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Molecular analysis of genetic diversity among different groups of potato (*Solanum tuberosum* L.)

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Abstract

Twenty one simple sequence repeat (SSR) markers were used to develop SSR profile in 169 genotypes of potato belonging to Indian accessions, tuberosum group (*Solanum tuberosum* ssp. tuberosum), breeding lines, neotuberosum, andigena group and tuberosum × andigena derivatives. All the 21 SSR markers showed polymorphism and were able to discriminate the genotypes studied. Molecular markers *viz*., STM0037, STI0012, STM1052, STM 5127, STG0001 and STI0030 were useful due to their high polymorphic information content and differentiating power. A high magnitude of genetic diversity was observed in andigena group (*Solanum tuberosum* ssp. andigena). Andigena accessions were also diverse from other groups of accessions as most of them formed a clear separate and distinct cluster. Tuberosum group germplasm, breeding lines, neotuberosum and Indian accessions formed a separate cluster, whereas Indian accessions were distributed widely. The Shannon Weaver diversity index for Indian accessions was higher than that of breeding lines, tuberosum germplasm, neotuberosum and tuberosum × andigena accessions. These results show that comparative genetic diversity of Indian accessions is good in comparison to other tuberosum group accessions.

Key words: Genetic diversity, Potato, *Solanum tuberosum*, simple sequence repeats markers

Introduction

Potato breeding programmes based on *Solanum tuberosum* L. have a narrow genetic base (Bradshaw and Ramsay 2005; Kumar et al. 2011). Most breeders agree that it is increasingly difficult to obtain improvement in yield and other traits from among recombinants produced by crossing presently available parental clones. Narrow genetic base of Indian potato selections developed since 1990 has also been reported earlier (Gopal and Oyama 2005; Kumar et al. 2011). North American (Mendoza and Haynes 1974; Plaisted and Hoopes 1989) and European varieties (Hawkes 1979; Ross 1986) have also been reported to have a narrow genetic base.

Molecular markers due to their simplicity, quickness and informativeness are being increasingly used to study the genetic divergence. Molecular markers have also been used in potato to assess genetic diversity (Milbourne et al. 1997; McGregor et al. 2000; Bornet et al. 2002; Chimote et al. 2004). Due to their co-dominant inheritance, robustness and amenability to high throughput, simple sequence repeats (SSRs) or microsatellites have become a tool of choice for investigations of critical importance to crop germplasm managers (Hokanson et al. 1998). The comparative genetic divergence study of Indian accessions compared to other cultivated tetraploid potatoes including primitive cultivated andigena accessions can provide information about genetic base of Indian accessions. The objectives of this study, therefore, were to: find usefulness of microsatellite markers for estimating genetic variation and relationships in tetraploid potato and to estimate the comparative genetic diversity of Indian accessions as compared to other cultivated tetraploid potato accessions of the world.

Materials and methods

The material used to study genetic diversity included 33 Indian accessions and 136 other germplasm accessions available at International Potato Centre

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(CIP) Lima, Peru (Table 1). Twenty one simple sequence repeats (SSRs) markers were selected out of 24 of Potato Genetic Identity Kit developed at CIP (Table 2) [International Potato Center (CIP) 2008].

Table 1. Plant material used in the present study and unique alleles in different groups of accessions

