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Native Plants to Arid Areas: A Genetic Reservoir for Drought-Tolerant Crops

*Ricardo Trejo-Calzada, Aurelio Pedroza-Sandoval,
Jesus G. Arreola-Avila and Fabian García-González*

Abstract

Droughts are common in arid areas. These cause important losses in crop production, while the increasing population demands more food and goods. Cultivars able to produce under drought conditions are required to avoid or reduce production losses. Plants have evolved different mechanisms to face drought, and many genes have been already discovered in model and cultivated plants that are involved in this trait. Some of these genes have been successfully transformed into cultivated plants for drought tolerance. Plants native to arid lands may possess variants of drought tolerance mechanisms as compared to mesophytic or model plants. Also, different drought-related genes can be revealed. Studies using high-throughput and bioinformatic tools may allow to discover new genes and give new insights on the mechanisms involved in drought tolerance. However, still scarce studies in plants native to arid lands show that there are many drought-related genes that have not been already characterized and potentially they may be novel genes. These novel genes may be used to improve crops for drought tolerance. Therefore, more physiological, transcriptomic, proteomic, and metabolomic studies are needed on plants native to the deserts.

Keywords: abiotic stress, water stress, drought-related genes, genetic diversity, deserts, vegetation, drought-tolerance mechanisms, oxidative stress, osmotic adjustment, differentially expressed genes

1. Introduction

Arid lands are defined by the United Nations Environment Programme (UNEP) based on the ratio of average annual precipitation and potential evapotranspiration or aridity index (AI). Arid lands are those with an AI lower than 0.65 [1]. Arid lands are widely spread around the world. They include around 41% of the earth's land surface [2]. These areas include hyperarid (1 billion ha), arid, semiarid, and dry subhumid (5.1 billion ha) regions distributed across virtually all the continents [3]. Arid lands are often affected by droughts, which disturb natural and managed ecosystems and cause less biomass production, biodiversity loss, poverty, and insecurity [2, 4].

Droughts are one of the main environmental factors that prevent plants from reaching their full genetic potential and strongly reduce plant growth and

productivity of native populations and in agricultural systems of arid and semiarid areas [5, 6]. Droughts are increasing in frequency and intensity on large regions of the world due to desertification processes. Desertification as a result of greater world's population, extensive agricultural practices, and the effects of the global climate changes has become a serious problem [7]. Droughts are not unusual when viewed from a geological or evolutionary perspective. Therefore, they represent a permanent, strong, and increasing factor for biological, ecological, agronomic, and economic processes [8].

Plants as sessile organisms are under strong selective pressure to adapt to their environment. Along the entire life cycle, plants are frequently subject to a combination of different biotic and abiotic stresses [9]. Drought is one of the major environmental factors that reduce the yield of crops by limiting water availability for plants' growth [10, 11]. Water deficit is one of the most important abiotic stresses that affect development and productivity of crop plants [12]. Water stress induces stomatal closure, restricts gas exchange, and reduces photosynthesis in plants [13]. Plants must cope with their environment through physiological acclimation and evolutionary adaptation. As a result, plants have evolved extraordinary mechanisms to perceive, respond, and survive some abiotic stresses and especially with water stress [8].

Most of the cultivated plants are very sensitive to drought and water stress [14, 15]. Thus, agricultural production is seriously limited by drought, while world population is continuously and increasingly demanding for food [16]. New cultivars that can keep or increase yields while using less water are needed in order to reduce the risk of grave yield losses and to reach the world food requirement [17, 18].

Some plant species have evolved morphological, physiological, and biochemical mechanisms that allow them to survive, grow, and reproduce in areas where drought is a common event. Plants may deal with water stress through escape, avoidance, and tolerance strategies [19, 20]. Escape is reached through plastic shifts in phenology in such a way that critical growth periods do not coincide with periods of water deficit. Avoidance includes adaptive responses to keep plant water status during drought. Tolerance strategies protect plant cells, tissues, and organs from water stress letting recovery after periods of water deficit and drought. These strategies are not mutually exclusive and may have different functions depending on species and duration, intensity, and timing of water stress [21, 22].

