



SSR marker based molecular characterisation of soybean (*Glycine max*) genotypes having differential response to yellow mosaic disease

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ABSTRACT

Yellow mosaic disease (YMD) is one of the major constraints limiting soybean [*Glycine max* (L.) Merrill] cultivation in South East Asian countries. The development and deployment of resistant varieties is the most economic and ecofriendly strategy for the YMD management. Recent advances in marker-assisted breeding have improved the efficiency of identifying and incorporating resistance genes into elite cultivars by enhancing selection accuracy and reducing breeding time. Hence, the present investigation was aimed for the identification of stable sources of resistance and to characterise soybean genotypes exhibiting differential responses to YMD using simple sequence repeat (SSR) markers. Forty-one soybean genotypes along with a susceptible and resistant check were screened against YMD under epiphytotic conditions for three consecutive years. The disease incidence and coefficient of infection ranged from 0.00–82.22% and 0.00–78.52 units, respectively. Sixteen cultivars were found highly resistant whereas eight were found resistant to YMD. A total of 26 alleles were amplified using 12 SSR markers with an average of 2.16 alleles/locus indicating a narrow genetic base of the genotypes. Among the markers, Satt 180, Satt 301, Satt 685, Sat 460, Satt 464 and GMHSP179 were polymorphic and had PIC values ranging from 0.12 (Satt 464) to 0.78 (Satt 180). Dendrogram based on the SSR marker profile of Satt 301, Satt 180, Satt 685 and GMHSP179 clearly differentiated the resistant and susceptible genotypes of soybean into separate clusters. Hence, these four markers can be successfully exploited for marker assisted selection of YMD resistant soybean genotypes.

Keywords: Polymorphism, Soybean, SSR Markers, Yellow mosaic

Soybean [*Glycine max* (L.) Merrill] is one of the oldest crops grown and is popularly known as “Miracle Crop or Golden Bean” owing to its multiple uses. In the South East Asian countries the crop is highly susceptible to the whitefly transmitted yellow mosaic disease (Singh and Aravind 2019). YMD has a significant effect on yield and yield linked agronomic traits with losses reported to range from 85–100% when the plant is infected at an early stage (Amrate *et al.* 2020). In India, annual yield losses of \$300 million in soybean, blackgram and greengram have been reported due to YMD (Varma and Malathi 2003). It is caused by Mungbean yellow mosaic India virus (MYMIV) in northern and western parts and by Mungbean yellow mosaic virus (MYMV) in southern and central parts of the country (Ramesh *et al.* 2016). Earlier, the disease was confined to the north-western plains, but its outbreak in central India in 2015 followed by sporadic appearance in South India

during *kharif* 2022–23 is threatening the soybean cultivation in the country (Khosla *et al.* 2021, Chavan *et al.* 2025).

As plant viruses continue to evolve rapidly and expand their host range under changing ecological conditions, the development of new varieties with stable and durable resistance is essential for their effective and sustainable management (Khosla *et al.* 2021). One of the key challenges for the development of such resistant varieties is the identification of genetically stable resistant donors. The morphological characterisation alone does not reliably portray the genetic diversity among the genotypes due to environmental interactions and unknown genetic control mechanisms (Reif *et al.* 2005). Hence, more attention is given for the marker-based strategy that can further enhance the accuracy and reduce time and resources in the breeding programmes (Surbhi *et al.* 2020). Among such markers, simple sequence repeat (SSR) markers are more popular due to their co-dominant nature, reproducibility and high polymorphism (Rani *et al.* 2016). They are widely employed for the genetic diversity assessment in different crops including soybean (Rakshit *et al.* 2011, Tantasawat *et al.* 2011). Hence, the present investigation was conducted to identify durable sources of resistance in soybean against

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YMD and to characterise such genotypes using SSR markers. The findings of the study can be vital for marker assisted selection of YMD resistant soybean genotypes.

