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RESEARCH ARTICLE

Tagging of cassava mosaic disease resistance gene in cassava (*Manihot esculenta* Crantz) using simple sequence repeat (SSR) markers

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Abstract

Cassava mosaic disease (CMD) is a major viral disease that causes severe yield loss in cassava cultivation in India. The host plant resistance breeding for CMD is the important strategy to control the disease spread. To understand the nature of disease resistance and identification of simple sequence repeat (SSR) markers closely associated with CMD resistance is important. To study the nature of resistance, seedling and clonal population developed by crossing Sree Jaya (Susceptible) and 9S127 (Resistant) and self-pollinating 9S127 parent were done and the population was evaluated for CMD disease scoring (1-5 scale) at 5 and 8 months after planting. The disease segregate in 1:1 ratio in the F_1 and C_1F_1generation of Sree Jaya × 9S127 cross and 3:1 in the S_1, C_1S_1 self-pollinated progenies of 9S127 parent. It confirms the gene in the resistant parent is heterozygous (Rr) and single dominant gene (RR) is controlling the resistance. In this mapping population, Sri Lankan Cassava Mosaic Virus (SLCMV) is prevalent in all the samples. A total of 14 CMD associated SSR markers were screened in the progenies using bulk segregant analysis (BSA) method. Out of 14 markers, two markers SSRY28, NS158 co-segregate with CMD resistance in the population. These markers can be used for marker assisted selection (MAS) for CMD screening in the seedling population to identify true resistant lines for further breeding trials.

Keywords: breeding; bulk segregant analysis (BSA); cassava; cassava mosaic disease (CMD); cassava mosaic virus (CMV); hybridization; simple sequence repeat (SSR) markers

Introduction

Cassava (*Manihot esculenta* Crantz) is one of the important tubers crops widely grown in tropical and subtropical regions. It belongs to family Euphorbiaceae and is a native crop of native to South America, from Brazil, Paraguay and parts of the Andes. Cassava cultivation areas expanded from their original place towards East Africa, West Africa, from there India and Sri Lanka. Cassava is one of the food sources for 800 million people and considered to be fifth important starchy staple food crop after Rice, Wheat, Maize, Potato (1-3). Cassava mosaic disease (CMD) is a major constraint to cassava production in Africa and India. Yield losses estimate in susceptible cultivars can be as high as 90 % and can be up to $2.7 billion USD. In India, 6.27 metric tonnes of cassava tuber produced from an area of 0.178 M/ha. with productivity of 35.24 t/ha (4). In India, due to CMD infection causes yield loss of 18-25 % in cassava (5). Therefore, losses due to CMD have an immediate impact on the food supply and threaten food security and the livelihoods of rapidly growing population. CMD is mainly spread by infected cuttings and transmitted by the whitefly (*Bemisia tabaci*). CMD is caused by a complex of at least 11 cassava mosaic begomoviruses (CMBs) worldwide, of which nine occur in Africa and two are found in the Indian subcontinent (ICMV, SLCMV) (6, 7).

The most widespread of cassava mosaic disease are particularly ravaging, with tuber yield losses as high as 100 % (8, 9). The use of resistant varieties and the supply of healthy planting materials is an effective strategy to mitigate the impact of the disease. Resistant varieties can significantly reduce yields losses and the source of inoculum of the virus in the field (10). India is the one of the major producers of cassava, hence marker-based approach to identify the CMD resistant lines will be great impact on the developing resistant varieties (11). There are several studies reveals the molecular markers such as AFLPs, RAPDs, simple sequence repeat (SSR), SNP, etc. are suitable for constructing linkage map and tagging the gene of interest (12).

Resistance to CMD was first identified by Nicholas, 1947 obtained from a cross between cassava and *Manihot glaziovii*. After three back crosses, the clone 58308 was selected and they used as the main source of resistance for decades. The several TMS and TME source of resistant genotypes are used to study

