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Root system architecture, physiological and transcriptional traits of soybean (*Glycine max* L.) in response to water deficit: A review

Rentao Xiong[a], Shuo Liu[a], Michael J. Considine[b], Kadambot H.M. Siddique[c], Hon-Ming Lam[d] and Yinglong Chen[a,c,*]

[a]State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, and Chinese Academy of Sciences, Yangling, Shaanxi, China
[b]School of Molecular Sciences, The University of Western Australia, LB 5005, Perth, Western Australia, 6001, Australia
[c]The UWA Institute of Agriculture, and UWA School of Agriculture and Environment, The University of Western Australia, LB 5005, Perth, Western Australia, 6001, Australia
[d]Center for Soybean Research of the State Key Laboratory of Agrobiotechnology, and School of Life Sciences, The Chinese University of Hong Kong, Shatin, Hong Kong

Correspondence
*Corresponding author,
e-mail: yinglong.chen@uwa.edu.au

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Drought stress is the main limiting factor for global soybean growth and production. Genetic improvement for water and nutrient uptake efficiency is critical to advance tolerance and enable more sustainable and resilient production, underpinning yield growth. The identification of quantitative traits and genes related to water and nutrient uptake will enhance our understanding of the mechanisms of drought tolerance in soybean. This review summarizes drought stress in the context of the physiological traits that enable effective acclimation, with a particular focus on roots. Genes controlling root system architecture play an important role in water and nutrient availability, and therefore important targets for breeding strategies to improve drought tolerance. This review highlights the candidate genes that have been identified as regulators of important root traits and responses to water stress. Progress in our understanding of the function of particular genes, including *GmACX1*, *GmMS* and *GmPEPCK* are discussed in the context of developing a system-based platform for genetic improvement of drought tolerance in soybean.

Introduction

Soybean is an important food crop with global production of over 340 million metric tons in 2016 (FAOSTAT 2017). Soybean is one of the five most important crops worldwide. The global import and export values of soybean have outstripped all of the other major crops such as wheat, rice and maize, even without the inclusion of soybean oil or other processed forms. However, it requires substantially more water than cereal crops for successful production. Soybean seeds are widely used in the food industry as a rich source of high-quality protein and edible oil (Niwińska et al. 2020). Soybean is grown in tropical, subtropical and temperate regions. However, the majority of global production is restricted by climate risk, particularly drought stress, because of the increasing variability in air temperature

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Abbreviations – ABA, abscisic acid; GmACX1, soybean Acyl-CoA oxidase; MAS, marker-assisted selection; PIC, polymorphic information content; RFLP, restriction fragment length polymorphism; ROS, reactive oxygen species; RSA, root system architecture; SOD, superoxide dismutase.

and rainfall, severe drought and limited agricultural water resources (Kunert et al. 2016). Drought pressures may worsen as a result of climate change, thereby reducing yields (Figs. 1 and 2; Trenberth et al. 2013, Li et al. 2015).

Rhizobium is the genus of rod-shaped gram-negative bacteria that coexist with leguminous plants to form nodules and fix nitrogen of the air for plant nutrition. Rhizobia invade plants through root hairs, lateral root forks or other parts of leguminous plants to form an invasive line into the root cortex, and stimulate the host cortex cells to form a nodule (Ferguson et al. 2010). Upon infection, the rhizobia are enveloped by a membrane envelope. Some bacteria can continue to propagate in the membrane envelope, and then stop proliferating and become mature bacterioides. Host cells and rhizobia synthesize leguminous hemoglobin, which acts as an oxygen carrier to regulate the oxygen content inside and outside the membrane envelope (Tu 1977). Bacterioides reduce molecular nitrogen to NH_3, secreting it into nodule cells. This provides a significant efficiency for the host legume, as NH_3 can be directly assimilated, whereas nitrates from the rhizosphere must first be reduced to NH_3 by the plant. In turn, the host provides carbon for energy and other essential nutrients for the rhizobia (Ferguson et al. 2019).

Drought tolerance refers to the ability of crops to grow, survive and form stable yields under drought stress, as determined by their genetic characteristics and interactions with the natural environment (Ainsworth et al. 2012). Soybean crops consume about 30% more water than cereal crops per unit of biomass. For each gram of biomass, soybeans consume 600–1000 g of water (Andriani et al. 1991). The degree of soybean sensitivity to water is closely related to the growth period. In soybean, short-term and moderate water deficits in vegetative growth period generally do not significantly reduce soybean yield (Kim and Hong 2000). On the contrary, soybean plants are more susceptible to drought stress during their reproductive period (Xu et al. 2018). Drought at the seedling stage can promote deep rooting, which is conducive to soybean growth and development, however this increases water demand during the flowering and pod stage (Zhang et al. 2011b). Episodes of drought stress during the flowering or pod stage will seriously affect yield potential. To achieve high and stable yield of soybean, scientists have characterized ecological aspects of drought tolerance to breed new soybean varieties with better adaptation to drought stress (Klukas et al. 2014).