MATERIALS AND METHODS

Field screening: The present study was carried out for three consecutive years i.e. 2018–2020 at Norman E Borlaug Crop Research Center, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar (29°00'52.9"N, 79°29'01.9"E), Uttarakhand, which is designated as a hotspot for YMD (AICRP soybean 2018, Gautam *et al.* 2025). Forty-one soybean varieties/promising genotypes from All India Coordinated Research Project on Soybean along with a susceptible (JS-335) and resistant check (UPSM-534) were screened against YMD under epiphytotic conditions. The experiment was laid out in randomised block design (RBD) with three replications. Sowing was done in 1st week of July in 3 rows of 3 m length with a spacing of 45 cm × 10 cm (Plot size: 3 m × 1.5 m). Two rows of the susceptible check variety JS-335 were sown as infector rows, after every three genotypes and as border rows, to ensure an even distribution of the virus load and vector population throughout the field. The disease assessment was based on the percent disease incidence (PDI) and coefficient of infection (CI). Coefficient of infection was calculated by multiplying the percent disease incidence to response value assigned for each severity grade (Table 1). PDI was calculated as:

$$\text{Disease incidence (\%)} = (X_1/X_2) \times 100$$

Where X_1 , Number of infected plants and X_2 , Total number of plants observed (Alice and Nadarajan 2007). Leaves showing YMD symptoms were counted from 10 randomly selected plants per plot and YMD severity was calculated using the formula:

$$\text{Disease severity (\%)} = (Y_1/Y_2) \times 100$$

Where Y_1 , Number of infected leaves per plant and Y_2 , Total number of leaves per plant. All the observations were recorded at an interval of 15 days starting from 10 DAS. The data from field screening were subjected to statistical analysis using IBM SPSS Statistical software.

DNA extraction: The seeds of 28 genotypes showing stable resistance/susceptible reaction for three consecutive years along with resistant and susceptible checks were used for growing seedlings by paper towel method at 25°C in a BOD incubator (Vieira *et al.* 2010). DNA was extracted from young leaves of 10–15 days old seedlings using CTAB method given by Doyle and Doyle (1990). The quantity of the isolated DNA was determined using a spectrophotometer and quality was assessed on 0.1% agarose gel.

SSR marker analysis: Twelve SSR primers previously reported to be linked to YMD resistance, showing high polymorphism were selected for characterisation of soybean genotypes varying in resistance to YMD (Table 2). The polymerase chain reaction (PCR) amplification profile consisted of initial denaturation at 94°C for 2 min followed by 35 cycles consisting of denaturation, primer annealing

Table 1 Rating scale for classifying disease reaction of YMD in soybean (Singh and Singh 2000)

Symptom	Severity grade	Response value*	Coefficient of Infection	Reaction
Symptoms absent	0	0	0–4	Highly resistant
Very mild symptoms up to 25% leaves	1	0.25	5–9	Resistant
Appearance of symptoms in 26–50% leaves	2	0.50	10–19	Moderately resistant
Appearance of symptoms in 51–75% leaves	3	0.75	20–39	Moderately susceptible
Severe disease symptoms in more than 75% leaves	4	1.0	40–69	Susceptible
			70–100	Highly susceptible

*Response value is based on disease severity which is calculated based on number of leaves showing symptoms in a single plant.

and extension at 94°C, 45–55°C and 72°C, respectively for 1 min each. The reaction mixture (20 µl) consisted of 50 ng DNA template, 1 µM of each forward and reverse primers, 1.5 mM dNTPs, 1U Taq polymerase and 1× buffer with $MgCl_2$ (Kumar *et al.* 2014). Scoring of the SSR alleles was performed manually and genetic similarity between the genotypes were measured by Jaccard's similarity coefficient based on the proportion of shared alleles using 'simqual' sub programme of software NTSYSpc version 2.11a software package (Rohlf 1997). The resulting distance matrix data was used to construct dendrogram using the un-weighted pair group method with an arithmetic average (UPGMA) subprogramme of NTSYSpc version 2.11a. The polymorphism information content (PIC) of the SSR markers was also calculated:

$$P_{ij} = 1 - \sum_{j=1}^n (P_{ij})^2$$

Where P_{ij} , Frequency of the j^{th} allele for i^{th} marker and summation extends over n alleles (Anderson *et al.* 1993).