Group of acc.*	No. of acc .*	Unique alleles
Indian acc.	33	STM $1052_{268 \text{ and } 270}$; STI$0003_{150, 160 \text{ and } 179}$ and STI0004_{83}
Andigena	61	STM 1064_{201}; STM$1053_{170, 183 \text{ and } 187}$; STM $0037_{95, 106, 109, 111, 120 \text{ and } 133}$; STM$0031_{195 \text{ and } 206}$; STM$1104_{182, 188 \text{ and } 192}$; STM$1052_{214, 239, 246, 256, 258, 262 \text{ and } 263}$; STM$1106_{163, 166 \text{ and } 214}$; STM$5114_{310 \text{ and } 317}$; STM$5127_{282}$; STG$0001_{140, 152, 153 \text{ and } 155}$; STG$0010_{181}$; STI$0003_{155, 166 \text{ and } 173}$; STI$0004_{89 \text{ and } 104}$; STI$0014_{127, 136 \text{ and } 151}$; STI$0030_{113 \text{ and } 137}$ and STI0033_{155}
Breeding lines	32	STM1052_{254}; STM 5127_{270} and STG0001_{159}
Neotuberosum	7	STM5114_{311} and STG$0010_{183 \text{ and } 186}$
Tuberosum germplasm	30	STM0031_{202}; STG0010_{192} and STI0012_{185}
Tuberosum x andigena	6	STM1064_{210}, STI0001_{200} and STI0033_{146}

*acc = accessions

Table 2. Polymorphic information content (PIC) for different SSR markers based on allelic phenotypes in different group of accessions

Marker	Adg	Bred	Neo	TBR	T×A	India	All 169
STM1064	0.77	0.77	0.65	0.76	0.61	0.78	0.81
STM1053	0.80	0.80	0.45	0.64	0.67	0.50	0.73
STM0037	0.96	0.94	0.65	0.60	0.83	0.92	0.97
STM0031	0.84	0.28	0.41	0.70	0.00	0.79	0.93
STM1104	0.94	0.85	0.82	0.86	0.67	0.78	0.93
STM1052	0.99	0.92	0.73	0.87	0.78	0.92	0.96
STM1106	0.91	0.70	0.61	0.87	0.78	0.53	0.87
STM5114	0.80	0.85	0.82	0.80	0.50	0.84	0.87
STM5127	0.97	0.96	0.78	0.88	0.83	0.84	0.96
STG0001	0.89	0.93	0.82	0.84	0.83	0.93	0.96
STG0010	0.80	0.87	0.78	0.81	0.67	0.86	0.88
STG0016	0.94	0.91	0.61	0.85	0.83	0.81	0.93
STG0025	0.65	0.37	0.41	0.50	0.61	0.50	0.59
STI0001	0.91	0.94	0.86	0.90	0.78	0.90	0.95
STI0003	0.93	0.89	0.86	0.86	0.78	0.90	0.95
STI0004	0.89	0.89	0.82	0.82	0.78	0.88	0.91
STI0012	0.95	0.91	0.86	0.93	0.83	0.92	0.97
STI0014	0.82	0.75	0.78	0.71	0.61	0.78	0.83
STI0030	0.97	0.87	0.86	0.92	0.83	0.87	0.96
STI0032	0.93	0.79	0.61	0.71	0.67	0.91	0.95
STI0033	0.81	0.84	0.69	0.80	0.78	0.88	0.91
average for population	0.88	0.81	0.71	0.79	0.70	0.81	0.90

Adg = andigena, Bred = breeding lines, Neo = neotuberosum, Tbr = tuberosum germplasm, TxA = tuberosum × andigena and India = Indian accessions

