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Research Progress on Drought Resistance of Soybean under Drought Stress

Shaohang Cui

School of Breeding and Multiplication(Sanya Institute of Breeding aand Multiplication) Hainan University, Sanya, China
20243005636@hainanu.edu.cn

Abstract. China is the world's largest customer of soybeans which supports its national food and agriculture. However, China's domestic industry remains under severe bottlenecks such as low yield per unit area and sensitive to pests and diseases. Drought has become one of the primary environmental pressures that severely limits soybean growth, physiological metabolism, and finally seed yield and quality. The investigation of the molecular basis of drought resistance and identifying key genes of resistance is becoming a critical prerequisite for supplying a stable supply of soybean. Increased drought tolerance by genetic means is an effective means to mitigate production risks and is an important prerequisite for sustainable agriculture. This review reviews the physiological and biochemical influence of drought stress on soybean agronomic traits and summarizes current research on drought-responsive genes, quantitative trait loci and underlying molecular regulatory networks. By summarizing recent development, this review could provide a model and guidance for future studies on genetic improvement of drought tolerance, discovering new genes and discovering more complex mechanisms of resistance.

Keywords: soybean, drought resistance, drought stress

1. Research background

Climate change, water scarcity, food shortage and population growth have become major threats and severe challenges facing human society [1]. These intertwined issues have exerted unprecedented pressure on the global agricultural production system. The increasingly severe water shortage in agricultural ecosystems has caused widespread impacts worldwide, leading to substantial yield reductions of various crops including soybeans and seriously threatening the stability of global food supply. As a key problem that continuously plagues crop growth, drought stress is recognized as one of the major constraints on global agricultural productivity [2], and its intensity and severity are predicted to keep increasing in the future.

Soybean, an important grain and oil crop originated in China with a cultivation history of over 5,000 years, is not only the main source of edible vegetable oil and plant protein for humans, supporting the nutritional balance of daily diet, but also occupies a core position in feed processing, industrial production (such as plastic and biodiesel manufacturing) and other fields [3]. Its planting area accounts for about 6% of the world's cultivated land [4] and shows an increasing trend year by year, playing an irreplaceable role in the global agricultural economy. However, soybean is relatively sensitive to water shortage. Drought stress can reduce soybean yield by up to 40% [5], interfere with its normal physiological activities, and cause damage to the photosynthetic system and inhibition of growth, which are specifically manifested as a series of phenomena such as decreases in fresh weight, dry weight and chlorophyll content, and increases in cell membrane permeability. Due to the rapid effects of drought stress on soybeans and other crops, it is ultimately crucial to fully understand the impact of drought stresses and genetic background. Relevant studies have provided the drought resistance of plants and crops at various levels. Since drought resistance in plants is an inherent trait, it involves collective responses at morphological, physiological, biochemical and cellular levels, and hence is highly challenging to improve crop quality.Soybeans mainly cope with drought through three mechanisms: escape (e.g., adjusting the growth cycle to complete the life cycle in advance) [6], tolerance (synthesizing osmoprotectants) , avoidance (reducing evapotranspiration) , as well as the variation law of soybean antioxidant enzyme activity [7]. These results provide a solid foundation for understanding drought resistance for crops such as soybeans, and provide a basis for a theoretical and technical explanation of soybeans drought resistance genetics. The development of water-efficient and drought-resistant soybean varieties can not only decrease the impacts of drought stress on soybean yield and ensure stable availability of this important grain and oil crop, but also can also help solve global problems of water scarcity and food scarcity, and ultimately help agricultural ecosystems develop in a sustainable manner.

2. Research on drought resistance characteristics of soybean

2.1. Root morphology

As the key organ for absorbing water and nutrients, soybean roots exhibit complex and sophisticated regulatory mechanisms during drought resistance. In terms of morphology, taproot elongation and lateral root development are important strategies for soybeans to cope with drought [3].