RESULTS AND DISCUSSION

Field screening of soybean genotypes against YMD: In the field study, mean disease incidence (DI) and coefficient of infection (CI) of genotypes ranged from 0.00–82.22% and 0.00–78.52 units, respectively (Table 3, Supplementary Table 1). Sixteen genotypes were found highly resistant with CI ranging from 0–4 whereas AMS-59 and AMS-58 were found highly susceptible (CI >70). Eight genotypes were found resistant (CI 5–9), five moderately resistant

Table 2 List of SSR markers used for assessment of molecular characterisation of soybean genotypes (Cregan *et al.* 1999, Song *et al.* 2004)

S.No.	Primer	Forward	Reverse	Chrom. No.
1.	GMHSP179	ATACCAGTTGATCTGCATATT	AAAACATCGTCTACTTAAGTC	17
2.	Satt301	GCGAAACACTCCTAGTTGATTACAAA	GCGATATAATGCACAAAGAAATTAAGA	17
3.	Satt180	TCGCGTTTGTTCAGC	TTGATTGAAACCCAATA	04
4.	Satt549	GCGGCAAACTTTGGAGTATTGCAA	GCGCGCAACAATCACTAGTACG	03
5.	Satt460	GCGCGATGGGCTGTTGGTTTTTAT	GCGCATACGATTTGGCATTTCATTG	06
6.	Satt167	AAGGCACTCTTCCATCAATACAA	TTGAGCCGAAAGTTCAATTCTA	09
7.	Satt464	GGGTTGGGAGAATTTAGGTT	TTTTGCATTAAAGGCTAATATGAA	17
8.	Satt481	GGGTTAACCGTCCACACATCTATT	GACGGTTTTAAACGGTAAGAAAAT	19
9.	Satt414	GCGTATTCTAGTCACATGCTATTTCA	GCGTCATAATAATGCCTAGAACATAAA	16
10.	Satt666	TGGCTTGTCATCTCTACTTTTATTAG	TCATGCATCTAATTTGTTTTATCTATCA	12
11.	Satt653	GCGAAACTCAAATTTGACACAACCTG	GCGCAAGGTAACTACTAACAAGACACA	10
12.	Satt685	ATCGTGGCATGTCTCACTAC	GAGGCGGAAGGAAATCTAAT	15

(CI 10–19), eight moderately susceptible (CI 20–39) and four were susceptible (CI 40–69). Genotype DS-3108 was found to be completely free from the disease and genotypes SL-1123, NRC-SL-1 and PS-1611 had less than one percent DI and CI.

All the 16 genotypes identified as highly resistant had CI<4 and the genotypes designated as susceptible/highly susceptible had CI>40 during the three years of study. This consistent performance over the year's emphasis on the minimum environmental influence and stringency of selection procedure adopted during the screening. The presence of resistance against YMD in soybean and other legumes has been reported by a number of scientists in India. Similar to our findings, Kumar *et al.* (2014), Bisht *et al.* (2017), Talukdar *et al.* (2013), and Chavan *et al.* (2025) have also observed a significant proportion of soybean genotypes to possess high level of resistance to YMD. Gautam *et al.* (2025) have reported that out of 60 soybean genotypes screened against YMD, 34 were highly

resistant, seven were resistant and 11 were moderately resistant. The resistance observed in genotypes SL 958, DS 3108, NRC-137, AMS 100-39, NRCSL1, PS-1613, and JS-20-34 corroborates earlier reports (Mishra *et al.* 2022, Chavan *et al.* 2025, Jhariya *et al.* 2025). These findings clearly indicate that stable sources of resistance to YMD are available in soybean germplasm and can be effectively exploited in breeding programmes for the development of YMD resistant cultivars.

SSR marker based characterisation: A total of 26 alleles (100–300 bp) were amplified using the 12 SSR markers with an average of 2.16 alleles per locus. Among the markers, six (Satt 180, Satt 301, Satt 685, Satt 460, Satt 464 and GMHSP179) were found polymorphic (2–5 alleles/marker) while the rest were monomorphic. Satt 180 and Satt 301 amplified five alleles each (Fig. 1, 2) whereas Satt 685 and Satt 464 amplified three alleles. PIC value of the polymorphic markers ranged from 0.12 (Satt 464) to 0.78 (Satt 180) with a mean of 0.52 (Table 4).