High-throughput phenotypic analysis is an important technique for analyzing plant phenotypic components. To quantify plant growth and analyze phenotypic traits, effective image processing performance and feature extraction are essential (Wang et al. 2006). Roots are the basis of plant growth: strong root systems could provide adequate nutrients and water for plants (Reynolds

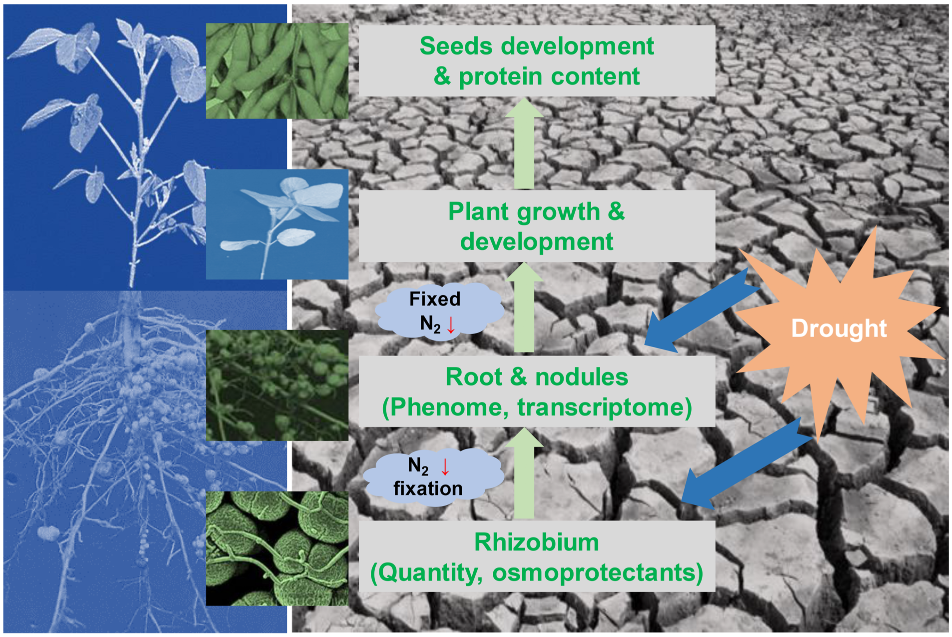

Fig. 1. Drought intervention of soybean-rhizobium symbiotic relations at various stages. Drought adversely affects the quantity and osmoprotectants of rhizobia in the rhizosphere of soybean and thus reduces (↓) nitrogen (N2) fixation; drought also limits root growth and nodule formation resulted in reduced (↓) the amount of fixed N2. It directly influences plant growth and eventually reduces seed development and protein content.

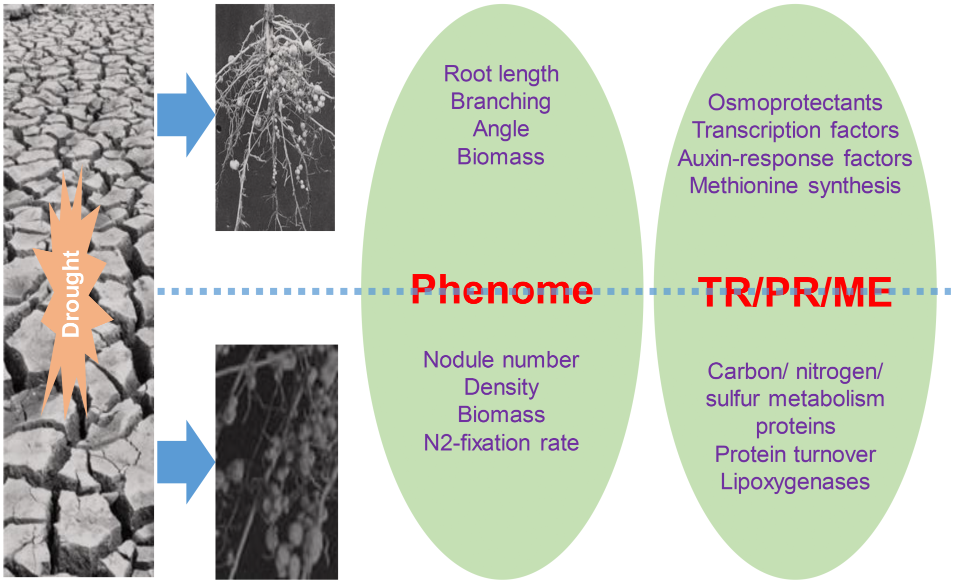

Fig. 2. Effects of drought on phenome, transcriptome (TR), proteome (PR) and metabolome (ME) of soybean roots and nodules. Drought stress has significant impact on root phenology and architecture traits (root length, branching, root angle and biomass, etc.) and nodulation (e.g. number, density and biomass, nitrogen-fixation rate), and on root physiology, transcriptome, proteome and metabolome.

