Plant Syst Evol (2011) 291:153–158
DOI 10.1007/s00606-010-0373-3

ORIGINAL ARTICLE

Characterization of *AhMITE1* transposition and its association with the mutational and evolutionary origin of botanical types in peanut (*Arachis* spp.)

M. V. C. Gowda · R. S. Bhat · V. Sujay · P. Kusuma · Varshakumari · S. Bhat · R. K. Varshney

Received: 23 September 2009 / Accepted: 4 October 2010 / Published online: 11 November 2010

Abstract *AhMITE1* is an active miniature inverted repeat transposable element (MITE) in peanut (*Arachis hypogaea* L). Its transpositional activity from a particular (FST1-linked) site within the peanut genome was checked using *AhMITE1*-specifc PCR, which used a forward primer annealing to the 5′-flanking sequence and a reverse primer binding to *AhMITE1*. It was found that transposition activation was induced by stresses such as ethyl methane sulfonate (EMS), gamma irradiation, environmental conditions, and tissue culture. Excision and insertion of *AhMITE1* at this particular site among the mutants led to gross morphological changes resembling alternate subspecies or botanical types. Analysis of South American landraces revealed the presence of *AhMITE1* at the site among most of the spp. *fastigiata* types, whereas the element was predominantly missing from spp. *hypogaea* types, indicating its strong association. Four accessions of the primitive allotetraploid, *A. monticola* were devoid of *AhMITE1* at the site, indicating only recent activation of the element, possibly because of the "genomic shock" resulting from hybridization followed by allopolyploidization.

M. V. C. Gowda (✉) · V. Sujay · P. Kusuma · Varshakumari · S. Bhat
Department of Genetics and Plant Breeding,
University of Agricultural Sciences,
Dharwad 580 005, India
e-mail: mvcgowda@sify.com

R. S. Bhat
Department of Biotechnology,
University of Agricultural Sciences,
Dharwad 580 005, India

R. K. Varshney
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Greater Hyderabad 502 324, India

Keywords *AhMITE1* · Transposition activation · Peanut · Allopolyploidy · Subspecies · Botanical types

Introduction

The cultivated peanut (*Arachis hypogaea* L.) originated from hybridization between diploid female species *A. duranensis* with the A genome and *A. ipaensis* with the B genome (Kochert et al. 1996). A single allotetraploidization event involved either chromosome doubling in diploid F_1 (Favero et al. 2006) or unreduced gametes in F_1 (Harlan and deWet 1975). Occurrence of diploid parental and wild allotetraploid species (*A. monticola*) indicates that the eastern foothills of the Andes in the region of northern Argentina and southern Bolivia could be the area of origin of *A. hypogaea* (Krapovickas and Rigoni 1957; Kochert et al. 1996; Ravi et al. 2010). Allotetraploid *Arachis* species were then put under selection for domestication (Kochert et al. 1996), and the domesticated peanut dispersed to South and Central America where both natural and artificial selection produced many landraces of domesticated peanut.

On the basis of several morphological differences, two subspecies *fastigiata* and *hypogaea* have been recognized in the cultivated peanut. Subspecies *hypogaea* is characterized by alternate branching, absence of flowers on the main axis, long duration (120–160 days), and presence of seed dormancy, whereas *fastigiata* is recognized by sequential branching, presence of flowers on the main axis, short duration (85–130 days), and lack of seed dormancy. On the basis of morphological differences, the two subspecies are subdivided into botanical varieties. Subspecies *hypogaea* is divided into var. *hypogaea* (Virginia bunch/runner) and var. *hirsuta* (Peruvian runner), whereas spp.

fastigiata is classified into var. *fastigiata* (Valencia), var. *vulgaris* (Spanish bunch), var. *aequatoriana*, and var. *peruviana* (Krapovickas 1969; Krapovickas 1973). Subspecies *hypogaea* is thought to have originated by a mutation from within subspecies *fastigiata* (Singh 1988).

