

Article

Impact of Molecular Genetic Research on Peanut Cultivar Development

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Abstract: Peanut (*Arachis hypogaea* L.) has lagged other crops on use of molecular genetic technology for cultivar development in part due to lack of investment, but also because of low levels of molecular polymorphism among cultivated varieties. Recent advances in molecular genetic technology have allowed researchers to more precisely measure genetic polymorphism and enabled the development of low density genetic maps for *A. hypogaea* and the identification of molecular marker or QTL's for several economically significant traits. Genomic research has also been used to enhance the amount of genetic diversity available for use in conventional breeding through the development of transgenic peanut, and the creation of TILLING populations and synthetic allotetraploids. Marker assisted selection (MAS) is becoming more common in peanut cultivar development programs, and several cultivar releases are anticipated in the near future. There are also plans to sequence the peanut genome in the near future which should result in the development of additional molecular tools that will greatly advance peanut cultivar development.

Keywords: genetic polymorphism; marker assisted selection; peanut; QTL; synthetic allotetraploid; TILLING; transgenic

1. Development of Tools to Enhance Molecular Breeding in Peanut

Genomic research can provide new tools and resources to revolutionize crop genetic improvement and production [1]. However, genomic research in peanut (*Arachis hypogaea* L.) is far behind that in other crops such as maize, soybean, wheat, sorghum, and potato due to the shortage of essential genome infrastructure, tools, and resources [2]. As a consequence, peanut has lagged behind other crops on the use of molecular genetic technology for cultivar development. The early technologies (isozyme, RFLP (Restriction Fragment Length Polymorphism), AFLP (Amplified Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), and SCAR (Sequence Characterized Amplified Region)) showed extremely low levels of polymorphism in *A. hypogaea* [3-11]. Those early struggles have been documented in several excellent reviews [2,12-14]. Recent advances in molecular genetic technology have allowed researchers to detect more frequent genetic polymorphism. These efforts have resulted in the construction of moderate density genetic maps for *A. hypogaea* [15-19] populated primarily with SSR (simple sequence repeat or microsatellite) markers that contrast with other PCR-based markers in their largely co-dominant vs. dominant (AFLP, RAPD, and SCAR) nature. Many of these SSR markers were developed from peanut ESTs (expressed sequence tags). Because of genome size and complexity, many plant EST libraries have been sequenced as an alternative to whole genome sequences, including peanut. EST data sets were foundational for functional genomics during the period when only a few plant genomes were sequenced and before the development of the second generation of high throughput sequencing technology. ESTs have been especially important resources for major crops or economically significant plants with large genomes (such as peanut) to enable gene discovery, gene expression analysis and molecular marker development.

The NCBI EST database contains 225,264 ESTs from peanut as of November 2011 [20]. There are 150,922 for *A. hypogaea* (including 745 for subsp. *fastigiata*), 35,291 for *A. duranensis*, 32,787 for *A. ipaensis*, and 6264 for *A. stenosperma*. Many of the *A. hypogaea* ESTs have been combined with short-read sequences to create a first generation transcriptome assembly (NCBI BioProject PRJNA49471). Before the completion of peanut whole genome sequence, sequencing large numbers of ESTs can create a formidable resource for studies in both biodiversity and gene-discovery. Sequence analysis tools have extended the scope of EST utility into the fields of proteomics, marker development and genome annotation. Although EST collections certainly are not intended to substitute for a whole genome sequence, the EST resource forms the core foundation for various genome-wide experiments, particularly for microarray gene expression study [21,22], marker development and genetic map construction [17], which will assist assembly of the whole genome. The ESTs will continue to be actively sequenced to fill knowledge gaps and complement the whole genome sequence.

In spite of the discovery of thousands of microsatellite-containing EST and genomic sequences from which markers have been developed [23], only ~10–20% detect multiple alleles among tetraploid peanut genotypes [24-27], although somewhat higher levels of polymorphism have been observed in several studies [28-32]. In spite of considerable molecular tool expansion for *A. hypogaea* over the past decade, low polymorphism resulting from a genetic bottleneck due to polyploidization [33] continues to limit the number of markers that can be mapped in populations from intraspecific biparental crosses. The discovery of SNP (Single Nucleotide Polymorphism) markers will further

enhance the molecular toolkit for peanut, although high-throughput SNP genotyping in the tetraploid will be challenging [23].

