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Genetic diversity and stability analysis of sweet potato accessions of north-eastern India grown under the mid-hill conditions of Meghalaya

Veerendra Kumar Verma, Amit Kumar, Heiplanmi Rymbai, Hammylliende Talang, M. Bilashini Devi, Pankaj Baiswar and S. Hazarika

ICAR Research Complex for NEH Region, Umiam-793103, Meghalaya, India

Research Article

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Corresponding author:
Veerendra Kumar Verma;
Email: verma.veerendra@gmail.com

Abstract

A total of 32 sweet potato genotypes were evaluated to assess the genetic diversity based on quantitative traits and molecular markers, as well as stability for yield and related traits. Wider variability was observed for the traits like vine length (181.2–501.3 cm), number of leaves/plant (103.0–414.0 cm), internodal length (3.20–14.80 cm), petiole length (6.5–21.3 cm), leaf length (8.50–14.5 cm), leaf breadth (8.20–15.30 cm), leaf area (42.50–115.62 cm^2), tuber length (7.77–18.07 cm), tuber diameter (2.67–6.90 cm), tuber weight (65.60–192.09 g), tuber yield (7.77–28.87 t ha^{-1}), dry matter (27.34–36.41%), total sugar (4.50–5.70%) and starch (18.50–29.92%) content. Desirable traits such as tuber yield, dry matter and starch content have shown high heritability (>60%) with moderate to high genetic advance. Under molecular analysis, a total of 232 alleles were observed from all 32 microsatellite markers, which ranged from 4 to 14 with an average of 7.77 alleles per locus. In the population, the average observed heterozygosity (0.51) was higher than the expected heterozygosity (0.49). The contribution of genotype, genotype by environment interaction to the total variations was found to be significant. Based on the multi-trait stability index (tuber length, tuber diameter, tuber weight and tuber yield), genotypes X-24, MLSPC-3, MLSPC-5, ARSPC-1 and TSP-12-12 were found to be most stable. Among them, the high-yielding and stable genotypes TSP-12-10 (26.0 t ha^{-1}) and MLSPC-3 (23.9 t ha^{-1}) can be promoted for commercial production or used as parental material in future crop improvement programmes.

Introduction

Sweet potato (*Ipomoea batatas* [L.] Lam) is a dicotyledonous plant which belongs to the family Convolvulaceae. It is the third-most important tuber crop in India after potatoes and tapioca. Globally, China is the leading country in terms of production of sweet potatoes, while India ranks ninth in production of sweet potatoes with an area of 0.13 million ha and a production of 1.5 million metric tonnes. It is grown in both the tropics and sub-tropics of the world. As far as the cultivation of sweet potatoes in India is concerned, North-Eastern states contribute 8.69% of the total area and 4.02% of the total country's production (NHB, 2018). Among the North-Eastern states, Assam, Meghalaya and Nagaland are the leading ones in terms of production of this particular crop. India is also earning value worth ≈0.49 million (USD) through the export of the tubers to various countries, namely, the United Arab Emirates, Nepal and Maldives (APEDA, 2022–23). Due to the wider adaptability of the crop, it is being grown over a wide range, i.e. from the valleys to the mid-hills of the region from March to November. In spite of the higher suitability of the crop to varying climatic conditions, the average productivity of the crop in the region is very low, i.e. 5.04 t ha^{-1} over the national average 10.57 t ha^{-1}(Press Information Bureau, 2022), which might be due to the use of poor-quality planting materials, crop management and cultivation on hill slopes as a rainfed crop under the reduced cycle of Jhum/shifting cultivation. The tubers of sweet potatoes are consumed boiled or roasted as snacks, whereas the foliage is used as green livestock feed. The tubers are rich in carbohydrates, carotene, ascorbic acid and vitamin B complex and thus play an important role in ensuring the nutritional security of the growers and other consumers.

Sweet potatoes are commercially propagated through cuttings, and due to poor flowering and seed set, most of the varieties have been developed through clonal selection. Nowadays, to develop cultivars higher in yield and richer in nutritional quality (starch, β-carotene, etc.), crop improvement through hybridisation and selection is gaining importance. Diverse genetic resources are of prime importance for developing desirable types of accessions. Despite having a wider diversity, no research work has been conducted on assessing the extent of the available genetic diversity in this particular region using both morphological and molecular markers and utilisation of this diversity in the identification of superior parental

lines. Globally, very few researchers have studied the genetic diversity present in the crop based on quantitative traits, isozyme and molecular markers (Prakash and He, 1996; Zhang *et al.*, 2000; Gichuru *et al.*, 2006; Karuru *et al.*, 2010; Nair *et al.*, 2017; Paliwal *et al.*, 2020; Narasimha Murthy *et al.*, 2021).

Being a cross-pollinated crop, sweet potatoes are highly heterozygous, and wider variability exists in the population. The presence of enormous variability in this crop determines the success of plant breeding as it facilitates the selection of superior genotypes with favourable attributes for their judicious utilisation (Leite *et al.*, 2016). The estimate of the genetic parameters has been found very useful in determining the nature and magnitude of the variability in the population, which is a prerequisite for crop improvement. Furthermore, principal component analysis (PCA) is also a very important tool to identify the important traits contributing to the diversity of the population. Afuape (2014) identified marketable and unmarketable root weight and total number of roots as important traits for forward selection of genotypes for total yield in sweet potatoes using multivariate analysis.

Tuber yield is a polygenic trait, and knowledge of its relationship with other yield-attributing traits is necessary to design the appropriate criteria for crop improvement. Selection of the genotype for higher yield based on component traits that are simply inherited rather than the total yield itself will be quite fruitful (Grafius, 1959). Furthermore, polygenic traits such as yield and quality attributes are heavily influenced by genotype, environment and their interactions; thus, knowledge of genotype and environmental interactions is critical for assessing the performance of varieties grown in different environments. Andrade *et al.* (2016) and Mustamu *et al.* (2018) identified the superior and stable varieties of sweet potato for different environmental conditions in Mozambique and West Java (Indonesia), respectively.

This experiment was carried out under the sweet potato improvement programme of the All India Coordinated Research Project (AICRP) on Tuber Crops project with the following objectives: to analyse the genetic parameters and trait association among the accessions of sweet potato; to study the genetic diversity based on quantitative traits and molecular markers; and to study the stability of the accessions for yield and related traits in the mid-hills of Meghalaya.