The morphological, physiological, and agronomic traits of cultivated peanuts are extremely variable. However, limited variation is found at the DNA level (Singh et al. 1998; Varshney et al. 2009; Khedikar et al. 2010) owing to the occurrence of a single polyploidization event followed by reproductive isolation from related diploid species (Young et al. 1996), self-pollination (Halward et al. 1991), and use of limited exotic germplasm in breeding programs (Knauft and Gorbet 1989). Hence it seems that most of the DNA-level variation among the cultivated types arose from various mutations (Perry 1968; Mouli et al. 1979; Prasad et al. 1984; Prasad 1989) rather than recombination. In a previous study, we hypothesized the important role of mutations possibly involving the activation of cryptic transposable elements (TEs) in the origin and evolutionary differentiation of the peanut (Gowda et al. 1996).

Miniature inverted repeat transposable elements (MITEs) are the predominant TEs among plant genomes (Wessler et al. 1995; Shan et al. 2005; Naito et al. 2006). Transposition preference for low copy genic regions emphasises the role of MITEs in modulating gene expression (Wessler 1998; Zhang et al. 2000; Wessler 2001) and aiding crop evolution (Shan et al. 2005; Naito et al. 2006). Previously, we reported an active peanut MITE (*AhMITE1*), the transposition of which was associated with the high-frequency origin of late leaf spot (LLS)-resistant mutants (Gowda et al. 2010). Here we have made an effort to study stress-induced activation of *AhMITE1*, and the relevance of its transposition with the mutational and evolutionary origin of botanical types.

Materials and methods

Plant material

Genotypes tested for *AhMITE1* transposition included parents and mutants generated by various stresses (Table 1), and thirty-three South American landraces representing different botanical types (Table 2) and four accessions of wild allotetraploid (*A. monticola*) with the AB genome combination (Table 3). Parental wild types and their mutants developed via mutagenesis with EMS and gamma irradiation, and those recovered from spontaneous mutation were selected from our mutant collection. These stabilized mutants were phenotypically studied and characterized for morphological changes (Motagi et al. 1996). TAG 24 and its mutant (TAG 24 (M)) recovered through tissue culture as somaclonal variant were obtained from Bhabha Atomic Research Centre (BARC), Mumbai, India. South American landraces and accessions of

Table 1 Activation of *AhMITE1* in peanut mutants

Parent	Mutant	Mutagen	*AhMITE1*[a]	Botanical type	Phenology
DER			0	–	Similar to ssp. *fastigiata*, but is prostrate in habit with short main axis, small seeds, and fresh seed dormancy and resembles some primitive forms of *A. hypogaea* and some forms of wild tetraploid progenitor of groundnut, *A. monticola*, in phenology
	SB 2, SB 4, SB 5, SB 6	Gamma	1	Spanish bunch	Increased pod size
	SB 10, SB 11	EMS	1	Spanish bunch	Increased pod size
VL 1			0	Valencia	Valencia mutant derived from DER
	28-2, 45, 110	EMS	1	Spanish bunch	Resistant to LLS, change in pod size and shape
28-2	28-2(s)	Spontaneous	0	Spanish bunch	Susceptible to LLS, change in pod size and shape
45	45(s)	Spontaneous	0	Spanish bunch	Susceptible to LLS, change in pod size and shape
110	110(s)	Spontaneous	0	Spanish bunch	Susceptible to LLS, change in pod size and shape
TMV 2			1	Spanish bunch	Cultivar
	NLM	EMS	0	Virginia bunch	Narrow leaf, drought-tolerant
JL 24			1	Spanish bunch	Cultivar
	VR 1, VR 2	Spontaneous	0	Virginia runner	Subspecies shift from Spanish bunch to Virginia runner
TAG 24			1	Spanish bunch	Cultivar
	TAG 24 (M)	Tissue culture	0	Spanish bunch	With some features of spp. *hypogaea*

[a] Amplification of 242-bp product upon *AhMITE1*-specific PCR (1: Yes, 0: No)

Table 2 Activity of *AhMITE1* at FST1-linked site among South American peanut landraces