et al. 2009). Crop growth and development result from the coordination of morphological functions of below ground and underground parts. The ability of crops to extract water from larger soil volumes is critical for maintaining yield stability when soil water is depleted. Under drought conditions, a deep root system potentially helps to increase yield (Costa et al. 2000). Root morphology, including root biomass, root length, root surface area, average root diameter and root volume (Vamerali et al. 2003), determine the ability of crops to obtain nutrients and water (Khan and Iqbal 2011). Quantitative trait loci (QTL) mapping, marker-assisted breeding and wild gene pool introductions are currently being used to improve drought tolerance (Zuo et al. 2013). QTL and association mapping methods have been found to be convenient for fine mapping and identification of genes affecting drought tolerance in wheat (Rahaman et al. 2017). The latest advances in high-throughput genotyping for root trait variability in large set of genotypes (Chen et al. 2011, 2015) and phenotyping methods, including high-throughput analysis of biophysical and biochemical properties of tissues, can help scientists make outstanding contributions to soybean research (Gupta et al. 2010).

Drought stress undermines dry matter accumulation, leaf area index and photosynthetic efficiency (Yan et al. 2017, Li et al. 2019). The temperature of the leaves increased because of the weakening of the ‘cooling’ effect resulted from reduced transpiration (Escalona et al. 2013). Water loss reduces plant cell expansion pressure and increases the permeability of cell membrane leading to cell lysis. Phenotypic changes such as increasing root growth and biomass, stomatal closure and leaf angle are associated with multiple genes and pathways, including signal transduction, protein metabolism, synthesis of compatible compounds, regulation of phytohormone synthesis and carbohydrate metabolism (Yamaguchi-Shinozaki and Shinozaki 2006, Harb et al. 2010, Osakabe et al. 2014). Additionally, drought stress may alter the composition of fatty acids, proteins and carbohydrates in soybean seeds (Dornbos and Mullen 1992).

Phenotypic division among soybean varieties is based on root morphology (Fried et al. 2019). Among soybean varieties, there are significant differences in root morphology, which can be roughly classified into three categories: (1) well-developed main root (taproot), (2) the main root is not obvious and (3) the branch root is longer, intermediate type – between the former two. The root morphology of soybean at the seedling stage is similar to that of the early stage of bulging. It can also be divided into the three categories mentioned above, but the root morphology of the seedling and the beginning of bulging are not exactly the same. The degree of root concentration and elongation speed is different, and the dynamic description should be more comprehensive when describing the root morphology (Gai et al. 2007a). Extensive genetic variations in root morphological and physiological traits in response to drought stress between soybean varieties indicate that the selection of root traits can be obtained to improve drought tolerance in soybean, which provides a new way and method for soybean breeding.

Lipids account for 23% of the dry weight in soybean seeds, mainly in the form of triacylglycerols produced during seed development (Nacer et al. 2013). Keto-acyl carrier protein synthase produced malonyl CoA during the initial cycles of fatty acid synthesis (Smith et al. 1989, Thelen and Ohlrogge 2002, Baud et al. 2008). Proteins can reach 41% of dry weight in soybean (Hajduch et al. 2005). The main storage proteins are glycine (11S globulin) and β-conglycinin (7S globulin), which account for 70% of the total. Co-inhibition of β-conglycinin glycine α′ subunit did not change the protein content in soybean seeds, which may be because of the compensatory effect of increasing glycine accumulation, indicating the importance of these major proteins in total content (Wolf 1977, Kinney et al. 2001, Yaklich 2001). Drought stress during seed filling affects the growth rate of soybean seeds by reducing photosynthesis, thus affecting the supply of assimilates converted into storage compounds. Under moderate and severe drought stress, seed size decreased by 9 and 35%, respectively (Nakagawa et al. 2018). The sucrose content of seeds decreased slightly (9%) in 7 d (Egli and Bruening 2004). These studies give new insights into the mechanisms of drought stress and genetic strategies.

Root system architecture traits

Root system architecture (RSA) determines the ability of crops to obtain nutrients and water. Root length, root surface area and root volume directly affect the ability of crops to absorb and transport nutrients and water (Rubio et al. 2001, Wang et al. 2019). For the root system, both the main and lateral roots have an apex. The apex is the most active part of the root's life and plays an important role in absorbing nutrients. Usually, the root hairs in the mature area of the root tip have a life span of only 1–2 weeks. After the root hairs die, the elongation zone will generate new root hairs to supplement and change the position of the roots in the soil to absorb nutrients (Piekarska-Stachowiak and Nakielski 2013). The formation of root hairs greatly increases the area where the roots absorb nutrients, but the root hairs are susceptible to the availability of soil moisture and develop poorly in arid soils. For the entire soil space, the root distribution only accounts for about 3% of the volume. It is not enough to rely on the roots to actively seek nutrients for crop growth. Therefore, the transfer of nutrients to the root surface is an important way for plants to obtain nutrients (Dayan et al. 2007, Kanase et al. 2019).

