



American Journal of  
**Plant Physiology**

ISSN 1557-4539



Academic  
Journals Inc.

[www.academicjournals.com](http://www.academicjournals.com)

## Drought Tolerance in Crop Plants

Beatriz Xoconostle-Cázares, Francisco Arturo Ramírez-Ortega,  
Leonardo Flores-Elenes and Roberto Ruiz-Medrano  
Departamento de Biotecnología y Bioingeniería,  
Grupo Interdisciplinario de Biotecnología,  
Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional,  
Av. IPN 2508, Zacatenco 07360, México

---

**Abstract:** One of the most important constraints for agriculture is water limitation. More recently, global warming may be worsening this situation in most agricultural regions. Thus, it is quite relevant to understand the mechanisms that enable plants to cope with water deficit. Indeed, plants show a wide range of adaptations, at different levels, to drought stress. The present review describes strategies used by plants to adapt to low water potential at the physiological, biochemical and molecular levels. This review also describes several approaches carried out by breeders in order to obtain varieties of agronomically-important crops with improved drought tolerance, such as traditional breeding and those based on molecular markers for drought tolerance. Strategies involving genetic engineering are also detailed, some of which show great promise. It is concluded that a combination of the aforementioned strategies will be necessary for crop production under generalized water limitation in the near future.

**Key words:** Drought tolerance, crops, breeders, genetic engineering

---

### INTRODUCTION

Drought stress has a tremendous effect on agriculture, thus negatively influencing human activities (NOAA, 2003). During crop domestication, it is assumed that plants were selected on the basis of different traits, water limitation tolerance being unlikely one them. Historical evidence links drought with the decay of Mayan civilization from 550 to 570 A.C. (Haug *et al.*, 2003). Moreover, the study of tree rings in the United States has identified droughts occurring as early as 1220, referring the longest season in 1276, which lasted 38 years (<http://science.jrank.org/pages/2165/Drought-History.html>).

More recently, drought episodes have resulted in extensive fires in North and Central America as well as in other regions of the world; a drought in northern China in 1876 dried up crops in an extensive region, producing famine and millions of human deaths. Russia also experienced severe droughts in 1890 and 1921, the latter producing up to five million deaths in the Volga river basin. Similar disasters have occurred in India and Africa, also producing famine, contagious diseases and deaths. More recent severe droughts occurred in England

---

**Corresponding Author:** Beatriz Xoconostle-Cázares, Departamento de Biotecnología y Bioingeniería, Grupo Interdisciplinario de Biotecnología, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Av. IPN 2508, Zacatenco 07360, México  
Tel: +525557473800, +52555541335224 Fax: 52-55-57473313

(1921, 1933-34 and 1976), Central Australia (1945-72) and the Canadian prairies (1983-85). According to the World Health Organization, drought is the cause of death for about half the people who are killed by natural disasters. Drought season can be predicted; however, erratic precipitation is modulated by climate changes such as imbalance in the cycle of haste, as well as by the increase in the global temperature and the El Niño Southern oscillation. All these alterations are related directly to human activities (Hoerling and Kumar, 2003). Since, it is predicted that the world precipitation pattern will change, either heavy rain or drought are similarly expected in the long term (Allen and Ingram, 2002). Therefore, drought will continue being a problem to be solved for crop production, since water limitation causes stress in plants and limits the production of important cultivations worldwide (Boyer, 1982). Even though field transformation through technification would substantially increase crop production, economic constraints limit these advances, as water availability does.

The need for new alternatives for a sustainable agriculture (Khush, 1999), such as drought-tolerant plants, will provide a practical solution to alleviate the problem of water limitation. Most of the alternatives are based either on accelerating the selection of natural varieties or/and inserting genes from other plant varieties or species with the capacity to provide drought tolerance (CIAT, 2001; CIMMYT, 2003). To achieve this goal, the biological base for drought tolerance needs to be understood.

#### **Physiological Adaptations to Water Deficit**

In nature, terrestrial plants have already developed a number of strategies, which are genetically encoded (Monneveux and Belhassen, 1996). One of the most striking adaptations consists in accumulating water to delay or escape from the stress. In contrast, drought-tolerant plants, such as resurrection plants, are able to cope with the stress by diminishing their metabolic functions, which are resumed once water potential increases (Chandler and Bartels, 1999; Bartels, 2005). Other plants are able to maintain their biological functions at low water potentials, although with limited development (Ramanjulu and Bartels, 2002). Other strategies to limit the loss of water to air include abscisic acid-mediated regulation of stomatal closure. Stomata, highly specialized cells involved in gas exchange, can account for a high water loss through leaf transpiration; the adaptation to drought consists in stomata closure during stress (Blum, 1996). This adaptation implies the accumulation of gases such as CO<sub>2</sub>, which diminish photosynthesis (Bohnert and Sheveleva, 1998). The result is a general energy imbalance, in which a net flow of electrons occurs toward oxygen giving rise to oxygen reactive species and oxidative processes (Levine, 1999). Regarding root development, an interesting general adaptation is hygrotopism, in which roots detect a water gradient and redirect its growth towards it (Lambers *et al.*, 2000).