SN	Landrace	Origin	Subspecies	Botanical type	*AhMITE1*[a]
1	ICG 1711	Bolivia	*fastigiata*	*vulgaris*	1
2	ICG 3746	Argentina	*fastigiata*	*vulgaris*	1
3	ICG 3775	Brazil	*fastigiata*	*vulgaris*	0
4	ICG 4750	Paraguay	*fastigiata*	*vulgaris*	1
5	ICG 5236	Chile	*fastigiata*	*vulgaris*	1
6	ICG 7190	Brazil	*fastigiata*	*vulgaris*	0
7	ICG 8567	Uruguay	*fastigiata*	*vulgaris*	1
8	ICG 15287	Brazil	*fastigiata*	*vulgaris*	1
9	ICG 9930	Zimbabwe	*fastigiata*	*vulgaris*	1
10	ICG 332	Brazil	*fastigiata*	*fastigiata*	1
11	ICG 5221	Argentina	*fastigiata*	*fastigiata*	0
12	ICG 6888	Brazil	*fastigiata*	*fastigiata*	1
13	ICG 8517	Bolivia	*fastigiata*	*fastigiata*	0
14	ICG 11144	Argentina	*fastigiata*	*fastigiata*	0
15	ICG 10890	Peru	*fastigiata*	*fastigiata*	1
16	ICG 15309	Brazil	*fastigiata*	*fastigiata*	1
17	ICG 10554	Argentina	*fastigiata*	*fastigiata*	0
18	ICG 8106	Peru	*fastigiata*	*fastigiata*	0
19	ICG 14630	Brazil	*fastigiata*	*fastigiata*	0
20	ICG 10044	Peru	*fastigiata*	*fastigiata*	0
21	ICG 10036	Brazil	*fastigiata*	peruviana	0
22	ICG 11088	Peru	*fastigiata*	peruviana	1
23	ICG 12625	Peru	*fastigiata*	*aequatoriana*	0
24	ICG 12719	Ecuador	*fastigiata*	*aequatoriana*	0
25	ICG 2857	Argentina	*hypogaea*	*hypogaea*	0
26	ICG 6993	Brazil	*hypogaea*	*hypogaea*	0
27	ICG 2381	Brazil	*hypogaea*	*hypogaea*	0
28	ICG 10479	Uruguay	*hypogaea*	*hypogaea*	1
29	ICG 6703	Paraguay	*hypogaea*	*hypogaea*	0
30	ICG 12276	Bolivia	*hypogaea*	*hypogaea*	0
31	ICG 12672	Bolivia	*hypogaea*	*hypogaea*	0
32	ICG 15207	Mexico	*hypogaea*	*hypogaea*	0
33	ICG 15206	Mexico	*hypogaea*	*hypogaea*	0

[a] Amplification of 242-bp product upon *AhMITE1*-specific PCR (1: Yes, 0: No)

A. monticola were obtained from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India.

Detection of *AhMITE1* insertion/excision

Genomic location of the *AhMITE1* was determined (Bhat et al. 2008) by recovering its 5′-flanking sequence tag from TMV 2, a Spanish bunch cultivar, using TAIL-PCR with a set of degenerate primers and nested primers designed based on the reported MITE sequence (Patel et al. 2004). Presence or absence of *AhMITE1* at this pre-determined site (FST1-linked site) in various genotypes/mutants was checked by developing an *AhMITE1*-specifc PCR (Gowda et al. 2010). The forward primer (5′ GGGAGAAGAA AAGGATGAGA 3′) was designed on the basis of the *AhMITE1* flanking sequence tag (FST1) recovered from the TMV 2 genotype of peanut (Bhat et al. 2008) whereas the reverse primer (5′ TCTCATGAAGATGCTTTGGT 3′) was specific to *AhMITE1* (Patel et al. 2004). Amplification of a 242-basepair (bp) product would indicate the presence of *AhMITE1* at the FST1-linked site in the genome.