The normal growth and development of crops is the result of the coordination of morphological functions between the ground and underground parts. The developmental responses of plants to drought stress were enhanced root growth and inhibited shoot growth, resulting in an increase in root:shoot ratio (Sharp et al. 2004, Yamaguchi and Sharp 2010, Xu et al. 2013). Kulkarni et al. (2017) found that a 20% faster root descent rate in soil combined with a more effective root system can more effectively extract water from the lower soil (roots below 60 cm) and provide yield benefits of 0.32–0.44 t ha^{-1} for soybean. Varieties with an increased proportion of deeper roots have greater yield under drought stress. The higher root proportion of plants (more root biomass than plants not under water stress) under water stress can effectively prevent from the damage caused by drought stress (Lopez et al. 2019).

Using field situ analysis, it was found that the average drought-tolerant subordinate function values (plant height, leaf area index, stem biomass and leaf biomass) of soybean were significantly and positively correlated with the relative root surface area and relative root biomass under drought stress (Gai et al. 2007b). Relative root surface area and relative root biomass could be used as important indicators to measure drought tolerance of soybean plants. The effect of drought on the root system varies with different drought patterns and degrees. In the vegetative growth stage, pod stage and grain filling stage, the root:shoot ratio gradually decreased with the increase of soil water content, and the effect of drought on the aboveground part was greater than that on the root system (Adams and Erickson 2017). Drought reduced root biomass and increased root:shoot ratio (Yanqi et al. 2018). Drought stress at seedling stage increased root volume, root length and total root surface area of soybean, whereas drought stress at other stages slowed down root morphological development (Wu et al. 2007). Under the condition of gradual drought (with field moisture contents ranged from 23 to 79%), roots grew best in mild drought (79%) and the worst in severe drought (23%). The average drought-tolerant subordinate function of soybean (vegetative and reproductive growth periods) was positively correlated with the relative root diameter, which indicated that only when the root diameter reached a certain thickness, the drought-tolerant ability of soybean plants could be effectively improved (Liu et al. 2011, Li et al. 2015).

Under extreme drought conditions, the key to increase grain yield is to maintain water absorption during grain filling period of soybean. Plant adaptation strategies to drought include closing stomata to regulate water loss and root morphology to slow the rapid water consumption of the soil. This can lead to reduced plant yields under drought conditions (Renu et al. 2017). The response of stomatal regulation to soil drying implies that there is a relationship between root system and leaf response in arid soil. The role of root signaling in stomatal control has been confirmed by many studies. A large number of data support a chemical signal: plant hormone abscisic acid (ABA) (Zhang and Davies 1990, Munns and Sharp 1993). ABA acts as a chemical signal involved in this rhizome communication process. Christmann et al. (2007) found that concentration of root-sourced ABA in Arabidopsis leaves regulates stomatal closure during soil drying. A molybdenum cofactor sulphurase (*LOS5/ABA3*, ABA-mediated low expression of osmotically responsive genes) improves drought tolerance and increases yield in soybean via enhanced ABA accumulation (Li et al. 2013). Stomatal closure under water deficit is a response to signals generated and transmitted by roots, and root characteristics may play an important role in the process of signal generation. Under drought conditions, soil water shortage promotes the de novo synthesis of ABA at the root and the translocation to the upper part of the plant, leading to the accumulation of ABA in the leaves, thereby promoting stomatal closure and reducing water dispersion loss to improve the tolerance of land plants to drought stress (Fig. 3; Tardieu et al. 2010). This helps plants as an early signaling mechanism to regulate stomata and conserve water (Renu et al. 2017).

Flow resistance (low conductance) in plant roots prevents water uptake and supply to the shoots. Radial flow is the biggest restriction for water uptake by roots to reach branches through both radial and axial channels (Audus and Garrard 1998, Bramley et al. 2009). In a former soybean study, after four-fifths of the sperm roots were removed, it was found that the increase in ABA and root water conductivity to meet transpiration demand was because of the redistribution of ABA from leaf to root. Therefore, ABA not only regulates stomatal function, but also regulates root water conductivity (Kudoyarova et al. 2011). Several studies have identified some compounds having significant ABA-agonist or antagonist activities, which could be potentially used to reverse the excessive or moderate ABA action as reviewed in Gupta et al. (2020).