From a cultivar development standpoint, however, these advances in technology have enabled the identification of molecular markers associated with quantitative trait loci (QTLs) for several economically significant traits. Recent research has resulted in the discovery of molecular markers associated with resistance to foliar diseases, rust and late leaf spot [18,34-36], resistance to *Cylindrocladium* black rot and early leaf spot [14], nematode resistance [37-40], resistance to TSWV [17], resistance to the aphid vector of groundnut rosette disease [41], drought tolerance [15,42], yield parameters [43], high oleic acid [44,45], and seed biochemical traits [46]. Many of these QTLs are not major, *i.e.*, they account for <10% of the phenotypic variation explained. Major QTLs identified for rust and late leaf spot in at least one germplasm source may be of wild species origin [18,36,47] as is the source of nematode resistance [40,48]. Many small effect QTLs were mapped in a population segregating for drought tolerance and its surrogate traits such as transpiration efficiency, specific leaf area, or dry weight and the percent of phenotypic variation explained was often low (<10%) [15,42]. Two additional populations confirmed that no major QTLs for drought tolerance could be identified [19]. The need to pyramid a large number of minor QTLs for drought tolerance may predetermine the most efficient breeding strategy to integrate with marker-assisted selection [49]. For example, marker-assisted backcrossing can efficiently combine only a few genes for foreground (trait-associated donor alleles) selection while conducting background selection using markers spanning the genome in order to rapidly recover the recurrent parent genotype plus the genes/alleles of interest. Foreground selection becomes more costly as the number of minor QTLs increases because population sizes increase dramatically. Up to now, neither background nor genome-wide selection has been practiced in peanut and must await the development of high-throughput, economical assays for large numbers of markers. For other traits such as high oleic acid or rust resistance, identification of major QTLs have or will enable efficient marker-assisted backcrossing [50].

2. Creating New Sources of Genetic Diversity in Peanut

Molecular breeding in peanut trails that of many crops [51,52] in part due to a lack of investment, but also because of low levels of molecular polymorphism among cultivated varieties. While polymorphism is abundant in diploid wild species, it is sparse in tetraploid peanut due to the genetic bottleneck imposed by its relatively recent origin [33]. Genomic research might also be used to enhance the amount of genetic diversity available for application in conventional breeding. The development of transgenic peanut, and the creation of TILLING populations and synthetic allotetraploids are three approaches that are being explored to create new sources of genetic diversity in peanut.

2.1. Transgenics

Transgenic research has resulted in the creation of new genetic diversity in peanut which could be very useful in cultivar development. The first successful transformation of peanut was achieved using the biolistic/bombardment technique with accompanying plant regeneration [53]. Since then several research groups have successfully employed this biolistic method using embryogenic cultures as the target tissues, and a few groups have utilized *Agrobacterium*-mediated transformation which relies

primarily on shoot-regenerating cultures. The biolistic method directly transfers target genes into plant cells by delivering DNA coated microprojectiles at a high velocity [54]. The direct delivery of transgenes makes the transformation less dependent on host genotype. As long as a peanut genotype can be regenerated from somatic embryo tissue culture, it can be transformed by bombardment. Three major peanut cultivar groups including runner, spanish and virginia have been transformed by this method. Besides the target gene of interest, DNA constructs for bombardment often include a selectable marker gene cassette expressing hygromycin phosphotransferase (*hph* or *hpt*). After bombardment, embryogenic tissues are cultured on selective medium to minimize non-transgenic escapes [53] and to yield highly proliferating transformed tissues that are further transferred to regeneration medium for shoot and root induction. Genetic transformation via bombardment has successfully transferred multiple genes for protein accumulation and RNAi-mediated gene silencing. Limitations for biolistic bombardment include: (1) it is a lengthy process which takes 12–14 months from initiation of tissue culture to the establishment of primary transgenic plants; and (2) infertility is frequent among tissue culture regenerants [53,55]. On the other hand, *Agrobacterium tumefaciens*-mediated transformation circumvents the tissue culture step and takes less time (usually 4–5 months) to obtain transgenic plants, but it is highly genotype dependent. In this case, a target gene of interest is engineered into the T-DNA region of a ‘disarmed’ plasmid and introduced into *A. tumefaciens*. The transgene within the T-DNA borders is further transferred into plant cells by cocultivation of *A. tumefaciens* and wounded plant tissue. Induction of *Agrobacterium* virulence genes is critical for transgene integration into the plant cell genome and is affected by exposure to phenolic compounds (such as acetosyringone), reducing monosaccharides and acidic pH by host cells [56,57].