C<sub>4</sub>, or CAM plants, have developed a strategy to fix carbon dioxide for sugar production with a minimum loss of water. This metabolism involves nocturnal assimilation of CO<sub>2</sub>; C<sub>4</sub> plants have developed a mechanism to efficiently channel CO<sub>2</sub> to RuBisCO. They have also developed a particular leaf anatomy where bundle sheath cells have chloroplasts, besides mesophyll cells as in C<sub>3</sub> metabolism. Instead of direct fixation in the Calvin cycle, CO<sub>2</sub> is converted to a 4-carbon organic acid, with the ability to regenerate CO<sub>2</sub> in the chloroplasts of the bundle sheath cells. These cells utilize CO<sub>2</sub> to synthesize carbohydrates by the conventional C<sub>3</sub> pathway. For this process stomata are opened in the night, allowing CAM plants to colonize hot environments, as their expense of water is very low in comparison with other plants (McNaughton, 1991; Zhu *et al.*, 2008). Anatomical adaptations are observed in tolerant plants, consisting of spongy tissues, acting as water reservoirs; growth is also impaired and plants reduce their foliar area to limit evaporation (Passioura, 1996). Similar

strategies are the rolling of the leaves, floral abscission and alteration in cuticle permeability (Taiz and Zeiger, 1998). Floral induction, associated to long-distance movement of FT protein, is also modulated by water limitation during plant development (Lin *et al.*, 2007).

### **Biochemical Responses**

Adaptive responses are based on complex changes to cope with stress, mainly focused to maintain water potential in key tissues. At the cellular level, the cell membrane as well as the endomembrane system change dramatically their disposition and limit organelle function as well as cell integrity in response to the stress (Gigon *et al.*, 2004). The cell wall, considered as a physical barrier, also provides protection; although limited due to its deforming properties (Murphy and Ortega, 1995). When a cell suffers dehydration, the rigidity of the cell wall can provide mechanical protection; however, this organelle is permeable, thus allowing desiccation if a stronger stress is applied (Verslues *et al.*, 2006). A common biochemical adaptation is osmotic adjustment, which is the result of certain newly-synthesized metabolites (Yancey *et al.*, 1982; Bartels and Sunkar, 2005). These are hydrophilic highly soluble molecules, able to produce a solvation surface, that capture water molecules to be later available during water limitation. Examples of these osmolytes are amino acids, glycine-betaine, sugars and sugar alcohols, which are non-toxic molecules at high concentrations, thus not interfering with cellular metabolism. Interestingly, other hypotheses consider osmolytes may have additional functions besides turgidity maintenance, such as coping with oxidative stress by quelling reactive oxygen species (Chen and Murata, 2002; Bartels and Sunkar, 2005). Sugars accumulated under drought stress are likely to stabilize membranes and prevent membrane fusion, together with other macromolecules such as LEA proteins. Trehalose, a disaccharide, is accumulated under drought stress and functions during embryo and flower development, as well as in the regulation of carbon metabolism and photosynthesis (Phillips *et al.*, 2002; Iturriaga *et al.*, 2009). Proline is ubiquitous in nature (McCue and Hanson, 1990) and also has osmolyte properties; however, other roles have been also described such as protection of plasma membrane integrity (Mansour, 2000), a source for carbon and nitrogen (Peng *et al.*, 1996) and a reactive-oxygen scavenger (Smirnoff and Cumbes, 1989; Hong *et al.*, 2000). Glycine betaine has been also described as osmoprotectant, maintaining water equilibrium in plant organs (Chen and Murata, 2002).

### **Responses at the Molecular Level**

Drought tolerance is considered a quantitative trait, involving the participation of a complex set of genes. The studies that have established this have been performed on model plants as well as in drought tolerant species (Seki *et al.*, 2001; Ozturk *et al.*, 2002; Yang *et al.*, 2004; Way *et al.*, 2005; Montalvo-Hernandez *et al.*, 2008). When drought stress is perceived by the plant, changes in the expression pattern have been monitored, ranging from genes whose products are involved in early response such as signal transduction, transcription and translation factors; to late response genes, such as water transport, osmotic balance, oxidative stress and damage repair. (Ramanjulu and Bartels, 2002, Shinozaki and Yamaguchi-Shinozaki, 2000; Knight and Knight, 2001; Zhu, 2001). Adaptive responses are observed as a consequence of such changes, including early flowering, growth inhibition, among others (Bray, 2002); detailed drought mechanisms are described below.

