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Recent Advances in the Acclimation Mechanisms and Genetic Improvement of Peanut for Drought Tolerance

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Abstract

Peanut (*Arachis hypogaea* L.) is one of the most important oilseed crops that are cultivated worldwide. Peanut production is now greatly limited by drought stress, which is a major environmental challenge. The urgent task for current peanut research is thus to study the underlying mechanisms of peanut drought tolerance, to identify genes that are closely associated with drought tolerance, and to create new germplasms/varieties with high drought tolerance. In this review, we summarize recent advances in the acclimation mechanisms to water deficiency and the genetic improvement of peanut for drought tolerance, and propose the perspectives for the future peanut research.

Keywords

Arachis hypogaea, Acclimation, Drought Tolerance, Genetic Improvement

1. Introduction

Cultivated peanut (*Arachis hypogaea* L.) is an allotetraploid crop (2n = 4x = 40, AABB) and belongs to *Arachis* section of *Leguminosae* family. It originates in South America and perhaps evolves from the hybridization of two putative progenitors, *Arachis duranensis* and *Arachis ipaënsis*, followed by genome duplication and domestication events. Recently, comparative karyotyping analysis via FISH (florescence in situ hybridization) reveals that chromosome organization is highly conserved in cultivated peanut and its two putative progenitors, especially in the B genome chromosomes. However, variations exist between *Arachis du-*

ranensis and the A genome chromosomes in cultivated peanut, especially for the distribution of ITRs (interstitial telomere repeats). Further analyses of additional *Arachis duranensis* varieties from different geographic regions reveal both numeric and positional variations of ITRs in their chromosomes, which are similar to the variations in tetraploid peanut varieties. These results provide evidence for the origin of cultivated peanut from the two diploid ancestors, and suggest that multiple hybridization events of *Arachis ipaënsis* with different varieties of *Arachis duranensis* may have occurred during the evolution of cultivated peanut (**Figure 1**) [1] [2]. The multiple hybridization hypothesis has also been partially supported by the results of genome sequencing for cultivated peanut and the two putative progenitors [3] [4] [5] [6].

Peanut is one of the most important oilseed crops and widely cultivated in the world. China is one of the main countries for peanut production and consumption, wherein the field for peanut cultivation and the annual yield are the greatest (4.608 million hectares and 17.092 million tons) among oilseed crops [7]. Peanut seeds are enriched in many kinds of nutrition such as unsaturated fatty acids, proteins, sugars, vitamins and mineral elements, and are usually used as fresh and processed foods as well as oil production, which are welcomed by

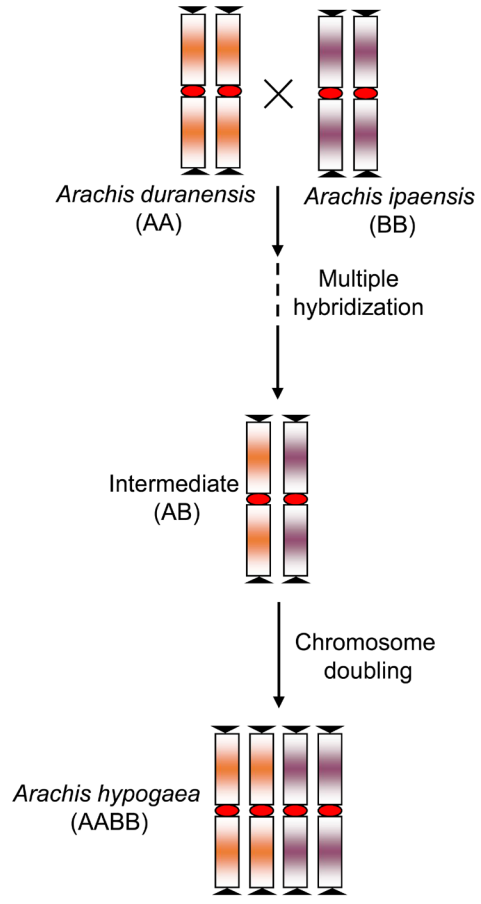

Figure 1. Schematic illustration for cultivated peanut origin and evolution [1].

billions of consumers. Nowadays, the supply and consumption of plant oil are largely unbalanced and over 60% of edible oil consumption depends on export to China, seriously threatening the national safety of edible oil [8]. In comparison to oilseed crops such as soybean and rapeseed, peanut displays many obvious advantages including higher yield per unit field, higher efficiency of oil production per unit weight and labor-saving field management, and therefore, plays a critical role in agricultural production in China [9].

