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Impact of Drought Stress on Peanut (*Arachis hypogaea* L.) Productivity and Food Safety

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1. Introduction

Peanut (*Arachis hypogaea* L.) is one of the world's most important legumes. It is grown primarily for its high quality edible oil and protein. Peanut is grown on 35.5 million ha across 82 countries in the world. More than half of the production area, which accounts for 70% of the peanut growing area fall under arid and semi-arid regions, where peanuts are frequently subjected to drought stresses for different duration and intensities (Reddy et al., 2003). An annual estimated loss in peanut production equivalent to over US$520 million is caused by drought. Further, drought is also known to predispose peanut to aflatoxin contamination (Blankenship et al., 1984; Cole et al., 1989) making them unfit for human consumption. Yield losses due to drought are highly variable in nature depending on timing, intensity, and duration, coupled with other location-specific environmental stress factors such as high irradiance and temperature. In the United States peanuts contribute to more than $4 billion to the country's economy each year. In USA majority of the peanut are grown under rain-fed conditions and only limited acreage is irrigated. Frequent failure of rains late in the season has resulted in decreased yield, poor quality peanuts and aflatoxin contamination. Furthermore, increased worldwide demand for water due to rapid population growth and irrigation practices have resulted in declines in aquifers limiting availability of water for irrigation. To meet future food-supply demands, crop production will have to increase, but it must do so under the constraints of less water and, most likely, less farm land. Agricultural Research Service (ARS) scientists with the Plant Stress and

Germplasm Development Research Unit, Lubbock, Texas, the National Peanut Research Laboratory (NPRL) in Dawson, Georgia, and ICRISAT, India are working with cooperators to help peanut farmers maintain and improve their production in a changing environment.
Drought-stressed plants lose moisture from pods which leads to the reduction in the seeds physiological activity, thereby increasing the susceptibility to fungal invasion. Besides affecting food quality, drought stress is also known to alter nutritional quality of peanut seed proteins. Since peanut lack desirable genetic variation in drought and aflatoxin tolerance several conventional as well as molecular breeding techniques were adopted to improve drought and aflatoxin tolerance (Mehan et al., 1986; Dorner et al., 1989; Holbrook et al., 2000). Recently several advanced molecular tools have been developed to screen drought tolerance in peanut genotypes. Effect of drought stress on peanut is being studied at the molecular and cellular level, which has generated enormous amount of genomic and proteomic data that displays the mechanism by which peanut plants respond to drought stress. Engineering peanuts to withstand drought stress has been achieved *via* different strategies, while few of them have succeeded in developing improved peanut genotypes that withstand drought stress others are in the process of developing advanced genotypes. This chapter will highlight selected as well as most significant achievements made to understand and overcome drought stress in peanuts.

2. Effect of drought on plant performance

2.1 Drought stresses reduce plant productivity

Drought stress has been the major environmental factor contributing to the reduced agricultural productivity and food safety worldwide. Drought stress perceived by the plant from its surrounding environment varies spatially and temporally at several different scales. Drought affects membrane lipids and photosynthetic responses (Lauriano et al., 2000) and yield in peanuts (Suther & Patel, 1992). Water deficit affects thylakoid electron transport, phosphorylation, carboxylation and photosynthesis. Changes in the lipid content and composition are common in water-stressed plants and this increases membrane permeability. This causes damage and membrane disruption as well as reduction in photosynthesis. Maintaining membrane integrity under drought conditions will determine the plants resistance towards stress. Plants have several mechanisms for adaptation to water and heat stress including stomatal conductance, paraheliotropism, and osmotic adjustments. Arid and semi-arid environments typically have hot days and cool nights. Since there is a lack of water vapor in the air, the temperature at night drops making the night cooler but the day hotter. This can be stressful to the plant.

2.2 Plant responses to drought

Drought stress has adverse influence on water relations (Babu & Rao, 1983), photosynthesis (Bhagsari et al., 1976), mineral nutrition, metabolism, growth and yield of groundnut (Suther & Patel, 1992). In addition, drought conditions influence the growth of weeds, agronomic management and, nature and intensity of insects, pests and diseases (Wightman et al., 1989). Parameters like relative water content (RWC), leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature influences water relations in peanut during drought. Stressed plants have lower RWC than non-stressed plants. For example, relative water content of non-stressed plants range from 85 to 90%, while in drought stressed plants, it may be as low as 30% (Babu & Rao, 1983). Peanut leaves

show large diurnal variation with high values in the morning when solar radiation and vapor pressure deficits are low, followed by low values around midday and gradual increase after midday (Erickson & Ketring, 1985). Osmotic potential follows the same pattern but ranges less widely than leaf water potential. Transpiration rate generally correlates to the incident solar radiation under sufficient water availability. However, drought stressed plants transpire less than unstressed plants. Subramaniam & Maheswari, (1990) reported that leaf water potential, transpiration rate and photosynthetic rate decreased progressively with increasing duration of water stress indicating that plants under mild stress were postponing tissue dehydration. Stomatal conductance decreased almost steadily during the stress period indicating that stomatal conductance was more sensitive than transpiration during the initial stress period. Stirling et al., (1989) found that under water deficit conditions the leaves exhibited marked diurnal variation in leaf turgor, while pegs showed less variation and maintained much higher turgor levels largely because of their lower solute potentials. Marked osmotic adjustment occurred in growing leaves but not in mature ones, allowing them to maintain higher turgor during periods of severe stress. This adjustment was rapidly lost when stress was released (Ali Ahmad & Basha, 1998). Bhagsari et al., (1976) reported that water potential of leaves and immature fruits were similar under drought stress conditions. It is a general observation that under severe moisture stress conditions, young pods lose their turgor and shrivel. Azam Ali (1984) reported that stomatal resistance of older leaves was greater than that of younger leaves. Leaves also become thicker under moderate drought stress (Reddy & Rao, 1968). The developing leaves of groundnut have an unusual thick layer of cells devoid of chloroplasts with lower epidermis below the sponge parenchyma. Cells of this layer are considered to be water storage cells (Reddy & Rao, 1968). During moisture stress, the opposing leaflets of tri-foliate leaf come together and orient themselves parallel to incident solar radiation, in an effort to reduce solar radiation load on the leaf. Leaf expansion is more sensitive to soil water deficit than stomatal closure (Black et al., 1985). Drought reduces leaf area by slowing leaf expansion and reducing the supply of carbohydrates. Reddy and Rao (1968) reported that severe drought stress decreased the levels of chlorophyll *a*, *b* and total chlorophyll. The decrease in chlorophyll was attributed to the inhibition of chlorophyll synthesis as well as to accelerated turnover of chlorophyll already present.