Table 3 Disease Incidence and coefficient of Infection of soybean genotypes (Pooled)

Sl. No	Cultivars	Pedigree	Disease incidence	Coefficient of infection	Disease reaction
1	UPSM-534 (R)	-	1.48 ^r	0.37 ^{op}	Highly Resistant
2	JS-335 (S)	JS-78-77 × JS-71-05	72.79 ^{cd}	68.87 ^b	Susceptible
3	SL-1123	Selection from AGS 751	0.74 ^r	0.19 ^{op}	Highly Resistant
4	Monetta	Exotic variety EC 2587	48.52 ^{efg}	28.43 ^{de}	Moderately Susceptible
5	Alankar	D 63-6094 × D 61-4249	44.07 ^{gh}	26.48 ^{efg}	Moderately Susceptible
6	BRAGG	Jackson × D 49-2491	25.56 ^{kl}	10.37 ^{jk}	Moderately Resistant
7	JS-20-27	JS 97-52 × JS 95-56	33.33 ^j	16.30 ⁱ	Moderately Resistant

Contd.

Table 3 (Concluded)

Sl. No	Cultivars	Pedigree	Disease incidence	Coefficient of infection	Disease reaction
8	DS-3108	-	0.00 ^r	0.00 ^p	Highly Resistant
9	KHSB-2	Manloxi × EC 39821	42.96 ^{hi}	23.15 ^{fgh}	Moderately Susceptible
10	PK-416	USPM-534 × Ankur	17.78 ^{nop}	4.44 ^{lmnop}	Resistant
11	NRC-SL-1	JS335 × SL525	0.74 ^r	0.19 ^{op}	Highly Resistant
12	PK-327	UPSM 82 × Semmes	10.00 ^q	2.50 ^{mnop}	Highly Resistant
13	PK-262	UPSM97 × Hardee	45.56 ^{fgh}	23.06 ^{gh}	Moderately Susceptible
14	VLS-59	(Pb1 × VLS2) × EC361336	10.74 ^q	2.69 ^{lmnop}	Highly Resistant
15	PS-1611	PS 1092 × VLS 47	0.74 ^r	0.19 ^{op}	Highly Resistant
16	NRC-7	Selection from S 69-96	23.33 ^{lm}	7.50 ^{jkl}	Resistant
17	PS-1225	PK515 × PK327	20.00 ^{mnop}	5.00 ^{lmno}	Resistant
18	MACS-58	JS2 × Improve pelican	38.52 ⁱ	16.39 ⁱ	Moderately Resistant
19	JS-72-280	EC 14437 × Bragg	73.33 ^{cd}	60.56 ^c	Susceptible
20	VLS-58	-	23.70 ^{lm}	5.93 ^{klm}	Resistant
21	Ankur	SPS from composite of 22 crosses	75.56 ^{bc}	57.50 ^c	Susceptible
22	AMS-100-39	Mutant of JS 93-05	2.96 ^r	0.74 ^{nop}	Highly Resistant
23	PS-1042	Bragg × PK 416	1.85 ^r	0.46 ^{op}	Highly Resistant
24	NRC-137	JS 97-52 × NRC 37	3.33 ^r	0.83 ^{nop}	Highly Resistant
25	Shilajeet	Single plant selection from EC 9309	23.70 ^{lm}	6.94 ^{iklm}	Resistant
26	JS-7546	Improved Pelican × Semmes	47.41 ^{fgh}	28.24 ^{de}	Moderately Susceptible
27	PK-472	Hardee × Punjab-1	42.96 ^{hi}	20.56 ^{hi}	Moderately Susceptible
28	JS-7244	D 60-9647 × EC 7034	49.63 ^{ef}	28.06 ^{def}	Moderately Susceptible
29	JS-97-52	PK 327 × L 129	31.11 ^j	11.02 ^j	Moderately Resistant
30	SL-958	SL 525 × SL 706	1.11 ^r	0.28 ^{op}	Highly Resistant
31	SL-688	PK416 × SL317	2.22 ^r	0.56 ^{nop}	Highly Resistant
32	AMS-59	-	82.22 ^a	78.52 ^a	Highly Susceptible
33	AMS-58	-	78.89 ^{ab}	73.24 ^b	Highly Susceptible
34	JS-20-53	-	18.52 ^{nop}	4.63 ^{lmnop}	Resistant
35	JS-93-05	Secondary selection from PS 73-22	68.89 ^d	55.93 ^c	Susceptible
36	PB-01	UPSM 82 × Semmes	21.85 ^{lmn}	5.46 ^{klmn}	Resistant
37	Shivalik	Selection from segregating PK 73-55	29.26 ^{jk}	10.28 ^{jk}	Moderately Resistant
38	MACS-450	Bragg × MACS 111	17.04 ^{op}	4.26 ^{lmnop}	Resistant
39	JS-20-34	JS98-63 × PK768	2.59 ^r	0.65 ^{nop}	Highly Resistant
40	SL-1068	SL 755 × SL 525	1.85 ^r	0.46 ^{op}	Highly Resistant
41	NRC-128	JS 97-52 × PBM-1-1-9-2-6-1	1.11 ^r	0.28 ^{op}	Highly Resistant
42	PS-1613	PS 1225 × PS 1042	2.96 ^r	0.74 ^{nop}	Highly Resistant
43	JS-99-89	-	52.59 ^c	32.96 ^d	Moderately Susceptible
	CV (%)		17.02	-	
	CD ($p=0.05\%$)		4.69	4.98	-
	SEM ±		1.67	1.77	-

