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Utility of AhTE Markers for Genetic and Genomic Studies in Groundnut (*Arachis hypogaea* L.)

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A B S T R A C T

Recombinant inbred line (RIL) and mutant populations of groundnut were employed to assess the utility of *Arachis hypogaea* transposable element (AhTE) markers, which detect the transposition polymorphism of *Arachis hypogaea* miniature inverted-repeat transposable element (*AhMITE1*), for the genetic and genomic studies to enhance the groundnut productivity. Of the two alleles (with and without *AhMITE1* insertion) at each locus, the latter was more frequent (0.56) across 79 AhTE markers among the genotypes. Observed heterozygosity (H_O) was higher for intergenic markers when compared to genic AhTE markers. Similarly, the AhTE markers from the A genome showed higher H_O when compared to those from B genome. Mutant population in general showed the higher heterozygosity over the RIL population. AhTE markers displayed as high as 65.82% polymorphism, based on which the genotypes could be classified into two groups. Thus, the study indicated the usefulness of the AhTE markers in the genetic and genomic studies in groundnut.

Introduction

Groundnut (*Arachis hypogaea* L.) has a genome of 2.8 Gb, and the diploid progenitors have been sequenced (Bertioli *et al*., 2016; Chen *et al*., 2016) for hastening the application of genomics in groundnut breeding for various traits to enhance the productivity (Bevan *et al*., 2017). Currently, genomics is providing new foundations and genomic innovations for crop-breeding systems in many crops (Bevan *et al*., 2017; Yuan *et al*., 2017). Of them, the development and use of DNA markers is the frontrunner with significant applications in developing new crop varieties with considerable genetic gain (Yuan *et al*., 2017). Though several types of marker systems are available in groundnut, most of them suffer from low polymorphism especially in cultivated groundnut (Song *et al*., 2010; Khera *et al*., 2013) over the wild types (Moretzsohn *et al*., 2009), which limits their application in crop improvement (for review, Holbrook *et al*., 2011).

Arachis hypogaea transposable element (AhTE) markers, which detect the transposition polymorphism of *Arachis hypogaea* miniature inverted-repeat transposable element (*AhMITE1*), have been developed in groundnut (Bhat *et al*., 2008; Gowda *et al*., 2010; Shirasawa *et al*., 2012a). Due to the large number and variation for transpositional activity of *AhMITE1*, AhTE markers show considerably high (27.4%)

polymorphism (Shirasawa *et al*., 2012a; Kolekar *et al*., 2016). In this study, an effort was made to analyze the population genetic parametersusing AhTE markers among a mutant population and a recombinant inbred line (RIL) population of groundnut to assess the utility of AhTE markers in genetic and genomic studies.

Materials and Methods

Two types of populations; the first consisting of the RILs (432) of TMV 2 × TMV 2-NLM, and the second consisting of mutants and their parents were used for assessing the genetic features of the AhTE markers. The AhTE markers used in this study were developed by (Shirasawa *et al*. 2012a and 2012b). Total genomic DNA was extracted from young leaves using modified cetyltrimethyl ammonium bromide (CTAB) method (Mace *et al*., 2003). A total of 79 AhTE markers were used for genotyping. PCR reactions were carried out with 50 ŋg of template DNA, 5 pmol of each primer, 10X of *Taq* polymerase buffer [500 mMKCl, 100 mM Tris-HCI (pH 8.5], 2.0 mM of $MgCl_2$, 0.25 mM of dNTPs and 0.15 U of *Taq* polymerase in a total volume of 10.0 µl. PCR was performed in Veriti 96-Well Thermal Cycler (Applied Biosystem), using the following PCR profile; 95°C for 5 min, 35 cycles of 1 min at 95°C, 1 min at 53°C and 1.30 min at 72°C, and a final extension step of 8 min at 72°C. The amplicons were analyzed by running on 1.8% agarose gel with 1X TAE at 80 V for 2 h using Bio-Rad gel electrophoresis unit. Amplified products were visualized using ethidium bromide under UV-transilluminator. The polymorphism information content (PIC), major allele frequency, heterozygosity and gene diversity were calculated for each marker using Power Marker ver. 3.25 (Liu and Muse, 2005). Principal co-ordinate analysis (PCoA) followed by cluster analysis was carried out using DARwin 6.0.14 (Perrier and Jacquemoud-Collet, 2006).