Various peanut tissues including leaf sections, cotyledonary nodes, longitudinal cotyledon halves, embryo axes, embryo leaflets, and hypocotyls have been tested for *A. tumefaciens* transformation [58–60]. Apical or axillary meristematic cells in these tissues allow for multiple shoot regeneration and have been targeted for gene transfer by *A. tumefaciens*. However, conditions for adventitious shoot formation through organogenesis vary widely, and cocultivation protocols with or without virulence inducing agents have been previously reviewed [61,62]. Complex host-pathogen interaction limits peanut genotypes that can be successfully transformed by *Agrobacterium*. Out of 19 publications on peanut transformation mediated by *A. tumefaciens*, 14 of them performed transformation mainly with either spanish (such as JL-24 and TMV 2) or valencia (such as New Mexico Valencia A) types of peanut. Runner cultivars account for 80% of the production in the U.S. Only one publication reported transgenic runner type peanut by *A. tumefaciens*-mediated transformation [63]. Differential expression of host genes in the first few hours of *A. tumefaciens* cocultivation can affect T-DNA integration and transformation efficiency as demonstrated in rice [64]. Recently, direct shoot organogenesis was achieved with a couple of US runner type cultivars Georgia Green [65] and Florida-07 [66] at a shoot production rate of 25% and 7% respectively [67], a frequency considerably lower than the 82–90% reported for the Indian cultivar JL-24 [59,68]. Further transformation study would potentially implement this transformation technology into major US peanut cultivars.

Specific details of peanut transformation events up to year 2005 have been documented in several reviews [62,69,70]. Peanut transgenic research since year 2006 is summarized in Table 1. Besides a couple of studies on transformation efficiency and selection conditions [68,71], more recent advances in peanut transformation mainly focus on integrating genes conferring resistance to biotic and abiotic

stresses. To improve peanut drought tolerance, *AtDREB1A*, a cis-acting transcription factor that binds to dehydration responsive element (DRE) from *Arabidopsis thaliana*, was transformed to peanut under the control of a stress inducible promoter from the *rd29A* gene [72]. One transgenic line demonstrated a 40% increase in transpiration efficiency (TE) in a greenhouse drought tolerance test. Further analysis of antioxidative responses from these transgenic lines cannot provide an explanation for the elevated TE performance [73]. In addition, improved greenhouse drought and salt tolerance was found among transgenic peanut lines transformed with *AtNHXI*, a vacuolar Na^+/H^+ antiporter [74]. Isopentenyltransferase (*IPT*), a key enzyme in the cytokinin biosynthesis pathway, driven by a drought inducible SARK promoter was used to transform peanut [75]. Transgenic lines demonstrated improved biomass retention in a greenhouse drought tolerance test and an average of 58% yield increase in a two-year field test. Transgenic peanut expressing a human Bcl-xL gene has improved tolerance to paraquat, a bipyridilium herbicide [76]. Fungal resistance in peanut was enhanced by transforming several genes including barley oxalate oxidase [77,78], mustard defensin [60], rice chitinase [79,80] and chloroperoxidase [81]. Evaluation of some transgenic lines was advanced to field studies such as resistance to *Sclerotinia minor*, which was confirmed in oxalate oxidase and rice chitinase transformed lines [78,79]. Synthetic *cry1* EC transformed peanut was shown to confer resistance to the larvae of *Spodoptera litura* [82].

Besides these applications in combating environmental challenges, peanut transformation has applications in vaccine development and peanut allergen silencing. Immunogen Ure B against the human bacterial pathogen *Helicobacter pylori* was overexpressed in peanut that potentially could be used as an oral vaccine [83]. The VP2 gene coding for the outer capsid of bluetongue virus (a sheep pathogen) was transformed in peanut [84]. In both cases, transgenic peanut has not been tested for the effectiveness of vaccination. Peanut endogenous proteins Ara h 2 and Ara h 6 were shown to be potent peanut allergens. Both were silenced by introducing an RNAi construct targeting homologous coding sequence, and human IgE binding to these proteins was greatly reduced in transgenic lines [63,85]. Ara h 2 was shown to have some trypsin inhibitor function [86], but silencing Ara h 2 did not promote *Aspergillus flavus* fungal growth. Collateral changes of proteins such as elevation in Ara h 10 (oleosin), 13-lipoxygenase and Ahy-3 (arachin) and decrease in conarachin among Ara h 2 silenced lines were identified by quantitative proteomics [87]. However, to date no released peanut cultivars are transgenic. There is public resistance to GMO food crops, particularly in the European countries, and it is very costly to meet the regulatory requirements for the release of GMO cultivars. In addition, there are significant issues regarding freedom to operate related to patented technologies.