Materials and methods

Experimental site

This experiment was conducted for 3 years (2016–2018) during March–November at the Horticulture Experimental Farm, ICAR Research Complex for NEH Region, Umiam, Meghalaya (latitude 25.41 N and 92.55 E longitude, elevation 960 m asl). The climate of the region is humid subtropical with an annual rainfall of 2200–2500 mm. The average maximum and minimum temperatures of the region during the crop period were 27.7 and 17.2°C, respectively. This location has inceptisol soils of sandy texture and acidic in reaction (pH: 5.5).

Germplasm collection

A total of 32 accessions (27 local collections from the north-eastern states and 5 advanced breeding lines/varieties, i.e. TSP-12-10, TSP-12-12, ST-14 and Gauri developed by research institutes located in other parts of the country) were collected and used for the studies (online Supplementary Table S1).

Crop evaluation

The crops were grown following a standard package of practices as standardised by the institute. The tubers were sown in the primary nursery in the first week of February. The vine cuttings of 20–25 cm in length from the secondary nursery were planted on ridges at a spacing of 60 × 45 cm between row and plant, respectively, in April. The farm yard manure of 15 t ha^{-1} was applied at the time of field preparation. In addition to that, 190 kg of urea, 375 kg of single super phosphate (SSP) and 150 kg of murate of potash (MOP) were also applied per hectare. One-third of urea and a full dose of SSP and MOP were applied at the time of land preparation, and the remaining dose of urea was applied in two equal splits at 30 and 60 days after planting. Manual weeding and earthing-up were done at 30 and 60 days after planting. The crop was harvested at full maturity in November, after the leaves had died. The experiment was carried out in a randomised block design with three replications.

The observations were recorded for growth and yield-related traits such as vine length (cm), number of leaves/plant, internodal length (cm), petiole length (cm), leaf length (cm), leaf breadth (cm), leaf area (cm^2), tuber length (cm), tuber diameter (cm), tuber weight (g) and tuber yield (t/ha). The length, width and area were measured using a leaf area metre (CI-203 Laser Area Meter). The mean values of six plants in each plot/replication were used for the statistical analysis.

Quality analysis

The quality parameters dry matter (%), total sugar (%) and starch (%) content were estimated from the tubers of the accessions using the standard procedure described by Rangana (1986).

Statistical analysis

The mean value of all six plants was used to constitute one replication, which was further used for analysis of variance as per Panse and Sukhatme (1978). The phenotypic (PCV) and genotypic coefficients of variance (GCV) of the genotypes were estimated as described by Burton and Devane (1953), heritability as described by Hanson *et al.* (1956) and genetic advance (GA) was estimated using the formula suggested by Johnson *et al.* (1955). The genotypic and phenotypic correlation coefficient and path coefficient were estimated as suggested by Dewey and Lu (1959). Clustering was performed using the Stats package in R 4.2.1 and visualised using the Factoextra package. PCA was performed using the Factoshiny package in R 4.2.1.

The additive main effects and multiplicative interaction (AMMI)-based stability parameters were measured as AMMI stability value (ASV) as described by Purchase *et al.* (2000), sums of the absolute value of the Interaction Principal Component (IPC) scores (SIPC) and averages of the squared Eigen value (EV) as proposed by Sneller *et al.* (1997), absolute value of the relative contribution of IPCs to the interaction (ZA) as per the procedure of Zali *et al.* (2012) and weighted average of absolute scores (WAAS) according to Olivoto *et al.* (2019) using the 'metan' package (v. 1.16.0) (Olivoto and Lucio, 2020) in R version 4.2.1 (http:// www.r-project.org/).

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Molecular characterisation

Plant materials

A total of 32 accessions, including popular cultivars, were used for molecular analysis.

Genomic DNA extraction

The total genomic DNA was extracted by using the CTAB method (Doyle and Doyle, 1987) with the addition of polyvinylpyrrolidone (1%) from young leaf tissue ground to a fine powder using liquid nitrogen. The DNA sample concentration was determined using a spectrophotometer and was diluted to 20 ng μl^{-1} prior to polymerase chain reaction (PCR) amplification.

Molecular analysis

Thirty EST-derived polymorphic SSR primers were selected (Wang *et al*., 2011; Baafi *et al*., 2015) and used for molecular analysis. The PCR analysis was carried out in 20 µl volume containing 40 ng template DNA, 0.5 U Taq DNA polymerase, 0.2 mM each dNTP, 0.2 µM forward and reverse primer each in (1 ×) reaction buffer that contained 10 mM Tris–HCl (pH 8.3), 50 mM KCl and 2.5 mM $MgCl_2$ (Thermo scientific, India). The amplification conditions (Applied BiosystemsVeriti™) were initial denaturation at 94°C for 5 min and 35 cycles at 94°C for 60 s and then 55–65°C for 60 s, and extension at 72°C for 2 min, followed by 10 min at 72°C and indefinite soak at 4°C. Amplified products were resolved on 3.5% Super fine resolution agarose gel containing ethidium bromide (10 mg/ml) at a constant voltage of 80 V for 3 h using a horizontal gel electrophoresis system (Biorad). The gel was run in 1× Tris-borate-EDTA buffer. A 50 bp DNA ladder (MBI Fermentas, Hanover, USA) was run alongside the amplified products to determine their approximate band size. Similarly, the amplified products were visualised under UV by image analysis (Bio-Rad Gel Doc XR+ Molecular Imager).

Data analysis

Only consistent, bright, reproducible (i.e. band absence was randomly verified) SSR bands were scored as per the allelic sizes, where each character state was treated independently. The allele frequencies were computed using an EM algorithm developed by Kalinowski *et al*. (2006). As disomic inheritance is different from polysomic inheritance, summary statistics of SSR markers such as number of alleles per locus, allele frequency, heterozygosity and polymorphic information index (PIC) were determined using POLYGENE 1.4 software with modifications in various parameters of genetic diversity. Genetic diversity was assessed using both a model-based approach and a distance-based approach. For the distance-based approach, the unrooted phylogenetic tree was constructed based on genetic distance as per Nei distance (Nei *et al*., 1983). Clustering using a model-based approach was also performed with a *K* value ranging from 1 to 10 in POLYGENE 1.4 software (Huang *et al*., 2020). The optimum *K* value was determined based on the delta *K* value calculated using excel. GenAlEx v.6.1 software was used for analysis of molecular variance (AMOVA) based on the quantitative traits (leaf shape and peel colour) and model-based clustering. Further, Mantel test was carried out to study the correlation between morphological and molecular clustering distance (Mantel, 1967).