### **Drought Sensing and Signal Transduction**

Although, the sensor for drought stress is still unknown, it is generally accepted that the organ with such ability is the root. The plant regulator abscisic acid (ABA) is a key

endogenous messenger mediating this stress response (Raghavendra *et al.*, 2010). Diverse hypotheses suggest that a redox imbalance could trigger the response to drought; a second possibility is changes in cell wall-membrane integrity (Kacperska, 2004). In *Arabidopsis*, two histidine kinase receptors (ATHK), belonging to the two-component family have been described as induced in early drought stress (Urao *et al.*, 1999). Additional protein kinases have been described, such as the *Arabidopsis* leucine rich protein RPK1 (Hong *et al.*, 1997) and SPK1 from *Phaseolus vulgaris* (Montalvo-Hernandez *et al.*, 2008), the most abundant transcript under drought stress. In *Arabidopsis*, SPK1 is induced by ABA, dehydration, salinity and low temperature, while its repression decreases sensitivity to ABA (Osakabe *et al.*, 2005). Since drought and salinity induce high levels of ABA, together with major changes in gene expression and adaptive physiological responses (Christmann *et al.*, 2007), it is considered that ABA has a central role in early plant response to drought. The recent discovery of the ABA receptor RCARs/PYR1/PYLs, which inactivates type 2C protein phosphatases (ABI1 and ABI) (Kang *et al.*, 2010), provides insights on ABA-dependent gene expression and ion channels. Other kinases identified as induced by stress (Conley *et al.*, 1997) are MAPKs (Jonak *et al.*, 1996), which are also induced by other abiotic factors, suggesting that reversible phosphorylation plays a key role in drought signaling (Mizoguchi *et al.*, 1996). Calcium-dependent protein kinases (CDPKs) are also induced when intra- or extracellular  $Ca^{2+}$  concentration increases, as a result of ABA-mediated stomatal closure (Schroeder *et al.*, 2001; Ramanjulu and Bartels, 2002). An important signal molecule is inositol triphosphate (ITP), a phospholipid induced by abiotic stress such as salinity, drought and cold in *Arabidopsis* (Hirayama *et al.*, 1995); in this plant, phospholipase D (PLD) is related to ABA sensing, regulating stomata opening and ion channel activity (Sang *et al.*, 2001). Drought tolerance is correlated to PLD accumulation in *Arachis hypogaea*, in contrast with susceptible plants, in which PLD accumulation is delayed (Guo *et al.*, 2006).

#### **Induced Genes at Transcriptional Level**

Plant gene expression is controlled at different levels and a significant number of drought-induced genes appear to be controlled at the transcriptional level. Massive transcriptome analyses using RNA microarrays have established that ABA-dependent and -independent signal transduction pathways operate in drought-stressed plants (Shinozaki and Yamaguchi-Shinozaki, 2000). Bioinformatics analyses have identified several Transcription Factors (TF) induced under drought stress (Bartels and Sunkar, 2005; Marcotte *et al.*, 1989; Abe *et al.*, 1997; Ashraf *et al.*, 2008; Ashraf, 2010). TF can be classified in six families: AP2/ERF (APETALA2/ethylene-response factor) (Marcotte *et al.*, 1989; Abe *et al.*, 1997), bZIP (Basic leucine-zipper protein); MYB/MYC, Zinc-finger protein (Rodríguez-Urbe and D'Connell, 2006; Abe *et al.*, 1997); CDT-1 (Furini *et al.*, 1997) and NAC families (Yamaguchi-Shinozaki and Shinozaki, 1994; Bartels and Sunkar, 2005; Umezawa *et al.*, 2006); Dreb (Stockinger *et al.*, 1997; Liu *et al.*, 1998). Considering the identification of TF through massive genomic analyses, transgenic plants expressing transcriptional activators have been developed for the production of drought-tolerant plants (Lam and Meisel, 1999).

#### **Drought-Induced Proteins**

Translational control is another mechanism regulating plant responses to abiotic stress. Synthesized proteins have direct functions in membrane and protein protection. They involve the acquisition of water and ions, as well as their transportation and homeostasis maintenance in basal cell functions. Late Embryogenesis Abundant protein (LEA) family belongs to this group and was described as highly accumulated in plant embryos

(Dure *et al.*, 1981; Galau *et al.*, 1986). LEA proteins are expressed at basal levels and can be induced to high levels during osmotic and drought stress (Ingram and Bartels, 1996; Barrera-Figueroa *et al.*, 2007). Five LEA groups have been described based on structural domains; groups 3 and 5 form dimers with a coiled-coil conformation that coordinate ions during stress (Dure *et al.*, 1989). Aquaporin (AQP) family is another example of stress-protecting proteins, facilitating water uptake and allocation by forming cellular water pores. AQP are membrane spanning proteins and can be located in plasma membrane or tonoplast (Johansson *et al.*, 2000). Differential accumulation has been shown in plant tolerant varieties (Montalvo-Hernandez *et al.*, 2008). Cold is another abiotic stress that induce AQP accumulation (Maurel and Chrispeels, 2001; Seki *et al.*, 2001) and also play an important role in plant recovery after the dehydration to resume cell growth and photosynthetic activity (Oono *et al.*, 2003).