Results and Discussion

The ability of a marker to distinguish the genotypes (polymorphism information content, PIC) is an important indicator of polymorphism (Hildebrand *et al*., 1994), which is useful in genomic studies. The AhTE markers varied greatly for their PIC (Table 1), with an average PIC of 0.317. Most of the markers recorded the PIC of 0.299 to 0.400. But AhTE0251 and AhTE0487 recorded more than 0.400 PIC.The type(s) and frequency of alleles provide an idea about the major and minor alleles, the extent of heterozygous loci and population structure. The AhTE markers, by their virtue, are able to detect only two types of alleles (with and without *AhMITE1*) at a locus. In this study, the alleles without *AhMITE1* insertion (B type) (0.56) were more frequent than those (A type) (0.44) with *AhMITE1*.The proportion of the major allele across the 79 AhTE marker loci ranged from 0.500 to 0.762, with an average of 0.595, indicating the overall abundance of the A type allele over the B type allele (Table 2).

For marker-trait association studies, the frequency of minor allele referring to the frequency at which the second most common allele occurs in a given population is important (Park *et al*., 2011) because the power of the statistical method encounters a challenge while discovering the low-frequency (≤0.05) phenotypic classes. Generally, an allele with a frequency of 5% or greater are targeted for genome-wide association studies. The minor allele frequency ranged from 0.238 to 0.504 with an average of 0.405 across the 79 AhTE marker loci (Table 2). Thus, the minor allele frequency in these populations allow the use of AhTE markers for genome-wide association studies.

The observed heterozygosity (H_O) for a locus denotes the proportion of the individuals heterozygous at that locus. It is related to the polymorphic nature of each locus. A high level of *Ho* at a locus generally correlates with high levels of genetic variation due to the adaptive response to environmental changes (Kotzé and Muller 1994). Our results showed a range of 0.000 to 0.240 with an average of 0.017 for H_O, indicating that on an average only 1.7% of the genotypes were heterozygous at each locus. No heterozygotes were observed at thirty-eight AhTE marker loci. Groundnut being a self-pollinated crop, a low level of observed heterozygosity is expected. However, certain *Arachis* species (e.g. *A. glandulifera*, *A. helodes* and *A. kuhlmannii*) showed moderate levels of observed heterozygosity (Bravo *et al*., 2006). *A. helodes* showed a heterozygosity of 0.0997, indicating that, on average, 9.97% of individual plants were heterozygous for a locus. Further, the high H_O in some species such as *A. kuhlmannii* (11.79%) shows that allogamy or other mechanisms to retain heterozygosity occur in *Arachis*.

The allele frequency expected under Hardy-Weinberg equilibrium (HWE) is known as expected heterozygosity (H_E). If the observed heterozygosity is lower than expected, the discrepancy can be attributed to forces such as inbreeding. If heterozygosity is higher than expected, an isolate-breaking effect (the mixing of two previously isolated populations) can be expected. As expected, H_O(0.017) was much less than the H_E (0.479). Such a high H_E over H_O were observed in the previous studies in groundnut (Palmieri *et al*., 2002) and chickpea (Sethy *et al*., 2006).

An attempt was made to compare the RIL and mutant population for the allele parameters. A difference in the minor allele frequency was observed between the RIL (0.488) and mutant (0.302) populations (Table 2). In addition, H_O was more in the case of mutant population (0.027) than in the RIL population (0.014). Because the genomic location of the AhTE markers was determined earlier, an effort was made to assess the population genetic parameters for the AhTE markers located on A genome with those present on B genome. The AhTE markers included 30 A genome-specific and 49B genome-specific markers. No major difference was observed between the A and B genome for the activity of *AhMITE1*. However, the B genome showed more activity of *AhMITE1* with mutagenesis over hybridization. The genic and intergenic location of the AhTE markers was already known, therefore an effort was made to compare the H_O for the genic AhTE markers with the intergenic AhTE markers. The AhTE markers included 45 genic and 34 intergenic markers. H_O was only 0.9% for the genic AhTE markers, while it was 2.7% for the intergenic markers, indicating a three-fold higher activity of *AhMITE1* in the intergenic region. Again, the mutant population showed higher H_O than the RIL population, and it was more pronounced for intergenic (0.048) AhTE markers.

Using these genetic parameters, the principal co-ordinate analysis (PCoA) was attempted to estimate and visualize the similarity between the genotypes, where the genotypes ordinated closer to each other were more similar than those ordinated farther away. In this study, the average distance (dissimilarity) between the genotypes was 0.6866. Twenty pairs of genotypes showed the lowest dissimilarity of 0.0002, while 120 pairs of the genotypes exhibited the highest dissimilarity (0.8598). The distance between the genotypes on graphical representation of the principal co-ordinate analysis confirmed the dissimilarity values (Figure 1). The genotypes showing the lowest dissimilarity failed to show any marker polymorphism, while those with the highest dissimilarity showed high polymorphism (up to 65.82%).