Results

Genetic variability for growth, yield and quality attributes

Among the (32) accessions, wide variability was observed for all the traits. Accessions were grouped into red (18), white (11) and orange (3 accessions) colours on the basis of peel colour; two leaf types, i.e. lobed (15) and cordate (17); and the number of leaf lobes was two or three or five (online Supplementary Table S1). The five-, three- and two-lobed leaf accessions were highly, moderately and very slight in depth of the margin, respectively. The quantitative traits showed significant variations for vine length (181.2–501.3 cm), number of leaves per plant (103.0–414.0), internodal length (3.20–14.80 cm), petiole length (6.50–21.30 cm), leaf length (8.50–14.50 cm), leaf width (8.20–15.30 cm), leaf area (42.10–115.62 cm^2), tuber length (7.77–18.07 cm), tuber diameter (2.67–6.90 cm), tuber weight (65.6–192.09 g) and tuber yield (5.07–28.87 t ha^{-1}). Similarly, quality parameters such as dry matter range from 27.34 to 36.41%, total sugar (4.50–5.70%) and starch content (18.5–29.92%) (Table 1).

TSP-12-12 had the highest yield (25.85 t ha^{-1}) among the accessions, followed by MWC-1, MLSPC-2, MLSPC-3 and SPC-1. Likewise, the highest starch content was observed in MZCP-3 (21.57%), followed by MWC-2 and BRC-2 (>20% each).

For all the traits, the contribution of both the GCV and PCV was significant (Table 1). Except for tuber length and quality attributes, all the growth and yield attributes have shown high heritability (>60%) and GA (>20%). Quality traits such as dry matter and starch content have also shown high heritability with moderate GA (>10%), whereas total sugar content has high heritability with low GA.

Correlation among yield and quality traits

The genotypic correlation was higher than the phenotypic correlation for all 14 traits (Table 2). Growth traits, namely vine length, showed a significantly positive genotypic and phenotypic correlation with the number of leaves and internodal length. Leaf area also showed a significant and positive genotypic and phenotypic correlation with leaf length, leaf width and petiole length. Economic traits such as yield per plant were positively correlated with tuber length, tuber diameter and tuber weight. Similarly, quality traits such as dry matter content showed a positive correlation with internodal length, tuber length, tuber diameter and tuber weight. Starch content as the most important quality trait also showed positive genotypic and phenotypic correlations with dry matter content, tuber length, tuber diameter and tuber yield, while it had a significant negative correlation with sugar content.

Principal component analysis (PCA)

The first five principal components (PCs; EV > 1.0) showed 69.63% cumulative variance of the total variance. Of the total variance, the first PC contributed 20.06%, which was dominated by growth-related traits (leaf length, leaf area, leaf width and petiole length); and the PC-II contributed 18.44%, which was dominated by quality and yield-attributing traits (dry matter, starch content, tuber length, diameter and yield); PC-III accounted for 14.16%, which was predominating by traits (number of leaves, vine length and internodal length); and PC-IV dominated yield traits (tuber weight, yield and tuber length). In addition, PC-II also separated the accessions superior for yield and quality traits from accessions vigorous in growth habit but poor in yield (Fig. 1).

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Table 1. Analysis of genetic parameters for growth, yield and quality attributes in sweet potato

Parameters	Max	Min	Mean	SE (mean)	CD (5%)	GCV	PCV	h^2	GAM
Vine length (cm)	501.30	181.20	297.68	10.86	30.71	27.61	28.32	0.95	55.43
No of leaves/plant	414.00	103.00	220.49	8.92	25.21	33.25	33.98	0.96	67.02
Internodal length (cm)	14.80	3.20	7.44	0.65	1.84	34.50	37.69	0.84	65.04
Petiole length (cm)	21.30	6.50	12.97	0.51	1.45	30.35	31.11	0.95	60.97
Leaf length (cm)	14.50	8.50	11.24	0.06	0.17	12.47	12.51	0.99	25.62
Leaf breadth (cm)	15.30	8.20	11.83	0.07	0.19	14.85	14.88	1.00	30.53
Leaf area	115.62	42.10	75.87	0.62	1.76	25.20	25.24	1.00	51.84
Tuber length (cm)	18.07	7.77	13.02	0.81	2.30	11.14	15.54	0.51	16.45
Tuber diameter (cm)	6.90	2.67	4.83	0.31	0.89	14.32	18.20	0.62	23.19
Tuber weight (g)	192.09	65.60	108.13	5.52	15.61	21.50	23.25	0.86	40.96
Tuber yield (t ha^{-1})	28.87	7.30	15.72	1.14	3.22	32.53	34.87	0.87	62.51
Dry matter content (%)	36.41	27.34	31.40	0.13	0.38	6.78	6.82	0.99	13.89
Total sugar %	5.70	4.50	4.90	0.06	0.17	4.32	4.82	0.80	7.98
Starch (%)	29.92	18.5	22.80	0.57	1.62	10.10	11.01	0.84	19.10

Genetic diversity

Genetic diversity based on quantitative traits

The 32 accessions were grouped into three major clusters on the basis of cluster analysis of 14 quantitative traits (Fig. 2a). Each cluster showed a mixture of cordate and lobed-type leaves. Cluster I comprised 18 accessions, including mixed red and white peel colour accessions; cluster II (4 accessions with red and white peel colours); cluster III (10 white, orange and red peel colour); while, orange-coloured accessions were distributed in clusters I (TSP-12-12) and III (ST-14 and BRC-3).

