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Exploring potato diversity: A comprehensive genetic and phenotypic analysis of quantitative and qualitative traits

Tasnim Khandaker Samiha[2], *Md Ataur Rahman*[1], *Saiful Islam*[1,3], *Nusrat Jalal*[2], *Aparna Islam*[2], *Abu Shamim Mohammad Nahiyan*[1]*

[1]*Advanced Seed Research and Biotech Centre, ACI Limited, Dhaka, Bangladesh*
[2]*Department of Mathematics and Natural Sciences, BRAC University, Mohakhali, Dhaka, Bangladesh*
[3]*National Key Laboratory for Germplasm Innovation & Utilization of Horticultural Crops, College of Horticulture and Forestry Sciences, Huazhong Agricultural University, Wuhan, P.R. China*

**Corresponding author: nahiyan80@hotmail.com*

Tasnim Khandaker Samiha and Md Ataur Rahman contributed equally to this work and share the first authorship.

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Abstract: For sustainable breeding in potato, a better understanding of genetic diversity within germplasm banks for sustainable breeding is needed. This study comprehensively characterised the molecular and phenotypic traits of 62 potato accessions, including advanced clones and indigenous potato varieties from Advanced Chemical Industries Limited (ACI Ltd.), Bangladesh, and 8 varieties from the Bangladesh Agricultural Research Institute (BARI). By using 9 SSR markers and 13 morphological traits, including both quantitative and qualitative traits, we observed correlation coefficients ranging from –0.3 to 0.7 for 8 quantitative traits, and Pearson's chi-square (χ^2 value) ranging from 24.3 to 135.4 for 5 qualitative characteristics. Molecular analyses identified 46 unique alleles, with 93.5% polymorphism. The markers STM0031 and STM1016 had the highest PIC value of 0.9. Genetic parameters for SSR markers included effective number of alleles per locus (*Ne*) = 5.6, unbiased expected heterozygosity (*uh*) = 0.8, diversity (*h*) = 0.8 and Shannon's information index (*I*) = 1.8. Jaccard's similarity coefficients ranged from 0.2 to 0.8, representing significant diversity. Cluster analysis, using unweighted pair-group method with arithmetic average (UPGMA), grouped the accessions into five clusters based on SSR profiles. An association was foud between the marker STM0031 and two traits: the number of tubers per hill and the content of reducing sugars in the tubers. This study provides information on genetic diversity and marker efficacy. It will guide future breeding programmes towards the development of high-yielding and industrially valuable potato varieties.

Keywords: gene bank; genotype; high yield; industrial trait; SSR marker

Potato (*Solanum tuberosum* L.), a key global food crop from the Solanaceae family, ranks third in worldwide consumption, boasting high yield potential (Islam et al. 2022). Its nutritional value and its adaptability contribute to increased production, particularly in developing nations like Bangladesh, where potato cultivation has notably expanded, averaging 22.9 Mt (BBS 2023). This growth holds promise for addressing the country's food and nutritional security concerns.

Potato production faces challenges such as disease susceptibility, requiring costly treatments, and limited availability of quality seeds (Tambi & Bobuin 2023). Developing resilient potato varieties with enhanced stress tolerance is crucial for improving productivity and meeting market demands (Tiwari et al. 2022). The diversity within potatoes is one of the essential factors for different trait-based potato breeding programs managed by germplasm banks like the International Potato Centre (CIP) and the Commonwealth Potato Collection (CPC) (Manrique-Carpintero et al. 2023). Furthermore, studying genetic diversity in potatoes in developing countries like Bangladesh is essential

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not only for developing disease-resistant and climate-resilient advanced lines, but also for improving yield, quality, and market al.gnment, enhancing potato breeding programs, promoting biodiversity, and ensuring sustainable agriculture.

The limitations of morphological markers in potato characterisation highlight the need for more reliable DNA markers (Tillault & Yevtushenko 2019). The availability of the potato genome sequence has accelerated cultivar development through gene-linked markers (Ghislain & Douches 2020). Simple sequence repeats (SSR) are ideal markers due to reproducibility, codominance, and extensive genome coverage (Islam et al. 2024), offering a cost-effective method for genetic identity determination in diversity analysis and breeding programs (Tillault & Yevtushenko 2019). Global studies using SSR markers have explored potato genetic diversity, providing valuable insights into different varieties (Liao & Guo 2014; Tillault & Yevtushenko 2019). Using SSR markers significantly enhances cultivar discrimination, genetic diversity analysis, and marker-assisted selection for commercially viable potato varieties.