Heat Shock Proteins (HSP), highly accumulated during stress and also known as molecular chaperones, are widely distributed in nature; they are involved in protein folding and assembly, as well as in the removal and disposal of non-functional proteins (Wang *et al.*, 2004). HSP are induced by drought and salinity (Alamillo *et al.*, 1995; Campalans *et al.*, 2001) and *in vivo* evidence suggests that HSPs prevent protein thermal aggregation (Lee *et al.*, 1995); thus facilitating the recovery of cell functions after abiotic stress. These proteins are classified according to their molecular weight: the Hsp70 family (family DnaK), the chaperonins (GroEL and Hsp60), the Hsp90 family, the Hsp 100 family (Clp) and the family of small Hsp (sHsp) (Wang *et al.*, 2004). Cyclophilin is a chaperon protein with systemic properties, involved in protein folding, highly induced during drought stress; overexpression of cyclophilin-encoding genes confers multiple abiotic stress tolerance (Gottschalk *et al.*, 2008; Sekhar *et al.*, 2010).

Turnover of damaged macromolecules in stress is a basic process to maintain cell homeostasis. An increase in cysteine protease activity has been also observed under drought conditions (Koizumi *et al.*, 1993; Seki *et al.*, 2002); polyubiquitin involved in labeling and targeting for hydrolysis in the proteasome is also up-regulated in stressed plants (Barrera-Figueroa *et al.*, 2007; Bartels and Sunkar, 2005).

### **Oxidative Stress**

One of the main effects of the dehydration in plants is the production of Reactive Oxygen Radicals (ROS) such as singlet oxygen, superoxide anion radicals, hydroxyl radicals and hydrogen peroxide (Smirnoff, 1998; Bartels, 2001). Since ROS are mainly produced in chloroplasts, the photosynthetic activity is compromised during stress; drought tolerance is unequivocally related to efficient antioxidant cellular processes (Kranter *et al.*, 2002; Montero-Tavera *et al.*, 2008). Factors participating in antioxidative activity are non-enzymatic and enzymatic (Bartels and Sunkar, 2005); among the former are vitamins C and E, glutathione, flavonoids, alkaloids, carotenoids, polyamines, etc. Enzymatic activities include catalase, super-oxide dismutase, peroxidase and metallothionein (Seki *et al.*, 2001).

The study of the molecular, biochemical and physiological mechanisms the plants employ to respond to drought stress has provided scientific knowledge for plant breeding. Despite drought tolerance being a quantitative trait, key genes can significantly contribute to ameliorate the damage produced by water limitation. A number of genetically-improved drought-tolerant crops have been developed by different approaches, such as conventional breeding, marker-assisted breeding and transgenic approach. For modern agriculture, a combination of the aforementioned techniques will likely be needed to produce new varieties showing drought tolerance in the field (Mittler and Blumwald, 2010). Regardless of the

approach, an interesting method to prove tolerance in the field was described by Salekdeh *et al.* (2009) based on yield quantification in function of the water use and harvest index.

### **Conventional Breeding**

Conventional improvement to obtain new individuals is based on their genetic variation and uses the selection to incorporate better characteristics into the progeny. For this purpose, two plants possessing desirable traits are selected and then crossed to exchange their genes, so that the offspring has new genetic arrangements. Individual plants are tested for the expression of the desirable characteristic and its maintenance in future plant generations (McCouch, 2004). In practice, drought tolerance is selected together with plant productivity; non-commercial varieties displaying drought tolerance are crossed with susceptible, higher-yield plants (McCouch, 2004; Hieng *et al.*, 2004; Lizana *et al.*, 2006).

### **Marker-Assisted Breeding**

Genetic improvement can be assisted by using recognizable tags linked to target genes; these are known as molecular markers, which are based on polymorphisms that occur naturally in the DNA sequence. Different methods are employed to detect linked markers such as RFLPs (Restriction Fragments length polymorphisms), SCARs (Sequence Characteristic Amplified Regions), the RAPDs (Random Amplified Polymorphic DNA), SSRs (Simple Sequence Repeats), AFLPs (Amplified Fragment Length Polymorphism), among others (Van Berloo *et al.*, 2008). The genetic factors responsible for part of the phenotypic variation observed for a quantitative characteristic are named QTLs (Quantitative Trait Loci). The use of molecular markers assisting the selection of new varieties has an enormous potential to accelerate this process (Asins, 2002; Ashraf and Akram, 2009; Ashraf, 2010).