Table.1 Population genetic parameters for the 79 AhTE markers among the RIL and mutant populations of groundnut

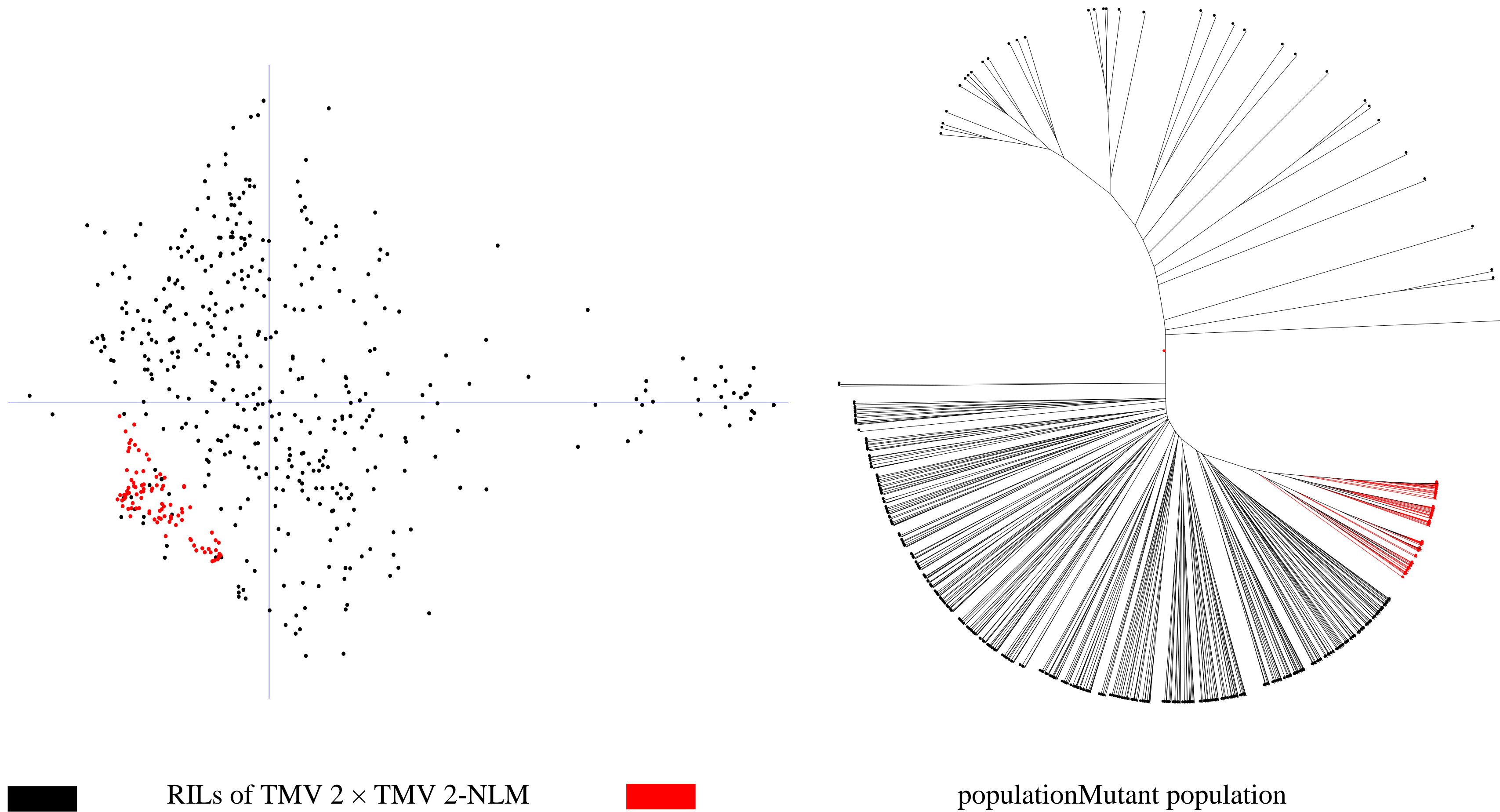
SN	Marker	Allele frequency		H_O	H_E	PIC
		Major	Minor			
1	AhTE0001	0.608	0.392	0.002	0.481	0.371
2	AhTE0005	0.736	0.264	0.000	0.389	0.313
3	AhTE0006	0.519	0.481	0.000	0.501	0.377
4	AhTE0010	0.707	0.293	0.126	0.416	0.331
5	AhTE0025	0.618	0.382	0.009	0.492	0.396
6	AhTE0032	0.506	0.494	0.000	0.507	0.386
7	AhTE0045	0.570	0.430	0.000	0.492	0.373
8	AhTE0050	0.534	0.466	0.023	0.508	0.390
9	AhTE0074	0.585	0.415	0.000	0.492	0.378
10	AhTE0101	0.513	0.487	0.000	0.503	0.380
11	AhTE0107	0.649	0.351	0.023	0.459	0.359
12	AhTE0113	0.548	0.452	0.017	0.505	0.389
13	AhTE0119	0.607	0.393	0.009	0.489	0.383
14	AhTE0121	0.497	0.503	0.028	0.511	0.392
15	AhTE0129	0.502	0.498	0.000	0.506	0.383
16	AhTE0130	0.638	0.362	0.015	0.479	0.385
17	AhTE0143	0.572	0.428	0.000	0.491	0.372
18	AhTE0148	0.555	0.445	0.011	0.505	0.390
19	AhTE0163	0.633	0.367	0.104	0.465	0.357
20	AhTE0164	0.598	0.402	0.019	0.482	0.368
21	AhTE0189	0.536	0.464	0.000	0.497	0.374
22	AhTE0191	0.529	0.471	0.002	0.504	0.382
23	AhTE0212	0.560	0.440	0.000	0.494	0.374
24	AhTE0218	0.519	0.481	0.011	0.499	0.375
25	AhTE0222	0.508	0.492	0.057	0.507	0.386
26	AhTE0232	0.694	0.306	0.000	0.424	0.334
27	AhTE0233	0.502	0.498	0.000	0.500	0.375
28	AhTE0237	0.540	0.460	0.000	0.499	0.376
29	AhTE0245	0.594	0.406	0.019	0.484	0.369
30	AhTE0249	0.517	0.483	0.000	0.501	0.377
31	AhTE0251	0.543	0.457	0.000	0.529	0.425
32	AhTE0254	0.598	0.402	0.019	0.481	0.365
33	AhTE0261	0.558	0.442	0.000	0.496	0.377
34	AhTE0278	0.665	0.335	0.006	0.449	0.353
35	AhTE0283	0.592	0.408	0.000	0.487	0.374
36	AhTE0296	0.592	0.408	0.023	0.487	0.374
37	AhTE0303	0.629	0.371	0.025	0.471	0.365
38	AhTE0305	0.562	0.438	0.000	0.500	0.384