Table 3 Activity of *AhMITE1* at FST1-linked site among the primitive allotetraploids of peanut

SN	Accession number	Species	Genome	*AhMITE1*[a]
1	ICG 13177	*A. monticola*	AB	0
2	ICG 8135	*A. monticola*	AB	0
3	ICG 8197	*A. monticola*	AB	0
4	ICG 8198	*A. monticola*	AB	0

[a] Amplification of 242-bp product upon *AhMITE1*-specific PCR (1: Yes, 0: No)

For *AhMITE1*-specifc PCR, genomic DNA of various genotypes and mutants was isolated from young leaves collected at the 3–4 leaf stage of the seedling using the GenElute™ plant genomic DNA miniprep kit (Sigma–Aldrich). A final volume of 20 µl containing 100 ng genomic DNA, 1× PCR buffer, 0.5 mM dNTPs, 10 pmol of each primer, and one unit of *Taq* DNA polymerase (Genei, Bangalore, India) was used for PCR. The amplification reaction was carried out in a Mastercycler® (Eppendorf, Germany) by setting the conditions for one cycle of pre-denaturation (94°C for 5 min), 35 cycles of denaturation (94°C for 1 min), annealing (60°C for 1 min), and extension (72°C for 1 min). One cycle of final extension (72°C for 1 min) was included before the PCR product was stored at 4°C until further use. Presence of the PCR product was checked on 1.2% agarose gel by electrophoresis.

Results

EMS and gamma mutagens and tissue culture could activate the transposition of *AhMITE1*. The parent Dharwad Early Runner (DER) did not amplify the 242-bp product (Fig. 1), hence was found to be free of *AhMITE1* insertion at the FST1-linked site. Mutants generated by gamma irradiation (SB 2, SB 4, SB 5, and SB 6) and EMS treatment (SB 10 and SB 11) amplified the 242-bp product with *AhMITE1*-specific PCR, indicating the insertion of *AhMITE1* into the FST1-linked site. These mutants resembled Spanish bunch type in their erect growth habit, lack of seed dormancy, and increased pod size compared

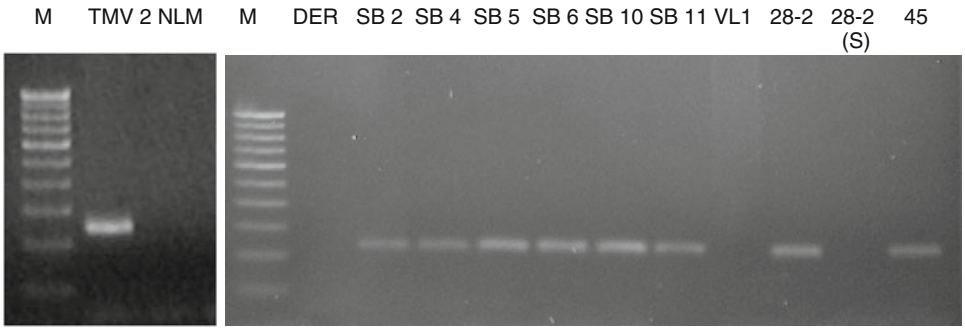

Fig. 1 Mutagen-induced transpositional activity of *AhMITE1* in some of the mutants and their parents. Amplification of the 242-bp product upon *AhMITE1*-specific PCR indicates the presence of the element at the FST1-linked site (*M*: 100 bp DNA ladder)

with the DER type (Table 1). Another EMS mutagenesis effort with VL 1, a Valencia mutant from DER, could generate three Spanish bunch mutants (28-2, 45, and 110). Compared with VL 1, these mutants had more primary and secondary branches, short main stem and primary branches, small leaves, high pod yield and test weight, and resistance to late leaf spot. They showed insertion of *AhMITE1* into the FST1-linked site. Contrastingly, EMS mutagenesis could also activate excision of *AhMITE1* from the FST1-linked site as observed with the narrow leaf mutant (NLM) from TMV 2. Origin of NLM, a Virginia bunch type mutant (with alternate branching and main stem flowering) belonging to spp. *hypogaea* from TMV 2, a Spanish bunch cultivar, involved excision of *AhMITE1* from the predetermined site, indicating a gross morphological change.