### **Plant Breeding Through Genetic-Engineering**

The capacity to stably insert a wide collection of drought-related genes to plant genomes has opened amazing opportunities for crop improvement. Recombinant DNA technology as well as plant regeneration is now applicable to a significant number of crop species (Gosal *et al.*, 2009). Key genes observed as induced under abiotic stress in other plants or microorganisms have been employed to generate transgenic plants.

Below are described advances in obtaining the most important drought-tolerant crops using conventional breeding, marker-assisted breeding and genetic engineering.

### **Maize**

Based on conventional breeding, researchers in the International Maize and Wheat Improvement Center (CIMMYT) located in Mexico have developed hybrids since 1970. These show both drought tolerance and higher stable productivity, calculated in 10 to 34% over normal improved varieties, depending on the site and seasonal conditions (Bänziger *et al.*, 2006). These varieties are employed in 13 African countries: Angola, Benin, Ethiopia, Kenya, Malawi, Mali, Mozambique, Nigeria, Tanzania, Uganda, Zambia, Zimbabwe and Ghana in the frame of the project "Drought Tolerant Maize for Africa" led by CIMMYT and the International Institute for Tropical Agriculture (IITA) (Rovere *et al.*, 2009).

A number of QTLs in maize has been identified for drought response (Lebreton *et al.*, 1995; Agrama and Moussa, 1996; Sari-Gorla *et al.*, 1999; Ribaut and Ragot, 2007; Tsonev *et al.*, 2009; Chenu *et al.*, 2009); some of them also associated to plant height, flowering and yield (Feng-lin *et al.*, 2008). However, no superior varieties have been commercialized using this powerful approach. The generation of transgenic maize, based on

the expression of selective markers will positively impact the market of maize production. The transcriptomic analysis of maize under drought stress has identified a number of candidate genes to obtain cisgenic lines (Zheng *et al.*, 2010). The overexpression of the bacterial gene encoding choline dehydrogenase (Quan *et al.*, 2004) provided higher tolerance to transformed plants when compared with wild type maize.

### **Wheat**

Wheat cultivation is linked to ancient and modern history. Indeed, the grain is employed to prepare flour, broadly used to prepare bread. Half of the wheat production is carried out under water limitation worldwide (Rajaram, 2005). At CIMMYT, conventional breeding yielded polyploid plants; among them, the cross of *Aegilops tauschii* and *Triticum turgidum* var. durum provided lines with new genetic variability and drought tolerance (Valkoun, 2001). In the world, conventional breeding is performed in both public and private research centers and it is worth mentioning the International Center for Agricultural Research in Dry Areas (ICARDA) located in Syria and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India. The location of a DNA fragment regulating ABA production in the 5A chromosome was reported by Quarrie *et al.* (1994). By means of genetic engineering, transgenic bread wheat lines containing the *Arabidopsis thaliana* DREB1A under the control of the stress inducible promoter rd29a were developed at CIMMYT Mexico, displaying drought tolerance.

### **Barley**

At ICARDA, new varieties have been developed with improved tolerance when compared with progenitor lines using conventional breeding; while QTLs associated to growth parameters and abiotic tolerance have been described (Teulat *et al.*, 1997) through analysis of water content and growth parameters. Interestingly, attempts to identify drought-associated QTLs in wild barley allowed the characterization of molecular markers in recombinant inbred lines for better productivity under drought stress (Baum *et al.*, 2003).

### **Rice**

Because of the importance of this millenary crop in feeding a high proportion of the world population, it represents a milestone for breeding. The International Rice Research Institute (IRRI) is focused on this task using different approaches; they developed rice hybrids with high yield (up to 360 kg ha<sup>-1</sup>) under drought stress by conventional crosses. The identification of QTLs (Flowers *et al.*, 2000; Lafitte *et al.*, 2004; Bernier *et al.*, 2008) associated with drought, established the basis for further selection based on this approach. Levi *et al.* (2009) obtained isogenic lines based on QTL selection obtaining superior varieties. QTLs associating drought tolerance and root length have been identified (Kamoshita *et al.*, 2008), as well as markers for grain productivity. Recently, Bernier *et al.* (2009) obtained new varieties with stacked properties: drought tolerance, earlier flowering and higher productivity. In the same year, Steele (2009) generated a high tolerant rice variety based on QTLs in upland India, showing also higher productivity and superior grain quality. Genetic engineering has allowed the overexpression of genes for trehalose accumulation driven by drought-induced promoters (Wu and Garg, 2003), providing also tolerance to cold and salinity. A similar phenotype was obtained by over-expressing LEA proteins (Xiao *et al.*, 2007).

### **Cotton**

The fiber of this staple is the most widely used natural-fiber in clothing today; this plant was traditionally grown in semiarid regions and displays some tolerance to salt and drought.