Native plants to arid lands must deal with extreme environmental factors such as high temperatures, high evaporation, low precipitation, salinity and high light intensity, and low soil moisture [23, 24]. These plants have evolved numerous mechanisms to survive drought. Some of those mechanisms have been described for model and cultivated plants [25]. However, wild populations frequently contain large pools of genetic and phenotypic diversity that can be useful for identifying new molecular strategies involved in drought tolerance. Detecting and understanding the roles of novel genes in drought tolerance may be the basis to improve or develop cultivars tolerant to drought [26, 27]. In this chapter we review some of the findings about drought-responsive genes in plants native to arid lands.

2. Drought tolerance genes

Plants' drought tolerance is a quantitative trait that is controlled by many genes with additive effects [28, 29]. In native plants to arid areas such as *Cynanchum komarovii* and *Prunus mongolica* Maxim, more than 3000 differentially expressed genes (DEG) under drought stress have been found [30, 31]. These genes and/or their products participate in at least two pathways involved in drought tolerance: ABA-dependent and ABA-independent pathways [25, 32]. According to their roles, these genes have been grouped

into two groups: (i) genes that code for regulatory proteins involved in signal transduction (transcription factors, protein kinases, ABA biosynthesis) and (ii) genes that code for functional proteins such as water and ion channels, detoxification enzymes, protective proteins (late embryogenesis abundant (LEA) proteins, chaperones), proteins involved in osmolyte biosynthesis, and proteases [25, 33].

2.1 Regulatory proteins

Plants must deal with drought by activating a complex signaling network that produces a variety of physiological responses and defense systems [34, 35]. The signaling pathways include a group of stress sensors, cellular signal transduction, and transcriptionally regulated networks. In order to respond to water stress, it must be perceived by specific receptors which transmit the stress signal into the cell and may trigger a series of signal transduction steps. [36]. The signal transduction in ABA-dependent pathways increasing ABA concentrations is sensed by receptors such as GTG1, GTG2, Mg protoporphyrin IX chelatase H subunit (CHLH/ABAR), and pyrabactin resistance 1/PYR1-like/regulatory component of ABA response 1 (PYR/PYL/RCARs) [37]. Once ABA binds to its receptor, ABI1 (ABA insensitive 1) phosphatase activity is blocked causing autophosphorylation and activation of an open serine-threonine kinase (open stomata 1, OST1). Then, transcription factors (TFs) known as ABA-responsive element-binding proteins (ABFs/AREBPs) are phosphorylated and activated by OST1. Besides OST1, calcium-dependent kinases (CDPKs) similarly activate SLAC1 and SLAH3 [38]. Afterwards, ABFs bind to DNA at specific ABA-responsive elements (ABREs). Finally, ABA-dependent gene expression is induced [39].

Gene expression at the transcriptomic level is strongly regulated by transcription factors [40]. TFs can be grouped into several families according to their structure and binding domains [41]. Several TFs belonging to MYB, MYC, NAC, bZIP, HD-ZIP, DREB, and WRKY families are involved in modulation of gene expression of plants in response to drought stress through ABA-dependent or ABA-independent pathways [42]. Even though many TF families have been found in several models and cultivated plants [43, 44], novel TFs are being described from plants native to arid lands. They may be used as a powerful tool for practical approaches for engineering drought stress tolerance in plants. For example, in the desert legume *Eremosparton songoricum*, a novel DREB2B (EsDREB2B) gene was identified. The transcript of EsDREB2B was upregulated by different abiotic stresses, among them drought stress [45]. Other novel DREBs from a desiccation tolerant moss (*Syntrichia caninervis* Mitt.) were isolated and used to transform yeast. The ScDREB enhanced stress tolerance to yeast [46]. In *Larrea tridentata*, a bush native and widely distributed to Northern American deserts, the LtWRKY21 transcription factor that functions downstream of ABI1 to control ABA-dependent expression of genes was found [47]. The PeDREB2L gene from the desert tree *Populus euphratica* Oliva was isolated and transformed into *Arabidopsis thaliana*. Transgenic plants showed an improved tolerance to drought and freeze [48]. Moreover, in *Sophora moorcroftiana*, an endemic Leguminosae shrub species native to arid and semiarid regions of the Qinghai-Tibet Plateau, a total of 1534 TFs were identified. Those TFs were classified into 23 different common families. The major group of TFs was the bZIP family (160, 10.43%), followed by MYB (115, 7.5%), bHLH (107, 6.98%), zinc finger (103, 6.71%), and WRKY (103, 6.71%) [49].

