cross. He also described three types of stem growth habits in chickpea: IDT, SDT and DT as in the case of soybean, pigeonpea and many other grain legumes. The inheritance of stem growth habit has been studied and found to be governed by two non-allelic genes with dominance epistasis (Hegde 2011). The two epistatic genes for stem growth habit are designated as *Dt1/dt1* and *Dt2/dt2* where *Dt1* have masking action on *Dt2* and *dt2.* The homozygous condition of *Dt1* (*Dt1Dt1Dt2Dt2* and *Dt1Dt1dt2dt2*) or heterozygous (*Dt1dt1Dt2*-and *Dt1dt1dt2dt2*) condition shows IDT growth habit. The absence of *Dt1* and homozygous condition of *Dt2* allele (*dt1dt1Dt2Dt2*) or heterozygous (*dt1dt1Dt2dt2*) condition produced SDT growth habit. The DT phenotype is obtained only in the presence of recessive alleles at both loci in homozygous (*dt1dt1dt2dt2*) condition. SDT types are relatively early, lodging resistant and found to be similar in their yield potential to that of IDT genotypes. A SDT mutant was more responsive to supplemental nitrogen as compared to its IDT parent (Shamsuzzaman et al. 2002). A change in plant type from IDT to SDT or DT is therefore required to improve the adaptation of chickpea plant to better agronomy and cool climate in order to achieve a breakthrough in its productivity. However, the inheritance of SDT stem growth habit is not well understood in chickpea. A better understanding of the inheritance of SDT growth habit would facilitate breeding of chickpea cultivars better responsive to cool climate and more productive environments.The SDT types are similar in their stem growth habit to that of indeterminate chickpeas during early vegetative growth stages and hence are difficult to differentiate IDT and SDT chickpeas in breeding populations. The molecular marker(s) linked to stem growth habit is not available in chickpea so far.Therefore, identification of a molecular marker linked to SDT stem growth helps to differentiate plant type in early stage itself and planning an appropriate selection strategy to design a new plant type with improved adaptation and grain yield in chickpea. The objectives of the present investigation were to: i) study the genetics of SDT stem growth habit in a newly developed chickpea genotype, BG 3078-1 and, ii) identify molecular marker linked to *Dt1* locus through Bulked Segregant Analysis (BSA).

Materials and methods

Plant materials used

The inheritance of SDT growth habit of a new-found chickpea genotype BG 3078-1 was studied in a cross between BGD 72 (IDT) x BG 3078-1 (SDT). BGD 72 is a high yielding widely adapted commercial cultivar released for general cultivation in central India. The IDT BGD 72 was crossed to the SDT BG 3078-1and the F_1 advanced to F_2 by self-fertilization. In each cross, seeds from F_1 plant, after confirming their true hybridity based on flower color, seed size or phenology were advanced to F_2. The two parents and F_2 plants were grown in an un-replicated trial in the 2016-17 post-rainy seasons. The two parents were sown in a single row plots of 4 m length and 8 rows of 4 m length in the F_2 population with a maximum of 20 plants per row. The spacing provided was 45 cm between rows and 20 cm between plants in a row. The crop was provided a basal fertilizer dose of 20 kg N and 40 kg P_2O_5/ha. The pod borer (*Helicoverpa armigera*) was effectively controlled by spraying 0.2 per cent Spinosad at 30, 45 and 60 days after sowing.

Inheritance of semi-determinate stem growth habit

For inheritance studies, F_1, F_2 and F_3 populations along with parental lines were tested for stem growth habit. The observation on stem growth habit was recorded at flowering and maximum pod formation stage on 5 plants in parents and F_1 and all plants individually in the F_2 population. Two distinct stem growth habits could be observed in F_2 of BGD 72 (IDT) x BG 3078-1 (SDT) cross. All the F_2 plants having elongated flowering branches that terminated with the vegetative bud classified as IDT; plants like IDT types in having elongated flowering branches but terminating with a flower bud or fully opened flower classified as SDT (Hegde 2011). The expected values corresponding to the observed values for IDT : SDT stem was calculated based on the assumed Mendelian ratio. The deviations of these were subjected to the chi-square (χ^2) test to determine the goodness of fit. The inheritance pattern observed for stem growth habit in F_2 was confirmed in F_3 during the post-rainy season of 2017-18. All the IDT and SDT plants phenotyped in F_2 were selected and evaluated their progenies along with their respective parents for the stem growth habit. Each F_3 progeny comprised of 15-20 plants. The crop production and protection practices remained the same

as those in the previous season. Each progeny was observed for stem growth habit on individual plant basis at maximum flowering and pod formation stage, classified them as non-segregating and segregating types for stem growth habit and subjected to the chi-square test to determine the goodness of fit.