Periodic water stress leads to anatomical changes such as a decrease in size of cells and intercellular spaces, thicker cell walls and greater development of epidermal tissue. Nitrogen fixation by leguminous plants is reduced by moisture stress due to a reduction in leg haemoglobin in nodules, specific nodule activity and number of arid regions. In addition, dry weight of nodules is significantly reduced in moisture stressed plants. Moisture stress also delays nodule formation in leguminous crops (Reddi & Reddy, 1995). There is considerable evidence that N, P and K uptake of peanut is reduced by drought stress (Kulkarni et al., 1988).

Leakage of solutes as a consequence of membrane damage is a common response of groundnut tissue to drought stress. Metabolic process is affected by water deficits. Severe water deficits cause decreases in enzymatic activity. Complex carbohydrates and proteins are broken down by enzymes into simpler sugars and amino acids, respectively (Pandey et al., 1984). Accumulation of soluble compounds in cells increases osmotic potential and reduces water loss from cells. Proline, an amino acid, accumulates whenever there is moisture stress. Accumulation of proline is greater in the later stages of drought stress and

therefore its concentration is considered a good indicator of moisture stress (Reddi & Reddy, 1995).

2.3 Effect of drought during flowering and pod formation

2.3.1 Flowering

The start of flowering is not delayed by drought stress (Boote & Ketring, 1990). The rate of flower production is reduced by drought stress during flowering but the total number of flowers per plant is not affected due to an increase in the duration of flowering (Gowda & Hegde, 1986; Janamatti et al., 1986; Meisner & Karnok, 1992). A significant burst in flowering on alleviation of stress is a unique feature in the pattern of flowering under moisture stress, particularly when drought is imposed just prior to re-productive development (Janamatti et al., 1986). When stress is imposed during 30–45 days after sowing the first flush of flowers produced up to 45 days do not form pegs during that time, however, flowers produced after re-watering compensated for this loss (Gowda & Hegde, 1986).

2.3.2 Pod formation

Peanut plants may experience water stress during pegging and pod development and then may have adequate amount of water (Jogloy et al., 1996). This would result in a drastic reduction of crop yield, and the magnitude of reduction would depend on peanut cultivars. Not only the yield of peanut but also the quality of products decreases under drought stress (Rucker et al., 1995). Peg elongation, which is turgor dependent, is delayed due to drought stress (Boote & Ketring, 1990). Pegs fail to penetrate effectively into air-dry soil, especially in crusted soils. Often, within 4 days of withholding water, the soil surface becomes too dry for peg penetration. Skelton & Shear (1971) reported that adequate root zone moisture could keep pegs alive until pegging zone moisture content is sufficient to allow penetration and initiation of pod development. Once pegs are in the soil, adequate moisture and darkness are needed for pod development. Adequate pod zone moisture is critical for development of pegs into pods and adequate soil water in the root zone cannot compensate for lack of pod zone water for the first 30 days of peg development. Dry pegging zone soil delayed pod and seed development. Soil water deficits in the pegging and root zone decreased pod and seed growth rates by approximately 30% and decreased weight per seed from 563 to 428 mg. Peg initiation growth during drought stress demonstrated ability to suspend development during the period of soil water deficit and to re-initiate pod development after the drought stress was relieved (Sexton et al., 1988). It has frequently been reported that under water stress, pegging and seed set responses of various peanut cultivars varied substantially, this leads to a large reduction in pod yield, and the reduction percentage also varies among peanut cultivars (Haris et al., 1988, Nageswara Rao et al., 1989).

2.4 Relationship of drought tolerance and aflatoxin contamination

Drought stress has a strong effect on biocompetitive (phytoalexins, antifungal proteins) or protective compounds (phenols), which influence the growth of *Aspergillus* fungus and aflatoxin synthesis, as well as the proper maturation of peanut seeds. Aflatoxin contamination threat increases with increasing seed maturity. As the seed moisture content decreases during drought, the capacity of seed to produce phytoalexins decreases resulting in *Aspergillus* invasion and aflatoxin production. Some of the enzymes that are induced in response to fungal attack such as chitinases, osmotins, peroxidases, and proteases are also

adversely affected during drought stress through cell membrane-mediated mechanisms. Drought stress and drought stress mediated-fungal infection compromise peanut defense and exacerbate aflatoxin formation in the seeds (Guo et al., 2005). Thus, breeding for drought tolerance has been accepted as one of the strategies for developing aflatoxin-tolerant peanut cultivars, which would not only minimize water usage but also help expand peanut production in marginal and sub-marginal soils. Success in this effort has been slow due to lack of genetic resources and lack of information on the relationship or interaction between the pathways affected due to drought and or pathogen invasion. However, to date, few peanut cultivars with natural pre-harvest resistance to aflatoxin production have been identified through field screening.

3. Breeding for crop improvement

3.1 Breeding towards drought tolerance

Efforts to improve peanuts that focus on yield as the only environmental method for screening of tolerance are seen to have a high variability in yield as well as differences in exactly reproducing stress conditions. A more-integrated approach for peanut breeding is needed to offer success in developing stress-tolerant varieties. Understanding physiological and molecular genetics may lead to the understanding of stress response and aid in development of new varieties with stress tolerance. So, a high-yielding cultivar that continues to produce well under drought conditions is a priority to enable stability of production. That is why much research for the last decade has attempted to improve performance by selecting plants with good pod yield under adverse conditions. As well as spending time testing plants in large-scale trials under different conditions, a study of plant physiology has revealed the features of the plant that correlate best with drought tolerance.