2.2 Functional proteins

Drought stress affects many processes in the plants and cause a variety of physiological and biochemical changes. Some of these changes include loss

of cellular turgor, changes in membrane fluidity and composition, changes in osmotic potential, and protein-protein interaction [10]. Cell turgor loss is perhaps the most evident indicator of water stress which affects integrity of cells, metabolism, and whole plant performance [50]. Maintaining cell turgor is critical for surviving and growth of plants. The changes in osmotic potential play a relevant role for that purpose. Loss of cell turgor, among other effects, may cause stomata closure and limitations of gas exchange which in turn decreases CO₂ supply for RuBisCo. Photosynthesis decreases, and the reducing power production exceeds the rate of its use by the Calvin cycle [51]. Consequently, overproduction and accumulation of reactive oxygen species (ROS) alter the redox status [52, 53]. ROS damage all major cell biomolecules impairing their function [53]. Plants may respond to these effects by activating several defense mechanisms that involve participation of numerous proteins such as late embryogenesis abundant (LEA) proteins, osmoprotectants, chaperons, detoxifying enzymes, and various proteases [25, 54].

2.2.1 Late embryogenesis abundant (LEA) proteins

A relatively well-known family of drought-responsive genes is the late embryogenesis abundant (LEA) gene family. LEAs are proteins that accumulate at late stage of development of many plant seeds. LEA proteins also accumulate in vegetative parts of plants as a response to water and osmotic stresses and ABA application [55]. It has been proposed that LEA proteins have an important role protecting cellular structures from water deficit [56]. LEA proteins have been grouped into at least eight different groups according to their amino acid sequence similarities and repeated sequence motifs (LEA1 to LEA6, dehydrins, and seed maturation protein). Most LEA proteins are highly hydrophilic, glycine-rich, and low-complexity proteins. They have a strongly disordered conformation in the hydrated state [57]. LEA genes are highly diverse and have been found in a wide range of plant species [58]. Up to 242 LEA genes have been found in *Gossypium hirsutum* [57]. The LEA genes have several stress-responsive cis-acting regulatory elements in the promoter region such as ABRE, DRE/CRT, MYBS, and LTRE [59]. The expression of LEA proteins is associated with acquisition of drought stress tolerance [60, 61]. The specific cellular role of LEA proteins is not well known. However, different studies have shown that LEA proteins may function in scavenging free radicals and ions; stabilization of enzymes, proteins, and membranes; interactions with RNA and DNA; and water retention during drought and other abiotic stresses [61].

Several novel LEA genes have been found in plants native to arid lands, and they have been successfully applied to transform plants for drought stress tolerance. For example, [62] cloned a LEA gene from *Tamarix androssowii*, a shrub that grows in arid or saline environments. The cloned LEA gene was transformed into tobacco. The transgenic plants showed less ion leakage and MDA content under drought than nontransgenic plants. Also, transgenic plants had a greater growth and lower number of wilted leaves. Also [63] use a *Tamarix androssowii* LEA gene (TaLEA) to obtain transgenic lines of *Populus simonii* × *P. nigra* which were compared to nontransgenic plants under salt and drought stress. They found that the constitutive expression of TaLEA in transgenic poplars improved salt and drought tolerance, which was attributed to the protection of cell membranes from damage. Moreover, [64] transformed a dehydrin protein from the desert grass *Cleistogenes songorica* (CsLEA) into alfalfa (*Medicago sativa* L.). Transgenic plants grew more than wild-type plants under drought stress. Moreover, transgenic plants were able to return to normal after rewatering. Identification of novel LEA genes in plants adapted to arid lands may be useful for improving drought tolerance of cultivated plants.