Mean followed by same letters does not differ significantly whereas mean with different letter differ significantly; Means with multiple shared letter indicates overlapping statistical groups.

Table 4 Number of alleles amplified and PIC value of SSR markers

Sl. No.	Primer	No. of alleles	PIC	Product size (bp)
1.	GMHSP179	2	0.46	100, 200
2.	Satt301	5	0.75	190, 200, 220, 240, 260
3.	Satt685	3	0.65	180, 190, 200
4.	Satt180	5	0.78	260, 270, 280, 290, 300
5.	Satt 460	2	0.32	200, 260
6.	Satt 464	3	0.12	170, 200, 220
7.	Satt481	1	0	200
8.	Satt 414	1	0	300
9.	Satt 666	1	0	240
10.	Satt 167	1	0	200
11.	Satt549	1	0	200
12.	Satt653	1	0	130

PIC, Polymorphism information content.

Several scientists have employed SSR markers for assessing molecular diversity in soybean genotypes (Tantasawat *et al.* 2011, Kumar and Lal 2015). Bhattacharya *et al.* (1999) and Talukdar *et al.* (2013) have reported the involvement of a single major gene contributing towards YMD resistance in wild type and cultivated soybean. Recently, the SSR marker BARC_14_1422 was found to have differential amplification in YMD resistant and susceptible genotypes (Gautam *et al.* 2025). The results obtained in the present investigation are in partial agreement with that of Kumar *et al.* (2014). Markers Satt 301 and GMHSP179 on chromosome 17 were found to be linked with YMD resistance in soybean and had a PIC value of 0.75 and 0.45, respectively which are in agreement with our results. Moreover, they have reported 10 other SSR markers

that were found associated with YMD resistance in soybean of which two, Satt 180 and Satt 685, were found to amplify different allelic fragments in the resistant and susceptible checks in the present investigation as well.

The average number of alleles per locus obtained in our study is low in comparison to reports published earlier (Li *et al.* 2008, Liu *et al.* 2011). In our study, a total of 26 alleles were amplified using the 12 markers with an average of 2.16 alleles per locus which indicated a narrow genetic base of the genotypes used in the study. The plant materials of this study consisted of more number of Indian released genotypes having a common parentage in their breeding programme which might have been one of the main causes for lower number of alleles per locus. Moreover, since our study focused on the YMD resistance, many of the diverse germplasm could have been eliminated during the field screening which might have added to the reduced diversity of the genotypes used in the molecular diversity analysis. However, our studies are in agreement with Rani *et al.* (2016), who reported an average of 2.41 alleles/locus and highest PIC value of 0.754 and with Kumar *et al.* (2014) who have reported 2.36 alleles/locus. A low average PIC content of 0.43 and 0.17 for SSR markers used for diversity analysis of soybean genotypes differing in response to YMD were reported by Mishra *et al.* (2022) and Saket *et al.* (2025), respectively.