39	AhTE0317	0.719	0.281	0.008	0.404	0.323
40	AhTE0324	0.575	0.425	0.004	0.507	0.399
41	AhTE0328	0.526	0.474	0.125	0.502	0.380
42	AhTE0332	0.668	0.332	0.000	0.445	0.348
43	AhTE0335	0.588	0.412	0.017	0.498	0.390
44	AhTE0357	0.570	0.430	0.000	0.493	0.375
45	AhTE0359	0.599	0.401	0.009	0.491	0.383
46	AhTE0369	0.658	0.342	0.011	0.457	0.363
47	AhTE0373	0.682	0.318	0.021	0.438	0.349
48	AhTE0381	0.632	0.368	0.000	0.465	0.357
49	AhTE0391	0.594	0.406	0.000	0.485	0.371
50	AhTE0416	0.557	0.443	0.064	0.499	0.380
51	AhTE0433	0.688	0.312	0.002	0.434	0.346
52	AhTE0437	0.658	0.342	0.019	0.452	0.353
53	AhTE0465	0.666	0.334	0.000	0.445	0.346
54	AhTE0470	0.715	0.285	0.004	0.409	0.327
55	AhTE0477	0.670	0.330	0.000	0.446	0.351
56	AhTE0482	0.509	0.491	0.000	0.509	0.389
57	AhTE0483	0.634	0.366	0.000	0.468	0.364
58	AhTE0486	0.608	0.392	0.000	0.481	0.371
59	AhTE0487	0.581	0.419	0.000	0.506	0.401
60	AhTE0491	0.575	0.425	0.026	0.489	0.369
61	AhTE0498	0.500	0.500	0.000	0.504	0.381
62	AhTE0501	0.528	0.472	0.000	0.504	0.382
63	AhTE0517	0.579	0.421	0.004	0.489	0.371
64	AhTE0523	0.762	0.238	0.008	0.363	0.299
65	AhTE0524	0.519	0.481	0.000	0.503	0.380
66	AhTE0536	0.625	0.375	0.000	0.477	0.374
67	AhTE0540	0.677	0.323	0.004	0.437	0.342
68	AhTE0550	0.643	0.357	0.174	0.460	0.356
69	AhTE0552	0.609	0.391	0.015	0.482	0.373
70	AhTE0563	0.664	0.336	0.000	0.447	0.349
71	AhTE0571	0.592	0.408	0.013	0.497	0.389
72	AhTE0572	0.685	0.315	0.000	0.433	0.341
73	AhTE0586	0.553	0.447	0.000	0.501	0.383
74	AhTE0590	0.553	0.447	0.000	0.503	0.385
75	AhTE0599	0.596	0.404	0.000	0.496	0.390
76	AhTE0607	0.599	0.401	0.002	0.483	0.370
77	AhTE0630	0.646	0.354	0.240	0.459	0.355
78	AhTE0661	0.552	0.448	0.002	0.498	0.378
79	AhTE0674	0.500	0.500	0.000	0.507	0.386