2.2.2 Osmoprotectants

Some plants respond to drought stress via organic and/or inorganic solute accumulation. Osmolytes or compatible solutes are produced in plants under drought or saline stress. They are small and neutral and do not affect plant metabolism even at relatively high concentrations [21]. These compounds are also called osmoprotectants and are included into three major chemical groups: amino acids (e.g., proline), polyols (e.g., mannitol, trehalose, fructans), and quaternary amines (e.g., glycine betaine and polyamines) [65]. Active accumulation of osmoprotectants may help plants to endure water stress by maintaining the fluidity of cell membranes, protecting and stabilizing proteins and macromolecular structures, detoxification of free radicals, and osmotic adjustment. Osmotic adjustment is a mechanism that allows plants to keep a flow of water to the cells. A greater concentration of osmolytes reduces the osmotic potential of cells, which in turn produces water movement to the cells, which allows maintenance of turgor. Osmotic adjustment also involves lowering of toxic concentrations of Na^+ by limiting influx, sequestration, or exclusion [66]. Therefore, cell activities take place at approximately normal speed for better growth and development of plants [67].

Several genes associated with synthesis of osmoprotectants have been identified, isolated, and cloned from a variety of plant species including those native to arid lands [68]. For example, the pyrroline-5-carboxylate synthase (P5CS) gene involved in proline synthesis was characterized in *Calotropis procera* from de novo assembled transcriptome contigs of a high-throughput sequencing dataset [69]. Also, [70] transformed wheat plants with a P5CS gene from *Vigna aconitifolia* a legume grown in arid and semiarid regions of India. They found that transgenic wheat acquired drought tolerance by proline accumulation, which may have protected plants against oxidative stress. A betaine aldehyde dehydrogenase (BADH) gene from *Atriplex canescens*, a perennial bush native to arid lands of Northern America, was introduced into a soybean cultivar. The expression of AcBADH increased after drought treatment of transgenic plants. Besides glycine betaine, proline content also increased, and transgenic soybean lines yielded up to 8.8% more than control plants under drought treatments [71]. A plasma membrane intrinsic protein (PIP) gene (ScPIP1) from *Simmondsia chinensis*, a typical desert shrub, was cloned and overexpressed in *Arabidopsis thaliana*. ScPIP1 conferred drought and salt tolerance probably by reducing membrane damage and increasing osmotic adjustment [72].

2.2.3 Detoxifying enzymes

Drought as other kinds of abiotic and biotic stresses may produce oxidative stress. The oxidative stress is caused by at least two processes: (i) an imbalance of production and detoxification of reactive oxygen species (ROS) and (ii) de novo ROS biosynthesis as a response for defense and adaptation to environment. These processes produce significant variations in the general cellular redox state [53, 73]. The term ROS includes substances with one or more activated atoms of oxygen that can be radicals. Some free radicals do not contain oxygen atoms. The key ROS are triplet oxygen, singlet oxygen, superoxide anion radical, hydrogen peroxide, and hydroxyl radical [53]. Oxidative stress causes lipid peroxidation that impairs membranes and induces loss of their barrier function, and consequently a breakdown of organelles occurs [74]. Plants have evolved defense systems against excess of ROS. Those systems include nonenzymatic and enzymatic responses. The enzymatic system consists of several enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and others that eliminate or scavenge ROS [75].