Two spontaneous mutants (VR 1 and VR 2) resembling Virginia runner were isolated from the Spanish bunch variety JL 24. These mutations represented the morphological changes from spp. *fastigiata* to spp. *hypogaea,* and accompanied the excision of *AhMITE1*. Likewise, 28-2(s), 45(s), and 110(s) obtained spontaneously from 28-2, 45, and 110, respectively, were also associated with excision of the transposable element. Significant morphological changes, for example susceptibility to late leaf spot and pod shape and size, were observed in these mutants. Tissue culture induced somaclone, TAG 24 (M), from TAG 24 indicated excision of the element. This excision resulted in discernible changes, for example increase in the number of branches, decrease in seed size, and prostrate habit. Thus, the origin of Spanish bunch mutants belonging to spp. *fastigiata* were generally associated with insertion whereas spp. *hypogaea* mutants were associated with excision of the TE from the FST1 site.

This association was further validated by checking South American landraces comprising native subspecies and botanical types for the presence of *AhMITE1*. Of the nine genotypes belonging to spp. *hypogaea*, only one (ICG 10479) had *AhMITE1* at the FST1-linked site. In the spp. *fastigiata*, four of the eleven Valencia, seven of nine in the Spanish bunch, and one of two *peruviana* (ICG 11088) had the *AhMITE1* insertion, and it was absent from the two *aequatoriana* genotypes tested. Proportions of the genotypes within the two subspecies carrying *AhMITE1* at the FST1-linked site were compared statistically using the z test (standard normal deviate test for proportion) (Nageswara Rao 2007). Because the calculated z value (2.06) was significantly higher than the critical value of 1.96 at the 5% level of significance, it was concluded that most of the landraces belonging to spp. *fastigiata* types had *AhMITE1* at the FST1-linked site, but spp. *hypogaea* types lacked it.

Four accessions of the allotetraploid *A. monticola* (AABB) and a cultivar (TMV 2) were screened for *AhMITE1* at the FST1-linked site to trace the possible time of transposition during the course of evolution and peanut domestication. It was found that all the accessions of *A. monticola* were devoid of the element at the site, indicating that insertion occurred late in the evolutionary differentiation of *A. hypogaea* into subspecies and botanical types.

Discussion

Among plants, allopolyploidy is common (Stebbins 1951; Masterson 1994; Leitch and Bennett 1997), and regarded as "dynamic" (Soltis and Soltis 1995) and a major force in evolution compared with diploidy (Liu and Wendel 2003). It is known to be of major importance in genome diversification and adaptation (Cronn and Wendel 2004). However, the underlying genetic and molecular basis of allopolyploidy-mediated evolution remains obscure. Recent studies indicate that epigenetic mechanisms, for example DNA methylation, chromatin remodelling, and RNA-silencing regulate reprogramming of the gene expression and developmental patterns in allopolyploids (Chen 2007). Methylation of cytosine and histone modifications are of major importance in regulating the activity of transposable elements (TE) belonging to both long terminal repeats (LTR) and MITEs (Wessler et al. 1995; Madlung et al. 2005) that are known to induce transposon-mediated variations fuelling adaptation and evolution (McClintock 1984).

Numerous reports record activation of a rice MITE, *mPing*, by diverse stresses such as gamma rays (Nakazaki et al. 2003), tissue culture (Jiang et al. 2003; Kikuchi et al. 2003), environmental conditions (Jiang et al. 2003), and genomic shock, because of interspecific hybridization (Shan et al. 2005). Enhanced transpositional activity was observed for *En-Spm*-like transposons of *Arabidopsis thaliana* after remodelling of CG methylation on allopolyploidization (Madlung et al. 2005). Hence, it seems that the response of a plant to such stresses may involve epigenetic changes leading to transpositional activity (Chen 2007).

In peanut, of the several copies of MITE identified using Southern hybridization, a particular MITE was induced by diethyl sulfonate (DES) to cause high oleate mutation (Patel et al. 2004). We named this *AhMITE1,* and determined its site of integration in TMV 2, a Spanish cultivar by recovering a 151 bp 5′-flanking sequence tag (FST1) (Bhat et al. 2008). Homology search indicated that a small region (23/24 bp) of the FST1 corresponded to a genomic sequence of *A. batizocoi* (GenBank acc. no. DX508954) of the methylation filtered library (LibID703) (Bhat et al. 2008). So the genomic location of *AhMITE1* as identified by the FST1 was referred to as the FST1-linked site.