In our study, 62 potato accessions from the gene bank of Advanced Chemical Industries Limited (ACI Ltd.) were analysed, using 13 phenotypic parameters and 9 SSR markers. Emphasizing the historical importance of phenotypic traits in potato breeding and prioritizing genetic diversity preservation, our goal is to uncover marker-trait associations. This enhances SSR marker utility for future genetic analyses and facilitates targeted breeding for commercially viable varieties ideal for industrial applications.

MATERIAL AND METHODS

Plant material. We assessed 62 potato accessions from the ACI gene bank comprising 54 ACI germplasm sources including advanced clones and indigenous potato varieties (IPV) and 8 exotic varieties released by Bangladesh Agricultural Research Institute (BARI) (Table S1 in Electronic Supplementary Material (ESM)). The selection criteria were established through field assessments conducted from 2015 to 2023 at ACI Regional Research Station, Debiganj, Panchagarh, one of the major potato growing region in Bangladesh. Numerical scales were used to assess 5 distinct qualitative characteristics: shape of tuber (ST), skin colour of tuber (SCT), flesh colour of tuber (FCT), eye colour of tuber (ECT) and eye depth of tuber (EDT) (Table 2). Quantitative traits such as plant height (PH), number of main stem/hill (NMS/H), number of tuber/hill (NT/H), weight of tuber/hill (WT/H), yield of tuber (YT), and growth duration (GD) were recorded during the field assessments of 62 potato accessions. In addition, DM and RS were also analysed in the ACI laboratory. Statistical analyses, including the determination of correlation coefficients among quantitative traits (PH, NMS/H, NT/H, WT/H, YT, DM, RS and GD) and Pearson's chi-square (χ^2) tests for qualitative traits, were performed using the R package, with significance set at $P < 0.05$.

DNA isolation, PCR and SSR analysis. Leaf samples from 62 potato accessions, 15-day-old healthy plants grown in the ACI greenhouse, Dhaka, underwent DNA extraction using a modified CTAB method (Raihan et al. 2016). Nine SSR markers known for their effectiveness in distinguishing cultivars were utilized (Tillault & Yevtushenko 2019). PCR amplification used a 10 µL reaction volume, including 1 µL DNA (50 ng/µL), 5 µL PCR-mix (EmeralAmp GT PCR master mix), 0.5 µL each of forward and reverse primers (0.5 µM/µL), and 3 µL ddH_2O. Cycling conditions involved an initial denaturation at 95 °C for 5 min, followed by 40 cycles at 95 °C for 20 s, primer-specific annealing for 20 s, extension at 72 °C for 45 s, and a final 10 min extension at 72 °C. PCR products were separated on a 1% polyacrylamide gel, stained with ethidium bromide, and documented using the UVsolo TS imaging system.

SSR evaluation and genetic diversity analysis. The detection of alleles and determination of their sizes were accomplished through image lab software (Ver. 6.0). The scoring of the number of peaks and profiles per marker was done by observing the amplification in different accessions. A data matrix involving 62 accessions was then generated, with entries indicating the presence (1) or absence (0) of the amplified SSR fragments. The polymorphic information content (PIC) for each SSR locus was computed using the formula mentioned below.

$$\mathrm{PIC} = 1 - \sum_{i=1}^{n} p_{i^2} - \sum_{i=1}^{n} \sum_{j=i+1}^{n} 2p_{i^2}\, 2p_{j^2}$$

where:

n – number of allele;

p_i – frequency of the i^{th} allele;

p_j – frequency of the j^{th} allele (Botstein et al. 1980).

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GenAlEx (Ver. 6.502) software was utilized to compute genetic diversity parameters, including the number of alleles per locus (*Na*), effective number of alleles per locus (*Ne*), unbiased expected heterozygosity (*uh*), and Shannon's information index (*I*). Jaccard's similarity coefficients were calculated using Past software (Ver. 4.03) based on 0–1 allele scoring. A dendrogram was constructed via an unweighted pair-group method with arithmetic average (UPGMA) cluster analysis to visualize accession clustering. The rate of distinguishing cultivars by cluster (RDCC) was determined from individual SSR-generated dendrograms to assess the cultivar differentiation ability within clusters (Liao & Guo 2014).

$$\text{RDCC} = \frac{N - N_i}{N}$$

where:

N – the total number of accessions evaluated;

N_i – the number of accessions that remained indistinguishable.