Plants native to arid lands may have antioxidant defense systems to limit the deleterious effects of ROS. For example, in *Oudneya africana*, a Saharan plant, water deficit caused variations in enzymatic and nonenzymatic antioxidants, differentially affecting the concentration of SOD and POX [76]. Transgenic poplar expressing the eukaryote translation initiation factor 5A (TaeIF5A1) from *Tamarix androssowii* showed greater superoxide dismutase (SOD) and peroxidase (POD) activities, lower electrolyte leakage, and improved tolerance to abiotic stresses [77]. Six plant species from semiarid Loess Hilly Region of China showed significant differences in SOD and POD activities when subject to drought along 3 months. Also there were significant interactions of SOD, CAT, and POD activities and MDA content between months and species [78]. A transcriptomic study under drought stress showed that *Prunus mongolica* Maxim, a species widely distributed in the Gobi Desert, increased transcription of iron superoxide dismutase and manganese superoxide dismutase which promoted drought stress tolerance [31].

3. Findings of novel genes in native plants from arid land areas

The development of high-throughput next-generation sequencing technologies offers opportunities for genome-wide transcription analysis of non-model plants and especially of desert plants and discovery of novel pathways and genes related to drought tolerance. These novel genes may be useful to improve drought tolerance in cultivated plants. Even though there are not many studies in plants native to arid regions, the results of some of the research that different groups have carried out allow insights over the abundance of potential novel genes for drought tolerance.

By using the analysis of subtracted expressed sequence tags (ESTs) in horse gram (*Macrotyloma uniflorum* (Lam.) Verdc.), 531 unigenes were found as upregulated by drought. Among these unigenes 366 showed significant similarity to known sequences in the database. Approximately 30% of the ESTs had no similarity to known proteins in the GenBank database. Those are considered as novel. Also, according to the functional classification, the most abundant ESTs were those related to stress responses (12%), DNA processing and nucleotide metabolism (10%), photosynthesis and electron transport (9%), and transcription factors (5%). There was redundancy in several known stress-responsive clones in dehydrated sample. The most prominent were metallothionein, glutathione S-transferase, RabGAP/TBC domain-containing protein, lipoxygenase, translationally controlled tumor protein, chaperon, lipid transfer protein, cysteine proteinase, calmodulin, calmodulin-binding protein, and sterol 24-C-methyltransferase [79]. Moreover, a protein-protein interactome study carried out in *M. uniflorum* showed that the highest number of PIPs occurred in shoot (416) and root (2228) tissues of a drought-tolerant genotype as compared to shoot (136) and root (579) tissues of a sensitive genotype. The PIPs most responsive to drought stress were kinase and transferase activities involved in signal transduction, cellular processes, nucleocytoplasmic transport, protein ubiquitination, and localization of molecules. These PIPs could be enclosed in mechanisms of drought tolerance of *M. uniflorum*. Also, they could provide new understandings of mechanisms involved in drought tolerance [80].

A transcriptomic analysis of the roots of *Ammopiptanthus mongolicus*, an endemic species to the Gobi Desert, allowed to identify 27 drought-responsive genes. These genes were grouped into the GO categories of response to osmotic stress, response to oxidative stress, response to hormone stimulus, and response to light stimulus. A total of 9771 (34%) out of 29,056 ESTs matched to known proteins recorded in the PlantGDB database. This means that many ESTs could be novel drought-responsive genes [81]. Another study of comprehensive transcriptome of *A. mongolicus*

identified up to 6102 DEGs under drought stress at 3 points of exposure. A group of 2028 DEGs were common for the 3 points. Among them 779 DEGs were upregulated and 1185 were downregulated by drought. The upregulated DEGs included a heavy representation of genes encoding ripening-related proteins, LEA proteins, peroxidases, transporters, enzymes of flavonoid biosynthetic pathways, protein kinases, ethylene receptors, and transcription factors. About 17.2% of the common DEGs had no homology to known functional proteins [82]. Similarly, Pang et al. [83] identified 1620 DEGs, including 1106 upregulated DEGs and 514 downregulated DEGs.