Genomic DNA was extracted using cetyltrimethylammonium bromide (CTAB) procedure of Doyle and Doyle (1990). Polymerase chain reactions (PCR) were performed in a 10 µl volume containing 90 mM Tris-HCl, 20 mM $(NH_4)_2SO_4$, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 30 nM of 700 or 800 IRDye-labeled M13 forward primer (LI-COR), 20 nM M13-tailed forward SSR primer, 30 nM reverse SSR primer, 1 unit of Taq polymerase, and 25 ng of genomic DNA. Polymerase chain reaction (PCR) was carried out in thermocycler using cycling profile of: 4 min at 94°C; 33 cycles of 50 seconds at 94°C, 1 min at annealing temperature (T_a) determined experimentally for each SSR primer combination and 50 seconds at 72°C; with a final extension step of 4 min at 72°C. Detection was done using LICOR DNA analyzing system. Alleles were sized with the IRDye 50-350 bp fragment size ladder (LI-COR, USA). SSR alleles were detected and scored using the SAGA Generation 2 software (LI-COR, USA). The SSR band/allele sizes reported in present study are for products multiplied by M13 - tailed primers and these are 19 nucleotides longer than products amplified by primers without this tail. Comparison of allele size in present study with other studies using untailed primer should take in account this 19 bp M13 sequence. Although SSR generate co-dominant markers, problems arise in identification of polyploids genotype based on band intensities. Banding patterns observed were therefore recoded as presence/absence matrix and are referred to as 'allelic phenotypes' (Reid et al. 2011). Genetic analyses were performed using the DARwin 4.0 software (http://darwin.cirad.fr/darwin/Home.php). Dissimilarity tree was built by the unweighted neighbour joining method using the dissimilarity matrix generated using Jaccard's

Coefficient. Polymorphic information content (PIC) and Shannon Weaver diversity index of each SSR marker as estimates of diversity were calculated and average diversity compared among accessions. As a measure of the information provided by each locus, heterozygosity was calculated as PIC values for each SSR marker using formula: $H = 1 \sum p_i^2$, where p_i is the frequency of allelic phenotype *i* (Nei 1973). Shannon Weaver diversity index (1949) was calculated using the formula:

Shannon Weaver diversity index $(H') = -\sum(p_i \ln p_i)$

where *pi* is the frequency of allele phenotype *i* in a specific group.

Results and discussion

Out of the 21 SSR markers 19 showed 1-4 bands per genotype. Only one accession I-1150 showed five bands with marker STM0037. For SSR marker STI0003 there were 5 accessions with 5 bands, two accessions with 6 bands and 1 accession with 7 bands. STM0031, STM1104, STM1106, STM5127, STG0016, STI0012 and STI0033 failed to amplify one accessions each, STM 5114 and STMI0003 failed to amplify two accessions each, while STG0010 failed to amplify 4 accessions. As repeated experiments gave consistent results, these accessions were considered to carry null alleles for these markers. Null alleles are presumably due to mutations in primer binding sites. As in the present study we were recorded banding pattern as allelic phenotype, possibility of other null allele present in other accessions can not be ruled out.

Polymorphic information content (PIC) values ranging from 0.59 to 0.97 were recorded in all the 169 accessions, while Indian accessions showed a range from 0.50 to 0.93 (Table 2). The lowest PIC was 0.59 for marker STG0025 and the highest was 0.97 for STM0037 and STI0012. Markers, STM1052, STM5127, STG0001 and STI0030 also had very high PIC value (0.96) including in Indian accessions. The number of alleles varied from 3 for STG0025 to 16 for STM1052 (Table 3). Marker STM5127 showed highest number of allelic phenotypes (68) and highest number of unique profiles (42). Marker STI0030 with 12 alleles showed 67 different profiles of which 34(20.1%) were unique. Marker STG0025 with very low PIC value had only 3 alleles and showed 4 different profiles of which none was unique. The occurrence of most common allelic phenotype ranged from 7.1% for STI0012 to 50.9% for STG0025. Markers STM0037, STI0012, STM1052, STM5127, STG0001 and STI0030 with high PIC value also had high number of unique profiles and low number of most common allelic phenotypes.