Research in the previous decade had developed low-cost, rapid and easily measured indicators for three significant physiological features of drought-tolerance *viz.* amount of water transpired (T), water-use efficiency (W) and harvest index (HI), thus allowing their potential quantification in large numbers of breeding populations. The application of this physiological model in peanut-breeding programs has not been possible because of practical difficulties associated with measurement of the traits under field conditions. The USDA germplasm collection numbers over 9000 accessions of *A. hypogaea* (Holbrook, 2001) and about 800 accessions of *Arachis* species. Large *Arachis* species collections are also maintained at Texas A&M University and N. C. State University. The US breeding program is focused more on yield, grade, seed size and developing disease tolerant germplasm, and less on drought tolerance. Identifying drought tolerant genotypes with emphasis to reduce preharvest aflatoxin contamination is being conducted at the USDA-ARS, Tifton, GA., The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India and The National Center of Genetic Resources (CENARGEN), Brazil. The largest collection of domesticated peanut germplasm is located at ICRISAT, where there are 14,310 accessions from 92 countries while CENARGEN has 413 accessions of *Arachis* species (Upadhyaya et al., 2001a). A new drought tolerant groundnut variety, ICGV 91114, is becoming very popular in Anantapur district in Andhra Pradesh, India, where it is now replacing a 7-decade old variety TMV 2. ICGV 91114 has also been released in Orissa, India and is doing very well in Karnataka, India.

In another study at Main Oilseeds Research Station, Junagadh Agricultural University, Junagadh, around 130 genotypes/crosses from different breeding trials (these were identified as potential drought tolerant with the help of visual observations such as retention of greenness at harvest, thickness of foliage, dwarfness combined with greenness, etc.) were screened for higher yield than local check varieties under simulated drought conditions in the summer season of 1999, 2000 and 1997. In the second phase of investigation, yield performance of these selected crosses/entries was assessed in comparison with three varieties GG-2, GG-5 (local checks) and J-11 (national check) at three naturally drought prone locations viz., at Targhadia (Main Dry Farming Research Station), Manavadar, Nanakandhasar and Jamkhambhalia, Gujarat, India in terms of pod yield. The basic advantage in selecting yield as the selection criteria is that it integrates all the additive effects of many underlying mechanisms of drought tolerance. Seven crosses and two genotypes with three controls (check varieties) were grown in a randomized complete block design with four replications for three consecutive Kharif seasons – 1999, 2000 and 2001. The results clearly indicated that the selected crosses/genotypes are at par with the local cultivated varieties of groundnut with respect to pod yields. In fact, they could even be termed superior because under extreme conditions of water deficit during 1999 and 2000 they recorded significantly higher pod yield than the local checks. Hence, the crosses GG-2 x NCAC 17135, GG-2 x PI 259747, J 11 x PI 259747, S 206 x FESR-8, Kisan x FESR-S-PI-B1-B, and the genotypes JB 223 and 224 could be termed as drought tolerant genotypes. Hence, it is suggested that these lines/genotypes could be grown under regions of limited rainfall. These lines may be also used as parents in breeding programs for developing drought tolerant groundnut cultivars.

3.2 Limitations of traditional breeding

Crop improvement in terms of production, desirable traits and resistance to drought stress is a pre-requisite in modern day agriculture. Conventional breeding for developing drought-tolerant crop varieties is time-consuming and labor intensive due to the quantitative nature of drought tolerance and difficulties in selection for drought tolerance (Ribaut et al., 1997). Combining high levels of resistance into higher yielding cultivars with acceptable market traits continues to be difficult (Holbrook & Stalker, 2003). Breeding programs, aimed at incorporating resistance genes from wild *Arachis* relatives have proved largely unsuccessful due to genetic incompatibility. Due to limitations of conventional peanut breeding either because of limited gene pool or the restricted range of organisms between which genes can be transferred, new *omics* techniques in addition to conventional methods are needed to develop peanut cultivars with resistance to drought and pre-harvest aflatoxin contamination.

4. Applications of molecular breeding tools for crop improvement

4.1 Genomic approach

Peanut is a polyploid with a large genome size, complete sequencing will be too expensive and labor intensive to perform with current resources. Research with molecular aspects of the peanut genome began in the 1980s when protein and isozyme variation in *A. hypogaea* was determined to be of little use for characterizing variation within the cultivated peanut. Although large numbers of polymorphisms were detected among other species in the genus (Lu & Pickersgill, 1993; Stalker et al., 1994), the number of markers was too small to be routinely used in breeding programs.

4.1.1 Molecular markers

Improvement of drought tolerance is an important area of research for groundnut breeding programs. Recent advances in the area of crop genomics offer tools to assist in breeding (Varshney et al., 2005, 2006). The identification of genomic regions associated with drought tolerance would enable breeders to develop improved cultivars with increased drought tolerance using marker-assisted selection (Ribaut et al., 1996). To make selection on large populations of progeny for breeding work, the accessions must be grown out and tested for traits. This is time consuming and subject to environmental variability. The scarcity of DNA polymorphism in cultivated peanut posses a considerable obstacle in genetic mapping of peanut. The Texas Peanut Breeding and Genetics Program is working on a long-term program to integrate modern physiological and molecular methods with plant breeding, to develop peanut varieties that can be grown efficiently under reduced water inputs and high heat stress. There are RFLP (Restricted Fragment Length Polymorphism) maps of wild type x cultivar crosses but the polymorphisms are too low for a cultivated x cultivated species cross; therefore, new markers are needed (Burow et al., 2001). Restricted Fragment Length Polymorphism markers also have disadvantages of using radioisotope, and results take longer to obtain than the use of PCR-based methods. Burow et al., (2001) study focused on finding traits useful in selecting genotypes for drought and heat tolerance. Heat stress was determined by fluorescence from cultivars grown in a high thermal stress greenhouse environment. Selections were made for drought and heat tolerance and crosses were made for further progeny evaluation. Further, they suggested that the research would entail sequencing cDNA in mapped RFLP clones to start the development of molecular markers in peanut.