Population structure analysis and marker-trait association. The collection structure analysis was conducted using STRUCTURE software (Ver. 2.3.4) (Mehmood et al. 2023) employing a Bayesian clustering method. *K*-values ranging from 1 to 10 were independently run five times, and the optimal *K* value (ΔK) was determined using STRUCTURE Harvester (Achilonu et al. 2023) following the method of Evanno et al. (2005), utilizing a burn-in length of 1 000 and 10 000 Markov chain Monte Carlo (MCMC) replications. For marker-trait association (MTA) analysis, genotypic and phenotypic data were processed using TASSEL (Ver. 5.0), following the approach by Hu et al. (2022). The analysis incorporated a general linear model (GLM) integrating Q-matrix and kinship matrix data derived from the STRUCTURE analysis.

Table 1. Quantitative traits of 62 potato accessions

	Min	Max	Average	SD	*CV* (%)
PH	28.1	95.0	60.7	15.6	25.8
NMS/H	1.2	8.2	3.2	1.6	50.8
DM	18.2	23.8	20.6	1.3	6.3
RS	0.2	0.7	0.4	0.1	33.9
NT/H	3.0	67.0	9.7	9.3	95.3
WT/H	234.0	713.7	448.9	101.0	22.5
GD	70.0	95.0	85.0	5.7	6.7
YT	28.0	59.5	35.26	5.2	14.8

PH – plant height (cm); NMS/H – number of main stem/hill; DM – dry matter (%); RS – reducing sugar (%); NT/H – number of tuber/hill; WT/H – weight of tuber/hill (g); GD – growth duration; YT – yield of tuber (t/ha); SD – standard deviation; *CV* – coefficient of variation

RESULTS AND DISCUSSION

Phenotypic trait analysis. Coefficients of variation ranged widely, emphasizing trait diversity, from 6.3% for dry matter content to 95.3% for number of tuber per hill (Table 1). Similar to our findings, lowest coefficients of variation of 12.1% for dry mat-

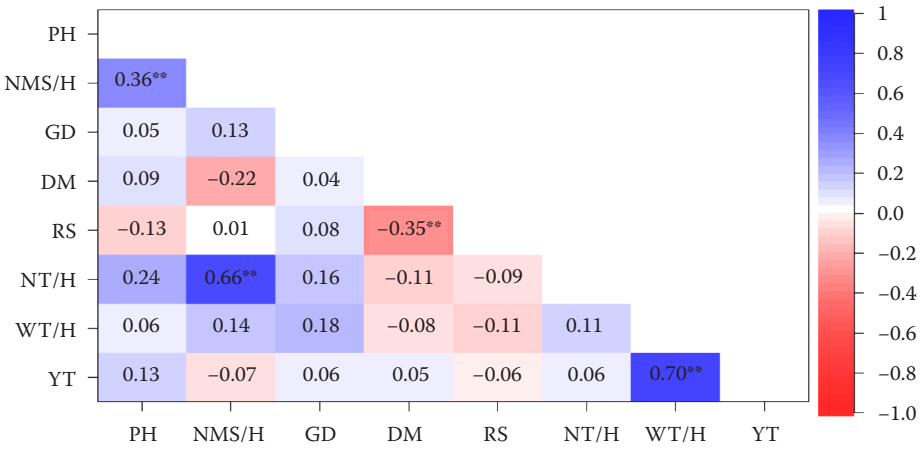

Figure 1. Correlation analysis of the 8 quantitative phenotypic traits on of the 62 potato accessions

PH – plant height; NMS/H – number of main stem/hill; GD – growth duration; DM – dry matter; RS – reducing sugar; NT/H – number of tuber/hill; WT/H – weight of tuber/hill; YT – yield of tuber; the strong correlation coefficients are indicated with **($P < 0.05$) and ***($P < 0.001$)

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ter content and highest 156.9% for flower colour were observed in the study of Hu et al. (2022). This variability underlines potential breeding efforts to enhance specific traits in potato cultivars (Rizvi et al. 2020; Gebhardt 2023). Plant height (PH) varied from 28.1 to 95 cm (average: 60.7 cm), and the number of main stems per hill (NMS/H) ranged from 1.2 to 8.2 (average: 3.2), indicating diverse growth duration. Dry matter content (%) ranged from 18.2% to 23.8%, and reducing sugar content (%) varied between 0.2% and 0.7%. Growth duration (GD) spanned 70 to 95 days (SD = 5.7), with an average tuber yield (YT) of 35.3 t