The length of taproots directly affects the depth of a soybean rooting in deep soil. The length of Taproots can be used as a proxy to determine the depth in which a soybeans can root, and will help to estimate the likelihood that a soyseto will eventually get deep water in the arid environment. In water-deficient environments, soybeans can induce meristematic cell activity [8], promote the massive production of lateral roots, and long-term drought stress will continuously increase the number of lateral roots, thereby expanding the absorption range of roots in the soil. Water limited habitats will adjust the amount of soybean biomass, increasing the amount (from the roots) to the roots, increasing root-shoot ratio and increasing the uptake in the roots.

Root structure, because it is positively correlated to drought resistance, can be used as an indicator of soybean stress tolerance. It is shown that in non-irrigation regions, soybeans have higher root elongation and growth rate and those developing a dense root structure at early growth yield good drought-resistant traits with valuable germplasm resources for breeding. Root trait improvements however are limited by the intractable screening method and the difficulty of selecting below-ground traits. To overcome these limitations, molecular and biotechnological approaches—specifically through candidate gene selection and association analysis—provide a viable pathway for studying and enhancing this complex trait [9].. By screening candidate genes such as RAB-18 and DREB for root traits, we can analyze root drought resistance regulation and guide soybean root trait improvement breeding.Studies on model plants show that circadian rhythm is linked to plant response to abiotic conditions.These drought-responsive genes in soybeans exhibit altered rhythmic expression patterns under drought stress, and certain cis-acting elements in their promoter regions are involved in stress and physiological clock regulation processes [10]. This provides a novel mechanism for controlling soybean root drought resistance at the molecular level based on rhythm.

2.2. Physiological characteristics

Different soybeans differ from drought conditions, and specific soybeans can be selected based on their physiological processes.

Cuticular conductance plays an important role in drought tolerance and can be used as one of the selection criteria for breeding drought-tolerant soybeans. In varieties adapted to arid environments, leaf cuticular conductance is lower [11]. Moreover, in soybeans, the diversity of cuticular conductance is independent of stomatal density. Low cuticular conductance has been found to be a selectable trait for breeding drought-tolerant varieties [12]. Trichome traits have negative effects on crops, such as reducing seed yield, increasing plant height, making crops prone to lodging and delaying maturity [3]. However, villin is the main protein to regulate actin dynamics. villin can maintain cytoskeleton formation and cytoplasm flow during dry fields. Before breeding it will be important to determine if the damage caused by this gene will affect research.WUE – the dry matter mass produced per unit weight of water in farmland transport. Increasing WUE of plants will result in better crops. In soybeans, the WUE can be improved by regulating the partial closure of stomata at specific soil water deficit levels [11].

Also in the presence of drought, plant will increase the cell sap concentration, reduce the osmotic potential, and increase the water absorbing or keeping capacity of cells in order to adapt to the water. We call this osmosis.Osmotic adjustment is conducive to maintaining stomatal conductance and photosynthesis under water stress [13], thereby delaying leaf death, reducing flower and pod abortion, and promoting root growth. Soybean varieties with high osmotic potential have a slower decrease in relative water content, thus maintaining turgor for a longer time [12].

3. Research on molecular mechanisms of soybean drought resistance

3.1. Nitrogen fixation

The symbiotic nitrogen fixation of soybeans with rhizobia is important for their growth and development, and drought will seriously hinder the nitrogen fixation, and hence soybean yield. Drought will decrease soybean nitrogen fixation activity with lower CO_2 accumulation and leaf area reduction, and cause protein synthesis and yield loss [12]Hierarchical aspects. In the case of drought, lower soil oxygen supply, reduced carbon flux, lower sucrose synthase activity, and increase in uridine and free amino acid contents prevent N_2 fixation, i.e., reduce the nitrogen metabolism; and increase nitrogen metabolism by crop yield, which is mainly mediated and regulated by important enzymes such as nitrate reductase (NR) and glutamine synthetase (GS) [12].