The SSR markers used in the study were very useful as all showed polymorphisms. The 21 used in the present study were reported by Ghislain et al. (2009a) to be single locus, high polymorphic content, and high quality of amplicons as determined by clarity and reproducibility. However in the present study two markers showed more than 4 bands in some accessions. These markers differentiated all the 169 genotypes. As only allelic phenotypes were scored, no data on allele frequency can be calculated. The chance of two genotypes showing identical profile can therefore not be derived from allele frequencies. However, an upper limit can be calculated based on frequency of most common allelic phenotype of each marker. An estimation of upper limit based on presented frequencies of most common allelic pheotypes of all 21 markers is $0.29 \times 0.379 \times 0.089 \times 0.16 \times 0.195 \times 0.083 \times 0.296 \times 0.243 \times 0.112 \times 0.112 \times 0.201 \times 0.16 \times 0.509 \times 0.13 \times 0.118 \times 0.213 \times 0.071 \times 0.29 \times 0.101 \times 0.112 \times 0.166 = 4.7 \times 10^{-17}$. This chance is 1 out of 2.1×10^{16} $(1/(4.7 \times 10^{-17}))$. The chance of two accessions yielding identical profile for 21 markers is infinitesimally small.

The identified markers with high PIC value were very useful in differentiating genotypes. The chance of two genotypes showing identical profile using these 6 markers is $0.089 \times 0.071 \times 0.083 \times 0.101 \times 0.112 \times 0.112 = 6.6 \times 10^{-7}$. This chance of 1 out of 1.5 millions $(1/(6.6 \times 10^{-7}))$ is also very rare. To verify the genetic identity only a few such SSR markers can be used. However, to study a large number of genotypes it will be better to use more number of SSR markers with wide genome coverage so that a precise estimate of genetic diversity can be obtained.

The DNA marker technique has been useful in studying the characterization and genetic relationship of germplasm. It is an efficient assay and has shown high levels of polymorphism in many crops including potato. In present study also the molecular markers have been successfully used for cultivar identification (Kawchuk et al. 1996; McGregor et al. 2000; Ghislain et al. 2000; Norero et al. 2002; Ghislain et al. 2004), to test differences between the two subspecies of *S. tuberosum* (Raker and Spooner 2002), to compare clones conserved *in vitro* with original clones maintained in the field (Perazzo et al. 2000), to detect genetic diversity (Provan et al. 1999) and for

Table 3. Characteristics of the 21 selected SSR markers

	Exotic accessions						Indian Accessions					
	No. of different alleles	No. of different profiles	No. of unique profiles	% of unique profiles	No. of most common allelic pheno-type	% of most common allelic pheno-type	No. of different alleles	No. of different profiles	No. of unique profiles	% of unique profiles	No. of most common allelic pheno-type	% of most common allelic pheno-type
STM1064	9	18	4	2.4	49	29.0	9	8	2	6.1	12	36.4
STM1053	6	8	2	1.2	64	37.9	5	2	0	0.0	17	51.5
STM0037	15	62	29	17.2	15	8.9	11	17	9	27.3	5	15.2
STM0031	10	35	13	7.7	27	16.0	10	11	7	21.2	13	39.4
STM1104	12	49	25	14.8	33	19.5	10	8	2	6.1	11	33.3
STM1052	16	55	26	15.4	14	8.3	16	18	11	33.3	5	15.2
STM1106	11	33	20	11.8	50	29.6	10	7	3	9.1	22	66.7
STM5114	9	24	8	4.7	41	24.3	9	11	4	12.1	10	30.3
STM5127	14	68	42	24.9	19	11.2	13	12	5	15.2	10	30.3
STG0001	16	59	32	18.9	19	11.2	16	21	14	42.4	5	15.2
STG0010	10	26	7	4.1	34	20.1	10	11	4	12.1	7	21.2
STG0016	9	37	14	8.3	27	16.0	8	10	3	9.1	11	33.3
STG0025	3	4	0	0.0	86	50.9	2	2	0	0.0	17	51.5
STI0001	7	38	11	6.5	22	13.0	7	16	6	18.2	8	24.2
STI0003	14	48	22	13.0	20	11.8	14	17	11	33.3	6	18.2
STI0004	11	46	26	15.4	36	21.3	9	15	9	27.3	7	21.2
STI0012	9	56	23	13.6	12	7.1	9	16	7	21.2	5	15.2
STI0014	7	16	8	4.7	49	29.0	6	7	2	6.1	11	33.3
STI0030	12	67	34	20.1	17	10.1	11	14	8	24.2	7	21.2
STI0032	8	50	28	16.6	19	11.2	7	17	9	27.3	7	21.2
STI0033	9	30	13	7.7	28	16.6	8	15	7	21.2	7	21.2

phylogenetic studies (Raimondi et al. 2005).