A considerable number of SSR sequences have been identified from peanut genome by several research groups (Hopkins et al., 1999; He et al., 2003; Ferguson et al., 2004; Moretzsohn et al., 2005; Proite et al., 2007; Cuc et al., 2008). SSR markers developed from these repeat sequences offer promising genetic and genomic tools in peanut research. Genetic diversity of peanut germplasm has been studied in Valencia (Krishna et al., 2004), mini-core collection (Barkley et al., 2007), and in Chinese (Tang et al., 2007) and Japanese peanut germplasm collections (Naito et al., 2008) using SSR markers. Genetic linkage maps with SSR markers have been constructed for diploid AA genome (Moretzsohn et al., 2005), BB genome (Moretzsohn et al., 2009), tetraploid AABB genome derived from a cross of cultivated with amphidiploids (Fonceka et al., 2009), and tetraploid AABB genome in the cultivated peanut (Hong et al., 2008, Varshney et al., 2009; Hong et al., 2010). Although an exceedingly large number of SSRs have been identified, the polymorphic SSR markers may not be sufficient for the construction of a saturated linkage map in the cultivated peanut, provide enough meaningful markers for marker-assisted selection in peanut breeding programs, or sufficient coverage of important domains of the peanut genome for functional genomics research.

To identify the genomic regions suitable for marker-assisted breeding strategies, it is important to establish accurate phenotyping methods, develop highly saturated molecular marker-based genetic linkage maps, and then identify QTLs (quantitative trait loci) associated with traits of interest. Several studies were conducted in the past that reported identification of QTLs for drought tolerance or related traits. A RIL mapping population comprising of 318 F8/F9/F10 lines derived from a cross of TAG 24 x ICGV 86031 was phenotyped for transpiration (T, g plant-1), transpiration efficiency (TE, g biomass kg-1 water transpired), SLA (cm2 g-1), SCMR, leaf area (LA, cm2 plant-1), shoot plus pod dry

weight (DW, g plant-1), and total dry matter (TDM, g plant-1, which includes root dry weight) and carbon discrimination ratio (d13C) during post-rainy season in 2004 and 2005 by Ravi et al., (2011). A genetic map containing 191 SSR loci based on a single mapping population (TAG 24 9 ICGV 86031), segregating for drought and surrogate traits was developed. This study suggests deployment of modern approaches like marker-assisted recurrent selection or genomic selection instead of marker-assisted backcrossing approach for breeding drought tolerance in peanut.

4.1.2 Gene expression during drought stress in peanuts

Abiotic stress is a growing concern for peanut cultivation. Many production areas are in semiarid environments or have unreliable rainfall, and global climate changes and growing demand for fresh water pose major challenges. Physiological adaptation and selection for drought tolerance have been studied by many researchers (Reddy et al., 2003). Study of peanut genomics has been limited by biological constraints, and many basic tools of genomics have yet to be developed (Gepts et al., 2005). The peanut genome is large, making insertional mutagenesis and whole-genome sequencing expensive using current technology, and requiring large genomic libraries for physical mapping and positional cloning. To date, 136,901 peanut sequences, including 87,688 ESTs from cultivated peanuts and 39,866 nucleotide sequences have been deposited in the NCBI EST database. Out of which 52 nucleotide sequences and 25,914 EST sequences are available in response to drought treatments.

One of the major molecular responses that plants exhibit to drought stress is altered expression of genes, related to different pathways associated with stress perception, signal transduction, regulators and synthesis of a number of compounds (Ramanjulu & Bartels, 2002; Sreenivasulu et al., 2007). Several hundred genes that respond to drought stress at the transcriptional level have been identified in model crop *Arabidopsis* by microarray technology and other means (Seki et al., 2002; Shinozaki and Yamaguchi- Shinozaki., 2007). The adaptive mechanisms under stress are a net effect of altered cell metabolism resulting from regulated expression of stress responsive genes. The resurrection plants have better capabilities to cope with severe drought conditions; hence, several studies have been conducted to discover what key genes are involved in enabling these plants to survive desiccation.

Differential display reverse transcriptase PCR was used to identify genes induced and suppressed in peanut seed during drought. A total of 1235 differential display products were observed in irrigated samples, compared to 950 differential display products in stressed leaf samples (Jain et al., 2001). In another experiment, seven transcripts were found induced following stress of which two transcripts were suppressed in drought stressed immature pods of tolerant variety K1375 (Devaiah et al., 2007) (Fig. 1). These products demonstrated qualitative and quantitative differences in the gene expression during drought stress in peanuts.

Subtractive hybridization was used to identify about 700 genes from cDNA library prepared from peanut plants that were subjected to gradual process of drought stress adaptation (Govind et al., 2009). Further, expression of the drought inducible genes related to various signaling components and gene sets involved in protecting cellular function has been described based on dot blot experiments. Many families of transcription factors including AP2/EREBP (AhWSI 279), bHLH (AhWSI 111, AhWSI 40), bZIP (AhWSI 20), CCAAT box (AhWSI 117), Homeobox (AhWSI6 11), Jumonji (AhWSI 72, AhWSI 116), NAC (AhWSI 153,

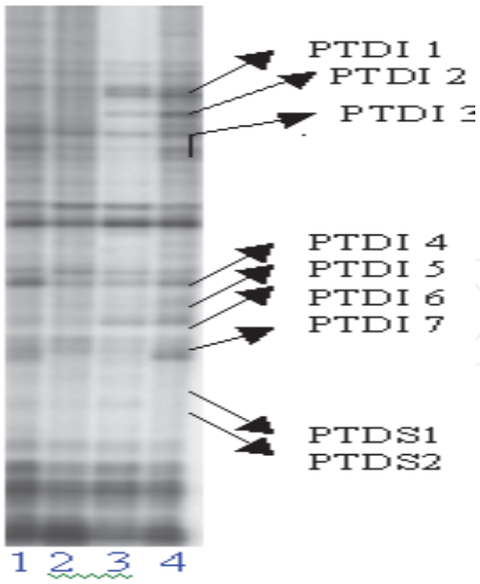

Fig. 1. DDRT PCR cDNA amplification from drought susceptible (JL-24) and drought tolerant peanut genotype (K1375). Arrows pointed upwards show peanut transcripts drought induced (PTDI) and arrows pointing downwards show peanut transcripts drought suppressed (PTDS).