It is worth noting that there is a synergistic relationship between root morphological characteristics and nitrogen fixation in response to drought [11]. A healthy root can support rhizobia to grow nodules and nitrogen fixation can also provide nutrients for root growth and grow root vitality and expansion. For instance, in drought, nitrogen fixation control is mostly performed locally. Split-root symbiosis studies show the nitrogen fixation capability of roots is lower with respect to carbon metabolism, amino acid metabolism, protein synthesis and growth of nodulated plants. This also indicates that nitrogen fixation is also affected by the overall root growth after the degradation of the root. Therefore further study of the synergy between root morphology and nitrogen growth under drought is very important for achieving drought resistance and yield.

3.2. Antioxidant defense system

The antioxidant defense system is composed of a series of enzyme systems and antioxidant substances that can scavenge reactive oxygen species (ROS), such as superoxide dismutase (SOD), peroxidase (POD), abscisic acid (ABA), ascorbic acid (AsA), etc. Under normal conditions, the ROS produced in plant cells is balanced with their scavenging system. However, when drought stress acts on plants for a long time, the produced ROS exceeds the capacity of the ROS scavenging system, leading to ROS accumulation and oxidative damage [14]. ROS first damages the membrane in particular stress-related phospholipids and fatty acids that lead to lipid peroxidation in biological membranes that enlarges membrane pores and permeates the membrane. A large amount of ions is released that relaxes the chlorophyll protein complex and also causes significant changes in chlorophyl content, and in these cases some plant deaths. The plant's antioxidant defense system has to help to resist ROS for drought stress.mportant ROS scavenging in drought stress.

SODs are the first line of defense against oxidative damage mediated by ROS free radicals. They can scavenge excess superoxide anion radicals in plants through the Haber-Weiss reaction ($2O^{2-}+2H^{+}\rightarrow H_2O_2+O_2$), and are key enzymes in the protective enzyme system. CAT specifically scavenges H_2O_2, but it is mainly localized in mitochondria, peroxisomes and glyoxysomes. The scavenging of H_2O_2 in chloroplasts is carried out through the Halliwell-Asada pathway, in which SOD, POD, catalase from micrococcus lysodeikticus (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) play important roles. POD has a dual role: on the one hand, POD is expressed in the early stage of stress or senescence, scavenging H_2O_2 and showing a protective effect, which is a member of the cellular ROS protective enzyme system; on the other hand, POD is expressed in the late stage of stress or senescence, participating in ROS generation, chlorophyll degradation, and triggering membrane lipid peroxidation, showing a damaging effect, which is a product of plants at a certain stage of senescence [15]. SOD and POD cooperate with each other to resist oxidative damage induced by drought stress.

As one of the plant endogenous hormones, ABA is the main moderator of drought [16] and it is crucial in controlling how plants grow, develop, and react to different environmental challenges.

Under drought, ABA closes a stomatal opening thereby reducing the transpiration rate and reducing the water loss in plants.ABA also assists plant drought adaptation by enhancing root water uptake capacity and promoting root growth.At the same time ABA inhibits drought-induced oxidative stress in soybean seeds by up-regulating key antioxidant enzymes SOD,POD,CAT, APX and GR that improve ROS scavenging mechanism, improve osmotic adjustment and reduce oxidative damage [17].It is an important part of the antioxidant defense system. Simultaneously, ABA plays a central role in mediating diverse physiological processes and activating molecular pathways in response to water deficit [18]. Drought stress signals are received by root and leaf to the shoots to initiate ABA formation, by protein kinases which have positive control for ABA signal transduction, metabolism and transport in drought conditions [19].Beyond core regulators, the expression and activity of specific genes and transporters also contribute to improving drought resistance by controlling the ABA signaling. For instance, GmCIPK2 in soybeans increases the expression of ABA and drought--responsive genes [20]. These reports indicate that ABA plays a key role in the research on the molecular mechanism of soybean drought resistance, and will also be one of the important paths in future research on improving soybean drought resistance.