Genetic diversity based on molecular analysis

The 35 SSR markers used in the study showed 30 amplifications and were polymorphic (online Supplementary Table S2). A total of 232 alleles were observed, and they ranged from four (IBS-7) to 14 (GDaas-0156), with an average of 7.77 alleles per locus. The effective number of alleles ranged from 1.45 (IBR-03) to 3.83 (GDaas-0930), with a mean value (2.05), and heterozygosity (observed, 0.35–0.75 and expected, 0.31–0.74). In all the 29 markers except GDaas-0930, the observed heterozygosity (0.51) was higher than the expected heterozygosity (0.49). Further, the polymorphism information content of the marker ranged from 0.31 to 0.71, with a mean value (0.47 per loci) and the Shannon's information index (SII) for each marker ranged from 0.83 to 1.73 with a mean value (1.16). Among markers, the maximum number of effective alleles (3.83), observed (0.75) and expected heterozygosity (0.74), polymorphism information content (0.71), and SII (1.73) were observed in marker GDaas-0930.

Based on Nei's genetic distance, sweet potato genotypes have been grouped into three major clusters (Fig. 2b). Cluster I was comprised of six genotypes, all of which were from Meghalaya, while clusters II and III had genotypes of different geographical origins. The popular cultivars Gauri, X-24, ST-14 and S-107 were grouped into a single cluster (III) and found genetically closer to the local landraces of the region. It was found that there is no relationship for differentiation among the genotypes on the basis of leaf shape or peel colours. Similarly, the accessions were distributed as mixed across the axis based on 30 molecular markers in the principal coordinate analysis (PCoA; online Supplementary Fig. S1). The red and orange peel accessions were found to be more diverse as compared to the white accessions. Both cluster and PCoA showed wider variability within and between the groups. The cluster-based AMOVA showed the presence of 50% variations within individuals and among the population. Based on group-wise Nei genetic distance analysis (Nei *et al.*, 1983), the accessions were grouped into six groups for peel colour and leaf shape. Among the groups, the maximum genetic distance (0.77) was observed between orange-cordate and white-lobed accessions, followed by orange-lobed to orange cordate (0.76) and orange cordate to red-lobed (0.74). However, the least genetic distance (0.30) was observed between white-lobed and red-lobed accessions. Moreover, the correlation between morphological and molecular diversity has shown a positive ($r = 0.0037$) and non-significant ($P < 0.05$) relationship with each other (online Supplementary Fig. S2).

Genetic structure and interrelationship

Genetic structure analysis carried out based on the 30 microsatellite markers has detected the maximal ΔK (37.06) at $K = 3$. The results have also shown an increase in the admixture from 6.25% ($K = 2$) to 25% ($K = 5$) at 95% threshold level in the population with an increase in K values, and it was 18.75% at optimal $K = 3$ (Fig. 3).

Stability analysis for yield-attributing traits

AMMI analysis of variance

The analysis of variance has revealed significant effects ($P < 0.01$) of genotypes (fixed), years/environments (random) and genotypes by environment interaction (GEI) on yield and yield-attributing traits (Table 3). Among the factors, genotype has explained significantly, i.e. 43.28 for tuber length, tuber

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Table 2. Phenotypic (above) and genotypic (below) correlation for growth, yield and quality attributes in sweet potato

Traits	Vine length (cm)	No of leaves/plant	Internodal length (cm)	Petiole length (cm)	Leaf length (cm)	Leaf breadth (cm)	Leaf area(cm^2)	Tuber length (cm)	Tuber diameter (cm)	Tuber weight (g)	Tuber yield (t ha^{-1})	Dry matter content (%)	Total sugar (%)	Starch (%)
Vine length (cm)		0.382**	0.234*	−0.179	−0.148	−0.245*	−0.026	−0.095	0.133	−0.125	0.200	−0.237*	0.096	−0.153
No of leaves/plant	0.396**		0.178	−0.289**	0.335**	0.061	0.316**	0.085	0.179	−0.13	−0.14	−0.220*	−0.018	−0.203*
Internodal length (cm)	0.267	0.171		−0.356**	−0.213*	−0.009	0.084	0.08	0.111	0.043	0.066	0.238*	−0.131	0.043
Petiole length (cm)	−0.182	−0.298	−0.391*		0.392**	0.321**	0.378**	−0.006	−0.172	0.133	−0.072	−0.217*	−0.027	−0.075
Leaf length (cm)	−0.152	0.343**	−0.238	0.409*		0.533**	0.658**	−0.015	−0.025	−0.01	−0.348**	−0.069	−0.420**	0.012
Leaf breadth (cm)	−0.255	0.063	−0.009	0.330*	0.536**		0.379**	−0.084	−0.031	−0.107	−0.154	0.038	−0.200	0.047
Leaf area (cm^2)	−0.025	0.324**	0.086	0.388*	0.662**	0.380*		0.1	0.159	0.077	−0.013	−0.004	−0.379**	0.138
Tuber length (cm)	−0.123	0.101	0.088	−0.009	−0.041	−0.117	0.147		0.270**	0.202**	0.164	0.206*	−0.213*	0.420**
Tuber diameter (cm)	0.219	0.247	0.127	−0.271	−0.03	−0.037	0.195	0.306		0.092	0.088	0.179	−0.071	0.223*
Tuber weight (g)	−0.138	−0.139	0.053	0.139	−0.012	−0.111	0.085	0.168	0.046		0.157	0.089	0.13	0.054
Tuber yield (t ha^{-1})	0.21	−0.142	0.078	−0.095	−0.369*	−0.17	−0.018	0.226	0.13	0.184		0.053	0.051	0.138
Dry matter content (%)	−0.245	−0.229	0.281	−0.218	−0.071	0.039	−0.003	0.336	0.236	0.092	0.065		−0.400**	0.602**
Total sugar (%)	0.129	−0.025	−0.188	−0.024	−0.466*	−0.22	−0.423*	−0.339	−0.154	0.102	0.093	−0.466**		−0.232*
Starch (%)	−0.166	−0.206	0.072	−0.064	0.008	0.047	0.153	0.646**	0.290	0.047	0.183	0.656**	−0.324**	

Note: The colour show the strength of the correlation among the traits.

diameter (57.51%), tuber weight (75.44%) and tuber yield (78.71%) of the total variation. The $G \times E$ interaction component was partitioned into the first two interaction principal components (IPCA), which were found to be non-significant. The IPCA1 explained 93.7, 89.6, 97.1 and 69.0% and the IPCA2 explained 6.2, 10.4, 2.9 and 31.0% of the $G \times E$ interaction for tuber length, tuber diameter, tuber weight and tuber yield, respectively. Thus, the first two PCs could explain 100% of the $G \times E$ variation.