Saranga *et al.* (2001) identified QTLs associated to this tolerance in commercial varieties, while Levi *et al.* (2009) characterized QTLs associated to physiological parameters present in two cotton drought-tolerant species. Genetic engineering was employed to introduce the gene that encodes the beta-endotoxin from *Bacillus thuringiensis*, thus producing insect-resistant cotton. Cotton has also been genetically modified for resistance to glyphosate; which is an inexpensive, highly effective, broad-spectrum herbicide.

### **Sorghum**

This plant is utilized for both human and animal consumption; also grown in semiarid conditions, in which selected varieties display acceptable tolerance. Sanchez *et al.* (2002) identified QTLs associated to drought tolerance; interestingly, different drought-related genomic regions were identified in vegetative and flowering stages. The stay-green phenotype, associated to drought tolerance, was associated to four QTLs (Harris *et al.*, 2007), demonstrating that maintenance of photosynthesis activity correlates to drought-tolerance.

### **Millet**

This cereal crop groups small-seeded varieties, widely grown around the world for human food and fodder; as sorghum, it has been grown in semiarid conditions and a number of tolerant lines are commercially used. Despite this, higher productivity needs to be obtained in tolerant backgrounds; for this purpose, Yadav *et al.* (2004) mapped QTLs for terminal drought and higher harvest index.

### **Soybean**

This legume native to East Asia, currently grown worldwide, is an important global crop that provides oil and protein. Soybean enriches the soil by fixing nitrogen in symbiosis with bacteria. Drought stress is a major constraint to the production and yield stability of soybean. In order to develop high yield lines under drought stress, a traditional approach has been employed over multiple locations (Manavalan *et al.*, 2009). Nineteen QTLs associated with productivity and ten with drought tolerance were mapped (Du *et al.*, 2009), thus providing the basis for further marker-assisted breeding. Soybean is a crop that has been genetically modified and it is being used in an increasing number of products. Soybeans have been genetically modified for resistance to the herbicide glyphosate, by expressing the gene EPSP (5-enolpyruvyl shikimic acid-3-phosphate) synthase. The substituted version is not sensitive to the herbicide (Padgett *et al.*, 1995). GmDREB2, a soybean DRE-binding transcription factor, was overexpressed in this crop; thus, conferring drought and high-salt tolerance to transgenic plants (Chen *et al.*, 2007).

### **Common Bean**

Considered as one of the most important cultivated plants, it serves as food for a great part of the world population (CIAT, 2001). It is estimated that bean was domesticated over 7,000 years ago in two centers of origin: Mesoamerica and the Andean region. A high genetic diversity was produced that gave rise to several traits, including drought tolerance (Beebe *et al.*, 2001; Broughton *et al.*, 2003). Among the Mesoamerican pool, the Durango race displays high abiotic tolerance, from which a number of tolerant varieties have been developed (Acosta-Gallegos *et al.*, 1995). Montalvo-Hernandez *et al.* (2008) demonstrated a correlation among the expression of drought-associated transcripts with photosynthetic parameters. Tari *et al.* (2008) analyzed contrasting genotypes under stress conditions and found a correlation between high water potential and photosynthesis with drought tolerance.

### **Concluding Remarks and Perspectives**

The generation of novel plant varieties displaying tolerance to abiotic stress is highly expected to cope with the unfavorable environmental challenges. Despite of the current knowledge on the scientific bases of drought tolerance, more information is needed to understand and be able to manipulate such complex quantitative trait. As described above, traditional breeding have provided an extense number of tolerant varieties; however new approaches are also available to obtain improved plant. The genetic engineering has already produced plants with important tolerance and is likely to be the best approach to obtain superior lines bearing abiotic tolerance, among other agronomically-important traits.

### **ACKNOWLEDGMENTS**

This study was supported in part by CONACyT to RR-M (50769), BXC (105985) and (ICyT DF to BXC (Pifutp08/147). FAR-O and LFE are CONACyT fellows. We apologize if some citations were not included, strictly due to space restrictions.