RSA is particularly important in the acquisition of soil resources by allocating root foraging to the soil regions with the greatest resource availability. Considering the enormous spatial variations in soil properties and the yield associated with root maintenance in exploring soil profiles indiscriminately (Lynch and Brown 2012). The subordinate function value of soybean drought tolerance was positively correlated with root diameter, root surface area, root volume and root biomass under drought stress, but negatively correlated with leaf area index, stem biomass and leaf biomass (Li et al. 2015). Studies in Arabidopsis have found new insights into the molecular and cellular biology of the occurrence and growth of contralateral roots. The effects of individual nutrients on lateral branches are different. Roots respond to the heterogeneous distribution of nutrients and other resources by changing the branching patterns. This plasticity is a challenge for scientists trying to change RSA through plant breeding (Drew and Saker 1978, Hodge 2006). Understanding root branching requires understanding not only the development of lateral roots, but also the development of other roots produced by lateral roots. The initiation and growth of these roots may be different from lateral root development, but they share signal elements with lateral root development. In leguminous plants, base roots and main roots form the scaffolds of RSA (Lynch 2019). The number of basal roots has a genetic basis, but the genetic determinants are not yet clear (Lynch and Brown 2012). Because roots are a huge and continuous metabolic cost for plants, it is important to understand how compensation mechanisms are combined with external signals to form one root type and another. Root development under drought stress is more conducive to improving the ability of plants to resist drought, whereas overgrowth of shoots, especially leaves, may increase water consumption of plants, which is not conducive to their tolerance to drought stress. These can be used as indicators to measure drought tolerance of soybean seedlings (Ambrocio 2015). Increased root growth and root length density in the deeper soil profile under water stress can effectively resist the damage caused by drought stress on crops. This can be used as an important index to measure drought tolerance of plants (Farooq et al. 2012). Larger root systems with greater root length and biomass improve drought tolerance, whereas higher aboveground biomass, especially higher leaf biomass, will reduce the drought tolerance of plants. This may be because root systems with superior (suitable) root traits are conducive to water absorption and drought tolerance, whereas higher aboveground biomass will increase the water consumption of plants. Transpiration loss of water is a major challenge for drought tolerance (Muchero et al. 2008, MacEwan et al. 2010).

Genes and QTL loci for RSA traits associated with improved tolerance to drought have been identified in many plant species as reviewed in Chen et al. (2018b) including soybean. For example, the soybean β-expansin protein is associated with an increased root cell division and elongation under drought stress (Guo et al. 2011). The uptake of genomics tools has accelerated the discovery of genetic and cellular networks that are the main components of root growth and development. These

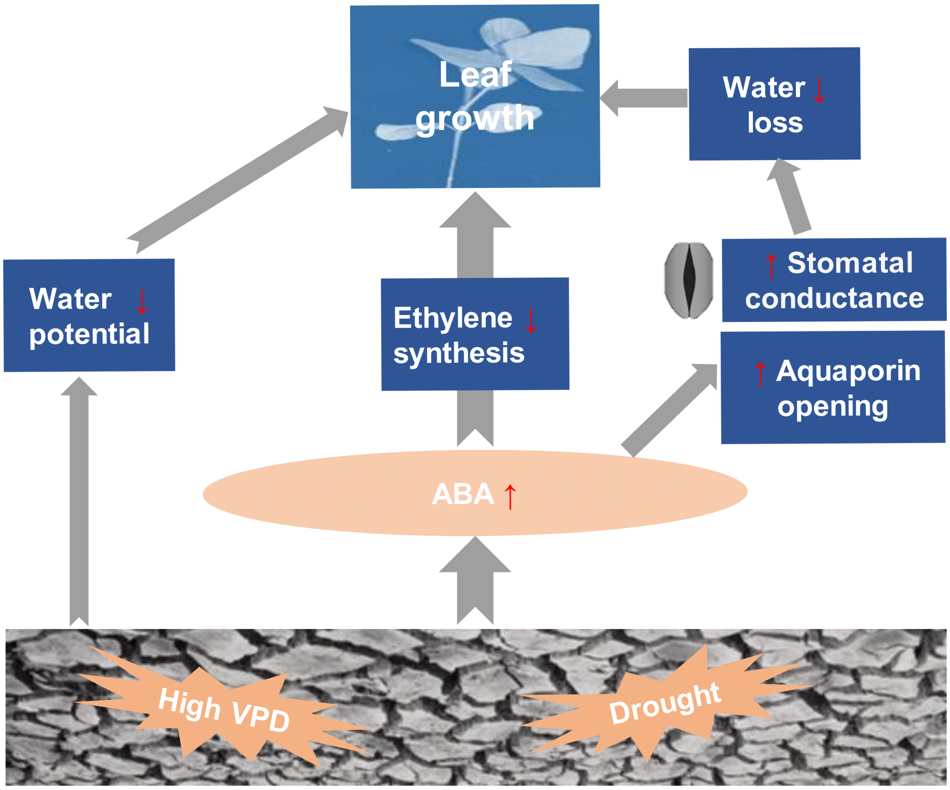

Fig. 3. Effect of drought and high vapor pressure deficit (VPD) on root-sourced ABA. Drying soil stimulates production of root-sourced ABA to transport to leaf, which regulate aquaporin (water channels) opening and stomatal conductance, and thus reduces leaf water loss to prevent leaf senescence. Drought inhibits ethylene synthesis in root and nodule tissue of legume plants and its signal transduction pathways generate a marked delay in senescence processes at early drought stages. The red thin arrows mean increase (↑) or decrease (↓).

processes will become valuable tools for the development of new crops with superior access to soil resources. Deployment of the information in crop improvement requires a detailed understanding of root phenology.