Genomic DNA isolation and PCR amplification

Tender and fresh leaves were collected from plants during flowering stage and DNA was isolated by following CTAB method (Murray and Thompson 1980). The RNA was digested and removed by treating the samples with 5 µl of RNase (10 µg/µl) and incubated at 37°C for 1 hour.

The purified DNA was quantified using a Nano drop machine. DNA samples were diluted with appropriate amount of TE buffer to yield a working concentration of 20 ng/µl and stored at 4°C. The PCR for SSR marker analyses were performed with 10 µl reaction volume in the 96-well PCR plates with thermal seal in thermal cycler (model "AppliedBioSystem") at temperature profile 94°C for 5 minutes followed by a 'touch-down' procedure with two steps. The first step had 18 cycles: denaturation at 94°C for 30 seconds, annealing at 52-65°C for 1 minute and extension at 72°C for 1 minute. The second step was set for 20 cycles: denaturation at 94°C for 30s, annealing at 55°C for 1 minutes and extension at 72°C for 1 minute. The final elongation was done at 72°C for 10 minutes. Amplification PCR products were separated on 3% Metaphor (Lonza). The amplified products were separated on horizontal electrophoresis system at 120 V for 3-4 h using 1.0X TBE buffer. The gels were stained by Ethidium bromide (10mg/ml) and visualized using Gel Documentation system (AlphaImager 2200, Alpha Innotech Corporation, and USA). Amplicons were scored as alleles for each marker loci. Scoring of the alleles was done manually and their sizes (in bp) were determined by comparing with 100 bp DNA ladder.

Parental polymorphism and Bulked Segregant Analysis (BSA)

The parental polymorphism was carried out between BGD 72 (IDT) and BG 3078-1 (SDT) with 581 SSR markers distributed across the chickpea genome on all 16 chromosomes. The primer sequences of all the microsatellite markers used in this study were obtained from the CGWR and NCBI web resources. The polymorphic markers obtained between the two parents were subjected to Bulked Segregant Analysis (BSA) as described by Michelmore et al. (1991). Two bulks *viz*., IDT bulk and SDT bulk were constituted separately by mixing equal amounts of DNA from 10 IDT and 10 SDT plants, respectively. Finally, both the bulks along with parents were tested with the polymorphic markers obtained from parental polymorphism to identify putatively linked markers to the gene of interest i.e. *Dt1* locus in BGD72.

Results and discussion

Plant morphology of SDT chickpea genotype, BG 3078-1

The plant morphology of the new found SDT genotype, BG 3078-1, was like that of the IDT parent, BGD 72, except that the primary and secondary branches of BG 3078-1 terminated by a flower bud or a fully opened flower (Fig. 1). The SDT genotype BG 3078-1 flowered

Fig. 1. Stem growth habit of BG 3078-1(SDT), Left and BGD-72(IDT) in early stage

in 56 days and matured in 119 days whereas BGD 72 (IDT) flowered in 74 days and reached maturity in 125 days after sowing (Harshavardhana 2018).

The inheritance of SDT growth habit was studied in a cross involving IDT (BGD 72) and SDT (BG 3078-1) parents. All the F_1 plants obtained from the cross between BGD 72 (IDT) x BG 3078-1 (SDT) were IDT in nature (Table 1) indicating that gene (s) governing the IDT stem was dominant over that of the SDT stem. The dominance of the IDT stem growth has also been reported by van Rheenen et al. (1994) and Hegde (2011) in chickpea. The IDT stem was also found to be dominant in soybean (Bernard 1972), pigeonpea (Waldia and Singh 1987; Gupta and Kapoor 1991) and broad bean (Filippetti 1986). The F_2 plants of BGD 72 (IDT) x BG3078-1 (SDT) segregated into 115 IDT: 33 SDT (Table 1). These numbers are in good fit with the ratio of 3 IDT: 1 SDT stem types (χ^2 value 0.58, P = 0.5-

Table 1. Segregation for stem growth habit in F_2 of a chickpea cross involving BGD 72 (IDT) and BG 3078-1 (SDT) parents

Cross	Total plants	Observed		Expected		Ratio tested	X^2 value	*P* value
		IDT	SDT	IDT	SDT			
BGD 72 x BG 3078-1								
BGD 72 (P1)	5	5	0					
BG 3078-1 (P2)	5	0	5					
F_1	5	5	0					
F_2	148	115	33	111	37	3:1	0.58	0.5-0.3

0.3) suggesting that the IDT and SDT parents involved in the cross differed for a single gene. The F_2 segregation pattern observed in this cross is as per the expected ratio predicted based on our previous study (Hegde 2011). Since the genetic constitution of IDT parent BGD 72 was already known as *Dt1Dt1Dt2Dt2* based on the previous study (Hegde 2011), the genotype of the newly identified SDT line BG 3078-1 is designated as *dt1dt1Dt2Dt2*.