In *Cynanchum komarovii*, a xerophytic plant species, up to 3134 unigenes were found as differentially expressed genes (DEGs) under drought stress. A total of 601 unigenes were induced, while 2533 unigenes were repressed. The most abundant upregulated DEGs were into the following GO groups: “oxidation-reduction process” with 120 DEGs, “single-organism metabolic process” with 185 DEGs, and “oxidoreductase activity” with 113 DEGs. The most downregulated genes were grouped into the following GO terms: “metabolic process,” “cellular component organization or biogenesis,” “cellular response to stimulus,” “macromolecular complex,” “cytoplasm,” “protein binding,” and “hydrolase activity.” KEGG pathway analysis allowed to identify that DEGs involved in “cutin, suberine, and wax biosynthesis” changed significantly, which may be due to the important role of this pathway for this plant species protection when exposed to drought [30].

Reaumuria soongorica is an extreme xerophyte shrub from Gobi and marginal loess of central Asia. A transcriptomic analysis identified 123 unigenes potentially associated with drought adaptation. A total of 46 unigenes were related to drought escape mechanisms, while 40 unigenes were potentially involved in drought avoidance. Also, 32 unigenes had identity to genes involved in ABA-dependent, while 8 unigenes had homology to some genes involved in ABA-independent pathways of drought tolerance. There was a 7.96% of unigenes that did not match any homologous genes in the known plant species [84]. Another study identified 1325 DEGs, including 379 upregulated DEGs and 946 downregulated DEGs under drought stress. Among DEGs, 20 genes encoded for kinases, and 14 encoded for transcription factors such as WRKY, NAC, MYC, TCP, and bZIP. Also 13 DEGs encoding for functional proteins such as LEA proteins, small heat shock proteins, and aquaporin (AQP) and proline transporter were identified. Moreover, 14 DEGs were found encoding for low-temperature-induced protein, dehydration-induced protein, defending precursor, resistance protein, universal stress protein, and protein involved in protein kinase [85].

Haloxylon ammodendron (C.A.Mey) is a desert tree distributed in Middle and Central Asia. By doing a transcriptomic analysis in this species, up to 1060 unigenes were identified as DEGs for drought stress. Among them, 356 DEGs were upregulated and 704 DEGs were downregulated. A total of 469 (44%) of DEGs did not show homology to genes in NCBI database. Approximately 12.1% of DEGs with homology to known genes were associated with nitrogen metabolism, starch and sucrose metabolism, and fatty acid metabolism. Also, 35 DEGs encoded known or putative transcription factors such as WRKY, MYB, and ethylene-responsive [86].

The expression of drought-responsive genes may depend on the stress intensity. A study in *Sophora moorcroftiana* revealed that more genes were differentially expressed under severe water stress than mild stress. Up to 5648 unigenes were differentially expressed between control and severe stress plants. Around 601 unigenes were common for mild and severe water stress. Eleven out of 1534 TFs were selected for expression analysis. Among these, seven were drought-responsive. Those encoding for DREB, zinc-finger protein (ZnF), zinc-finger protein kinase (ZFPK), MYB, NAC, and WRKY were upregulated, while ERB was downregulated. Three selected aquaporins (AQPs) and one sugar transporter (SUT) genes were upregulated by

drought. Genes encoding for scavenging reactive oxygen species such as POD, PRX, and GPDH were induced by drought stress [49].

Prunus mongolica is a plant native to the Gobi Desert. In this species a total of 3365 differentially expressed transcripts (DETs) for water stress were identified, counting 1876 transcripts upregulated and 1489 transcripts downregulated. Among these, 42 transcripts coding for 5 aquaporin subfamilies were found. Also, 15 potential plasma membrane intrinsic proteins (PIPs) were upregulated and 1 downregulated. Interestingly, 177 transcripts related to ROS scavenging were identified. Approximately 28% of them were predicted as SOD. Several significant pathways were identified to be related to drought tolerance of *P. mongolica*. These pathways included transcription factors and plant hormone signal transduction, starch and sucrose metabolism, and cysteine and methionine metabolism [31].

Artemisia sphaerocephala is a species found in sand dunes in the deserts of Northwest China. A transcriptomic analysis in this species identified 108 unigenes related to drought stress tolerance. These had homology to 17 kinases, 2 potential chaperones, 52 enzymes, 6 transporters and channels, and 3 aquaporins. Even though, transcription factor were not identified, 25 out of the 108 unigenes were among the 1000 most highly expressed genes [87].