Table 2. Pearson's chi-square (χ^2) analysis of 5 qualitative traits among the 62 potato accessions

Traits	Numerical scale	Phenotype	Frequency	χ^2	df	*P*-value
ST	1	round	13	24.3	6	0.0004681
	2	round-oval	3			
	3	oval	11			
	4	oval-oblong	18			
	5	oblong	11			
	6	oval-long	4			
	7	oblong-long	2			
	8	long	0			
SCT	0	white	26	135.4	11	2.20E-16
	1	yellowish	1			
	2	yellow	5			
	3	pinkish white	1			
	4	white with pink spot	1			
	5	pink	1			
	6	red with white patches	4			
	7	light red	1			
	8	red	17			
	9	deep red	2			
	10	blue white	1			
	11	purple	2			
FCT	0	white	32	102.4	6	2.20E-16
	1	light yellow	5			
	2	yellow	20			
	3	deep yellow	1			
	4	yellow with marginal pink ring	2			
	5	pink	1			
	6	purple	1			
ECT	0	white	28	65.5	5	8.62E-13
	1	yellow	6			
	2	pink	2			
	3	red	22			
	4	purple	1			
	5	black	3			
EDT	1	deep	16	40.3	2	1.78E-09
	2	moderate deep	3			
	3	shallow	43			

df – degrees of freedom; ST – shape of tuber; SCT – skin colour of tuber; FCT – flesh colour of tuber; ECT – eye colour of tuber; EDT – eye depth of tuber

https://doi.org/10.17221/10/2024-CJGPB

per ha (SD = 5.2) (Table 1). Correlation analysis revealed coefficients among 8 quantitative traits ranging from –0.3 to 0.7 (Figure 1). Significant differences ($P < 0.001$) were observed in five instances, with two instances showing significant differences ($P < 0.05$) in trait correlations. Notably, three coefficients exceeded 0.6, indicating strong associations, while two surpassed 0.4, denoting robust relationships. Positive correlations were found between plant height and the number of main stems per hill, as well as between total tuber yield and weight. Additionally, the number of tubers per hill exhibited a notable positive relationship with the number of main stems per hill, accompanied by a moderate negative correlation with tuber shape reported by Rizvi et al. (2020). In our comprehensive analysis of 62 potato accessions, we also evaluated 5 qualitative traits, revealing significant variability through χ^2 test of these accessions (Table 2) which revealed χ^2 value ranging from 24.3 for ST to 135.4 for SCT. Our findings highlights substantial diversity in agronomic traits among the evaluated potato accessions, offering valuable insights for future breeding programs aimed at targeting specific characteristics in potato cultivars.

SSR marker evaluation. The genetic analysis of 62 potato samples employing 9 SSR markers located on chromosomes 1, 7, 8, 10, and 12 (Table 3). Amplicon sizes ranged from 95 to 809 bp (Table S2 in ESM), revealing 3 to 11 alleles per marker with the average of 7.3 alleles. This indicates substantial genetic diversity among the studied materials (Tillault & Yevtushenko 2019). STM1052 primer pair showed the fewest bands, while STM0031 detected the most. Among 46 alleles, 43 were polymorphic (93.5% polymorphism). Genetic variance analysis indicated 7 to 11 alleles per locus (*Na*), averaging 7.33 alleles per locus (Table 4). The effective number of alleles per locus (*Ne*) averaged 5.6, with unbiased diversity (*uh*) ranging from 0.6 to 0.9 and a mean Shannon's information index (*I*) of 1.8. PIC values ranged from 0.5 to 0.9, averaging 0.8 per SSR marker. This aligns with previous studies on potato diversity and other crops (Elibariki et al. 2013; Anoumaa et al. 2017). The RDCC varied from 9.7 to 67.7; SSR markers STM0031 and STM1106 demonstrated high discriminatory power, distinguishing about 40 accessions each. Conversely, STM1049 discriminated only 6 out of the 62 cultivars. These SSR markers provided valuable information for decoding genetic diversity and cultivar differentiation in the studied potato population, as it has also been stated by Rocha et al. (2010) and Anoumaa et al. (2017).