The segregation pattern observed in F_2 was confirmed by studying the breeding behavior of 148 F_3 progenies of BGD 72 (IDT) x BG3078-1(SDT) (Table 2). The segregation pattern in F_3 progenies showed that all 33 SDT 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 (χ^2 value 1.00, *P* = 1.00). Of the 114 progenies of IDT plants 43 were non-segregating while 71 segregated into IDT and SDT plants. The proportion of non-segregating and segregating progenies observed in F_3 of IDT F_2 plants are in good fit with the expected ratio of 2 segregating: 1 non-segregating (χ^2 value 0.99, *P* = 0.5-0.3). Based on the F_2 phenotypic ratio 3 IDT: 1 SDT, 1/3 (*Dt1Dt1Dt2Dt2*) of the IDT plants are expected to be non-segregating in F_3 while 2/3 (*Dt1dt1Dt2Dt2*) of the IDT plants expected to segregate into IDT and SDT plants. All the SDT (*dt1dt1Dt2Dt2*) plants are expected to be non-segregating and breeding true in F_3. Thus, the F_3 segregation pattern observed for IDT and SDT stem types confirmed the segregation observed in F_2. These results obtained in the present study are similar to the inheritance of the stem growth habit reported in pigeonpea (Gupta and Kapoor 1991). The F_2 and F_3 segregation in BGD 72 (IDT) x BG 3078-1 (SDT) also confirmed the genotype of the new found SDT line BG 3078-1 as *dt1dt1Dt2Dt2*.

Parental polymorphism survey between IDT parent 'BGD 72' and SDT parent 'BG 3078-1' was conducted by using 581 chickpea SSR markers available in the Pulses Research Laboratory, Genetics Division, ICAR-IARI, New Delhi. Among them, 50 SSR markers showed polymorphism between the two parents involved in the cross. The representative gel picture of SSR markers showing parental polymorphism is presented in Fig. 2. Bulked Segregant Analysis was used to rapid identification of molecular marker linked to oligogenic traits in crops based on the principle of near isogenic lines (Michelmore et al. 1991). Bulked Segregant Analysis (BSA) was performed to identify putatively linked markers to the *Dt1* locus utilizing the markers that are polymorphic between the two parents differing in stem types. Both

Table 2. Segregation for stem growth habit in F_3 of a chickpea cross involving BGD 72 (IDT) and BG 3078-1 (SDT) parents

Cross	Phenotypic class	No. of progeny	Observed		Expected		Ratio tested	χ^2 value	Table value
			Segregating	Non-segregating	Segregating	Non-segregating			
BGD 72 X BG 3078-1	IDT	114	71	43	76	38	2:1	0.99	0.5-0.3
	SDT	33	0	33	0	33	0:1	0.00	1.00

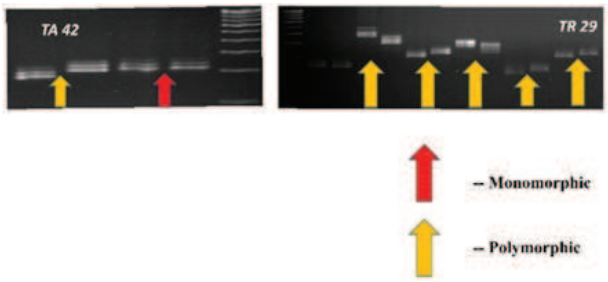

Fig. 2. ParentalPolymorphic survey of BGD-72(IDT) and BG 3078-1(SDT)

IDT bulk and SDT bulk were constituted separately by mixing equal amount of DNA from 10 IDT and 10 SDT F_2 plants, respectively after thorough phenotyping. BSA has identified two SSR markers, *TA42* and *TR29*, putatively linked to *Dt1* locus in chickpea (Fig. 3). These

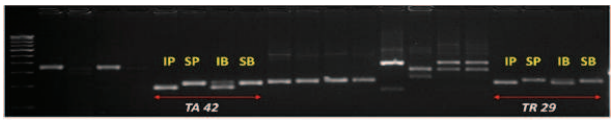

Fig. 3. Bulked Segregant Analysis (BSA) showing putatively linked marker. IP = IDT parent; SP = SDT parent; IB = IDT bulk; SB = SDT bulk

two markers were confirmed in 15 IDT and 15 SDT plants individually (Figs. 4 and 5). These two markers were also validated on 3 IDT, 8 SDT and 3 DT genotypes which showed co-segregation with the *Dt1*