Various techniques like pedigree analysis (Gopal and Oyama 2005; Kumar et al. 2011), RAPD (Chakrabarti et al. 2001) and SSR (Chimote et al. 2004; Ghislian et al. 2006) have been previously employed to study genetic diversity in Indian potato varieties. Most of these studies have indicated narrow genetic base of Indian varieties. Pedigree analysis of 77 advanced potato selections showed that their origin could be traced to only 49 ancestors (Gopal and Oyama 2005). However, wide genetic base of Indian varieties was estimated using RAPD analysis (Chakrabarti et al. 2001). Most of these studies were based only on Indian varieties. Comparing the genetic diversity of potato accessions belonging to a particular country/ region with CIP germplasm accessions can be useful as CIP gene bank maintains the largest collection of potato in world. Wang et al. (2013) compared genetic diversity of Chinese cultivars with that of CIP potato germplasm using amplified fragment length polymorphism (AFLP) markers and found that diversity of CIP potato resources was higher that of Chinese cultivars. In morphology based divergence study poor divergence was observed in exotic as well as Indian varieties bred from *tuberosum*, with most of them clubbed together with very small intra-cluster distance (Gaur et al. 1978).

The average PIC value for Indian accessions was more than that of breeding lines, tuberosum germplasm, neotuberosum and tuberosum × andigena accessions (Table 2). It was, however, less as compared to that of andigena accessions. Estimates

of diversity as Shannon Weaver diversity index (*H'*) were highest for andigena accessions (Table 4). Shannon Weaver diversity index of Indian accessions was more than that of tuberosum germplasm, breeding lines, neotuberosum and tuberosum × andigena accessions. However, Shannon Weaver diversity index of Indian accession was lower than that of andigena accessions.

Most of andigena (*Solanum tuberosum* ssp. andigena) accessions formed a clear separate and distinct cluster in dissimilarity tree (Fig. 1). Out of 217 alleles generated by 21 SSR markers, 44 belonging to 16 different SSR markers were present in andigena accessions only (Table 1). Tuberosum group germplasm, breeding lines, neotuberosum and Indian accessions formed a separate second cluster. Neotuberosum accessions were not grouped with andigena accessions. Some tuberosum × andigena accessions were grouped with andigena accession cluster while others were present in other major cluster. Indian accession I-1039 and some breeding lines were grouped at one end of andigena accession cluster indicating that these were more diverse than other