CMD resistance (13). The first CMD-resistant varieties, developed by IITA in Nigeria, were hybrids obtained with *M. glaziovii*, found in Brazil, which conferred multigenic resistance (*CMD1*). Currently, three CMD genes, *CMD1* (polygenetic, recessive), *CMD2* (monogenetic, dominant) and *CMD3* (QTL - quantitative trait loci) conferring resistance were discovered and important molecular markers associated with *CMD2* and *CMD3* have been identified (14, 15). Five CMD associated markers used to screen CMD resistance in 1224 accessions by genotyping (16). The major QTL region in the chromosome 8 is responsible for CMD resistance up to 66 % and the potential candidate genes in this region is two peroxidases and one thioredoxin (17). By comparing the cassava disease score and CMD marker genotypic data to predict the resistant progenies at 52 % accuracy (18). Two new SNP markers (S12_7926132 and S14_4626854) for CMD screening were reported, that predict accuracy of SNP marker S12_7926132 (true positives and negatives) of the major *CMD2* locus on chromosome 12 was 80 % in the CMD resistant population used (19). The above two SNP markers associated with CMD resistance could not be used to select for CMD resistance in diverse populations but could predict the CMD resistance in segregating populations (20).

Bulked segregant analysis (BSA) is a rapid procedure for identifying the genetic markers, to a particular trait of interest such as, disease resistance or susceptibility (21). This technique involves, making two pooled DNA from all the selected opposite samples for the trait of interest. By studying resistance in the Nigerian landrace TME3, identified *CMD2* gene, is a single dominant gene flanked by three markers SSR28, NS158 and RME -1 (14) using BSA technique. Three SSR28, SSR106 and an AFLP (E -ACC/M-CTC-225) marker linked with CMD resistance is identified (22). Similarly, for early tuber bulking (23) was studied in nine cassava hybrid populations, as a result, nine SSR markers found to be associated with early bulking. In potato, BSA technique used for study genetic basis of embryo spot formation (24) and potato virus-A resistance (25). The present study aimed to identify SSR markers associated to *CMD2* gene using bulked segregant analysis.

Materials and methods

Genetic material

The two cassava genotypes, 9S-127 a CMD resistant genotype and Sree Jaya, a CMD susceptible, short duration (6-7 months) variety, was hybridized to develop 165 F_1 progenies and the seedlings, its clones (F_1, C_1F_1) were evaluated for morphological characters during 2022-23 and 2023-24 at ICAR-Central Tuber Crop Research Institute (CTCRI), Thiruvananthapuram (Table 1, Fig. 1).

Phenotypic screening for CMD resistance

CMD scoring was recorded in the seedling, clonal progenies based on the level of symptom expression in the leaves and over all plants (26) based on 1-5 scoring pattern (Table 2, Fig. 2). CMD segregate in the progenies in the ratio of 1:1, it shows the gene in the resistant parent is in heterozygous condition. To know the nature of CMD gene in the resistant parent (9S-127), is self-pollinated and CMD symptom appearance recorded in the seedlings (S_1) and clonal progenies (C_1S_1) at 5, 8 MAP during 2023-2025. The phenotypic score was tested for 1:1 and 3:1 segregation ratio using chi-square test (R statistical package) and no significant difference among the resistant/susceptible progenies.

DNA extraction

Genomic DNA of the parents and 20 F_1 progenies (10 each resistant, susceptible) isolated from young fresh leaves

Table 1. Characteristics of selected progenies and parents

Parents/Hybrid	Emerging leaf colour	Leaf lobes	Petiole colour	Male flower	Female flower	Fruit colour
Sree Jaya	Purple	7-lobes, two down (S. Jaya)	Pink	Green - pink top	Green, pointed	Deep Green
9S-127	Light green	Five upward lobes	Deep purple	Light green	Light Green	Light Green
R1	Purple	Upward lobes (9S-127)	Pink	Green	Green, pointed	Light green
R2	Light green	Upward lobes (9S-127)	Pink	Green - pink top	Light pinkish	Light green
R3	Purple	7-lobes, two down (S. Jaya)	Purple	-	-	-
R4	Light green	Upward lobes (9S-127)	Deep purple	Pink colour	-	Light green
R5	Light green	7-lobes, two down (S. Jaya)	Deep purple	Green	-	-
R6	Purple	7-lobes, two down (S. Jaya)	Pink	-	-	Light green
R7	Light green	7-lobes, two down (S. Jaya)	Pink	-	-	-
R8	Light green	Upward lobes (9S-127)	Pink	-	-	Light green
R9	Purple	Upward lobes (9S-127)	Pink	Pink	-	Light green
R10	L. Purple green	Upward lobes (9S-127)	Pink	Purple green	-	Light green
S1	Purple green	Upward lobes (9S-127)	Deep purple	-		Light green
S2	Purple	7-lobes, two down (S. Jaya)	Pink	-	-	-
S3	Light green	7-lobes, two down (S. Jaya)	Pink	-	-	Light green
S4	Light green	Upward lobes (9S-127)	Pink	Light pink	Green pointed	Light green
S5	Purple	7-lobes, two down (S. Jaya)	Pink	-	-	-
S6	Light green	Upward lobes (9S-127)	Pink	Light pink	Light pink	Green
S7	Light green	7-lobes, two down (S. Jaya)	Pink	-	-	Green
S8	Light green	Upward lobes (9S-127)	Pink	Green - pink top	-	Green
S9	Light green	Upward lobes (9S-127)	Pink	Green - pink top	Pink pointed	Green
S10	Purple	Upward lobes (9S-127)	Pink	Green - pink top	Pink pointed	Green