Stability analysis by the AMMI model

Genotype environment signals (GEs) were calculated (Gauch, 2013) to ascertain the appropriateness of the data for AMMI analysis. GEs were calculated by subtracting GE_N (GE noise) from GEI. For calculating GE_N, error mean sum of square and degrees of freedom (df) for GE are required. Thus, the first step included the calculation of GE_N by multiplying the error mean sum of square with the df for GE ($0.64 \times 62 = 39.93$ for tuber length; $0.053 \times 62 = 3.34$ for tuber diameter; $73.5 \times 62 = 4557.00$ for tuber weight and $1.15 \times 62 = 71.30$ for tuber yield). Further, GEs were computed (370.14–39.93 = 330.21 for tuber length; 54.75–3.34 = 51.42 for tuber diameter; 17012.8–4557.00 = 12455.80 for tuber weight and 724.78–71.30 = 653.48 for tuber yield). The analysis has shown a lower value for the sum of square due to GE_N over GEI sum of square for all the yield-attributing traits.

AMMI stability value (ASV) and other stability parameters

The accessions have shown a wide range of variations for ASV (online Supplementary Table S3), and it ranged from 0.50 to 18.40 for tuber length, 0.11 to 9.86 for tuber diameter, 0.58 to 249.0 for tuber weight and 0.11 to 3.25 for tuber yield. The genotype with the lowest ASV is considered a stable genotype for the traits. Among the accessions, the most stable genotypes with the lowest ASV value were identified as MZCP-1, BRC-2, X-24, MLSPC-2 and ST-14 for tuber length; SPC-6, MZCP-1, SPC-1 and SPC-4 for tuber diameter; SPC-2 and Kokrajhar Local for tuber weight; and MWC-4, TSP-12-10, Meghalaya Local and MLSPC-3 for tuber yield per hectare.

Like ASV, the other stability indices, such as the SIPC, the AMMI stability index, the average of the squared EV, ZA and the WAAS, were significant and positively correlated with each other. Based on all the stability indices, genotypes viz. MWC-4, TSP-12-10, MLSPC-5, Meghalaya Local and X-24 were identified as stable genotypes for tuber yield.

Multi-trait stability index (MTSI) and genotype selection

Based on MTSI, out of 32 accessions, five accessions (X-24, MLSPC-3, MLSPC-5, ASPC-1 and TSP-12-12) were found suitable for selection at 10% selection intensity for yield-related traits (online Supplementary Fig. S3a). Further, based on all the traits, the genotypes were found stable and selected as MLSPC-3, X-24, S-107, SPC-1 and SPC-3 (online Supplementary Fig. S3b). Moreover, the strength–weakness analysis based on the multi-trait genotype–ideotype distance index revealed that genotypes MLSPC-3, X-24, S-107, SPC-1 and SPC-3 are stable for the maximum number of factors with the minimum contribution (online Supplementary Fig. S4). From both analyses, two genotypes, namely MLSPC-3 and X-24, were found stable for yield as well as other traits.

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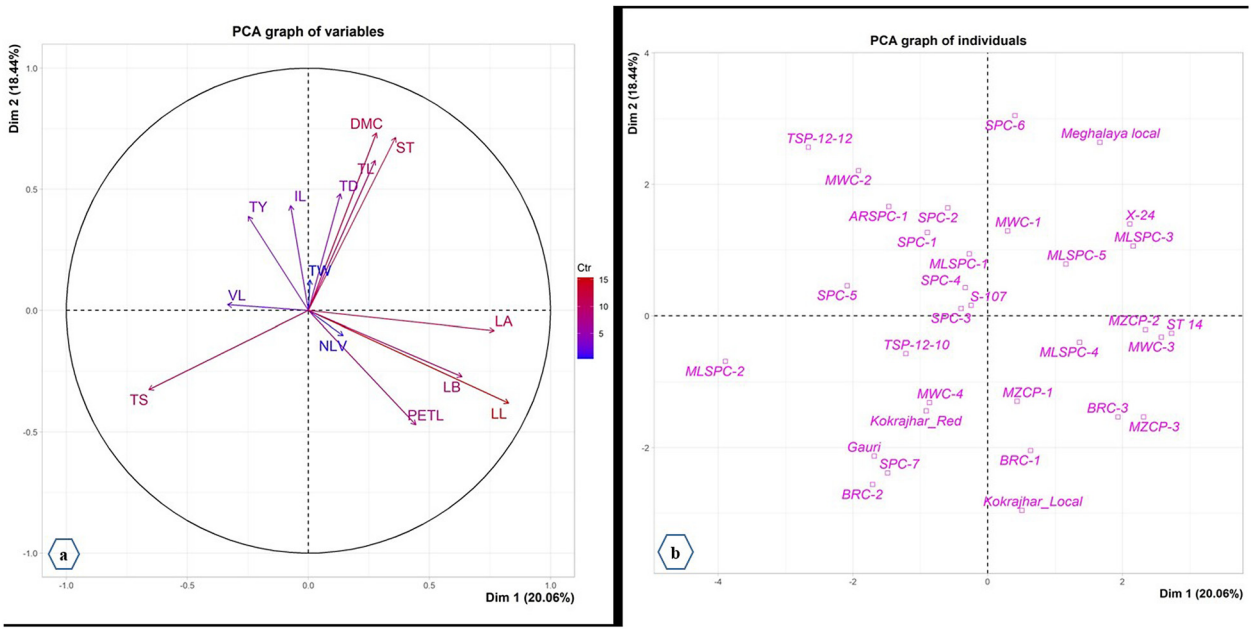

Figure 1. Biplots showing distribution of traits (a) and genotypes (b) over principal components in sweet potato for quantitative traits.

The results of factor analysis (FA) linked to correlated traits have been explained by five factors. The correlated traits for each factor are presented in online Supplementary Table S4. Among the traits highly responsive to the selection were the number of leaves per plant (52.35), followed by tuber weight, vine length, leaf area and tuber yield. Moreover, traits for leaf breadth, tuber length and total sugar were negative for response to selection.