AhWSI 308) and several zinc finger protein transcripts are preferentially induced under drought treatments in peanut plants. Also among the upstream signaling components they observed induction of transcripts of calmodulins (AhWSI 227, AhWSI 228), G protein (AhWSI 551), MAPKK (AhWSI 28) and several receptor kinases during drought treatments. In addition, specific upregulation of hormone responsive genes such as auxin-repressed proteins (AhWSI 306, AhWSI 468, AhWSI 467), brassinosteroid responsive BRH1 (AhWSI 36), cytokinin-repressed protein CR9 (AhWSI 465), GA like proteins (AhWSI 291, AhWSI 464) was observed during drought treatments. Insights gained from this study would provide the foundation for further studies to understand the question of how peanut plants are able to adapt to naturally occurring harsh drought conditions. Guo et al., (2006) identified a novel PLD gene in peanut, encoding a putative phospholipase D (a main enzyme responsible for the drought-induced degradation of membrane phospholipids in plants). PLD expression was induced faster by drought stress in the drought-sensitive lines than in the drought-tolerant lines, suggesting that peanut PLD may be involved in drought sensitivity responses, which could be useful as a tool in germplasm screening for drought tolerance. Gene expression in leaves of peanut plants submitted to progressive drought stress was studied by Drame et al., (2007). This study revealed that a good correlation exists with the agronomical and physiological responses during drought in peanuts. This study demonstrated that phospolipase Dα and LEA transcripts accumulation could contribute to reduced water loss and protection of cellular components.

4.1.3 Microarray based screening for monitoring gene expression during drought

Microarray technology employing cDNAs or oligonucleotides is a powerful tool for analyzing gene expression profiles of plants exposed to abiotic stresses such as drought,

high salinity, or cold, or to ABA treatment (Seki et al., 2001, 2002a, 2002b; Kreps et al., 2002). There are two predominant varieties of microarray technology available; the cDNA microarray (Seki et al., 2001, 2002a, 2002b) and the oligonucleotide microarray. cDNA Microarray was used to screen peanut genotypes by Luo et al., (2005). In this study, resistance genes in response to *Aspergillus parasiticus* infection under drought stress were identified using microarray and real-time PCR. A peanut genotype (A13) which is believed to be tolerant to drought and pre-harvest aflatoxin contamination was used to study gene expression. A total of 52 up-regulated genes were detected in response to drought apart from genes that were expressed due to biotic stress. Reactive oxygen scavengers glutathione S-transferase GST, superoxide dismutase (Cu–Zn), lactoylglutathione lyase, ascorbate peroxidase, lipoxygenase 1, Lipoxygenase 1, lactoylglutathione lyase, superoxide dismutase (Cu–Zn), stress proteins like drought-induced protein RPR-10, cytochrome P450, NOI protein, cold-regulated LTCOR12, low temperature and salt responsive protein, LTI6B, auxin-induced protein, ultraviolet-B-repressible protein, embryonic abundant protein, salt tolerance-like protein, proline-rich protein APG isolog, 10 kDa protein precursor, salt tolerance-like protein, NOI protein, embryonic abundant protein, ultraviolet-B-repressible protein, auxin-induced protein, osmotin-like protein, cell-autonomous heat shock cognate protein 7 and heat shock protein 81-2 were observed to be induced during drought.

High-density oligonucleotide microarray was developed for peanut using 49,205 publicly available ESTs and the utility of this array were tested for expression profiling in a variety of peanut tissues (Payton et al., 2009) to identify putatively tissue-specific genes and demonstrate the utility of this array for expression profiling in a variety of peanut tissues, transcript levels in pod, peg, leaf, stem, and root tissues. A set of 108 putatively pod-specific/abundant genes, as well as transcripts whose expression was low or undetected in pod compared to peg, leaf, stem, or root was detected. The transcripts significantly over-represented in pod including genes responsible for seed storage proteins and desiccation (e.g., late-embryogenesis abundant proteins, aquaporins, legumin B), oil production, and cellular defense were also observed. This Microarray chip represents sequences available from various drought stress treatments and hence, can be used as tool to monitor gene expression profile in genotype screening for drought tolerance.

4.1.4 Micro RNA could modify regulator gene expression during drought in peanuts

Micro RNAs are a new class of small, endogenous RNAs that play a regulatory role in the cell by negatively affecting gene expression at the post-transcriptional level. MicroRNAs have been shown to control numerous genes involved in various biological and metabolic processes. Recently MicroRNAs (miRNAs) were isolated in peanuts by Zhao et al., (2010). In this study, they used next generation high through-put Solexa sequencing technology to clone and identify both conserved and species-specific miRNAs in peanut. Next generation high through-put Solexa sequencing showed that peanuts have a complex small RNA population and the length of small RNAs varied, 24-nt being the predominant length for a majority of the small RNAs. Combining the deep sequencing and bioinformatics, they discovered 14 novel miRNA families as well as 75 conserved miRNAs in peanuts. All 14 novel peanut miRNAs were considered to be species-specific because no homologs have been found in other plant species except ahy-miRn1, which has a homolog in soybean. qRT-PCR analysis demonstrated that both conserved and peanut-specific miRNAs were expressed in peanuts. This study led to the discovery of 14 novel and 22 conserved miRNA families from peanut. These results show that regulatory miRNAs exist in agronomically-

important peanuts and may play an important role in peanut growth, development, and response to environmental stress.