Table 2. CMD scoring based on the symptom expression in the plant

Sl. No.	Symptoms description	Score
a	Unaffected shoots, no symptoms	1
b	Mild chlorosis, mild distortions at bases of most leaves, while the remaining parts of the leaves and leaflets appear green and healthy	2
c	Pronounced mosaic pattern on most leaves, narrowing and distortion of the lower one-third of the leaflets	3
d	Severe mosaic distortion of two thirds of most leaves and general reduction of leaf size and stunting of shoots	4
e	Very severe mosaic symptoms on all leaves, distortion, twisting, mis-shapen and severe leaf reductions of most leaves	5

Source Ref. (26).

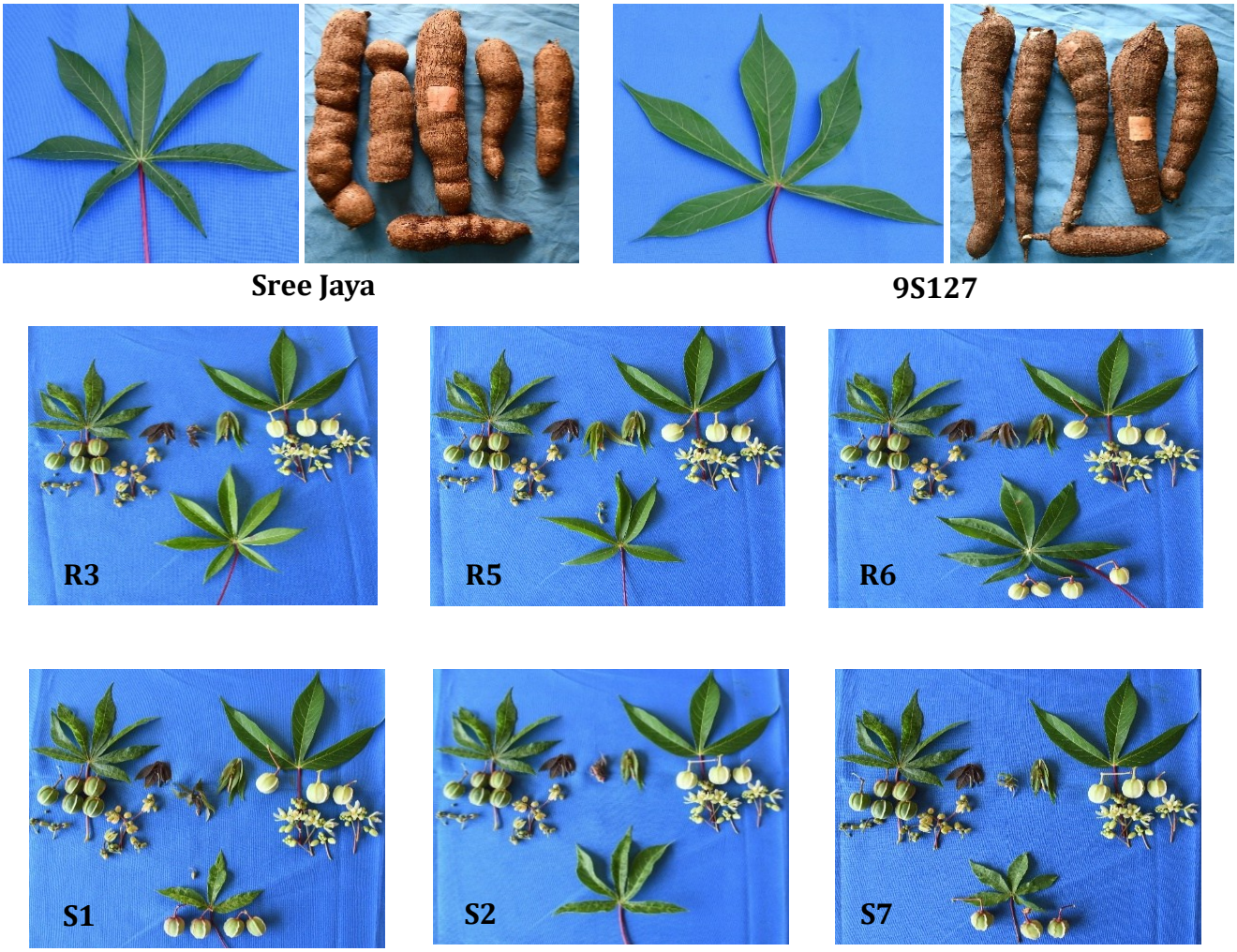

Fig. 1. The morphological characters of parents and its progenies.

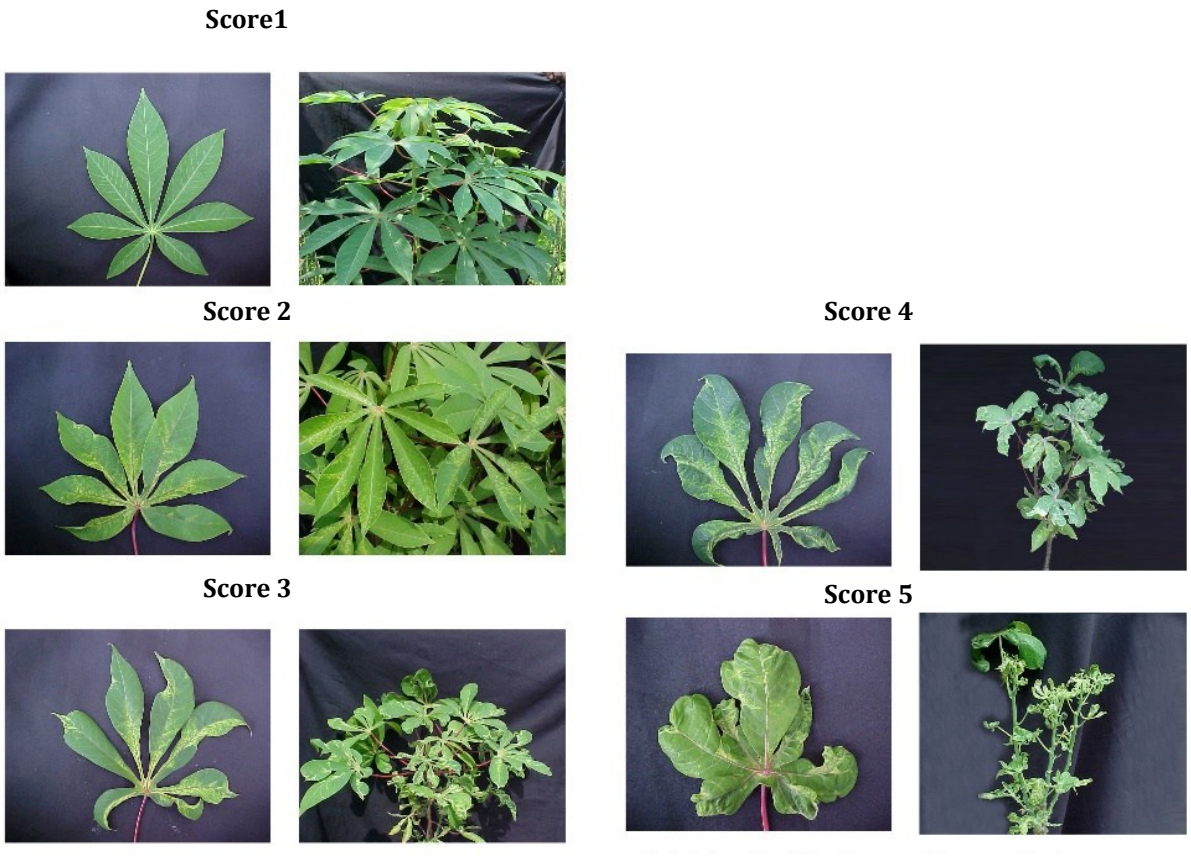

Fig. 2. Severity of the disease and the respective damage core.

according to CTAB method (27). The DNA of individual sample was quantified by using Nano-Spectrophotometer (NABI, Microdigital, South Korea) and its quality was checked on using 0.8 % Agarose gel. And finally, DNA concentration adjusted to 100 ng/µL for PCR reaction. To screen the SSR markers associated with CMD resistance gene, bulk segregant analysis (BSA) method was used.