4. Soybean drought-resistant genes

Drought-resilient genes are regulated genes and functional genes (structural genes) for their respective roles. Though different in action hierarchy, mode and application value, they constitute the drought-resiliency molecular network. Regressive genes are upstream regulatory hubs that do not directly resist stress. They intervene in signal transduction through their expression products, regulate multiple functional genes and one regulatory gene may achieve multiple functional gene effects in transgenic applications with large applications [21].Functional genes are downstream execution units which determine the structure of a particular protein or enzyme and perform stress-resistant physiological process after expression, but are controlled by regulatory genes and a single gene can only be a function of multiple transgenes. This is a "upstream regulation-downstream execution" that gives ideas for plant drought resistance. In this chapter, I will describe the progress of soybean drought resistant genes from the aspects of regulatory genes (protein kinase genes and transcription factor genes) and functional genes.

4.1. Protein kinase genes

The signal system composed of CBL and CIPK is an important regulatory network for abiotic stress responses [22]. In soybean hairy roots, the GmCIPK2 gene is induced to express by drought and ABA, which improves the drought resistance of soybeans, and regulates soybean drought resistance by controlling the expression of the GmCBL1 gene. RLK function as crucial regulators in enabling soybeans to withstand drought and other abiotic stresses [23].The heterologous expression of the Catharanthus roseus CrRLK1L20 gene in soybean hairy roots has been shown to significantly improve drought tolerance.This is achieved by boosting antioxidant enzyme activity and upregulating a suite of stress-responsive genes,including GmMYB84, GmWRKY40, GmDREB-like, GmGST15, GmNAC2 and GmbZIP78,which encode R2R3-Myeloblastosis proteins, dehydration-responsive element binding protein-like (DREB) [24], glutathione s-transferase 15 (GST15), NAC transcription factors [NAM (no apical meristem), ATAF1 (arabidopsis transcription activation factor 1), ATAF2, CUC2 (cup-shaped cotyledon 2)] and basic leucine zipper 78 (bZIP78) respectively.They can enhanc the drought resistance of soybeans [25]. In addition, expressing the Arabidopsis thaliana ERECTA dominant negative mutant AtΔKinase in soybeans encodes a truncated ERECTA protein with a leu-rich repeat receptor-like ser/thr kinase (LRR-RLK) domain. Under normal conditions, the soybean plants become shorter, the number of branches increases, the number of leaves decreases, and the leaf area reduces; while under drought stress conditions, the relative water content of soybean leaves increases, the transpiration rate and stomatal conductance decrease, the drought resistance is enhanced, and the yield is increased [26].

4.2. Transcription factor genes

At present, the discovered transcription factor genes regulating soybean drought resistance mainly include AP2/ERF, NAC, NFY and MYB genes. Overexpressing or silencing these transcription factor genes can improve the drought resistance of soybeans.Comprising a large number of members, AP2/ERF proteins act as a central regulatory hub, integrating signals to coordinate plant growth and development with adaptive responses to both environmental (e.g., drought) and biological stresses [27]. At present, the discovered AP2/ERF family genes that can improve soybean drought resistance are mainly from the DREB subfamily [28]. Studies on the DREB subfamily reveal that overexpression of the AtDREB1Agene enhances soybean drought tolerance at both vegetative and reproductive stages. At the seedling stage, transgenic plants exhibit improved resistance, primarily due to the upregulation of drought-responsive genes such as GmPI-PLC, GmSTP, GmGRP and GmLEA14, alongside increased stomatal conductance, photosynthetic rate, chlorophyll content, and abaxial cuticle thickness, coupled with a reduced transpiration rate [29].At the reproductive time, drought tolerance also brings yield properties, such as higher number of grains per plant, effective pods and total number of pod.

NAC transcription factors, unique to plants, are pivotal regulators in soybean drought adaptation. Studies have demonstrated that the overexpression of specific NAC family members can markedly improve drought resistance in soybeans [30]. Functional experiments show that GmNAC4, the GmAd-Demic, expression-driven gene, is positively active in drought adaptation. Extended gene GmCAC4 increases soybean drought resistance with coordinated antioxidant defense and osmotic homeostasis. Extensive gene GMNAC3 increases soy drought tolerance. It boosts gene expression of stress-sensitive genes such as LEA14, APX2, GSH-PX, 6PGD, and P5CS in hairy roots along with increased activity of associated antioxidant enzymes [31]. thereby enhancing soybean drought resistance [32]. This implies that GmNAC3 mediates enhanced drought tolerance in soybean by transcriptionally regulating a suite of genes, including those encoding ROS-scavenging enzymes (GSH-PX, APX2) and osmoregulators (P5CS, LEA14, 6PGD) [33].