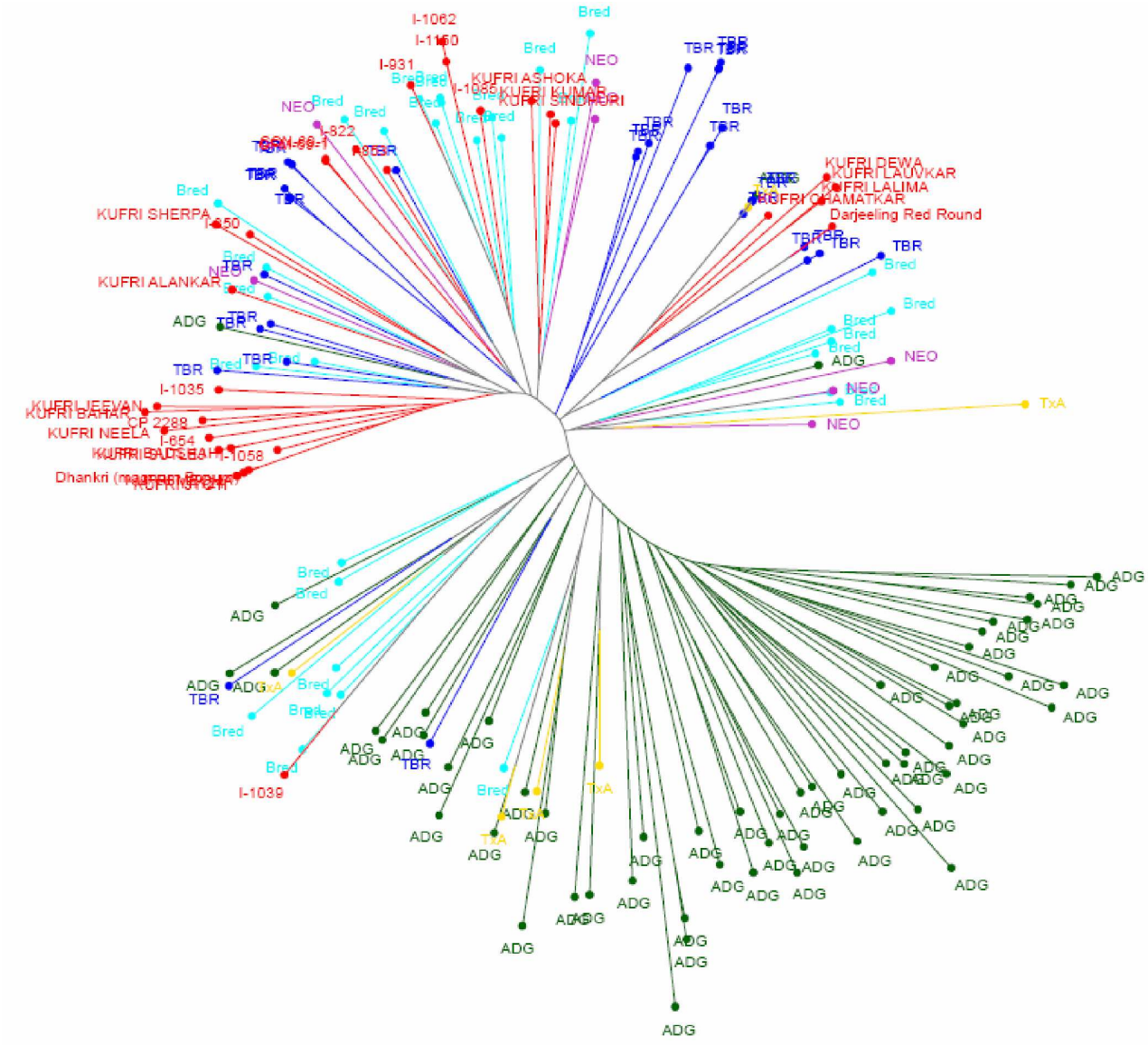

Fig. 1. Radial tree (Neighbour Joining) of Indian accessions (shown as individual accession name, (*red*), tuberosum germplasm (TBR, *blue*), breeding lines (Bred, *cyan*), Tuberosum × andigena (T × A, *yellow*), neotuberosum (NEO, *purple*) and andigena (ADG, *green*) accessions

cultivated tuberosum genotypes. Indian accessions were distributed widely in second cluster. There were 6 alleles which were present in Indian accessions only. Three alleles each were present only in tuberosum germplasm, neotuberosum, tuberosum × andigena and breeding lines.