The communality ranged from 0.51 (tuber yield and tuber diameter) to 0.86 (leaf length) and the unique factors ranged from 0.14 (leaf length) to 0.49 (tuber yield and diameter) for all these 14 different biometric traits (online Supplementary Table S4). The maximum uniqueness value for tuber diameter and tuber yield (0.49 each) is followed by leaf breadth (0.46), vine length and total sugar (0.38). In the present study, common variance explains approximately 66.02% of the total variance present among all 14 measures.

Discussion

To develop new cultivars with desirable traits through hybridisation and clonal selection, a diverse population or accessions is required. In the present study, the accessions (32) had demonstrated greater variability in agro-morphological and quality attributes (Table 1). Except dry matter, sugar and starch content, all the traits showed high heritability (>60%) and GA (>20%), indicating that the majority of these traits are governed by additive genetic action and there is potential for selection. The high heritability and moderate GA traits, such as dry matter and starch content, indicate the equal contribution of additive and non-additive

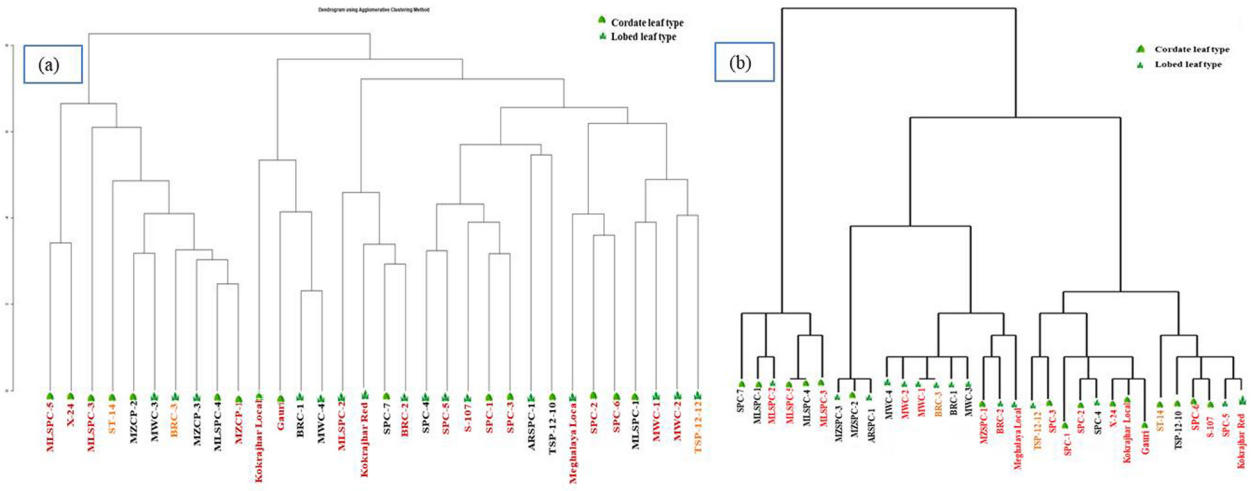

Figure 2. Cluster analysis among the sweet potato genotypes (a) based on quantitative traits (b) based on SSR markers.

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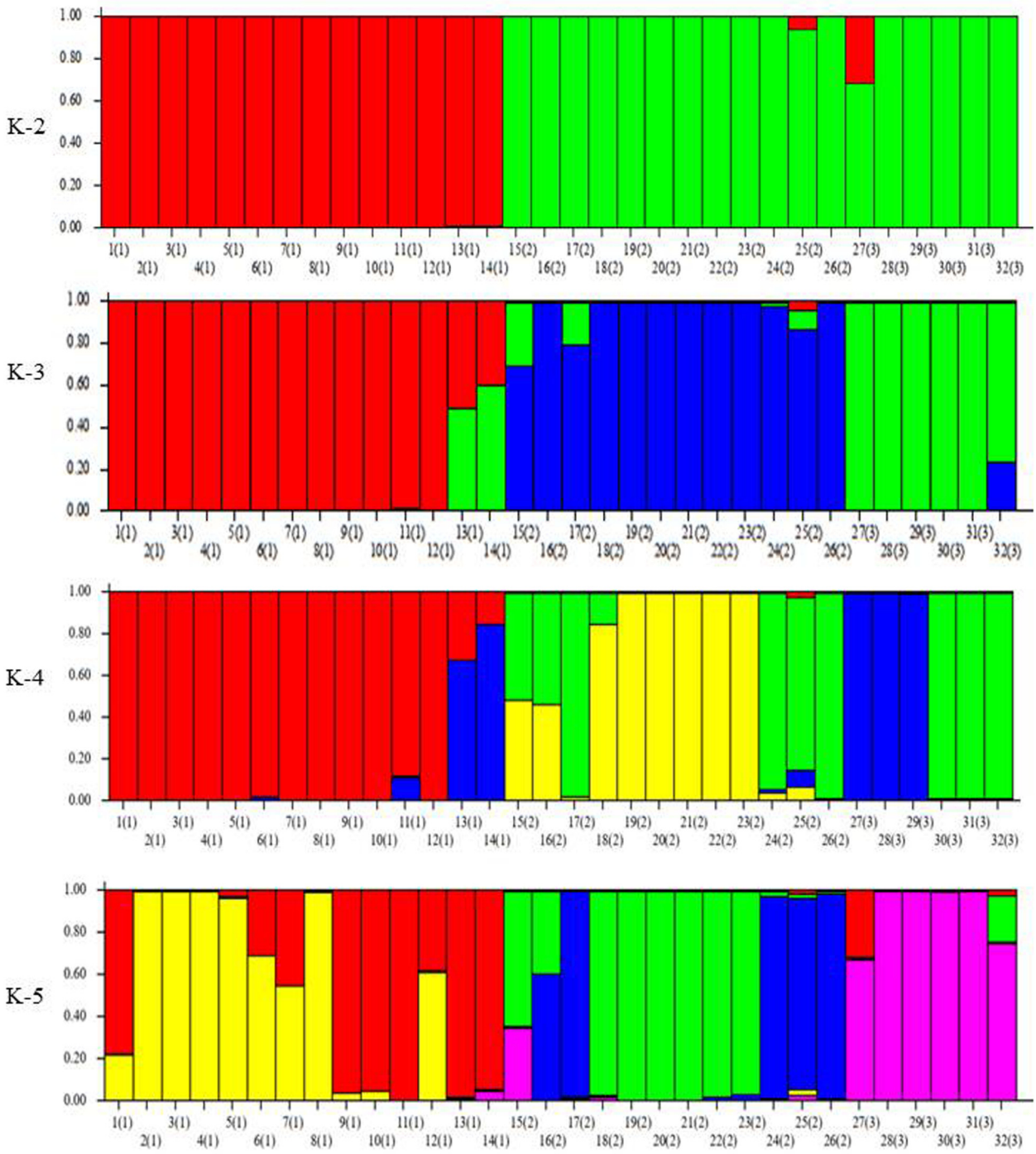