4.2 Proteomic approach

4.2.1 Protein expression during drought stress

Proteomics studies have been carried out in leaf and immature peanut pods in response to drought stress. Identification and development of drought-tolerant genotype/s is the potential means to reduce aflatoxin contamination. Difference in biochemical response of peanut genotypes with varying degree of drought tolerance was monitored by withholding irrigation for various intervals. Changes in seed protein composition in response to drought stress were measured using two-dimensional electrophoresis followed by Mass spectroscopy. Mass spectroscopy analysis revealed down-regulation of methionine rich proteins (MRPs) and arachin proteins in drought-susceptible (DS) genotypes, while these proteins continue to express in drought-tolerant (DT) genotypes. Up-regulation of mRNA transcripts in DT genotypes indicated their association with stress tolerance. Continued expression of these proteins seems to enhance drought tolerance, reduce aflatoxin level and enhance nutritional value of peanut. These studies have revealed that drought stress suppresses expression of several seed storage proteins such as arachin, methionine-rich proteins, conarachin, etc (Basha et al., 2007).

Changes in the seed protein content and composition during 14 days of desiccation was determined by Mazhar and Basha (2002) using a combination of electrophoretic and immunochemical techniques. Following desiccation, the protein content of 'white' (most immature) and 'orange' (Intermediate maturity stage: Drexler and Williams, 1979) seed increased, while that of the 'brown' (more mature) seed were not affected. Sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) showed no major qualitative differences in protein composition during desiccation. However, immunoblotting with anti-dehydrin antisera revealed presence of several new proteins in the desiccated samples compared with the controls. One of the dehydrin-like proteins, was found to be related to water-stress, while the other proteins appeared to be the storage proteins accumulated as the seed matured *in vitro*. Capillary electrophoresis (CE) showed major changes in protein quantity and quality of 'white' seed (Immature) during the 0–14 days of desiccation. In contrast, in the 'orange' and 'brown' seeds (more mature) changes in protein composition were less significant. Their results indicated that several dehydrin-like proteins expressed in peanuts during desiccation but not all of them are related to drought stress.

In 2007, Basha and his co-workers carried out a study to determine changes in seed polypeptide composition among drought-tolerant (Vemana and K-1375) and drought-susceptible peanut genotypes (M-13 and JL-220) following water stress (WS) for 7, 14 and 28 d. They found that water stress had variable effect on peanut seed polypeptide composition (Fig. 2A) among the DT and DS genotypes. WS affected polypeptides with apparent molecular weight (Mr) around 70, 35, 25, 20, 18 and 14 kDa, and isoelectric points between 4.0 and 6.0 pH. The maximum response to WS occurred between 0 to 7 d, and additional periods (14 and 28 d) of stress caused only limited changes in seed polypeptide composition. These responses included over-expression, suppression, and appearance of new proteins in water-stressed seed compared to irrigated control. These data revealed that seed polypeptide composition of drought-tolerant peanut genotypes (Vemana and K-1375) was least affected while that of drought-susceptible genotypes (M-13 and JL-220) significantly altered due to WS (Fig. 2).

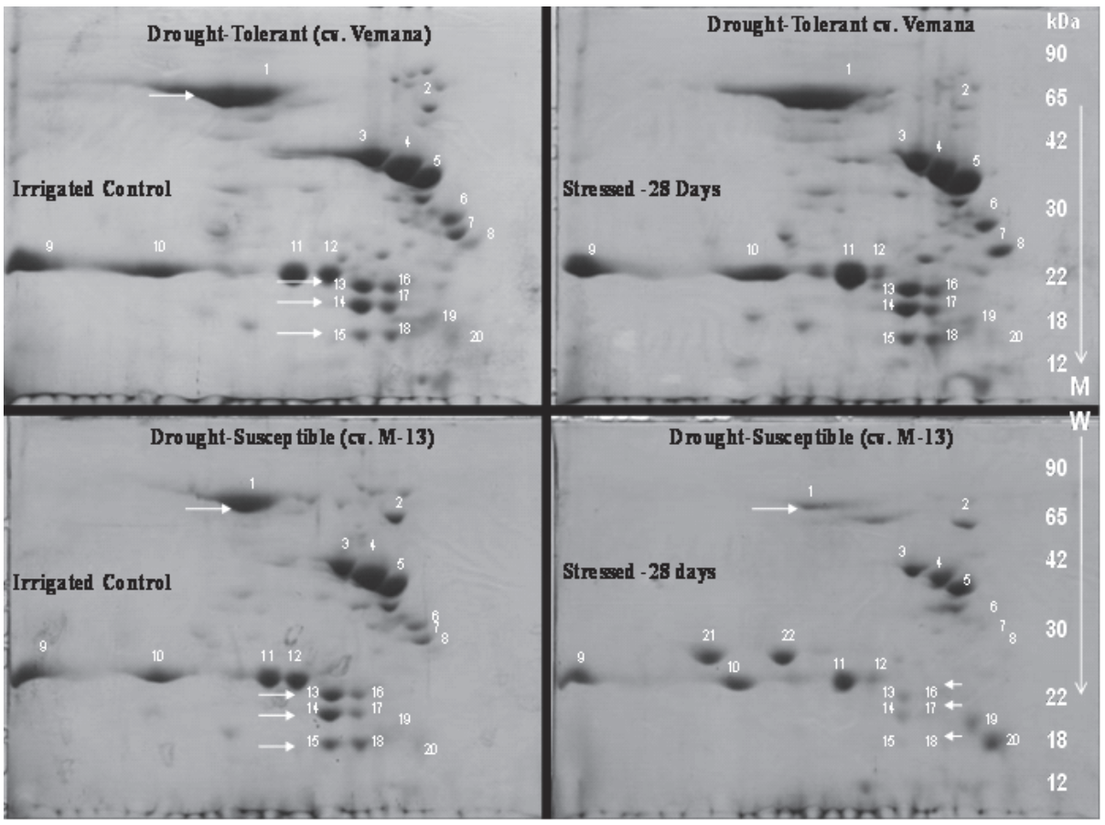

Fig. 2. Differential response of seed proteins of Drought Tolerant and Drought Susceptible Peanut Genotypes to Water Stress