Drought stress affects lipid regulation and protein metabolism

Drought stress significantly reduced the oil content of seeds at the later stage of grain filling in soybean (Martin et al. 2019). Dornbos and Mullen (1992) found that serious water shortage during seed filling reduced oil content by 12.4% and oleic acid content by 11.1% at the same time. The expression of lipid biosynthesis-related genes in soybean, pyruvate kinase, biotin carboxyl carrier protein and ketoacyl acyl carrier protein synthase, in mature seeds decreased between days 19 and 29 of drought stress (Nakagawa et al. 2018). Meanwhile, the expression of Acyl-CoA oxidase (*GmACX1*), malate synthase and phosphoenolpyruvate carboxykinase, which are key genes of lipid degradation, increased under drought stress at 24 and 29 d. The gene expression of homologs of *GmACX2*, *GmACX1* and *GmACX4* also increased during drought stress. Lipid biosynthesis of mature seeds was inhibited, whereas lipid degradation and sugar accumulation were promoted under drought condition (Martin et al. 2019). These sugars can be used to maintain basic growth and metabolism, as well as to regulate seed germination, seedling development, flowering, senescence and eventual drying (Gibson 2005, Buitink et al. 2006).

Lower enzyme activity leads to lower soluble sugar content because lipids and proteins are stored for gluconeogenesis to produce sugar. The biosynthesis of seed lipids depends on the supply of photosynthates in plant tissues. One reason why drought stress reduces lipids is the reduction of stomatal conductance that decreases the rate of photosynthesis control (Rylott et al. 2003, Baud and Lepiniec 2010). Among the genus *Glycine*, *GmGY1-5* showed significant changes under drought stress, including *β-conglycine* that also encodes storage protein and decreased on 10, 19 and 24 d under drought treatment (Nakagawa et al. 2018). The expression level of *GmCYSP1* during stress differed to that of *GmCYSP2* which increased on 10 and 19 d (Ling et al. 2003).

Drought stress induces the expression of cysteine protease that is very important to decompose stored proteins into free amino acids (Vierstra 1996). Amino acids released by cysteine proteases are used in the ab initio synthesis of stress-adaptive enzymes. It is caused by increasing the activity of cysteine protease under salt and drought stress (Forsthoefel et al. 1998). Drought stress reduces the dry weight of soybean seeds through reducing the content of lipid and protein in seeds, reducing their biosynthesis and promoting their degradation (Desclaux et al. 2000, Wei et al. 2016). Further research on lipid regulation and protein metabolism is in progress.

Association between simple sequence repeat markers and yield traits

In recent years, with the rapid development of simple sequence repeats (SSR) marker technology, a variety of molecular markers have been widely used in soybean yield traits and correlation analysis (Galeano et al. 2012, He et al. 2012, Lightfoot and Iqbal 2013). Ning et al. (2017) studied the polymorphism of 36 soybean cultivars under drought and high temperature treatments and detected 156 alleles in 49 polymorphic markers. The Shannon index of marker loci ranged from 0.4506 to 1.3265 with the average of 0.9662. Marker *Sat_418* (in response to control the QTL of linoleic acid and environmental interaction) had the highest Shannon index value marker *Satt679* had the lowest value. The Shannon index is used to describe the disorder and uncertainty of individual species. The higher the uncertainty, the higher the diversity. Thirty-six soybean materials were divided into two subgroups under high temperature and drought treatment. Polymorphic information content (PIC) value ranged from 0.2454 to 0.9059, the average is 0.6060. The maximum PIC index is *Sat_195* and the minimum is *Sct_187*. PIC refers to the value of a marker for detecting polymorphisms in a population. PIC depends on the number of alleles detected and their frequency distribution. Its value is equal to 1 minus the sum of the squares of all allele frequencies. The correlation analysis showed that 12 loci were correlated with yield traits of soybean. *Satt362* is related to the degree of wilting (Charlson et al. 2009). *Satt575*, *Satt185*, *Satt428* and *Sat_312* are related to production (Wang et al. 2004, Reinprecht et al. 2006). *Satt380* is related to flowering and pod-setting stages (Tasma et al. 2001). *Satt452* is related to maturity and yield (Rossi et al. 2013). The phenotypic effects of *Satt575-2*, *Sat_201-1* and *Satt686-2* were excellent allele variants, which provided the basis for parent selection and marker-assisted breeding in later hybrid breeding (Wang et al. 2004).

Effects of soybean varieties on physiological characteristics and interpretation rates of phenotypic variations in correlation between physiological indexes and grain weight are affected by high temperature stress. Related to the first flowering days in normal and high temperature conditions, the expression of *Satt380* was increased, whereas *Satt452* decreased. There was no detailed information of *Sat_201* in the database and thus it needs to be verified by future QTL mapping. *Satt575* and *Satt185* are the two loci related to the initial flowering stage under high temperature and drought conditions. They are all related to yield in the SoyBase database, and their roles might change under high temperature and drought stress (Zhang et al. 2012). The ways and mechanisms involved in changing the stress intensity and process need to be further studied.