PCR amplification and SSR screening

A total of 14CMD associated SSR markers are selected for PCR amplification (Table 3). Initially screening, all the primer amplification done with two parents (Sree Jaya, 9S127) and two bulks consist of ten progenies each susceptible and resistant (susceptible bulk-SB and resistant bulk-RB). PCR amplifications were performed (28) on a PCR Thermal Cycler (PTC Tempo Thermal Cycler, Bio-Rad, USA), with thermal temperature of 94 ° C for 5 min followed by 30 cycles of 1 min at 94 °C, 1 min at 58 °C and 1 min at 72 °C with final extension for 5 min at 72 °C. The amplified products were running on 2 % agarose gel and the gel was visualized by gel documentation system (GeldocGo Image System, Bio-Rad, USA). The primer shows polymorphic bands or co-segregating markers used for PCR amplification with 20 F_1 progenies along with two parents and two bulks.

Screening for CMV virus

The parents and selected progenies were screened for presence of cassava mosaic virus (CMV), namely ICMV (*Indian cassava mosaic virus*) and SLCMV (*Sri Lankan cassava mosaic virus*), these two are predominant virus prevailing in India. The parent and progenies DNA were PCR amplified with ICMV and SLCMV specific primers (Table 4) using a multiplex PCR protocol (29).

Results

Morphological

In the present study, the Sree Jaya variety was crossed with a hybrid line 9S127 to develop seedling progenies resistant to CMD. Sree Jaya is a released variety of cassava having good cooking quality, short duration (6-7 months) and susceptibility to CMD. The 9S127 is a hybrid progeny developed from a population received from CIAT (Central Institute of Tropical Agriculture, Columbia) has high starch, high yield, highly resistant to CMD disease with drought & PPD tolerance. Both parents are profusely flowering and good seed sett percentage of 75-80. From these parents, 325 F_1 hybrid progenies have been developed. From this population, 165 C_1F_1 progenies selected for CMD resistance study and ten randomly selected seedling progenies of CMD-resistant and susceptible F_1s were used for the recording morphological characters (Emerging leaf colour, petiole colour and nature of leaf, male/female flower and fruit colour) (Table 1, Fig. 1) and CMD-associated SSR markers studies.

CMD resistance screening

The plants Sree Jaya and 9S127 and its 325 F_1progenies were observed for the presence of CMD symptoms in the leaves and overall plants. A total of 168 progenies were resistant and 157 were susceptible, resulting in a phenotypic segregation ratio of 1:1. The 165 C_1F_1 clonal progenies screened for resistance to CMD, indicated wide variation for the level of resistance among the progenies (Fig. 3).

To confirm the resistance in the 9S-127 parent is heterozygous, 85 S_1 - seedling progenies developed by self-pollinating 9S127 parent, evaluated for symptom expression and CMD score segregated for resistance (61), susceptible (24) in 3:1 ratio. The same progenies evaluated in C_1S_1 generation confirm the same phenotypic ratio. The frequency distribution of progenies C_1S_1 coming under various categories of damage score is shown in Fig. 4.

Bulk segregant analysis (BSA) for CMD resistance

Fourteen SSR primer pairs associated with CMD resistance were used for BSA. Out of 14 SSR primers, two markers (SSR28, NS158) showed polymorphic bands in the parents, bulks and progenies

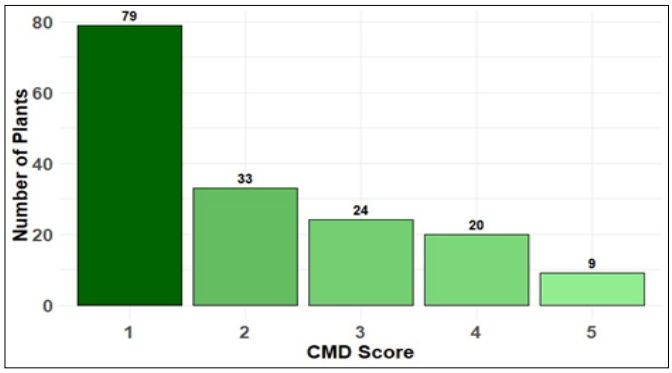

Fig. 3. CMD resistant score of C1F1 population of Sree Jaya/9S127.