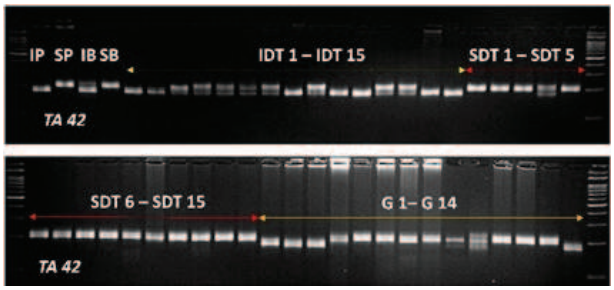

Fig. 4. Confirmation and validation of marker *TA42* linked to *Dt1* locus in chickpea genotypes

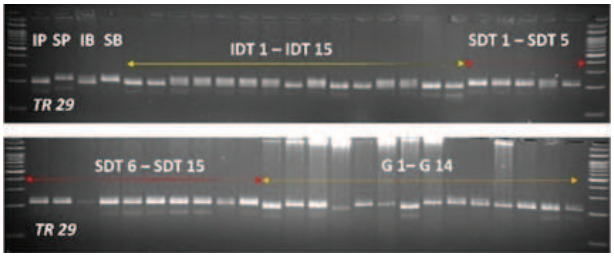

Fig. 5. Confirmation and validation of marker *TR29* linked to *Dt1* locus in chickpea genotypes

locus. Thus, it was demonstrated that the evaluated plants (Figs. 4 and 5) exhibited the expected DNA profile. The IDT cultivars BGD 72, BG 362 and BGM 547 and 1 to 15 IDT plants selected in F_2 exhibited *Dt1Dt1* (*Dt1dt1* for heterozygous locus) genotype. Table 3 provides the list of IDT, SDT and DT chickpea

Table 3. List of IDT, SDT and DT chickpea genotypes used for validation of markers in the study

Code	Genotype	Stem growth habit	Origin	Seed type	Geno-type status
G1	BGD 72	IDT	IARI	Desi	RV
G2	BG 362	IDT	IARI	Desi	RV
G3	BGM 547	IDT	IARI	Desi	RV
G4	BG 1053	SDT	IARI	Kabuli	RV
G5	BGD 2701-20	SDT	IARI	Desi	BL
G6	BGD 2701-57	SDT	IARI	Desi	BL
G7	BGD 2701-63	SDT	IARI	Kabuli	BL
G8	ICCV 88201	SDT	ICRISAT	Desi	G
G9	BG 1044	SDT	IARI	Desi	BL
G10	BG 3078-1	SDT	IARI	Desi	BL
G11	BG 1099	SDT	IARI	Desi	BL
G12	BGD 9971	DT	IARI	Desi	BL
G13	BGD 2701-79	DT	IARI	Desi	BL
G14	BGD 2702-53	DT	IARI	Desi	BL

RV = Released variety; BL = Breeding line; G = Germplasm

genotypes used for validation of markers in thestudy. The SDT genotypes BG 1053, BGD 2701-20, BGD 2701-57, BGD 2701-63, ICCV 88201, BG 1044, BGD 3078-1 and BG 1099 and determinate genotypes BGD 9971, BGD 2701-79 and BGD 2702-53 showed *dt1dt1* genotype. No information is available on the identification of molecular marker associated with stem growth habit in chickpea. This is the first report on the identification of markers linked to *Dt1* locus in chickpea. However, a closely linked marker *TA34* for stem growth habit has been identified in soybean (Vicente et al. 2016) and IDT growth habit locus (*Dt1*) was mapped to CcLG03 (Varshney et al. 2013; Saxena et al. 2017) in pigeonpea.

These two markers, *TA42* and *TR29*, have already been mapped to Linkage Group 7 with 10.4 cM distance between them (Nayak et al. 2010). With this information it is expected that the *Dt1* allele controlling IDT stem growth habit is located on the same Linkage Group

(LG7). Further studies on mapping *Dt1* and *Dt2* alleles are required for locating the exact genomic region involved in the inheritance of stem growth habit in chickpea.The markers identified for *Dt1* locus help to differentiate stem termination types of chickpea in its early growth stage itself and can be efficiently utilized in Marker Assisted Selection (MAS) for changed plant type in chickpea.

Authors' contribution

Conceptualization of research (VSH, HYS); Designing of the experiments (VSH, HYS); Contribution of experimental materials (VSH); Execution of field/lab experiments and data collection (HYS, MKS, SKC, RKS); Analysis of data and interpretation (HYS, VSH, ST, RSR, PKJ, KG, CB, RK); Preparation of manuscript (HYS, VSH).

Declaration

The authors declare no conflict of interest.

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