Physiological and transcriptional responses

Soybean cultivar Williams 82 was used to study how antioxidant enzymes were involved and which genes and molecular pathways responded to drought. Some identified soybean genes and pathways can be used as targets for genetic engineering or molecular breeding to improve its drought tolerance (Xu et al. 2018). Williams 82 results in the total differential expression of 6609 transcripts under drought conditions, including many genes related to hormones (auxin/ethylene), carbohydrates, cell wall-related secondary metabolism and transcription factors controlling root growth (Song et al. 2016, Xu et al. 2018). Under drought stress, plants might partially or fully close stomata to reduce water loss. Under drought stress, excessive reduction of photosynthetic electron transport chain forces excitation energy to dissipate through non-photochemical quenching, resulting in reactive oxygen species production (Alam et al. 2010). Harmful reactive oxygen species (ROS) are usually produced under plant growth stress. One of the mechanisms of plant evolution is the production of antioxidant enzymes to mitigate damage (Noctor et al. 2014). The activities of catalase and superoxide dismutase (SOD) dismutase in plants under drought stress were higher, but no change was found for G protein and peroxidase protein. The increase of catalase and SOD activities in soil indicated that drought stress caused by soil water loss resulted in oxidative stress to soybean plants.

In plants under drought stress, bioinformatic annotations, such as Gene ontology (GO), Clusters of Orthologous Groups, Differentially Expressed Gene (DEG) and Kyoto Encyclopedia of Genes and Genomes (KEGG) databases, enhance our understanding of the gene regulation. Under drought stress, 2771 genes were differentially expressed, of which 1798 genes were upregulated and 973 genes were downregulated in Williams 82. The most abundant categories bounded by fold-change >2 are 'general functional prediction' (395 DEGs), followed by 'transcription' (253 DEGs), 'replication, recombination and repair' (206 DEGs) and 'signal transduction mechanisms' (265 DEGs). The expression genes of William 82 under drought stress can be divided into three categories: biological processes, cellular components and molecular functions (Xu et al. 2018, Ribichich et al. 2019). The 1867 DEGs assigned to the GO classification fall into three broad categories: biological processes, cellular components, and molecular functions. Among drought-stressed plants, 'cellular processes', 'metabolic processes' and 'monomeric processes' are the most responsive groups in the biological process category. 'Cellular part' and 'cell' are the fastest responding groups in the cell component category; 'binding' and 'catalytic activity' are the most sensitive groups in the molecular functional category (Dinakar et al. 2010).

Studies on gene manipulation involving isoflavone synthesis alone or in combination with the alteration of pathways related to ROS removal provide insight to improved drought tolerance of soybean plants. Soy isoflavones react with superoxide anions to prevent the initiation of free radicals, chelate with metal ions to prevent the generation of hydroxyl free radicals, and react with lipid peroxidation groups to prevent the lipid peroxidation process (Legang et al. 2004). Physiological studies had shown that the accumulation of flavonoids, having a potential role in protecting against oxidative damage, increases under water stress. Initially, plant secondary metabolite production may increase under drought stress because carbohydrates are redirected to the synthesis of these products. However, if severe drought persists, the number of secondary metabolites may decrease (Sun and Han 2005). Phenylpropionate-related enzyme protein decreased under drought stress. Their expression often returns to the control level after recovery, indicating their dynamic role in drought response (Hernández et al. 2009, Abebe et al. 2010).

WRKY transcription factors are important in the development and physiological functions of soybean. This gene has been extensively studied for its role in abiotic stress tolerance in many plant species, including wheat, common bean and canola (He et al. 2016, Phukan et al. 2016, Wu et al. 2017). Upregulation of *WRKY* transcription factor at protein level under drought stress shows that *WRKY* transcription factor plays a direct role in drought tolerance (Tripathi et al. 2014). Expression of four members of the *WRKY* family (*WRKY55*, *WRKY50*, *WRKY15* and *WRKY2*) in soybean plants was induced under drought stress. Members of this gene family have been found to be involved in many types of plant physiological regulation, such as stomatal movement, flower control and wax synthesis (Rabara et al. 2013). *MYB* is another group of transcription factor identified from soybean plants (Buchanan-Wollaston et al. 2003, Klukas et al. 2014) that have been found to be involved in many types of plant physiological regulation, such as stomatal movement, flower control and wax synthesis (Baldoni et al. 2015). The decreased expression of *MYB118* and *MYB139* and the induced expression of *MYB48* in soybean plants under drought stress indicated that transcription factors can be regulated to improve soybean drought tolerance (Bian et al. 2017, Yan et al. 2017).

Compared with the differentially expressed genes of *MYB* and *WRKY* families, the most significant induction of gene expression was observed in many genes of *NAC* family. The drought tolerance of *Arabidopsis thaliana*, wheat and tomato could be improved by controlling the expression of *NAC* gene (Tran et al. 2004, Chen et al. 2018a). Except for *NAC4*, overexpression of *NAC29*, *NAC25* and *NAC72* in leaves only leads to increased drought tolerance in reproductive stage (Hussain et al. 2017). These studies also indicate the importance of studying genome-wide variations of different transcription factors and improving drought tolerance by using allele variations.