Table.2 Population genetic parameters for the AhTE markers among the RIL and mutant populations of groundnut

Population	**Major allele frequency**		**Minor allele frequency**		**Gene diversity**		**Heterozygosity**		**Polymorphism information content**	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
All AhTE markers (79)										
Mapping population	0.580	0.500-0.730	0.488	0.270-0.500	0.488	0.395-0.536	0.014	0.000-0.259	0.376	0.319-0.435
Mutant population	0.698	0.510-0.989	0.302	0.010-0.490	0.390	0.020-0.500	0.027	0.000-0.674	0.308	0.020-0.375
Pooled population	0.595	0.500-0.762	0.405	0.238-0.500	0.479	0.363-0.529	0.017	0.000-0.240	0.317	0.299-0.425
A genome AhTE markers (30)										
Mapping population	0.599	0.500-0.722	0.401	0.278-0.500	0.482	0.402-0.528	0.021	0.000-0.259	0.373	0.323-0.421
Mutant population	0.740	0.510-0.990	0.260	0.010-0.490	0.352	0.020-0.500	0.012	0.000-0.153	0.282	0.020-0.375
Pooled population	0.621	0.500-0.736	0.379	0.264-0.500	0.469	0.389-0.508	0.019	0.000-0.240	0.365	0.313-0.399
B genome AhTE markers (49)										
Mapping population	0.569	0.501-0.730	0.431	0.270-0.499	0.491	0.395-0.536	0.010	0.000-0.155	0.378	0.319-0.435
Mutant population	0.672	0.510-0.929	0.328	0.071-0.490	0.414	0.133-0.500	0.036	0.000-0.674	0.324	0.124-0.375
Pooled population	0.578	0.500-0.762	0.422	0.237-0.500	0.485	0.363-0.529	0.015	0.000-0.126	0.373	0.299-0.425
Genic AhTE markers (45)										
Mapping population	0.588	0.500-0.730	0.412	0.270-0.500	0.484	0.395-0.536	0.009	0.000-0.194	0.374	0.319-0.435
Mutant population	0.714	0.510-0.999	0.286	0.010-0.490	0.373	0.020-0.500	0.011	0.000-0.174	0.296	0.020-0.375
Pooled population	0.605	0.502-0.762	0.395	0.238-0.498	0.474	0.363-0.529	0.009	0.000-0.174	0.368	0.299-0.425
Intergenic AhTE markers (34)										
Mapping population	0.570	0.502-0.663	0.498	0.337-0.498	0.492	0.448-0.515	0.022	0.000-0.259	0.378	0.350-0.408
Mutant population	0.677	0.520-0.939	0.323	0.061-0.480	0.414	0.115-0.499	0.048	0.000-0.674	0.324	0.108-0.375
Pooled population	0.581	0.500-0.707	0.419	0.293-0.500	0.485	0.416-0.511	0.027	0.000-0.240	0.373	0.331-0.399

Fig.1 Principal co-ordinates (a) and clusters for the genotypes (b)



The genotypes were also subjected to cluster analysis using DARwin. Two diverse groups could be clearly distinguished (Figure 2). One small group consisted of only RILs, and the other large group contained both RILs and the genotypes of mutant population.

To conclude, the AhTE markers which detected the polymorphism due to *AhMITE1* insertion both in genic and intergenic regions of groundnut genome, showed high PIC and polymorphism. AhTE markers could be successfully used to group the genotypes based on the principal co-ordinates. Therefore, AhTE markers might provide an efficient marker system, like SSR markers (Li *et al*., 2011; Ren *et al*., 2014), for genetic and genomic studies in groundnut. Recently, AhTE markers have been successfully employed for trait mapping in groundnut (Shirasawa *et al*., 2012b; Kolekar *et al*., 2016). They were also used to identify and clone the gene governing various traits (Lee *et al*., 2006; Monden *et al*., 2009; Sato *et al*., 2013) since the transposable element served as a DNA tag.

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