Table 4. CMV specific primers used in the study

Locus	Primer sequence (5¢-3¢)	Product size (bp)
ICMVA-F_1	GCTGATTCTGGCATTTGTAN	900
SLCMVA-F_2	TGTAATTCTCAAAAGTTACAGTCN	599
I/SLCMVA-R	ATATGGACCACATCGTGTCN	-

Source Ref. (29).

Table 3. List of SSR primers used for PCR amplification

Locus	Forward Primer (5¢-3¢)	Reverse Primer (3¢-5¢)	Product size (bp)
SSR6	TTTGTTGCGTTTAGAAAGGTGA	AACAAATCATTACGATCCATTTGA	298
SSR7	TGCCTAAGGAAAATTCATTCAT	TGCTAAGCTGGTCATGCACT	250
SSRY21	CCTGCCACAATATTGAAATGG	CAACAATTGGACTAAGCAGCA	192
SSR28	TTGACATGAGTGATATTTTCTTGAG	GCTGCGTGCAAAACTAAAAT	180
SSR40	TGCATCATGGTCCACTCACT	CATTCTTTTCGGCATTCCAT	231
SSR42	TTCCTCCAAAGTTATCTAGAACCA	CAATCCTTGTAGTAGCCAGTCTCA	221
SSR77	CAGGAGGTGGCAGATTTTGT	GCATGTTCCACCTGCATAAG	275
SSR106	GGAAACTGCTTGCACAAAGA	CAGCAAGACCATCACCAGTTT	270
SSR235	CAGCTTTGCCATCCAATTTT	CAGCAAAATGACATGAGTGTATCTC	216
SSR324	CGCTTACAACACCACCTTCA	GCTTGATCTCAGCCATGTCA	206
NS136	GACTATTTGTGATGAAGGCTTGC	GGTTCAAGCATTCACCTTGC	120
NS158	GTGCGAAATGGAAATCAATG	TGAAATAGTGATACATGCAAAAGGA	166
NS169	GTGCGAAATGGAAATCAATG	GCCTTCTCAGCATATGGAGC	319
NS198	TGCAGCATATCAGGCATTTC	TGGAAGCATGCATCAAATGT	196

Source Ref. (14, 22, 30).

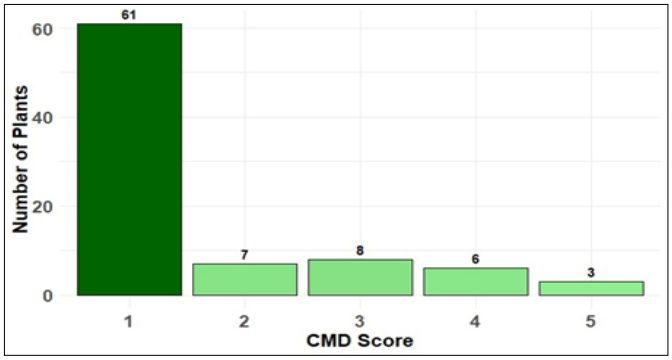

Fig. 4. CMD resistant score of C1S1 self-pollinated progenies of 9S127.

in the similar pattern, which were associated with the *CMD2* gene resistance. Among the remaining 12 SSR primers (SSR6, SSR7, SSR40, SSR42, SSR77, SSR106, SSR235, SSR324, NS136, NS169 and NS198) showed mono/polymorphic bands in parents and bulks (Fig. 5).

The BSA reveals that primer SSR28, with a band size of 180 bp, shows double bands in the susceptible parent Sree Jaya and single band in the resistant parent 9S127. The same results were observed in both bulks, as well as 10 susceptible/resistant progenies (Fig. 6). Similar banding (166 bp) pattern noted in the CMD gene associated marker NS158 (Fig. 7). Out of the 14 SSR primers tested, only SSR28 and NS158 were polymorphic and showed clear differentiation between resistant and susceptible lines, indicating a strong association with the *CMD2* resistance gene.

Detection of cassava mosaic virus

Screening of parents and their 20 F_1 progenies (susceptible/resistant) for ICMV and SLCMV was tested using virus specific primers. The PCR diagnostics detected the presence of SLCMV virus, with a band size of 599 bp in all samples (Fig. 8).