Table 3. Primers information for the 9 SSR markers

SSR marker	Primer sequences (5' to 3')	Chromosome No.	Motif	Reference
STM 0030	F: AGAGATCGATGTAAAACACGT R: GTGGCATTTTGATGGATT	XII	(GT/GC)(GT)8	Ghislain et al. (2009)
STM 0031	F: CATACGCACGCACGTACAC R: TTCAACCTATCATTTTGTGAGTCG	VII	(AC)5...(AC)3 GCAC (AC)2 (GCAC)2	Milbourne et al. (1998); Ghislain et al. (2009)
STM 0037	F: AATTTAACTTAGAAGATTAGTCTC R: ATTTGGTTGGGTATGATA	XII	(TC)5 (AC)6 AA (AC)7 (AT)4	Milbourne et al. (1998); Tillault and Yevtushenko (2019)
STM 1016	F: TTCTGATTTCATGCATGTTTCC R: ATGCTTGCCATGTGATGTGT	VIII	(TCT)9	Tillault and Yevtushenko (2019)
STM 1049	F: CTACCAGTTTGTTGATTGTGGTG R: AGGGACTTTAATTTGTTGGACG	I	–	Favoretto et al. (2011)
STM 1052	F: CAATTTCGTTTTTTCATGTGACAC R: ATGGCGTAATTTGATTTAATACGTAA	VII	(AT)14 GT (AT)4 (GT)6	Milbourne et al. (1998); Kandemir et al. (2010)
STM 1106	F: TCCAGCTGATTGGTTAGGTTG R: ATGCGAATCTACTCGTCATGG	X	(ATT)13	Milbourne et al. (1998); Kandemir et al. (2010)
STM 2013	F: TTCGGAATTACCCTCTGCC R: AAAAAAGAACGCGCACG	VII	(TCTA)6	Tillault and Yevtushenko (2019)
STM 3009	F: TCAGCTGAACGACCACTGTTC R: GTTTGATTTCACCAAGCATGGAAGTC	VII	(TC)13	Milbourne et al. (1998)

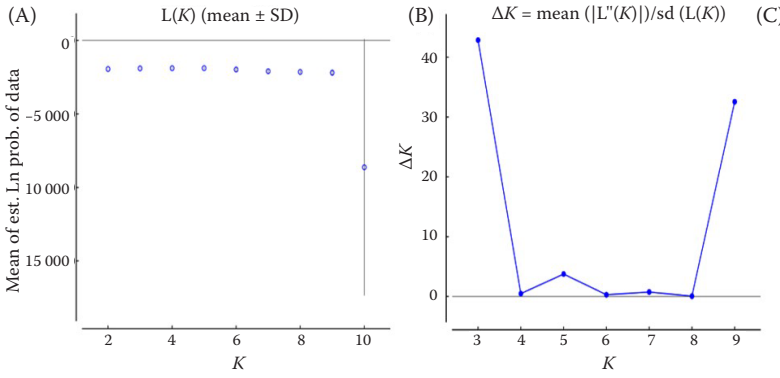
https://doi.org/10.17221/10/2024-CJGPB

Table 4. Genetic diversity of the 62 potato accessions using 9 SSR markers

Marker	*Na*	*Ne*	*uh*	*h*	*I*	PIC	*Ni*	*Nd*	RDCC (%)
STM0030	8	6.2	0.8	0.8	2.0	0.8	39	23	37.1
STM0031	11	8.8	0.9	0.9	2.3	0.9	20	42	67.7
STM0037	8	8.0	0.9	0.9	2.1	0.8	47	15	24.2
STM1016	10	7.4	0.9	0.9	2.1	0.9	37	25	40.3
STM1049	5	4.3	0.8	0.8	1.5	0.7	56	6	9.7
STM1052	3	2.6	0.6	0.6	1.0	0.5	44	18	29.0
STM1106	7	4.3	0.8	0.8	1.7	0.7	24	38	61.3
STM2013	7	4.2	0.8	0.8	1.6	0.7	52	10	16.1
STM3009	7	4.5	0.8	0.8	1.7	0.7	53	9	14.5
Mean	7.3	5.6	0.8	0.8	1.8	0.8	41.3	20.7	33.3

Na – the number of alleles per locus; *Ne* – the effective number of alleles per locus; *uh* – unbiased diversity; *h* – diversity; *I* – Shannon's information index; PIC – polymorphic information content; *Ni* – number of indistinguishable accessions; *Nd* – number of distinguishable accessions; RDCC – rate of distinguishing cultivars by cluster