Analysis of several spontaneous and induced mutants originating from mutagenesis (EMS and gamma irradiation) and tissue culture revealed *AhMITE1* transposition. EMS-induced NLM from TMV 2 involved excision of *AhMITE1* from the FST1-linked site. Most interestingly, this mutation involved morphological changes from subspecies *fastigiata* (TMV 2) type to those resembling *hypogaea* (NLM), for example sequential branching to alternate branching and main stem flowering to main stem non-flowering. Likewise, many mutations characterized previously (Motagi et al. 1996), were associated with drastic morphological changes resembling alternate subspecies or botanical types, and the presence of *AhMITE1* at the FST1-linked site was predominant in spp. *fastigiata*. As in the previous studies (Prasad et al. 1984; Gowda et al. 1996), the origin of mutants belonging to spp. *hypogaea* from spp. *fastigiata* types was more common than the other way round. This could be because of higher chances of excisions of *AhMITE1* at the FST1-linked site compared with fresh insertions at that site.

Among the cultivated species of peanut, spp. *fastigiata* (both Spanish bunch and Valencia) were found to carry an *AhMITE1* insertion at the FST1-linked site, whereas genotypes classified under spp. *hypogaea* rarely contained *AhMITE1*, indicating a strong association between *AhMITE1* transposition and intraspecific differentiation. Such preferential activity of MITEs has been reported in *japonica* versus *indica* types of rice (Jiang et al. 2003). The exceptions, for example VL 1, a Valencia type mutant from DER, and some genotypes belonging to different botanical types in spp. *fastigiata,* which were devoid of the element, indicated a probable role of additional mechanisms. Genotypes belonging to *A. hypogaea* spp. *fastigiata* var *aequatoriana* missed *AhMITE1* at the site, similar to many spp. *hypogaea* types. Previous efforts with AFLP markers also indicated its closer resemblance to spp. *hypogaea* than to spp. *fastigiata* (He and Prakash 2001).

Lack of *AhMITE1* at the FST1-linked site in four accessions of *A. monticola* but its presence in some forms of cultivated species indicates de-repression of MITE, possibly because of "genomic shock" triggered by hybridization followed by allopolyploidization (Shan et al. 2005; Naito et al. 2006). As far as we are aware, this is the first report indicating the role of an MITE in peanut genome differentiation that took place after allopolyploidization. This unique association supports the view that the spp. *hypogaea* is much closer to the wild allotetraploid (Paik-Ro et al. 1992; Singh et al. 1993; He and Prakash 2001), and that *AhMITE1* transposition at an FST1-linked site could have been of major importance in the origin of spp. *fastigiata*.

This study reveals a possible reason for extensive morphological diversity, despite low DNA polymorphism in the cultivated species. MITEs, by virtue of their inherent property, are preferentially inserted into low copy genes and their regulators (Singh et al. 1998), and the transpositions are known to modulate gene expression because of methylation, gene disruption, and frame-shift mutations (Nakazaki et al. 2003; Shan et al. 2005). Such events could also be important precursors generating morphologically distinct subspecies and botanical types. Genomic characterization of the FST1-linked site for candidate gene and future elucidation of other MITEs/LTRs using the transposon display technique (Van den Broeck et al. 1998) in mutant collection, landraces, and wild types will lead to better understanding of peanut genome differentiation and domestication.

Acknowledgments The authors are grateful to Dr H.D. Upadhyaya, ICRISAT, for providing the wild peanut species, and to Mr Ravi Koppulu, ICRISAT, for technical help.