Discussion

The mapping population from the cross between Sree Jaya, 9S127 are shows high level of heterozygosity for different morphological characters including CMD resistance. The expression of the resistant parent 9S127 is more in the progenies compare to the susceptible parent Sree Jaya, including tuber characters (Fig. 1). The result shows high heterozygous nature of the crop is due to its high cross pollination and clonal propagation of the cassava by fixing the heterosis in the progenies.

The CMD resistance analysed by conventional or classical genetic breeding shows 1:1 gene segregation in the Sree Jaya, 9S127 population both in F_1 and C_1F_1 progenies (Fig. 9). The result from the study, confirms the single dominant gene in resistant parent is heterozygous condition and segregate in the population for CMD (14, 22). To validate this observation, the selfed progenies of 9S127 screened for CMD symptom and 3:1 segregation ratio (S_1 and C_1S_1) noted (Fig. 9), thereby confirming that a dominant gene is responsible for *CMD2* type of resistance in cassava (16). The resistant progenies in the 9S127 population both homozygous and heterozygous condition, it can be identified by SSR, SNP markers associated with CMD resistance

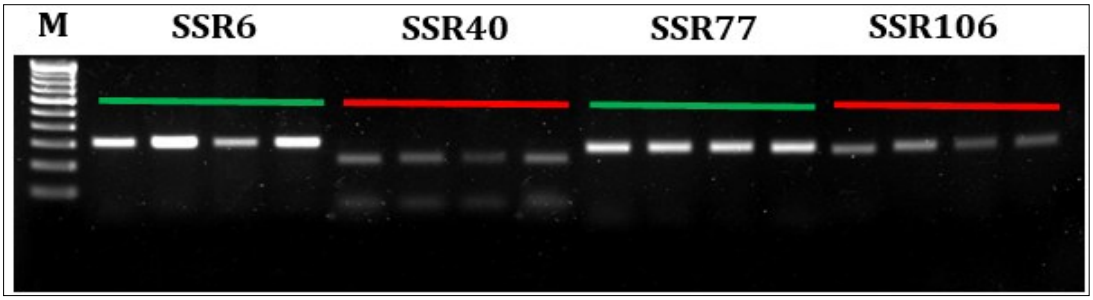

Fig. 5. Primer Screening with CMD associated SSR markers.

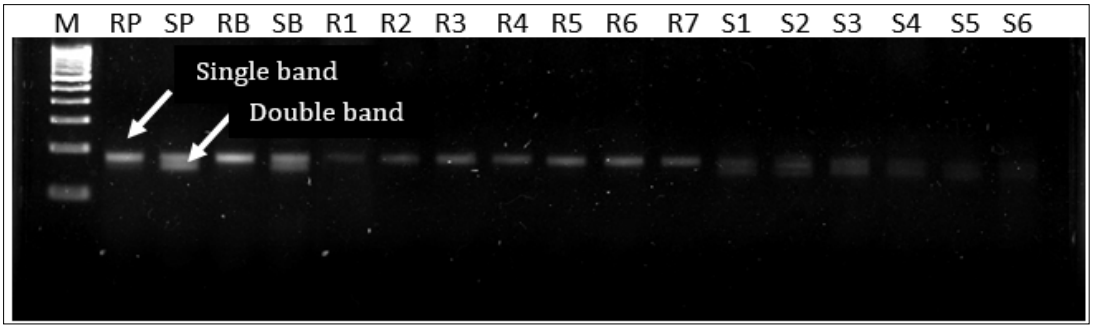

Fig. 6. SSR28 CMD marker amplification using BSA.

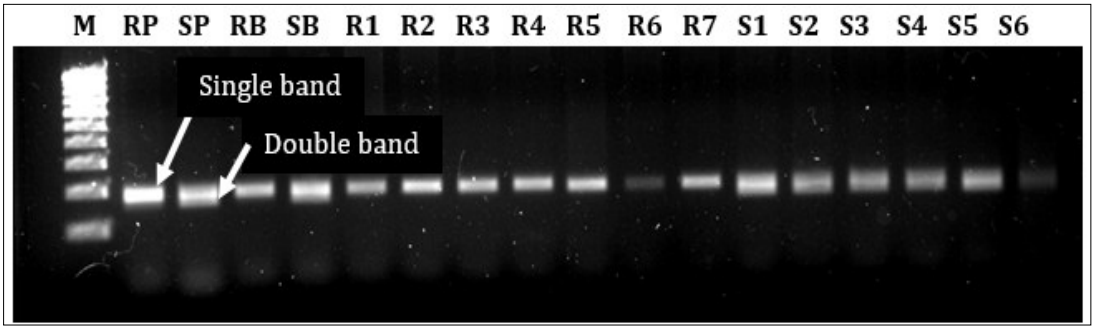

Fig. 7. NS158 CMD marker amplification using BSA.