### **REFERENCES**

- Abe, H., K. Yamaguchi-Shinozaki, T. Urao, T. Iwasaki, D. Hosokawa and K. Shinozaki, 1997. Role of Arabidopsis MYC and MYB homologs in drought-and abscisic acid-regulated gene expression. *Plant Cell*, 9: 1859-1868.
- Acosta-Gallegos, J.A., R. Ochoa-Márquez, M.P. Arrieta-Montiel, F. Ibarra-Pérez, A. Pajarito-Ravelero and I. Sanchez-Valdez, 1995. Registration of 'Pinto Villa' common bean. *Crop Sci.*, 35: 1211-1212.
- Agrama, H.A.S. and E.M. Moussa, 1996. Mapping QTLs in breeding for drought tolerance in maize (*Zea mays* L.). *Euphytica*, 91: 89-97.
- Alamillo, J., C. Almogura, D. Bartels and J. Jordano, 1995. Constitutive expression of small heat shock proteins in vegetative tissues of the resurrection plant *Craterostigma plantagineum*. *Plant Mol. Biol.*, 29: 1093-1099.
- Allen, M.R. and W.J. Ingram, 2002. Constraints on future changes in climate and the hydrologic cycle. *Nature*, 419: 224-232.
- Ashraf, M.J., H.R. Athar, P.J.C. Harris and T.R. Kwon, 2008. Some prospective strategies for improving crop salt tolerance. *Adv. Agron.*, 97: 45-110.
- Ashraf, M. and N.A. Akram, 2009. Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. *Biotechnol. Adv.*, 27: 744-752.
- Ashraf, M., 2010. Inducing drought tolerance in plants: Recent advances. *Biotechnol. Adv.*, 28: 169-183.
- Asins, M.J., 2002. Present and future of QTL analysis in plant breeding. *Plant Breed.*, 121: 281-291.
- Barrera-Figueroa, B., J. Pena-Castro, J.A. Acosta-Gallegos, R. Ruiz-Medrano and B. Xoconostle-Cazares, 2007. Isolation of dehydration-responsive genes in a drought tolerant common bean cultivar and expression of a group 3 late emb yogenesis abundant mRNA in tolerant and susceptible bean cultivars. *Functional Plant Biol.*, 34: 368-381.
- Bartels, D. and R. Sunkar, 2005. Drought and salt tolerance in plants. *Crit. Rev. Plant. Sci.*, 24: 23-58.
- Bartels, D., 2001. Targeting detoxification pathways: An efficient approach to obtain plants with multiple stress tolerance. *Trends Plant Sci.*, 6: 284-286.
- Bartels, D., 2005. Desiccation tolerance studied in the resurrection plant *Craterostigma plantagineum*. *Integrative Comp. Biol.*, 45: 696-701.

- Baum, M., S. Grandol, G. Backes, A. Jahoor, A. Sabbagh and S. Ceccarelli, 2003. QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross Arta H. spontaneum 41-1. *Theor. Applied Genet.*, 107: 1215-1225.
- Beebe, S., J. Rengifo, E. Gaitan, M.C. Duque and J. Tohme, 2001. Diversity and origin of Andean landraces of common bean. *Crop Sci.*, 41: 854-962.
- Bemier, J., A. Kumar, R. Serraj, D. Spaner and G. Atlin, 2008. Review: breeding upland rice for drought resistance. *Sci. Food Agric.*, 88: 927-939.
- Bernier, J., A. Kumar, R. Venuprasad, S. Impa and R.P. Gowda, 2009. The large effect drought-resistance QTL qtl12.1 increases water uptake in upland rice. *Field Crops Res.*, 110: 39-46.
- Blum, A., 1996. Crop responses to drought and the interpretation of adaptation. *Plant Growth Regul.*, 20: 135-148.
- Bohnert, H.J. and E. Sheveleva, 1998. Plant stress adaptations-making metabolism move. *Curr. Opinion Plant Biol.*, 1: 267-274.
- Boyer, J.S., 1982. Plant productivity and environment. *Science*, 218: 443-448.
- Bray, E., 2002. Abscisic acid regulation of gene expression during water-deficit stress in the era of the Arabidopsis genome. *Plant Cell Environ.*, 25: 153-161.
- Broughton, W.J., G. Hernandez, M. Blair, S. Beebe, P. Gepts and J. Vanderleyden, 2003. Bean (*Phaseolus* sp.) model food legumes. *Plant Soil*, 252: 55-128.
- Bänziger, M., P. Setimela, D. Hodson and V. Biniganavile, 2006. Breeding for improved abiotic stress tolerance in maize adapted to southern Africa. *Agric. Water Manage.*, 80: 212-224.
- Campalans, A., M. Pages and R. Messeguer, 2001. Identification of differentially expressed genes by the cDNA-AFLP technique during dehydration of almond (*Prunus amygdalus*). *Tree Physiol.*, 21: 633-643.
- Chandler, J. and D. Bartels, 1999. Plant Dessication. In: *Plant Responses to Environmental Stresses: from Phytohormones to Genome Reorganization*, Lerner, H.R. (Ed.). Marcel Dekker, New York, USA., pp: 575-590.
- Chen, M., Q. Y. Wang, X.G. Cheng, Z.S. Xu and L.C. Li *et al.*, 2007. GmDREB2, a soybean DRE-binding transcription factor, conferred drought and high-salt tolerance in transgenic plants. *Biochem. Biophys. Res. Commun.*, 353: 299-305.
- Chen, T.H.H. and N. Murata, 2002. Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Curr. Opin. Plant Biol.*, 5: 250-257.
- Chenu, K., S.C. Chapman, F. Tardieu, G. McLean, C. Welcker and G.L. Hammer, 2009. Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize: A gene-to-phenotype modeling approach. *Genetics*, 183: 1507-1523.
- Christmann, A., E.W. Weiler, E. Steudle and E. Grill, 2007. A hydraulic signal in root-to-shoot signaling of water shortage. *Plant J.*, 52: 167-174.
- CIAT, 2001. Centro internacional de agricultura tropical. Project IP3, Improved Cassava for the Developing World, Annual Report. Apdo Aereo 6713, Cali, Colombia.
- CIMMYT, 2003. Centro internacional de mejoramiento de Maizy Trigo. [http://es.wikipedia.org/wiki/Centro\\_Internacional\\_de\\_Mejoramiento\\_de\\_Ma%C3%ADz\\_y\\_Trigo](http://es.wikipedia.org/wiki/Centro_Internacional_de_Mejoramiento_de_Ma%C3%ADz_y_Trigo).
- Conley, T.R., R.E. Sharp and J.C. Walker, 1997. Water deficit rapidly stimulates the activity of a protein kinase in the elongation zone of the maize primary root. *Plant Physiol.*, 113: 219-226.
- Du, W., M. Wang, S. Fu and D. Yu, 2009. Mapping QTLs for seed yield and drought susceptibility index in soybean (*Glycine max* L.) across different environments. *J. Genet. Genomics*, 36: 721-731.