Table 1. Peanut Genetic transformation since year 2006.

Peanut Genotype	Transformation Method	Explant	Promoter	Transgene	Selectable Marker	Trait Evaluation	Reference
JL-24	<i>A. tumefaciens</i> strain GV2260	cotyledonary node	CaMV 35 S	GUS	<i>nptII</i>	none	68
JL-24	<i>A. tumefaciens</i> strain C58	cotyledon	<i>A. thaliana</i> rd29A	<i>AtDREB1A</i>	<i>nptII</i>	green house tests for drought tolerance antioxidative response to drought stress	72 73
JL-24	<i>A. tumefaciens</i> strain EHA105	embryo axes	CaMV 35 S	mustard defensin	<i>nptII</i>	detached leaf assay and greenhouse tests for late leaf spot resistance	60
JL-24	<i>A. tumefaciens</i> strain EHA101	cotyledon	CaMV 35 S	synthetic <i>cryIEC</i> gene	<i>hph</i>	leaf feeding bioassay on <i>Spodoptera litura</i>	82
JL-24	<i>A. tumefaciens</i> strain C58	cotyledon	CaMV 35 S <i>A. thaliana</i> oleosin	rice chitinase maize phytoene synthase	<i>none</i> <i>none</i>	none none	71
Golden and BARI-2000	<i>A. tumefaciens</i> strain LB4404	cotyledonary node	CaMV 35 S	rice chitinase-3	<i>hph</i>	inoculation with <i>cerospora arachidicola</i>	80
Golden and BARI-2000	<i>A. tumefaciens</i> strain LBA4404	cotyledonary node	CaMV 35 S	<i>AtNHXI</i>	<i>nptII</i>	green house salt and drought tolerance	74
N/A	<i>A. tumefaciens</i> strain EHA105	embryo leaflets	Peanut oleosin	Ure B	<i>nptII</i>	none	83
New Mexico Valencia A	<i>A. tumefaciens</i> strain EHA104	cotyledon	drought inducible SARK	Isopentenyltransferase	<i>nptII</i>	Field drought tolerance test	75
Georgia Green	<i>A. tumefaciens</i> strain EHA105	hypocotyl	CaMV 35 S	<i>arah 2</i> RNAi	<i>nptII</i>	Allergenicity by human Ig E	63
Okrun	Biolistic	somatic embryo	CaMV 35 S	rice chitinase Alfalfa glucanase	<i>hph</i>	fungal resistance and agronomic traits evaluated in a 3-year field study	79
Georgia Green	Biolistic	somatic embryo	CaMV 35 S	<i>arah 2</i> RNAi	<i>hph</i>	Allergenicity by human Ig E	85
Georgia Green	Biolistic	somatic embryo	CaMV 35 S	chloroperoxidase	<i>hph</i>	In vitro and in situ <i>A. flavus</i> inoculation	81
JL-24	Biolistic	somatic embryo	CaMV 35 S	Bluetongue VP2	<i>nptII</i>	none	84
Georgia Green	Biolistic	somatic embryo	CaMV 35 S	Bcl-xL	<i>hph</i>	In vitro paraquat assay	76
Wilson, Perry, NC-7	Biolistic	somatic embryo	CaMV 35 S	Barley oxalate oxidase	<i>hph</i>	Field evaluation of transgenic lines for Sclerotinia minor resistance	77-78

2.2. Tilling

New sources of genetic variation can also be generated by TILLING (targeting induced local lesions in genomes) [88]. Tilling is a reverse genetic technique that requires knowledge of gene sequences since mutants are detected by screening for DNA sequence changes rather than phenotypic differences (forward genetics). A peanut TILLING population of over 3400 mutant lines from the cultivar Tifrunner [89] was generated using chemical (ethylmethane sulfonate -EMS) mutagenesis and screened for mutations in six genes [90]. This resulted in the discovery of gene knockouts or functional mutations in genes encoding the major allergen proteins, Ara h 1 and Ara h 2, and one of the genes that controls the oleic to linoleic acid ratio in peanut seed (FAD2). As more sequence data become available for peanut, this TILLING population should be useful for functional genomic studies as well as to discover mutations of potential value for cultivar development.