However, global climate change is dramatically aggravated and has resulted in frequent occurrences of drought with gradually increased seriousness, which imposes negative influences on peanut production such as yield loss, lowered seed quality, and increased damages from diseases and pests. It has been reported that over 30% of peanut yield loss is attributed to water deficiency in approximately 70% of peanut cultivation area in China [10]. Drought stress is thus considered as the most serious environmental stress in peanut production in China [11]. To unveil the underlying mechanisms about peanut acclimation to drought stress has become an urgent need for current peanut research in China. Peanut genes related to drought tolerance are needed for the creation of new peanut germplasms with high drought tolerance as well. In this review, we summarize recent advances in peanut research about the acclimation mechanisms underlying drought tolerance and its genetic improvement, and propose some perspectives for future peanut research.

2. Effects of Drought Stress on Cultivated Peanut

2.1. Effects of Drought Stress on Growth, Development and Yield of Peanut

Under drought stress, peanut organs can be influenced to different extents. For example, peanuts grown under moderate drought stress display the increased root to shoot ratio and the enhanced root length and density, particularly in the deep soil, in comparison to those grown under normal growth condition [12] [13]. Peanut root activity can be stimulated by water deficiency, and thus water absorption and root growth can be returned to the normal level rapidly after re-watering [12] [13]. Peanuts under long-term drought stress can greatly decrease root length, root density, total area of absorption and activity [14] [15]. Consequently, the water usage efficiency, internode length, node and tiller numbers of peanut plants can be significantly lowered [14] [15]. Sankar *et al.* [16] also reported that in comparison to plants under normal growth condition, peanuts stressed by water deficiency displayed some seriously damaged phenotypes including the smaller and curled leaves, the decreased thickness of leaf epidermis and hypodermis, the altered structure and number of mesophylls, the dwarfed aerial parts and the deceased accumulation of assimilates. In addition, peanut yield can be largely reduced by drought stress because of the delayed flower bud differentiation and anthesis, the reduced flower and pod numbers, and the extended growth period [15] [17].

Because of the variations in water demand, peanut usually displays variable tolerance to drought stress at different developmental stages. Water demand is the least at germination stage and the occurrence of drought stress at this stage can inhibit the germination of peanut seeds [18]. Consequently, the germination rate is significantly decreased [18]. The growth of aerial parts of peanut seedlings is largely limited under drought stress, while great complementary effects can be observed in drought stressed seedlings after re-watering [19]. Therefore, water control at seedling stage can benefit peanut growth and yield [19]. Peanut at flowering and podding stages becomes very sensitive to water deficiency, and the limitation of water supply can largely decrease flower and pod numbers, thus reducing peanut yield [20]. The occurrence of water limitation at seed-filling stage has negative effects on peanut quality and yield such as the decreasing of pod fullness, the lowering of kernel to pod ratio, and the declining of oil content [21].

2.2. Effects of Drought Stress on Physiological and Biochemical Processes in Peanut

Water deficiency can alter physiological and biochemical processes in cultivated peanut. Zhang *et al*. [22] reported that peanut plants withered under drought stress because of water leakage and the decreased tensions of cells and tissues. The disorders of plant hormones and soluble metabolites together with the inhibition of protein and fat biosynthesis were also observed in stressed plants [22]. Photosynthesis is a basic physiological process and plays a critical role in plant growth, development and production. Under drought stress, chlorophyll content in peanut leaves is changed in a variety-dependent manner. The increased content of chlorophyll is observed in the leaves of peanuts with high drought tolerance, while that in the leaves of drought sensitive peanuts is dramatically decreased [23]. However, the lowered ratio of chlorophyll a to chlorophyll b can be found in the leaves of both drought tolerant and sensitive varieties [23]. Qin *et al*. [24] reported that light and dark reactions such as primary light-energy conversion, electron transfer and photophosphorylation were greatly inhibited in drought stressed peanuts, resulting in the disturbance of photosynthesis. Water deficiency leads to the dissociation of oxidative phosphorylation and photophosphorylation, and further inhibits the biosynthesis of ATP (adenosine triphosphate) [25]. As a result, the metabolism of assimilates and energy is interrupted and respiration is also decreased in peanut plants [25]. In addition, nitrogen fixation and mineral element absorption are negatively influenced in peanuts under water deficiency condition [26].

3. The Underlying Mechanisms for Peanut Drought Tolerance

Peanut can adopt three different strategies to cope with water deficiency: drought escape, drought avoidance and drought tolerance. A plethora of studies have provided morphological, physiological, biochemical, and molecular expla-

nations for the mechanisms regarding peanut drought tolerance.