Genetic similarity analysis. STRUCTURE analysis of 62 potato accessions revealed three subpopulations (Q1: 17 cultivars, Q2: 15 cultivars, and Q3: 30 cultivars) based on Δ*K* analysis (Figure 2), providing insights into the genetic structure of the collection (Lee et al. 2021; Bhardwaj et al. 2023). Jaccard's similarity coefficients (Figure 3) ranged from 0.2 to 0.8 (average: 0.4), signifying substantial genetic diversity (Favoretto et al. 2011; Liao & Guo 2014). The highest similarity coefficient (0.8) occurred between acces-



(C)

K	Reps	LnP(*K*) mean	LnP(*K*) SD	Ln'(*K*)	|Ln''(*K*)|	Δ*K*
2	3	−1 949	0.8185	–	–	–
3	3	−1 904	0.7638	44.933	32.733	42.858
4	3	−1 891	21.019	12.2	9.7333	0.4631
5	3	−1 889	25.886	2.4667	96.833	3.7408
6	3	−1 983	82.057	−94.37	22.667	0.2762
7	3	−2 100	95.044	−117	69.8	0.7344
8	3	−2 148	69.877	−47.23	2.8	0.0401
9	3	−2 198	196.07	−50.03	6 382.5	32.552
10	3	−8 630	8 695.4	−6 433	–	–

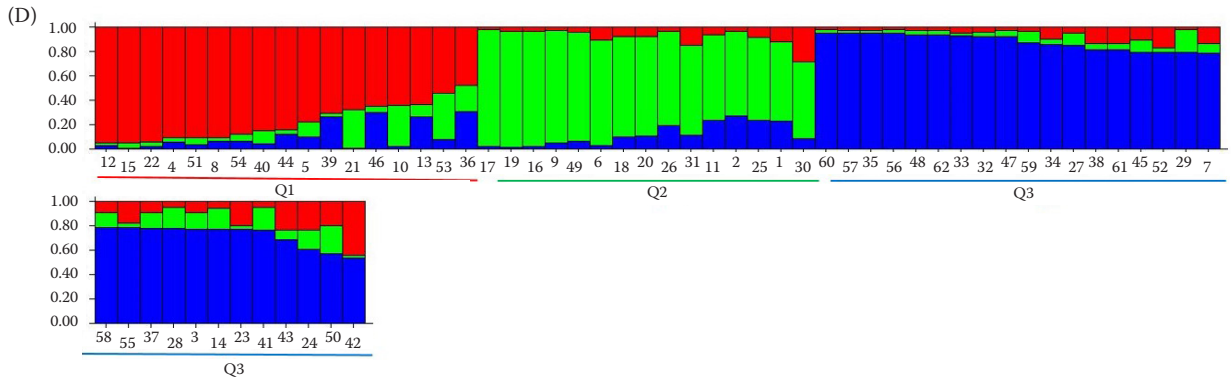


Figure 2. Population structure analysis of 62 potato accessions: mean log-likelihood, L(*K*) (mean ± SD) (A); population estimation using LnP(D) derived Δ*K* (B); *K* values from 1 to 10, based on the Evanno approach (C); population structure analysis for Δ*K* = 3 (D)

The three populations (Q1, Q2, Q3) are represented by the colors red, green, and blue, respectively

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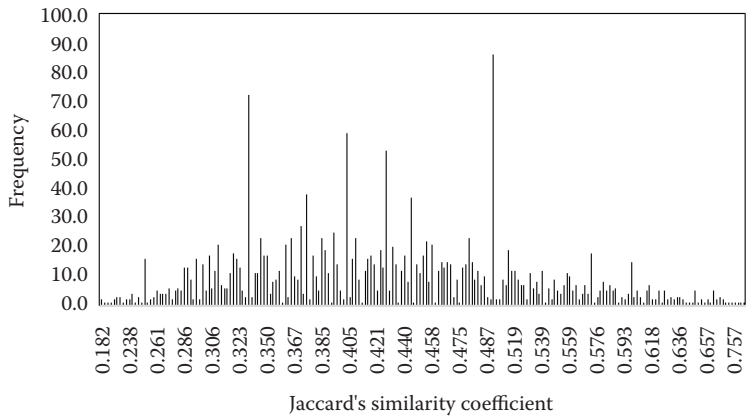

Figure 3. Frequency distribution of Jaccard's similarity coefficients among 62 potato accessions