Zygophyllum xanthoxylum is a succulent halophyte adapted to arid environments. In this plant a total of 1723 DEGs were identified as upregulated in leaves of plants under osmotic stress (−0.5 MPa) during 24 h. Up to 53 DEGs related to ROS scavenging were also identified as upregulated, most of them encoded for glutathione S-transferase (GST) and peroxidases (POD). Also, 31 DEGs homologous to transporters were upregulated in the roots under salt and osmotic stress. However, 23 DEGs related to photosynthesis were downregulated under osmotic stress [88].

Cleistogenes songorica is a C4 xerophyte widely distributed in the arid regions of Northwest China. A mining study for LEA genes identified at least 44 putative LEA proteins. They were named CsLEA1 to CsLEA44 and classified into eight subfamilies. These LEAs were characterized, and two unusual LEA stress-related domains, water stress and hypersensitive response (WHy), and LEA14-like desiccation-related proteins were detected. Most LEAs within the same family showed similar structures and properties. All the CsDehydrin proteins contained the YKS segments which are essential for keeping the capacity to adjust their conformation and maintain cellular homeostasis under stress conditions. Among the cis-regulatory elements of the LEA genes, more than three G-Boxes were registered for each *dehydrin*, *LEA_2*, and *SMP* genes and more than two MBS for *dehydrin* and *LEA_2* subfamily gene [89].

Prosopis juliflora is a species native to arid lands of Mexico and widely distributed in arid and semiarid regions of Central and South America. In this species 6874 DEGs were found under salt and drought stress. Approximately 42.6% (2932 DEGs) had homology to genes with GO annotation. Among these, 1339 DEGs were upregulated, while 1596 were downregulated. More DEGs under salt and drought stress were found in roots than those of leaves. Under drought stress, there was more upregulation than downregulation in leaves, while in roots there was more downregulation. A total of 30 unigenes were recognized as exclusively responsive to drought stress. One of these genes encoding for *Arabidopsis* ortholog ABR1 was downregulated. Two upregulated genes encoded for transcription factors involved in diminishing intracellular H₂O₂ levels. Also, three highly upregulated DEGs encoded for “pq-loop repeat family protein transmembrane family protein” which has been assigned with a potential role in stress tolerance. Many drought-responsive genes were tissue specific. For example, 1040 genes were specifically expressed in root tissues. Up to 805 genes were commonly regulated by drought and salt stress in root tissue. Upregulated genes included those coding for dehydration-responsive

protein rd22, pectinesterase-2, LEA protein, and POD. Moreover, 74 DEGs were commonly upregulated in leaf tissues and 16 were downregulated. The induced genes included pectinesterase-2, non-specific lipid-transfer protein, delta-1-pyrroline-5-carboxylate synthase, and ras-related protein rabc2a [90].

4. Conclusions

Drought stress tolerance is a complex quantitative trait that involves several mechanisms and multiple genes to produce the defense responses of the plants for dealing with environmental conditions of drought. Studies in model plants have found some of the main mechanisms, genes, and proteins that are activated upon drought stress. However, not enough studies have been carried out in plants native to arid lands. The new sequencing technologies and bioinformatic tools applied to some plants native to desert areas have allowed to identify many of the already characterized genes and proteins involved in drought stress tolerance. The most important is that this kind of studies has shown that myriads of drought-related transcripts are not characterized and may belong to novel genes. These may be part of the already known pathways of plants responses to drought or may participate in novel ways to tolerate drought, and after further studies may be used to improve drought tolerance in crops.

Conflict of interest


The authors of this work declare no conflict of interest.

Author details

Ricardo Trejo-Calzada*, Aurelio Pedroza-Sandoval, Jesus G. Arreola-Avila
and Fabian García-González
Chapingo Autonomous University, Bermejillo, Durango, México

*Address all correspondence to: rtrejo@chapingo.uruza.edu.mx

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