Figure 3. Population structure of 32 sweet potato accessions based on 33 SSR markers at different *K* value (2–5). *X*-axis indicating the genotype in order of (1) SPC-3, (2) TSP-12-12, (3) Kokrajhar Red, (4) SPC-5, (5) Gauri, (6) Kokrajhar-Local, (7) SPC-4, (8) X-24, (9) SPC-2, (10) SPC-1, (11) TSP-12-10, (12) ST-14, (13) S-107, (14) SPC-6, (15) MZSPC-1, (16) Meghalaya-Local, (17) BRC-2, (18) MWC-4, (19) BRC-1, (20) MWC-3, (21) MWC-2, (22) BRC-3, (23) MWC-1, (24) SPC-7, (25) MLSPC-2, (26) MLSPC-1, (27) MLSPC-3, (28) MLSPC-4, (29) MLSPC-5, (30) ARSPC-1, (31) MZSPC-3, (32) MZSPC-2. The numbers in parenthesis indicate their respective cluster.

gene action (Shelby, 2000). Sugar content had high heritability (>60%) with low GA (<10%), indicating that it was highly influenced by environmental factors in this trait. A high heritability and GA for yield and low GA for dry matter content were earlier reported (Otoboni *et al.*, 2020). Therefore, the high heritability also indicated that these traits can be exploited through selection as they maintain dominance and epistasis effect through clonal propagation (Gonçalves Neto *et al.*, 2012).

Genotypic correlation coefficients were higher than phenotypic correlation coefficients for the majority of the traits, except internodal to vine length, leaf area to dry matter content, petiole length to starch and sugar content, and tuber weight to starch and

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Table 3. Additive main effect and multiplicative interaction analysis (AMMI) analysis of variance for yield-attributing traits in sweet potato

Source	DF	Tuber length (cm)			Tuber diameter (cm)			Tuber weight (g)			Tuber yield (t ha^{-1})		
		Mean square	*F* value	% Explained	Mean square	*F* value	% Explained	Mean square	*F* value	% Explained	Mean square	*F* value	% Explained
ENV	2	67.578**	23.98	7.58	0.1901*	1.81	0.14	2262.4**	5.44	2.11	123.55**	14.66	2.32
REP (ENV)	6	2.817			0.1046			415.8			8.42		
GEN	31	24.898**	38.66	43.28	5.1828**	96.22	57.51	5139.7**	69.90	74.44	247.11**	213.06	78.71
GEN:ENV	62	5.97**	9.22	20.75	0.8832**	16.39	19.54	274.4**	3.73	7.95	11.69**	10.08	8.30
PC1	32	10.842	16.84	93.7	1.5327	28.46	89.6	516.4	7.02	97.1	15.63	13.48	69.0
PC2	30	0.774	1.20	6.3	0.1903	3.53	10.4	16.2	0.22	2.9	7.48	6.45	31.0
Residuals	186	0.644			0.0539			73.5			1.15		
Total	349	5.112			0.8058			613.3			27.57		

Note: *Significant at $P \leq 0.05$ and **significant at $P \leq 0.01$.

sugar content. The lesser magnitudes of phenotypic correlation coefficients than genotypic correlation coefficients had also been reported (Tsegaye *et al.*, 2006; Dash *et al.*, 2015; Mekonnen *et al.*, 2020), which reveals the presence of inherent genetic relationships among various characters and the phenotypic expression of these traits is less influenced by the environment. Economical traits (tuber yield) were positively correlated with tuber length, tuber diameter and tuber weight. Quality traits (dry matter and starch content) were significant and positively correlated with each other as well as with yield, while both traits were negatively correlated with total sugar content. This could be due to the inverse relation (interconversion) between the starch and sugar content in the tubers, as earlier reported in potatoes (Islam *et al.*, 2022).

PCA is an important tool to identify the plant traits that contribute to variations within a group of genotypes for the selection of the parental lines. The cumulative variance of 69.63% contributed by the first five PCs indicates that the identified traits within these axes exhibited great influence on the phenotype of the landraces and could effectively be used for selection among these lines. Leite *et al.* (2022) also observed 82.46% of the cumulative variance in the first five PCs. The distribution of variance over multiple PCs may be due to poor correlation among the contributing traits, such as yield and growth traits, that attribute to a higher diversion of the photosynthates towards vegetative growth than accumulation in tubers. Like PCA, the cluster analyses grouped the genotypes into three major clusters and showed the presence of wider diversity within and between the clusters. The accessions from the diverse cluster can be utilised for the hybridisation and selection of new recombinants.

Allele richness (AR), or allelic diversity, is a measure of genetic diversity and is indicative of a population's long-term potential for adaptability and persistence. Our study had a higher level of allelic diversity in the population as indicated by AR range (4.0–14), which was also observed earlier in sweet potatoes (Tumwegamire *et al.*, 2011; Gwandu *et al.*, 2012; Rodriguez-Bonilla *et al.*, 2014). The higher number of alleles in sweet potatoes can be explained by the autopolyploidy (hexaploidy) nature of the crop. Higher AR helps in population's potential adaptation to future environmental changes since diversity is the raw material for evolution by natural selection (Fisher, 1930). Further, wide variations were also observed for the effective number of alleles (1.45–3.83), indicating the differential contribution of the alleles towards heterozygosity. The amount of heterozygosity is a general indicator of the amount of genetic variability present in a population. The higher observed heterozygosity (0.51) at all the loci than the expected heterozygosity (0.49) indicated the isolated breaking effect (the mixing of two previously isolated populations). High levels of heterozygosity have also been observed in sweet potatoes from Tropical America (0.37), Latin American (0.60) and Kenyan (0.75) (Karuri *et al.*, 2010; Roullier *et al.*, 2013). This could be due to the outcrossing and self-incompatible nature of the plant (Zhang *et al.*, 1999). For instance, this self-incompatibility in the field conditions might have resulted in chance seedlings from crossings, another means of increasing genetic diversity (Yada *et al.*, 2010). Moreover, the heterozygosity-based hybrid vigour presence in the population could be exploited through clonal selection (Dobzhansky, 1952).