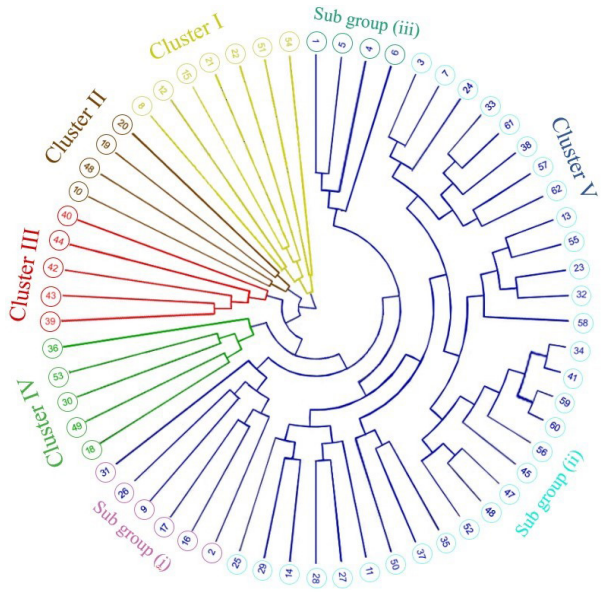

Figure 4. Dendrogram constructed via unweighted pair-group method with arithmetic average cluster analysis of 62 potato accessions using 9 SSR markers

sions 16 and 17, while accession 57 showed the lowest coefficient (0.2), indicating the greatest genetic distance. Cluster analysis (Figure 4) grouped accessions into five clusters (I, II, III, IV, and V), with cluster V containing the majority of accessions (41) and further subdividing into three groups (Table 5). This pattern suggests both clusters and subgroups shared unique genetic traits among accessions. STM0031 and STM1016 SSR markers effectively separated 56 of the 62 accessions. The combination of the four best primers (STM0030, STM0031, STM0037, and STM1016) based on PIC values highlighted genetic diversity, emphasizing marker utility in population structure analysis (Lee et al. 2021) and offering valuable information for breeding programs and conservation efforts (Anglin et al. 2021) (Figure S1 in ESM). These results contribute to a comprehensive understanding of potato genetic diversity, providing a foundation for informed breeding strategies and germplasm conservation.

Marker-trait associations. Associations between SSR markers and phenotypic traits were explored using TASSEL software's general linear model. A total of 598 marker-trait association tests revealed significant connections, such as loci STM0031_1, STM0031_2, and the number of tubers per hill, and locus STM0031_4 with reducing sugar content. Manhattan and QQ plots illustrated robust correlations between these markers and the mentioned traits (Figure 5, 6). Genetic diversity in sweet po-

Table 5. Potato accessions grouped in clusters formed by unweighted pair-group method with arithmetic average and Jaccard's coefficient

Cluster No.	I	II	III	IV	V		
					subgroup *i*	subgroup *ii*	subgroup *iii*
No. of accessions	7	4	5	5	6	31	4
Accession No.	8, 12, 15, 21, 22, 51, 54	10, 48, 19, 20	39, 43, 42, 44, 40	18, 49, 30, 53, 36	2, 16, 17, 9, 26, 31	3,7,24,33, 61,38,57,62,13, 55, 23, 32, 58, 34, 41, 59,60,56, 45,47 46, 52, 35, 37, 50, 11, 27, 28, 14, 29, 25	1,5,4,6

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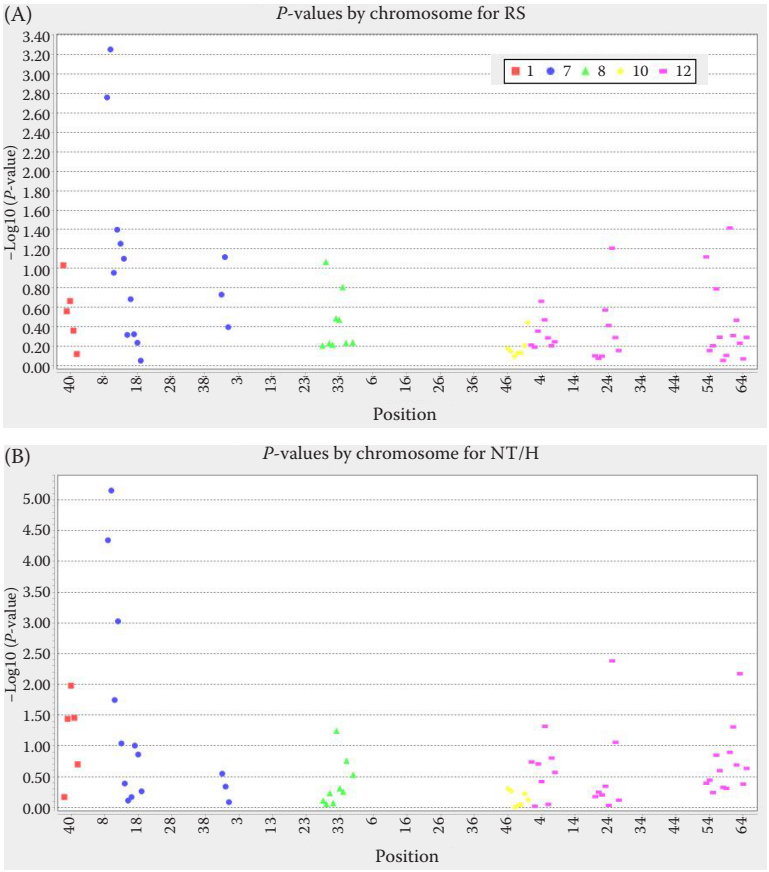