Upregulation and downregulation of multi-transcription factors in soybean indicates that the control of upstream regulation genes is the main mechanism for plants' response to drought stress. Because each transcription factor can regulate a series of downstream response genes, manipulation of some individual or combined transcription factors may lead to improvement of drought tolerance in soybean plants (Laufs et al. 2004, Xie et al. 2019). The recent publication of a reference-grade genome of wild soybean will enable further bioinformatic approaches to advance our understanding of the genetic and transcriptional diversity of responses to drought and other stresses (Xu et al. 2018).

Breeding technologies

The development of modern molecular biology provides a new way for breeding soybean and improves the drought tolerance heredity of soybean (Quarrie 1996). At present, there are two main methods adopted: one is transgenic breeding, which transfers endogenous or exogenous genes related to drought tolerance at high efficiency into soybean varieties; the other is gene mapping and cloning through molecular marker-assisted selection (MAS) of soybean, and introducing genes with high drought tolerance or high water-use efficiency into

Table 1. Transcription factors and functional genes of drought tolerance in soybean and other crops.

Transcription factor family	Response gene	Other response species crops
Aquaporin	GmPIP2, GmPIP3, GmPIP4, GmPIP5, GmPIP6, ZjPIP2, PmPIP1, VhPIP1	Arabidopsis thaliana
Protein phosphatase	GsPP2C clade D	Arabidopsis thaliana
Pectin lyase	PL-18, Glysoja_033298	Arabidopsis thaliana
Basic leucine zipper	GmbZIP44, GmbZIP62, GmbZIP78	Arabidopsis thaliana, Nicotiana tabacum, Malus pumila, Oryza sativa, Vigna radiata, Cucumis sativus
WRKY	WRKY57, AtWRKY15	Arabidopsis thaliana, Oryza sativa
MYB	AtMYB60, AtMYB21, MdMYB121, MdSIMYB1	Arabidopsis thaliana, Nicotiana tabacum, Oryza sativa, Malus domestica
NAC	NAC72, NAC24, NAC5	Arabidopsis thaliana, Triticum aestivum, Solanum lycopersicum
AP2/EREBP	OsDREB1A, OsDREB1F, GmDREB2, ZmDREB2A	Arabidopsis thaliana, Oryza sativa, Zea mays

soybean varieties by means of hybridization and backcross (Nguyen et al. 1997, Kelly et al. 2003).

Cloning, recombining and transferring genes related to drought tolerance into plant genome are one of the most effective methods to cultivate drought-tolerant soybean varieties (Thudi et al. 2014). At present, the main target genes for drought-tolerant transgenic breeding are enzymes that synthesize various osmotic protectants, enzymes of antioxidant system and protein kinase genes related to transcription factors acting in stress-tolerance and signal transduction (Yue et al. 2006). *Agrobacterium*-mediated, gene gun, pollen tube pathway and protoplast methods are the main methods used for gene transformation. At present, many studies have carried out tolerance screening using polymerase chain reaction detection and Southern hybridization detection of soybean transgenic plants, proving that foreign genes have been integrated into the soybean genome. Some of the 'tolerance' genes have also been functional tested. Transgenic breeding is changing from single gene transformation to multi-gene transformation (Wang et al. 2006).

In recent years, with the rapid development of various disciplines in the field of biology, the construction of molecular genetic maps of various crops with markers and location of important trait genes provides a new method for improving crop drought tolerance (Sorkheh et al. 2008). Difficulties in quantifying complex traits can be assisted by restriction fragment length polymorphism (RFLP) or other molecular marker methods. Drought-related genes can be marked by molecular markers. Complex quantitative traits can be decomposed into simple quality traits to study (Tanksley et al. 1989). Using RFLP molecular marker and linkage map, the QTLs related to water use efficiency and leaf ash were identified among 120 F4 families of soybean hybrid combinations (Mian et al. 1996). Some important trait genes have been labeled and mapped. Segregation analysis was used to analyze the genetic characteristics of drought-tolerant related root traits and QTL mapping (Zhang et al. 2011a). At present, many genes related to drought tolerance of soybean have been cloned, and some of them have been introduced into soybean to obtain transgenic plants (some cloned genes related to soybean drought response have been introduced into crops as shown in Table 1). However, in order to truly improve the genetic improvement of drought tolerance of soybean, further research is needed; multiple genes should be transferred and combined for systematic integration analysis. Molecular breeding and conventional breeding are complementary and inseparable (Lightfoot 2008).

Conclusion

Root biology is a new frontier which can be used to systematically study many processes involved in plant water and nutrient mobilization, uptake and transport. Identified suitable root traits can be used for more efficient screening in a controlled environment, or labeled with molecular markers, and then incorporated into other varieties by MAS or transgenic methods. Such research will help us understand the drought tolerance mechanism of soybean and the theory and practice of genetic improvement of soybean varieties. However, more in-depth research with additional application and theoretical research is needed to develop crop varieties with improved water-use efficient and enhanced adaption to drought environments.

Author contributions

R.X. and Y.C. initialed the conception and structure of this review. R.X. wrote the first draft. Y.C. reproduced figures. All co-authors reviewed and revised the manuscript.

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Data availability statement

All relevant data is contained within the article: The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding author.

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