4.3. Functional genes

The GmDHN9 gene shows a very obvious response under drought induction. Under drought stress, the germination rate, root length, chlorophyll content, proline content, relative water content and antioxidant enzyme content of transgenic Arabidopsis thaliana are all higher than those of wild-type plants. Moreover, the activities of SOD, POD and CAT are increased, which significantly reduce the contents of O_2^- and H_2O_2, improve ROS scavenging ability, and enhance plant drought resistance [34].

GmERA1s. This gene encodes a protein that is negatively affected by ABA signaling in soybean guard cells which prevents the hormone from signaling. The expression level of GmERA 1s may be further regulated by the gene to enable soybeans to close their mouths in a faster manner under water [35]. Therefore, GmERA1 is implicated in the dehydration stress response of soybeans, which is a useful strategy to enhance soybean drought resistance.

GsEXLB14 expansin gene is root-specific for wild soybeans, and its transcription is highly regulated under drought conditions. Functional analysis showed that overexpression of GsEX LB14 of the hairy roots leads to root number, length, weight, and can increase over those of the control group. During drought conditions, genes encoding peroxidase, calcium/calmodulin dependent protein kinase, dehydration-varying protein kinases, and expansin (EXPB/LB) genes in transgenic hairy roots are increased. Different transcriptional regulation of the mentioned genes might explain the improved drought tolerance of soybean hairy roots by overexpressing GsEXLB14. Finally, the expansing gene GsEXLB14 is likely to be an effective target for molecular breeding to improve soybean stress robustness.

5. Conclusion

In summary, soybeans respond to drought stress through the coordination of complex morphological and physiological adaptations and molecular networks. At the physiological level, soybeans mainly maintain water balance through strategies such as optimizing root architecture, reducing cuticular conductance, regulating water use efficiency and osmotic adjustment. At the molecular level, key genes play a core role. Key upstream regulators, such as protein kinases (GmCIPK2, CrRLK1L20) and transcription factors (DREB, NAC family members), function collaboratively. They establish a coordinated drought-response network by orchestrating the expression of downstream effector genes that mediate antioxidant defense and osmotic protection.

In addition, drought stress significantly affects the efficiency of soybean symbiotic nitrogen fixation, and its synergistic relationship with root development is the key to maintaining nitrogen nutrition. The ABA signaling pathway plays a core hub role in integrating drought perception with physiological responses such as stomatal closure and antioxidant defense.

Under the global water scarcity environment, the demand for stable soybean production has increased significantly. Future research will further construct a systematic research framework of "multi-omics integration - gene network analysis - molecular breeding application", providing innovative paths for breaking through the bottleneck of synergistic improvement of high yield and drought resistance traits in soybeans. By integrating multi-dimensional data from transcriptomics, proteomics, metabolomics and epigenomics, combined with cutting-edge technologies such as CRISPR/Cas9 precise editing and GWAS (genome-wide association study) analysis, new molecular regulatory mechanisms of soybean response to drought stress will be revealed, excellent alleles with breeding value will be excavated, and an efficient molecular breeding system will be established to realize the rapid transformation of excellent gene resources into new varieties. The research results will fill the theoretical gap in the synergistic regulation of high yield and drought resistance in soybeans, provide core technical support for breeding new soybean varieties with stress resistance and stable yield, and have important scientific value and strategic significance for improving the stress-resistant production capacity of global soybeans, ensuring food security and addressing agricultural challenges caused by climate change. It will also provide a reference technical paradigm for the stress-resistant and high-yield breeding research of other crops.

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