Recently, Kottapalli and co-workers (2009) analyzed peanut genotypes from the US mini-core collection for changes in leaf proteins during reproductive growth under water-deficit stress. One and two-dimensional gel electrophoresis (1- and 2-DGE) was performed on soluble protein extracts of selected drought-tolerant and drought-susceptible genotypes. A total of 102 protein bands/spots were analyzed by matrix-assisted laser desorption/ionization–time-of-flight mass spectrometry (MALDI–TOF MS) and by quadrupole time-of-flight tandem mass spectrometry (Q-TOF MS/MS) analysis. Forty-nine nonredundant proteins were identified, implicating a variety of stress response mechanisms in peanut. Lipoxygenase and 1L-myo-inositol-1-phosphate synthase, which aid in inter and intracellular stress signaling were found to be more abundant in tolerant genotypes under water-deficit stress. Acetyl-CoA carboxylase, a key enzyme of lipid biosynthesis increased in relative abundance along with a corresponding increase in epicuticular wax content in the tolerant genotype, suggesting an additional mechanism for water conservation and stress tolerance. They also found a marked decrease in the abundance of several photosynthetic proteins in the tolerant genotype, along with a concomitant decrease in net photosynthesis in response to water-deficit stress. In contrast, Katam et al. (2007) found up-regulation of leaf proteins following drought stress in DT genotypes and down-regulation in DS genotypes. Differential regulation of leaf proteins involved in a variety of cellular functions (e.g. cell wall strengthening, signal transduction, energy metabolism, cellular detoxification and gene regulation) indicates that these molecules could affect the molecular mechanism of water-deficit stress tolerance in peanut.

5. Transgenic peanut tolerant to drought

The mechanisms of drought response have been investigated extensively in *Arabidopsis* (Bray et al., 1997; Shinozaki et al., 2003). However, the response of peanut to drought stress has not been extensively studied using genetic engineering. Classical breeding for drought tolerance in peanut is difficult because of variability in time, intensity, and duration of stress. In certain breeding programs, plants with genetic variability to drought have been identified and used to introduce this trait in genotypes with desirable agronomic characteristics. Thus in peanut classical breeding has and continues to have some success but the process is slow and limited by the availability of suitable genes for breeding. Beyond this there has been limited progress in breeding for drought tolerance because of limited characterization of associated traits and the fact that potential component traits of drought tolerance such as Transpiration, Transpiration Efficiency, or Harvest Index (Passioura, 1977) do not have simply additive effects (Bhatnagar-Mathur et al., 2007) in peanut. Molecular markers have been used to aid in the breeding process, but the low level of polymorphism in cultivated peanut has interfered with this approach. Although peanut germplasm with reduced drought tolerance have been identified and screened in breeding populations (Holbrook et al., 2000), peanut growers currently cannot rely fully on the available drought tolerant cultivars, as they are location specific. Therefore, the use of genetic engineering technology to over-express drought tolerant genes in peanut is an attractive prospective way to improve tolerance.

5.1 Developing drought tolerant peanut through genetic engineering

Development of drought tolerant peanut by genetic engineering requires the identification of key genetic determinants underlying stress tolerance in peanut plants, and introducing these genes into peanut crops. The effect of drought can trigger a wide array of physiological responses in plants, and this can affect a large number of genes. For example, Sahi et al., (2006) through their gene expression experiments have identified several hundred genes which are either induced or repressed during drought. *Arabidopsis* has played an important role in the elucidation of the basic processes underlying stress tolerance, and the knowledge achieved has been transferred to several food crops (Zhang et al., 2004). Most of the genes that are known to be involved in stress tolerance were initially isolated from *Arabidopsis*. Several stress induced genes that have been introduced in other plants by genetic engineering have resulted in increased tolerance of transgenic plants to drought. Therefore the same techniques that have been used in other crops can be used in peanut.

5.2 ABA-independent gene regulation to drought stress

There are two transcription factors *DREB1* and *DREB2*, which have been identified to be important in the ABA-independent drought tolerant pathways that induce the expression of drought tolerant genes. When the native form of *DREB1* and the constitutively active form of *DREB2* are over-expressed, tolerance of transgenic *Arabidopsis* plants to drought is increased. Even though these genes were initially identified in *Arabidopsis* plants, their existence and function in stress tolerance have been reported in many other important plants, such as tomato, barley, rice, canola, maize, rye, wheat, maize and soybean. This is an indication that these genes are conserved, and they perform a universal stress defense mechanism in plants. This is why the *DREB* genes can be used as suitable targets for peanut improvement for drought tolerance through genetic engineering.

5.3 Peanut transformation systems

Peanut transformation has been accomplished by several different methods. Ozias-Akins et al., (1993) reported the first successful transformation of peanut with accompanying plant regeneration by utilizing the microbombardment technique. Micro-bombardment has since been completed in peanut with a number of genes conferring disease resistance (Ozias-Akins & Gill, 2001; Magbanua et al., 2000; Yang et al., 1998; Higgins et al., 2004; Athmaram et al., 2006). However, its efficiency levels remain low and the process takes several months from when the initial transformation event is induced until plant maturity (Egnin et al., 1998). A highly-efficient and faster technique is needed to transform peanut, and *Agrobacterium*-mediated transformation appears to offer the possibility to achieve this goal. Cheng et al., (1996) used this method on a Valencia-type peanut, but other investigators have been unable to expand the methodology to other genotypes thus restricting its usefulness. To date, biolistic methodologies are more reliable in peanut than other transformation methodologies and single constructs can be inserted into the peanut genome. Individual genes that confer agronomic traits have been integrated into the peanut genome such as bialophos resistance (*bar*) for herbicide tolerance (Brar et al., 1994), *Bacillus thuringiensis* (*Bt*) toxin *cryIA(c)* for insect resistance (Singsit et al., 1997), viral nucleocapsid or coat protein genes for virus resistance (Higgings et al., 2004), chitinase, glucanase, and oxalate oxidase to control fungal diseases (Chenault et al., 2005; Livngstone et al., 2005; Rohini and Rao, 2001). But, in studying drought tolerance in transgenic peanut plants, Bhatnagar-Mathur et al., (2007), introduced a transcription factor *DREB1A* from *Arabidopsis thaliana*, in a drought-sensitive peanut cultivar JL-24 through *Agrobacterium tumefaciens*-mediated gene transfer (Fig.3). The stress inducible expression of *DREB1A* in these transgenic plants did not result in growth retardation or visible phenotypic alterations. They were successful in developing transgenic events of peanut with the *DREB1A* transcription factor that is specifically expressed under a stress responsive promoter such as *A. thaliana rd29A*. Thus, their study opens ways to other scientist to dwell more on producing transgenic peanut with drought tolerance.