3.1. Morphological Basis for Peanut Drought Tolerance

Previous studies have demonstrated that in comparison to drought sensitive ones, peanuts with high tolerance have more complex root system including greater root fresh weight, total length and surface area, and can well adjust water usage efficiency when exposing to water deficiency condition by optimizing the spatial distribution of root such as the increasing of root length, surface area and volume in soil, especially in the deep soil [5]. Under heavy drought stress, the inhibitory effects on the growth of root and aerial parts are lighter for drought tolerant peanuts than sensitive ones [27]. Different leaf morphologies have also been observed among peanut plants with different drought tolerance and the higher leaf thickness, the greater ratio of palisade cells to spongy mesophyll, the greater specific leaf weight and leaf area per plant are detected in drought tolerant peanuts than in the sensitive ones under both normal growth condition and water deficiency condition [28].

3.2. Physiological Basis for Peanut Drought Tolerance

Osmotic regulation is one of the most significant mechanisms underlying the acclimation of plants to drought stress. There are two main categories of osmotically active substances: one is the absorbed inorganic ions by root such as Na^+ and K^+, and the other is small organic molecules that are synthesized endogenously in plants such as soluble sugars, soluble proteins, and proline [29]. The dramatically increased content of soluble proteins and free amino acids can be observed in peanut leaves very shortly after the exposure of plants to drought stress, while the content of these osmotically active substances is gradually decreased with the extension of water deficiency period [30]. The increased content of osmotic substances can be detected in drought stressed peanuts overall developmental stages, especially during flowering period [30]. The capacity of osmotic regulation is different among these osmotic substances, and the best is soluble proteins followed by soluble sugars, free amino acids and finally proline.

Oxidation-reduction enzyme system plays crucial roles in the acclimation of peanut to water deficiency as well. In a study regarding the effects of drought stress on redox system in peanut root nodes, Furlan *et al*. [31] reported that the activities of POD (peroxidase), APX (ascorbateperoxidase) and GR (glutathione reductase) were increased significantly, while no significant changes were observed in the activity of SOD (superoxide dismutase). Xiong *et al*. [20] investigated the responses of redox system to water deficiency in peanuts with different tolerance and found that the activity of CAT (catalase) was significantly enhanced in the leaves of high tolerant varieties, while in drought sensitive varieties the activity of CAT was increased slightly or decreased and the content of MDA (malondialdehyde) was increased greatly, leading to growth inhibition and yield loss. In comparison to other developmental stages, physiological processes,

agricultural traits and yield of peanut were influenced mostly during podding period, indicating a development-dependent response of redox system to drought stress in peanut [20].

In addition, the involvement of plant hormones such as ABA (abscisic acid) has been revealed in the acclimation of peanut to water deficiency [32]. For example, the content of ABA is significantly increased in plant root when water supply is limited, and the accumulated ABA is further transported to aerial parts of stressed plants via xylems for the adjustment of osmotic potential and the regulation of stomatal movement, thus protecting plants from excessive water loss under drought stress [33] [34]. Moreover, the drought-induced variations of ABA content display a variety-dependent manner and greater ABA accumulation is observed in plants with high drought tolerance [32].

3.3. Molecular Basis for Peanut Drought Tolerance

Recently the rapid development of molecular biology and related technologies has deepened our understanding on the mechanisms of drought tolerance in peanut, and genes that encode drought tolerance-related proteins and peptides have been successfully cloned in peanut. For example, Dramé *et al.* [35] investigated the expression profiles of *PLDα* (*phospholipase Dα*), *cysteine protease*, *tryptophan protease* and *LEA* (*late embryogenesis abundant*) proteins in the leaves of peanut seedlings that were grown under water-limited condition and re-watering condition, respectively, and found that the expression of *PLDα* and *LEA* was dramatically enhanced, while the expression of *cysteine protease* and *tryptophan protease* was decreased significantly in high tolerant peanuts than that in drought sensitive ones. After re-watering, the expression of the above mentioned four genes was returned to the normal level faster in the drought tolerant peanuts than in the sensitive ones [35]. The authors thus proposed that the distinct expression profiles of these four genes might be important reasons for the variable drought tolerance of peanuts underwater-limited condition [35]. Proteomic analysis has been performed on peanuts with different drought tolerance by Kottapalli *et al.* [36], and the results reveal that genes such as*ACC* (*acetyl CoA carboxylase*), *LOX* (*lipoxygenase*) and *IPS* (*inositol phosphate synthase*) might be involved in the acclimation of germinated peanut seeds to water deficiency [36]. Furthermore, a number of drought-responsive transcriptional factors such as *bZIP* (*basic leucine zipper*), *MYB* (*v-myb avian myeloblastosis viral oncogene homolog*) and *AP2-EREB* (*APETALA2/ethylene responsive element binding*) have been uncoveredvia high throughput sequencing in peanut [37] [38]. By analyzing ESTs (expressed sequence tags), Pruthvi *et al.* [39] observed that the expression of *CTL* (*cyclin T-like*), *ARL* (*aldehyde reductase-like*), *CKL* (*cholin kinase-like*) and *PAPL* (*proline amino peptidase-like*) was greatly stimulated in drought stressed peanut plants. Functional analysis of peanut *ATL*1 (*ABA transporter-like* 1) has been performed by Ge *et al.* [40], who showed that overexpression of peanut *ATL*1 in *Arabidopsis* decreased the sensitivity to