The results in present study show that andigena accessions were most diverse as estimated by Shannon Weaver diversity index. High diversity of Andigena accessions is due to large number of unique alleles present in Andigena accessions and this resulted in their forming a separate distinct cluster on dissimilarity tree. Spooner et al. (2005) also reported that rare SSR alleles were identified predominately from andigena group and andigena accessions formed a cluster separate from Chilean landraces, modern European cultivars and Indian putatively extant group andigena clones. High diversity in primitive cultivated potatoes of *Solanum tuberosum* group andigena is well known as andigena is considered to be a rich source of genetic diversity (Kumar et al. 2008). Group Andigena display a wide range of morphological variations, including diversity in colours of flower and tuber shapes. The group Andigena is distinguished morphologically from group Tuberosum by narrower leaflets and upright leaves with acute leaf angle with the stem. The diverse andigena accessions with wide range of valuable traits can be useful parents in breeding programmes. The Tuberosum accessions from different parts of world including breeding lines and Indian accessions were developed mainly from material received from Europe. Considering the high diversity of andigena accessions, broadening of the tuberosum genebase was undertaken in Europe and America by creating long-day adapted Neo-tuberosum (N-T) from large populations of andigena. This took six or more cycles of recurrent mass selection (Simmonds 1976; Rasco et al. 1980). Varieties with N-T in their pedigrees include the New York releases Rosa, which is 50% N-T, and Eva, 25% N-T. Neo-Tuberosum accessions in present study group with Tuberosum and other accessions cluster instead of Andigena accessions cluster. This supports earlier findings that Neo-Tuberosum materials are clearly not the product of strict inter-Andigena breeding (Ghislain et al. 2009b).

Table 4. Shannon Weaver diversity index for different group of accessions based on allelic phenotype

Marker	Adg	Bred	Neo	TBR	T×A	India	All 169
STM1064	1.83	1.65	1.08	1.56	1.01	1.74	2.03
STM1053	1.80	1.35	0.80	1.14	1.24	0.69	1.55
STM0037	3.39	2.91	0.60	2.47	1.79	2.66	3.73
STM0031	2.22	0.64	0.60	1.58	0.00	1.96	2.98
STM1104	3.12	2.22	1.75	2.23	1.24	1.75	3.26
STM1052	1.61	2.66	1.48	2.24	1.56	2.70	3.55
STM1106	2.85	1.55	1.15	2.18	1.56	1.19	2.58
STM5114	1.97	2.13	1.75	1.94	0.87	2.09	2.47
STM5127	3.64	1.54	1.55	2.25	1.49	2.15	3.71
STG0001	2.81	2.81	1.75	2.15	1.79	2.88	3.57
STG0010	2.05	2.13	1.55	1.83	1.24	2.13	2.57
STG0016	2.99	2.63	1.00	2.07	1.79	1.96	3.05
STG0025	1.13	0.67	0.60	0.69	1.01	0.69	1.00
STI0001	2.69	2.87	1.95	2.43	1.56	2.56	3.24
STI0003	2.96	2.43	1.95	2.04	1.56	2.54	3.42
STI0004	2.55	2.45	1.75	2.07	1.56	2.41	3.07
STI0012	3.25	2.66	1.95	2.77	1.79	2.62	3.68
STI0014	1.95	1.53	1.55	1.44	1.01	1.66	2.01
STI0030	3.60	2.29	1.95	2.69	1.49	2.31	3.82
STI0032	3.06	1.92	1.15	1.56	1.24	2.61	3.44
STI0033	2.14	2.24	1.28	1.89	1.56	2.36	2.80
average for population	2.55	2.06	1.39	1.96	1.35	2.08	2.93

Adg = andigena, Bred = breeding lines, Neo = neotuberosum, Tbr = tuberosum germplasm, T×A = Tuberosum × andigena and India = Indian accessions, respectively

The comparative genetic diversity of Indian accessions based on Shannon Weaver diversity index was higher than all other groups of accessions except andigena accessions. Six alleles were present in Indian accessions only. Wide distribution of Indian accessions in second cluster comprising of accessions other than andigena accessions and with one Indian accession at one end of andigena accessions cluster also shows that comparative genetic diversity of Indian accession is good in comparison to other tuberosum group accessions which include breeding materials from different countries available at International Potato Centre (CIP) Lima Peru.

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