References

Bhat RS, Patil VU, Chandrashekar TM, Sujay V, Gowda MVC, Kuruvinashetti MS (2008) Recovering flanking sequence tags of miniature inverted-repeat transposable element by thermal asymmetric interlaced-PCR in peanut. Curr Sci 95:452–453

Chen ZJ (2007) Genetic and epigenetic mechanisms for gene expression and phenotypic variation in plant polyploids. Annu Rev Plant Biol 58:377–406

Cronn R, Wendel JF (2004) Cryptic trysts, genomic mergers, and plant speciation. New Phytol 161:133–142

Favero AP, Simpson CE, Valls JFM, Vello NA (2006) Study of the evolution of cultivated peanut through crossability studies

among *Arachis ipaensis*, *A. duranensis,* and *A. hypogaea*. Crop Sci 46:1546–1552
Gowda MVC, Nadaf HL, Sheshagiri R (1996) The role of mutations in intraspecific differentiation of groundnut (*Arachis hypogaea* L.). Euphytica 90:105–113
Gowda MVC, Bhat RS, Motagi BN, Sujay V, Varshakumari, Bhat S (2010) Association of high-frequency origin of late leaf spot resistant mutants with *AhMITE1* transposition in peanut. Plant Breed 129:567–569
Halward TM, Thomas Stalker H, Larue EA, Kochert G (1991) Genetic variation detectable with molecular markers among unadapted germplasm resources of cultivated peanut and related wild species. Genome 34:1013–1020
Harlan JR, de Wet JMJ (1975) On Ö Winge and a prayer: the origins of polyploidy. Bot Rev 41:361–390
He G, Prakash C (2001) Evaluation of genetic relationships among botanical varieties of cultivated peanut (*Arachis hypogaea* L.) using AFLP markers. Genet Resour Crop Evol 48:347–352
Jiang N, Bao Z, Zhang X, Hirochika H, Eddy SR, McCouch SR et al (2003) An active DNA transposon family in rice. Nature 421:163–167
Khedikar Y, Gowda M, Sarvamangala C, Patgar K, Upadhyaya H, Varshney R (2010) A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). Theor Appl Genet. doi:10.1007/s00122-010-1366-x
Kikuchi K, Terauchi K, Wada M, Hirano HY (2003) The plant MITE *mPing* is mobilized in anther culture. Nature 421:167–170
Knauft DA, Gorbet DW (1989) Genetic diversity among peanut cultivars. Crop Sci 29:1417–1422
Kochert G, Stalker HT, Gimenes M, Galgaro L, Lopes CR, Moore K (1996) RFLP and cytogenetic evidence on the origin and evolution of allotetraploid domesticated peanut, *Arachis hypogaea* (Leguminosae). Am J Bot 83:1282–1291
Krapovickas A (1969) The origin, variability and spread of the groundnut (*Arachis hypogaea*). In: Ucko RJ, Dimbledy WC (eds) The domestication and exploitation of plant and animals. Gerald Duckworth Co. Ltd, London, pp 427–441
Krapovickas A (1973) Evolution of the genus *Arachis*. In: Moav R (ed) Agricultural genetics-selected topics. Wiley, New York, pp 135–151
Krapovickas A, Rigoni VA (1957) Nuevas especies de Arachis vinculadas al problema del origen del mani. Darwiniana 11:431–455
Leitch IJ, Bennett MD (1997) Polyploidy in angiosperms. Trends Plant Sci 2:470–476
Liu B, Wendel JF (2003) Epigenetic phenomena and the evolution of plant allopolyploids. Mol Phylogenet Evol 29:365–379
Madlung A, Tyagi AP, Watson B, Jiang H, Kagochi T, Doerge RW et al (2005) Genomic changes in synthetic Arabidopsis polyploids. Plant J 41:221
Masterson J (1994) Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. Science 264:421–424
McClintock B (1984) The significance of responses of the genome to challenge. Science 226:792–801
Motagi BN, Gowda MVC, Sheshagiri R (1996) Mutants resistant to foliar diseases in groundnut (*Arachis hypogaea* L.). Curr Sci 71:582–584
Mouli C, Kale DM, Patil SH (1979) Sequential flowering large pod Trombay groundnuts (Abst.) Symposium on the Role of Induced Mutations in Crop Improvement Hyderabad, India