the exogenous application of ABA and drought tolerance in comparison to Mock plants, revealing the negative involvement of *ATL*1 gene in peanut drought tolerance. In addition, miRNAs and epigenetically modified histone proteins have been reported to be involved in the adaption of peanut to water deficiency [41] [42] [43] [44] [45]. More efforts have been paid on the identification of drought-responsive genes in previous research regarding peanut drought tolerance, while functional analysis of these genes should be strengthened in the future.

4. Genetic Improvement of Peanut for Drought Tolerance

4.1. Genetic Breeding

Genetic hybridization has been the most widely used breeding strategy for the improvement of peanut drought tolerance. Peanut drought tolerance varies greatly among different germplasms. More tolerant varieties are found in the dragon type peanut such as "A596" and "Rugaoxiyangsheng" (**Table 1**), followed by Virginia type, Spanish type, intermediate type and Valencia type peanuts. Dragon type, Virginia type and Spanish type peanuts are widely used as parental lines for breeding drought tolerant varieties.

In comparison to cultivated ones, wild peanut varieties have higher genetic polymorphisms and contain more beneficial genetic resources that are responsible for drought tolerance, disease resistance and high productivity. Therefore, these wild peanut varieties are considered as invaluable germplasm resources for the improvement of cultivated ones. For example, by using wide crossing between wild and cultivated peanuts, scientists have successfully generated high oleic acid varieties, low palmitic acid varieties, early maturation varieties and

Table 1. Recently identified peanut germplasms with high drought tolerance.

Peanut germplasms with high drought tolerance	References
"Tangke 8", "Jihua 2", "Jihua 4", "Huayu 25", "Huayu 17", "Huayu 22", "Datangyou" and "Huayu 21"	[14]
"Huayu 17", "Huayu 25", "Tangke 8", "Fenghua 1", "Luhua 14", "Jihua 4" and "Huayu 27"	[46]
"Shanhua 11", "Rugaoxiyangsheng" and "A596"	[47]
"A596", "Shanhua 11" and "Rugaoxiyangsheng"	[28]
"L19", "L121" and "L146"	[48]
"Yuanza 9307"	[49]
"#11", "#34" and "#49"	[50]
"Zhonghua 8" and "Xianghua 55"	[51]
"Taihua 4", "Xuhua 13", "Tai 0125" and "Tai 0005"	[52]
"Yueyou 7"	[45]
"Yuanza 9102", "Ji 0212-4", "Xianghua 2008" and "NC6"	[53]

disease resistance varieties [54] [55] [56] [57] [58]. However, there are still bottlenecks limiting the application of wide crossing in current peanut breeding such as hybridization incompatibility, low survival rate of hybrids, sterility of hybrids and the segregation of elite traits [59].

4.2. Mutation Breeding

Mutation breeding is an important method for crop improvement. Mutations are commonly produced by radiation and chemical reagents. Compared to conventional genetic hybridization, mutation breeding can rapidly create large numbers of novel genetic alleles that do not exist in nature. For example, by using radiation breeding, new peanut germplasms with drought tolerance, saline-alkaline tolerance, disease resistance and so on, have been created [59]. In addition, peanut mutants with high yield, big or small seeds have been generated via chemical mutagenesis [60] [61] [62] [63].

4.3. Cyto-Engineering Breeding

Cyto-engineering breeding is a strategy for creation of new plant germplasms or new varieties with improved agronomic traits through modifying plant cells according to the expected targets of breeding. This technology is developed on basis of totipotency of plant cells and can be classified as anther culture, embryo culture, protoplast culture, somatic hybridization, chromosome transferring and so on. The greatest advantage of cyto-engineering is the overcoming of hybridization barriers as comparing with other breeding strategies, and thus lots of genetically improved crops including wheat, tomato, potato and orange have been created [59]. However, the application of cyto-engineering breeding in current peanut improvement still lags behind other crops largely due to the lack of basic knowledge about peanut cyto-engineering and physiological mechanisms, the low efficiency of hybrid regeneration, and so on [64] [65].