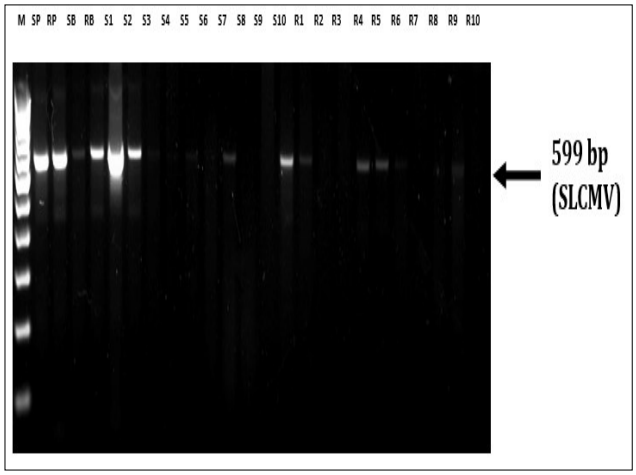

Fig. 8. Detection of ICMV, SLCMV using virus specific primers.

(14, 22, 30). By identification of homozygous resistant progeny from the above population very much useful for developing 100 % resistant progenies when it crossed with susceptible parent, can avoid 1:1 segregation. In general, SLCMV is the predominant virus present in the cassava population in Kerala.

The marker associated resistance assessed by using 14 CMD markers used for BSA technique, out of the fourteen markers studied SSR28 and NS158 markers co-segregation with disease. In the resistant parent only one allele noticed, but in the susceptible parent two alleles appeared. The presence of extra allele may be responsible for susceptibility to disease; however, this needs to be confirmed by studying large population and sequencing. The markers SSR28 and NS158 both are reported in the same linkage group in the cassava map in the nearby locus next to the resistant gene *CMD2* and many previous studies also report the same result (14, 16, 22, 30). So, these markers can be the candidate marker for Marker Assisted Selection (MAS) for screening the CMD in seedling stage.

Conclusion

From the present study, hybrid progenies of Sree Jaya/9S127 are showing lot of morphological variation like 9S127 parent. The resistant gene in the population segregate in the 1:1 ratio and self -pollinated progenies (9S127) segregates in 3:1 ratio, confirms the monogenic inheritance. CMD associated marker screening, it is concluded that the SSR markers SSR28, NS158 were linked to CMD resistance in cassava and used for MAS for CMD selection. Further marker discovery needs to be identified with close association to CMD from sequence data of genome, transcriptome specific to the disease.

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Authors' contributions

NC - helped in SSR marker analysis; SJ and AA - conducted field observation and photos; KMS - carried out field observation, lab work; TM - performed CMD scoring & CMV amplification; JS - done statistical analysis; AVVK - conducted field work, graphical analysis and data analysis; and CM - performed mapping population, field observation, CMD scoring and SSR marker work. All authors read and approved the final manuscript.

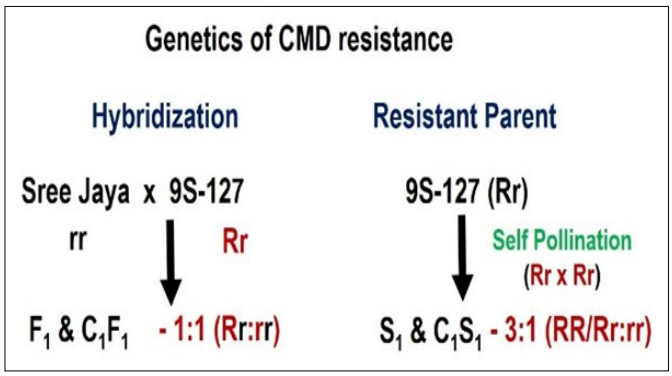

Fig. 9. Genetics of CMD resistant in the present study.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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