6. Future research

Classical plant breeding programs, which are relatively inexpensive, are not well adapted for utilizing advanced technologies associated with genomics. Hence, a large percentage of scientists who perform genomic research are mainly interested in the molecular function of specific genes or processes and are usually less interested in marker development for phenotypic selection applications. On the other hand, plant breeders need markers to facilitate selection and are generally not interested in developing large data sets for sequencing specific genes. Although the gap between the producer of genomic information (molecular biologist) and the user (plant breeders) is very wide, there is enormous potential for interactions among disciplines for plant improvement. Indeed, increasing research efforts in engineering for production of drought-tolerant peanut crops should be employed. There are certain genes that are expressed at elevated levels when a plant encounters stress, and it is important to understand that tolerance to drought is a complex process, and it is unlikely to be under the control of a single gene. Therefore, it is wise to combine conventional screening efforts, marker assisted selection and genetic engineering to switch on a transcription factor regulating the expression of several genes related to drought tolerance.

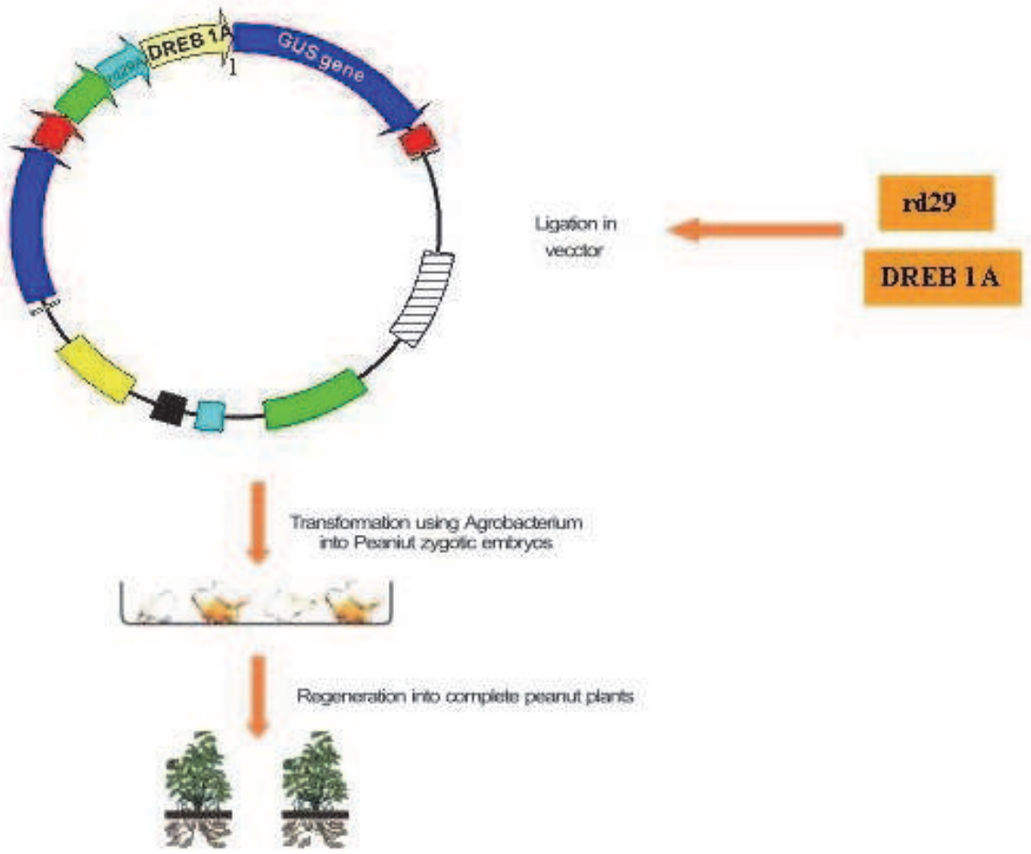

Fig. 3. Schematic representation of Cloning and Agrobacterium mediated genetic transformation in peanut

7. Conclusion

Although significant progress is being made to elucidate the genetic mechanisms underlying drought tolerance in peanut, considerable challenges still remain. In field conditions, peanut plants are subjected to variable levels of multiple stresses, and hence, the response of peanut to a combination of stresses deserves much more attention. In other words, the response of plants to multiple stresses cannot be inferred from the response to individual stress. Therefore, it is very important to test newly developed varieties to multiple stresses, and to perform extensive field studies under diverse environments to assess their tolerance.

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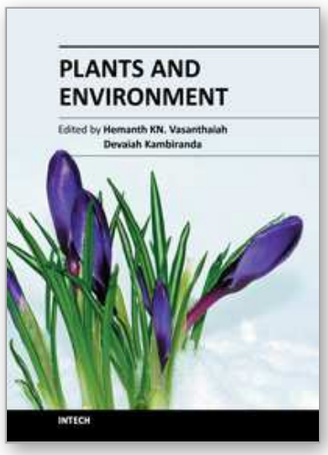

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Changing environmental condition and global population demands understanding the plant responses to hostile environment. Significant progress has been made over the past few decades through amalgamation of molecular breeding with non-conventional breeding. Understanding the cellular and molecular mechanisms to stress tolerance has received considerable scientific scrutiny because of the uniqueness of such processes to plant biology, and also its importance in the campaign â€œFreedom From Hungerâ€. The main intention of this publication is to provide a state-of-the-art and up-to-date knowledge of recent developments in understanding of plant responses to major abiotic stresses, limitations and the current status of crop improvement. A better insight will help in taking a multidisciplinary approach to address the issues affecting plant development and performance under adverse conditions. I trust this book will act as a platform to excel in the field of stress biology.

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