Out of the 6 polymorphic markers, five markers, viz. GMHSP179, Satt 301, Satt 180, Satt 685 and Satt 460 showed differential allele amplification in resistant and susceptible check. The dendrogram constructed using these SSR marker profile grouped the genotypes into 2 major clusters designated as A and B which possessed a similarity coefficient of 0.12 (Fig. 3). The major cluster A contained a total of 13 highly resistant genotypes grouped into two sub-clusters, viz. A-I and A-II. Major cluster B was further divided into 2 sub clusters with a similarity

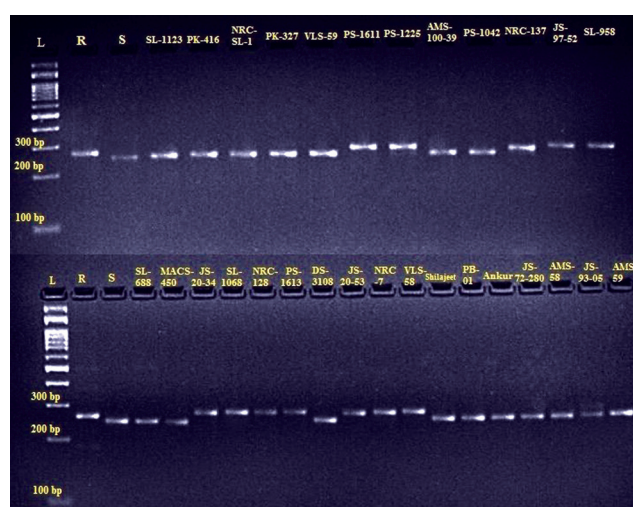


Fig. 1 Amplification profile of the polymorphism among soybean genotypes generated by SSR marker Satt 180. L, Ladder; R, Resistant Check; S, Susceptible Check; 1–28, Soybean genotypes.

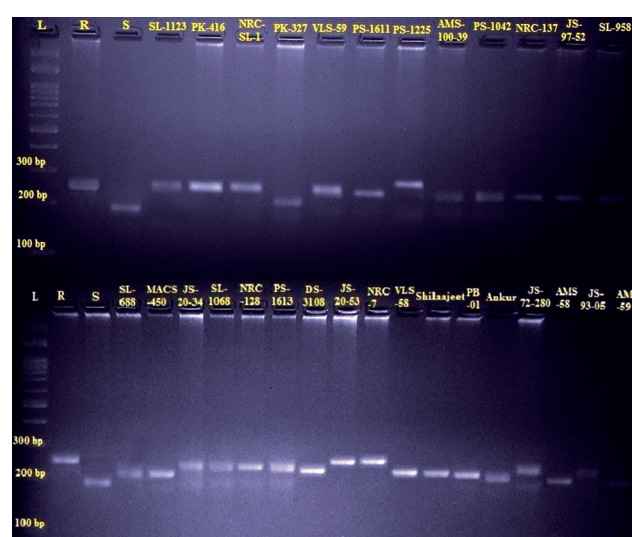


Fig. 2 Amplification profile of the polymorphism among soybean genotypes generated by SSR marker Satt 301. L, Ladder; R, Resistant Check; S, Susceptible Check; 1–28, Soybean genotypes.