Nageswara Rao G (2007) Statistics for agricultural sciences. Oxford and IBH Publishing company, New Delhi, pp 98–99
Naito K, Cho E, Yang G, Campbell MA, Yano K, Okumoto Y et al (2006) Dramatic amplification of a rice transposable element during recent domestication. Proc Natl Acad Sci USA 103:17620–17625
Nakazaki T, Okumoto Y, Horibata A, Yamahira S, Teraishi M, Nishida H et al (2003) Mobilization of a transposon in the rice genome. Nature 421:170–172
Paik-Ro OG, Smith RL, Knauft DA (1992) Restriction fragment length polymorphism evaluation of six peanut species within the *Arachis* section. Theor Appl Genet 84:201–208
Patel M, Jung S, Moore K, Powell G, Ainsworth C, Abbott A (2004) High-oleate peanut mutants result from a MITE insertion into the *FAD2* gene. Theor Appl Genet 108:1492–1502
Perry A (1968) A radiation breeding experiment with peanuts, iv. Effects of the vegetative and reproductive phases of the branching system (NC4–18.5 KR). Rad Bot 8:109–119
Prasad MVR (1989) Genetic differentiation in *Arachis hypogaea* L. In: Farook SA, Khan IA (eds). Recent advances in genetics and cytogenetics. Premier Publishing House Hyderabad, India, pp 53–55
Prasad MVR, Kaul S, Jain HK (1984) Induced mutants of Peanut for canopy and pod bearing characters. Indian J Genet 44:25–34
Ravi K, Hari U, Sangam D, David H, Varshney RK (2010) Genetic relationships among seven sections of genus *Arachis* studied by using SSR markers. BMC Plant Biol 10:15
Shan X, Liu Z, Dong Z, Wang Y, Chen Y, Lin X et al (2005) Mobilization of the active MITE transposons *mPing* and *Pong* in rice by introgression from wild rice (*Zizania latifolia* Griseb.). Mol Biol Evol 22:976–990
Singh AK (1988) Putative genome donors of *Arachis hypogaea* (Fabaceae), evidence from crosses with synthetic amphidiploids. Plant Syst Evol 160:143–151
Singh AK, Gurtu S, Jambunathan R (1993) Phylogenetic relationships in the genus *Arachis* based on seed protein profiles. Euphytica 74:219–225
Singh AK, Smartt J, Simpson CE, Raina SN (1998) Genetic variation vis-à-vis molecular polymorphism in groundnut, *Arachis hypogaea* L. Genet Resour Crop Evol 45:119–126
Soltis DE, Soltis PS (1995) The dynamic nature of polyploid genomes. Proc Natl Acad Sci USA 92:8089–8091
Stebbins GL (1951) Variation and evolution in plants. Columbia University Press, New York
Van den Broeck D, Maes T, Sauer M, Zethof J, De Keukeleire P, D'hauw M et al (1998) Transposon Display identifies individual transposable elements in high copy number lines. Plant J 13:121–129
Varshney RK, Bertioli DJ, Moretzsohn MC, Vadez V, Krishnamurthy L, Aruna R et al (2009) The first SSR-based genetic linkage map for cultivated groundnut (*Arachis hypogaea* L.). Theor Appl Genet 118:729–739
Wessler SR (1998) Transposable elements associated with normal plant genes. Physiol Plant 103:581–586
Wessler SR (2001) Plant transposable elements. A hard act to follow. Plant Physiol 125:149–151
Wessler SR, Bureau TE, White SE (1995) LTR-retrotransposons and MITEs: important players in the evolution of plant genomes. Curr Opin Genet Dev 5:814–821
Young ND, Weeden NF, Kochert G (1996) Genome mapping in legumes (Family Fabaceae). In: Paterson AH (ed) Genome mapping in plants. Landes Biomedical Press, Austin, pp 211–277
Zhang Q, Arbuckle J, Wessler SR (2000) Recent, extensive, and preferential insertion of members of the miniature inverted-repeat transposable element family Heartbreaker into genic regions of maize. Proc Natl Acad Sci USA 97:1160–1165