The PIC values are a reflection of allelic diversity and frequency among the accessions and are estimators of the usefulness of any marker system for genotype distinction and genetic diversity analysis. In the present study, SSR markers had high

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discriminatory power in differentiating the accessions, as shown by the PIC value (0.31–0.71) and also indicating the presence of a higher level of genetic diversity among the accessions, as shown by the high polymorphism (medium > 0.25 to high > 0.5) for each of the 15 markers out of 30. A higher PIC value has also been reported in South African (0.85) and CIP (0.7816) accessions (Anglin *et al.*, 2021; Naidoo *et al.*, 2022), while a lower value (0.188–0.204) was reported in the accessions of China having collections from other countries (Yang *et al.*, 2015). Further, a higher SII value (1.16) indicated a high level of genetic diversity among the accessions. Our study was similar to previously reported in South African accession and higher than the Central European accession with a lower SII value (0.86) (Naidoo *et al.*, 2022).

The cluster analysis revealed three distinct groups and the local landraces of different geographic origins distributed in the clusters (II and III), indicating the existence of a wide range of variation for breeding and strategic conservation (Nair *et al.*, 2017). Similarly, PCoA differentiated the genotypes into three major groups, and the accessions Meghalaya Local and MZSPC-3 (both red and cordate) were found close to each other in a separate group. Likewise, SPC-3 and TSP-12-12 were found closer to each other with red and orange peel colours, respectively, and cordate leaf shapes. These genotypes can be used for breeding for some specific traits. Moreover, the relationship between morphological and molecular diversity has also indicated the poor association of these EST markers with the traits under study. This could be due to the large, complex genome ≈2–3 GB in size (Ozias-Akins and Jarret, 1994) and uses of the limited number of markers in the study.

AMOVA among and within groups of sweet potato populations was based on leaf shape and peel colour. The significantly higher variation (81.65%) was observed within the population, followed by among the populations (18.35%). Moreover, molecular cluster analysis-based AMOVA showed 50% variations among the individuals and between the populations. Yang *et al.* (2015) observed similar findings in the sweet potato accessions of China. Further, group-wise Nei genetic distance has also revealed the presence of wider diversity among the groups, and orange cordate was found to be the most diverse from the white-lobed, followed by orange cordate and orange-lobed. Here, leaf shape (lobed/cordate) was a prominent factor for grouping over the peel colour.

The genetic structure analysis based on the 30 microsatellite markers differentiated the accessions into three genetic groups, and the proportion of admixture in the population was comparatively low (18.75% at the 95% threshold level at optimal $K = 3$), which may be attributed to different geographical origins. Moreover, among the genotypes, TSP-12-10 had the least admixture, and accessions SPC-3, MLSPC-3 and SPC-7 (all from Meghalaya) had alleles from all three groups. This shared variation indicated an ancient lineage among the genotypes propagated clonally.

In the present study, the AMMI model of stability for yield and related traits was analysed, and the ANOVA showed the significant contribution of the G and GEI on the expression of all the yield-attributing traits over the years under mega environment (online Supplementary Table S3). Further, the higher value for the sum of square due to GEI over the GEN sum of square for all the yield-attributing traits also indicated that the interactions are signal-rich and not buried in the noise. This marked the usefulness of AMMI analysis in the study. Moreover, Kivuva *et al.* (2014) observed a significantly higher contribution of the environment to tuber yield under managed drought stress conditions. The FA revealed that important traits like tuber weight, tuber yield, dry matter and starch content are responsive to selection in the present population under the mega-environment (humid subtropics). Moreover, traits such as leaf breadth, tuber length and total sugar were negative for response to selection. Further, higher uniqueness values for tuber diameter, tuber yield and leaf breadth indicated that variance for these traits is explained by specific factors, i.e. unrelated to common factors (online Supplementary Table S4). Uniqueness is the part of the variance associated with the error term. Growth-related traits such as leaf length, internodal length, leaf area and dry matter have shown higher communality and lower uniqueness, suggesting that variance for these traits is explained by a common factor and is highly effective to account for total variations as compared to other traits.

The MTSI has been proven useful for selecting genotypes with multiple traits based on performance and stability (Olivoto and Nardino, 2021). The MTSI for tuber length, tuber diameter, tuber weight and tuber yield indicates stable selection in genotypes X-24, MLSPC-3, MLSPC-5, ARSPC-1 and TSP-12-12. Among these selected stable genotypes, the high-yielding accession TSP-12-12 (26.0 t ha^{-1}) can be promoted for commercial production under a mega environment, and the local collection MLSPC-3 (23.9 t ha^{-1}) with a stable and higher yield can be further promoted for advanced varietal trials under multi-location testing. Furthermore, a stable genotypic background of high-yielding unstable genotypes such as MLSPC-2 (24.7 t ha^{-1}) and MWC-1 (25.0 t ha^{-1}) can be used in improvement programmes.

Conclusion

Sweet potato accessions collected from various parts of the region showed greater variability in growth, yield and quality traits. Molecular analysis also revealed a wider diversity among the accessions. The desirable traits such as tuber yield, dry matter and starch content showed additive gene action as depicted by high heritability and GA and were also highly responsive to selection. Both quality traits, namely dry matter and starch content, were significant and positively correlated with each other, while both were negatively correlated with total sugar. The G and GEI contributed significantly to the total variations. All the stability measures were positively correlated and were able to identify the common stable genotypes. Based on the MTSI (tuber length, tuber diameter, tuber weight and tuber yield), genotypes X-24, MLSPC-3, MLSPC-5, ARSPC-1 and TSP-12-12 were selected.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S1479262123001041

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Competing interests. None.

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