Figure 5. Manhattan plots for marker-trait associations: reducing sugar (RS) content (A); number of tubers per hill (NT/H) (B)

tato resources was assessed through a combination of morphological, qualitative, and molecular markers, including 14 hypervariable microsatellite markers (Palumbo et al. 2019). Correlations between plant morphology, tuber quality traits, and market preferences were considered vital for commercial viability and consumer acceptance (Slater et al. 2014; Das et al. 2021). In a potato diversity study, SSR markers

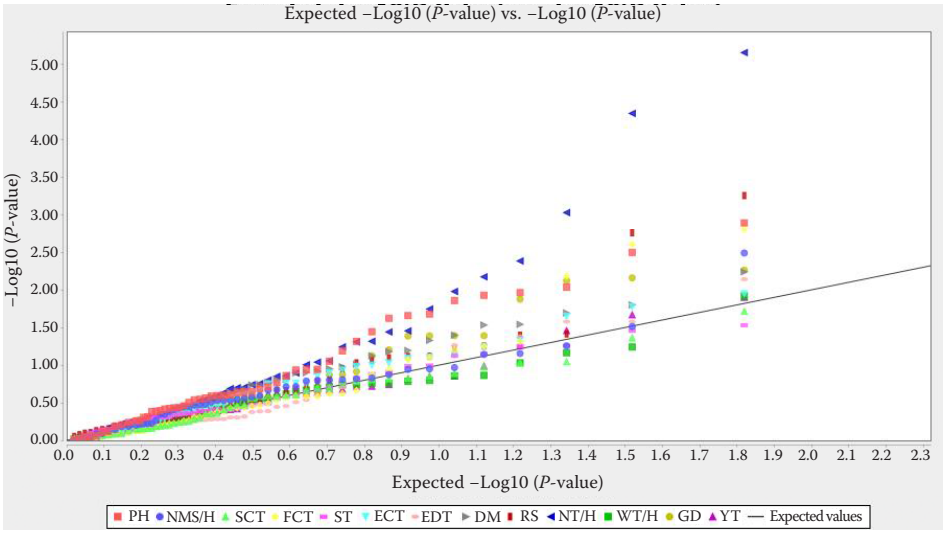

Figure 6. QQ plots from marker–trait association study involving 13 traits in the potato population
PH – plant height; NMS/H – number of main stem/hill; SCT – skin colour of tuber; FCT – flesh colour of tuber; ST – shape of tuber; ECT – eye colour of tuber; EDT – eye depth of tuber; DM – dry matter; RS – reducing sugar; NT/H – number of tuber/hill; WT/H – weight of tuber/hill; GD – growth duration; YT – yield of tuber

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proved efficient tools for examining genetic diversity within a potato diversity panel (Liao & Guo 2014; Bhardwaj et al. 2023). Another investigation involving new potato varieties utilized 10 SSR markers for genotyping, revealing insights into the genetic makeup of varieties developed by a private breeder (Tillault & Yevtushenko 2019).

CONCLUSION

The study utilized 9 SSR markers to distinguish all 62 potato accessions from the ACI gene bank, revealing significant variability in 13 agronomic traits. Key markers, STM0031 and STM1016, demonstrated their importance in genetic analysis with high PIC values (0.9) for the 62 potato accessions in this study. Cluster analysis using Jaccard's coefficient indicated an average genetic distance of 0.4, confirming substantial variation. These SSR markers are robust tools for characterising potato varieties, essential for maintaining germplasm diversity. Future efforts will explore deeper associations between SSR markers and specific industrial potato traits, potentially revolutionizing production efficiency and enhancing desired traits.

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