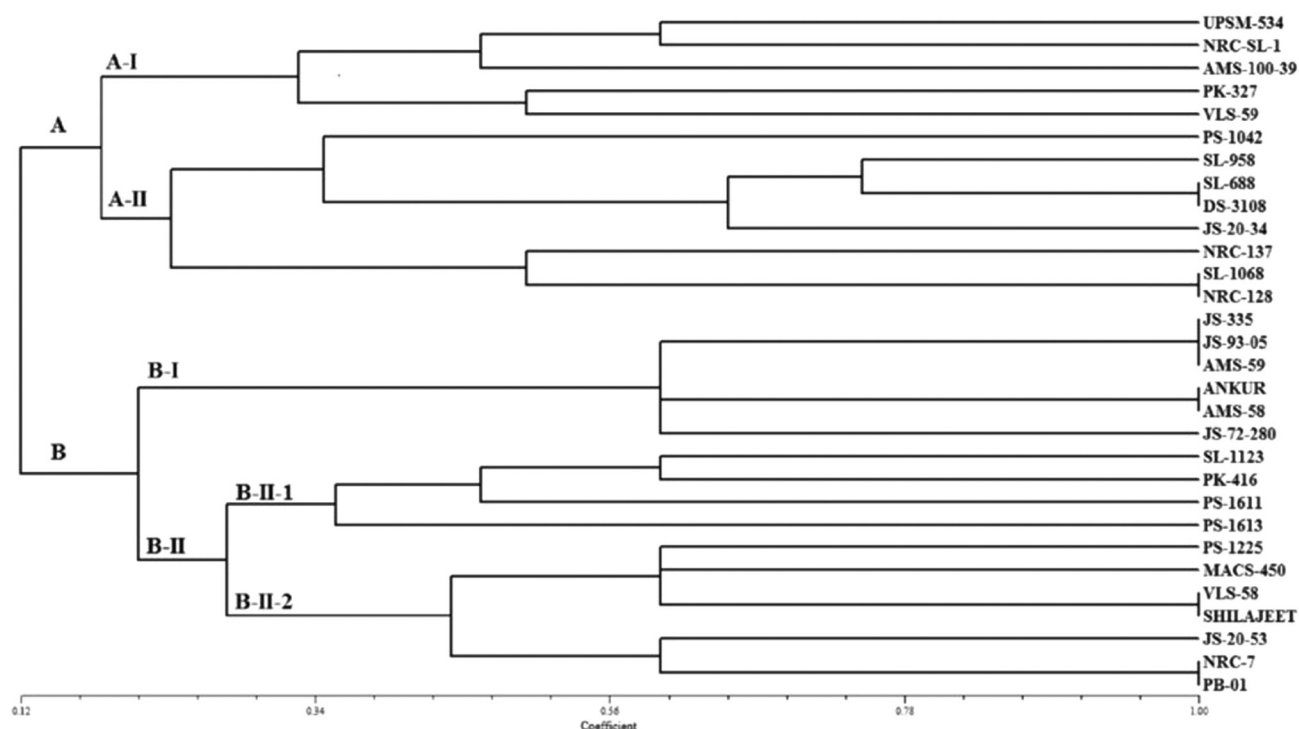


Fig. 3 UPGMA dendrogram showing similarity coefficients and genetic relationships among soybean genotypes based on SSR marker profile.

coefficient of 0.20. The sub cluster B-I contained the susceptible check (JS-335) and all other highly susceptible/susceptible genotypes. Sub-cluster B-II was further divided into two groups B-II-1 and B-II-2. Group B-II-1 contained three highly resistant genotypes (SL-1123, PS-1611 and PS-1613) and one resistant genotype (PK-416). All the remaining resistant genotypes clustered in group B-II-2. The cluster analysis based classification of YMD resistant and susceptible genotypes have been reported by Kumar *et al.* (2014) and Mishra *et al.* (2022). According to Kumar *et al.* (2014), dendrogram constructed using SSR marker profile classified the soybean genotypes into three clusters with the pair-wise genetic similarity ranging from 0.39–0.95 with an overall mean of 0.65. The biggest cluster had 45 genotypes collected from Taiwan and Madhya Pradesh (India) which were susceptible to YMD. They had the highest level of genetic similarity among them and with JS335 which is highly susceptible to YMD. Mishra *et al.* (2022) observed that in UPGMA cluster analysis, soybean genotypes were grouped into two clusters one minor and one major. Minor cluster contained only four genotypes namely AMS-100-99, JS-20-116, MACS-1520 and NRC-2 which were resistant to YMD. Similarly, clustering of genotypes based on their differential response to YMD assessed by SSR markers have also been reported by Sahu *et al.* 2024 and Saket *et al.* (2025).

The findings of the present investigation clearly indicated the presence of resistance sources against soybean YMD. The resistant sources identified can be further incorporated into the plant breeding programmes for developing high

yielding YMD resistant soybean cultivars for deployment in the endemic regions. The four SSR markers identified to give differential amplification in resistant and susceptible genotypes can be successfully exploited for validation of field data and marker assisted selection of YMD resistant soybean genotypes.

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