4.4. Molecular Breeding

Cultivated peanut is one of the only two tetraploidy species in the *Arachis* family and is reproductively isolated from wild peanut varieties, of which most are diploid. Therefore, wild germplasm resources that can be used for genetic improvement of cultivated peanut varieties have been greatly limited. In the past several years the technologies for peanut somatic embryogenesis and agrobacterium-mediated transformation have been well developed, thus promoting the improvement of cultivated peanut via genetic engineering. There are two systems for peanut transformation: bombardment-mediated transformation of calli and agrobacterium-mediated transformation of explants such as embryo leaflets, cotyledons and hypocotyls, and both can generate transgenic plantlets through somatic embryogenesis [66] [67].

Drought tolerance can be improved via genetic engineering. Bhatnagar-Mathur *et al*. [68] transformed "JL24", a drought sensitive peanut variety, with *Arabi-*

*dopsis DREB*1*A* (*dehydration-responsive element-binding protein* 1*A*) gene that was driven by a stress-inducible promoter, and the improved transpiration efficiency was observed in transformed peanut plants. Vadez *et al*. [69] and Devi *et al*. [70] reported significantly increased drought tolerance of peanut "JL24" when it was transformed with a peanut-derived *DREB1A*gene, of which the overexpression improved water usage efficiency of transgenic "JL24" via the stimulation of root system and the decreasing of transpiration rate. Tan *et al*. [71] overexpressed a *NCED*1 (9-*cis-epoxycarotenoid dioxygenase*1) gene under the 35S promoter in cultivated peanuts and observed that ABA content was significantly increased in the aerial parts of transgenic plants. After exposing to 10-h PEG6000-medaited drought stress, the expression of *NCED*1 gene was dramatically stimulated and the content of endogenous ABA was enhanced, while the level of reactive oxygen species was lowered in the leaves of *NCED*1-overexpressed peanuts [71]. Additionally cultivated peanuts that overexpress *Arabidopsis*-derived *IPT* (*adenylate isopentenyltransferase*), or *NHX*1 (*sodium/hydrogen exchanger*1), or *AVP*1 (*pyrophosphate-energized vacuolar membrane proton pump* 1), or *Aeluropus sinensis*-derived *DREB*1*A* display significantly increased drought tolerance in comparison to wild type plants under water deficiency condition, and the improvement of growth performance, photosynthesis and transpiration is observed in the transgenic peanut plants, thus obtaining higher yield [53] [72] [73] [74].

5. Perspectives

Peanut is one of drought tolerant crops, and has great potentials in the utilization of arid/semi-arid field and the development of dryland agriculture in China. However, high drought tolerant peanut varieties such as dragon type (**Table 1**) often display bad agronomic performance while those with good agronomic performance are often sensitive to water deficiency. There is an urgent need to study the molecular mechanisms underlying peanut drought tolerance and to identify genes responsible for drought tolerance, which will benefit the breeding of new peanut varieties with both good agronomic performance and high drought tolerance in the future.

In the past several years, targeted genome engineering technologies such as CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats/CRIPSR-associated protein 9) have been successfully used for mutation of target genes in crops [75] [76], demonstrating the great potentials in crop improvement. The CRISPR/Cas9 system is commonly composed of a Cas9 endonuclease and a sgRNA. The sgRNA that harbors a 20- or 19-bp sequence base-pairing with target site in plant genome can form a complex with Cas9 and then guides this complex to bind the target site. Thereafter the Cas9-mediated breakage occurs at the target site. The mutations/modifications will be introduced into the plant genome when the breakage site is repaired. With the aid of CRIPSR/Cas9 technology, we could obtain new peanut germplasms with high drought tolerance. For example, the identified negative regulators such as peanut

*ATL*1 (*ABA transporter-like* 1) [40] could become candidate targets for genetical modifications via CRISPR/Cas9 system, enabling peanut plants to be resistant to drought stress. Although complete knockouts of these negative regulators might compromise the normal growth and production of peanut under non-stress condition, the engineered peanuts could be used in the arid/semi-arid area, where water deficiency is constantly threatening the peanut production. Most importantly, these engineered materials will be transgene-free because the construct of CRISPR/Cas9 can be segregated in the siblings by genetic hybridization, thus being able to be accepted by the public.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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