2.3. Synthetic Allotetraploids

Peanut cultivar development would greatly benefit from simplified access to the genetic diversity available in related diploid species of *Arachis*. Of great interest are the extremely high levels of resistance to many pests and diseases that occur in wild *Arachis* [91]. Introgression of traits using conventional breeding is a long and arduous task due to the cross incompatibilities and ploidy barriers between diploid wild and tetraploid cultivated along with poor agronomic performance of interspecific material. Two pathways for introgression have been tested in peanut, one involving a triploid intermediate from hybridization of cultivated tetraploid with wild diploid and the other a synthetic tetraploid hybrid crossed with cultivated tetraploid [48,92]. The latter is the most direct route for introgressing useful genes into *A. hypogaea*. Since much higher levels of molecular polymorphism occur in diploid *Arachis* in comparison to *A. hypogaea* [3,7], the use of molecular genetic technology on hybrids between wild and cultivated lines should allow for much more rapid and efficient introgression of desirable traits while maintaining acceptable agronomic performance. A synthetic tetraploid has been derived through crosses between the two putative progenitors of *A. hypogaea* (*A. duranensis* and *A. ipaensis*) and is being used as a springboard to access the diploid gene pool to mine for disease resistance, drought tolerance, and other traits [92,93].

3. Examples of Molecular Breeding in Peanut Cultivar Development

The first successful example of marker assisted selection (MAS) was the introgression of nematode resistance through an amphidiploid pathway into cultivated peanut [48], and the subsequent development of a nematode resistant cultivar, NemaTAM [94]. Although this cultivar has near immunity to the peanut root-knot nematode, it is not suitable for cultivation in the Southeastern U.S. due to extreme susceptibility to *tomato spotted wilt tospovirus* (TSWV) [95]. A goal of our peanut breeding program was to develop a cultivar with resistance to both TSWV and the peanut root-knot nematode. We chose to pursue this objective using phenotypic selection because the early markers were expensive, low throughput, and produced a significant amount of inaccurate data. Using a conventional breeding approach we produced ‘Tifguard’, the first peanut cultivar with high levels of resistance to both the peanut root-knot nematode and TSWV [95].

The next goal of the breeding program was to combine the high oleic fatty acid trait with resistance to both the peanut root-knot nematode and TSWV. Due to recent advances in molecular marker technology we decided to pursue this goal using a backcross breeding program accelerated by MAS. Research by Chu *et al.* [39] and Nagy *et al.* [40] resulted in the development of molecular markers for nematode resistance that can be used in high throughput systems and are more amenable for large breeding populations. Chu *et al.* [44,45] developed molecular markers for both genes which control the high oleic fatty acid trait in peanut. To achieve our breeding goal, Tifguard was used as the recurrent female parent and two high oleic cultivars were used as donor parents for the high O/L trait. ‘Tifguard High O/L’ was generated through three rounds of backcrossing using as the pollen donors BC_nF₁ progenies selected with molecular markers for these two traits. The high O/L trait is recessive but the use of a co-dominant molecular marker allowed backcrossing with heterozygous lines. Selfed BC₃F₂ plants yielded marker-homozygous individuals identified as Tifguard High O/L. Use of this MAS backcross breeding procedure compressed the hybridization and selection phases of the cultivar development process to less than 3 years [50], allowing for more rapid initiation of preliminary yield trials.

It is anticipated that more peanut cultivars developed using molecular technology will be released in the near future. Recent research has resulted in the development of several molecular markers or QTLs that should be useful for peanut cultivar development. Stalker *et al.* [96] presented a table with 14 references documenting molecular markers associated with traits in peanut, and efforts are ongoing to use the molecular markers associated with the QTL for leaf rust to incorporate leaf rust resistance into three elite cultivars at ICRISAT, India [23].

4. Concluding Comments

Efforts to shepherd initiatives for increased research on peanut genomics at the 2001 U.S. Legume Crops Genomics Workshop and at subsequent meetings of the International Peanut Genome Consortium have been described by Stalker *et al.* [96] and Feng *et al.* [20]. Recent updates are posted on <http://www.peanutbioscience.com>. These efforts have resulted in quantum leaps of knowledge about the peanut genome, and have facilitated ongoing marker assisted breeding programs. These efforts have also stimulated the development of molecular genetic tools and RIL populations that should result in additional quantum leaps of knowledge. In addition, these efforts have laid the foundation for plans to sequence the peanut genome in the near future. This should result in the development of additional molecular tools that will greatly advance peanut cultivar development.

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