- Dure, L., M. Crouch, J. Harada, T.D. Ho and J. Mundy *et al.*, 1989. Common amino acid sequence domains among the LEA proteins of higher plants. *Plant Mol. Biol.*, 12: 475-486.
- Dure, L., S.C. Greenway and G.A. Galau, 1981. Developmental biochemistry of cottonseed embryogenesis and germination: Changing messenger ribonucleic acid populations as shown by *in vitro* and *in vivo* protein synthesis. *Biochemistry*, 20: 4162-4168.
- Feng-lin, F.U., F. Zhi-Lei, G. Shi-bing, Z. Shu-feng and L. Wan-chen, 2008. Evaluation and quantitative inheritance of several drought-relative traits in maize. *Agric. Sci. China*, 7: 280-290.
- Flowers, T.J., M.L. Koyama, S.A. Flowers, C. Sudhakar, K.P. Singh and A.R. Yeo, 2000. QTL: Their place in engineering tolerance of rice to salinity. *J. Exp. Bot.*, 51: 99-106.
- Furini, A., C. Koncz, F. Salamini and D. Bartels, 1997. High level transcription of a member of a repeated gene family confers dehydration tolerance to callus tissue of *Craterostigma plantagineum*. *EMBO J.*, 16: 3599-3608.
- Galau, G.W., D.W. Hughes and L. Dure, 1986. Abscisic acid induction of cloned cotton Late Embryogenesis Abundant (LEA) messenger RNAs. *Plant Mol. Biol.*, 7: 155-170.
- Gigon, A., A.R. Matos, D. Laffray, Y. Zuily-Fodil and A.T. Pham-Thi, 2004. Effect of drought stress on lipid metabolism in the leaves of *Arabidopsis thaliana* (Ecotype Columbia). *Ann. Bot.*, 94: 345-351.
- Gosal, S.S., S.H. Wani and M.S. Kang, 2009. Biotechnology and drought tolerance. *J. Crop Improvement*, 23: 19-54.
- Gottschalk, M., E. Dolgener, B. Xoconostle-Cazares, W.J. Lucas, E. Komor and C. Schobert, 2008. *Ricinus communis* cyclophilin: Functional characterisation of a sieve tube protein involved in protein folding. *Planta*, 228: 687-700.
- Guo, B.Z., G. Xu, Y.G. Cao, C.C. Holbrook and R.E. Lynch, 2006. Identification and characterization of phospholipase D and its association with drought susceptibilities in peanut (*Arachis hypogaea*). *Planta*, 223: 512-520.
- Harris, K., R. Klein and J. Mullet, 2007. Sorghum stay-green QTL individually reduces post-flowering drought-induced leaf senescence. *J. Exp. Bot.*, 58: 327-338.
- Haug, G.H., D. Günther, L.C. Peterson, D.M. Sigman, K.A. Huguen and B. Aeschlimann, 2003. Climate and the collapse of maya civilization. *Science*, 299: 1731-1735.
- Hieng, B., K. Vgrinovic, J. Sustan-Vozlic and M. Kidric, 2004. Different classes of proteases are involved in the response of drought of *Phaseolus vulgaris* L. Cultivars differing in sensitivity. *J. Plant Physiol.*, 161: 519-530.
- Hirayama, T., C. Ohto, T. Mizoguchi and K. Shinozaki, 1995. A gene encoding a phosphatidylinositol-specific phospholipase C is induced by dehydration and salt stress in *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci.*, 92: 3903-3907.
- Hoerling, M. and A. Kumar, 2003. The perfect ocean for drought. *Science*, 299: 691-694.
- Hong, S.W., J.H. Jon, J.M. Kwak and H.G. Nam, 1997. Identification of a receptor-like protein kinase gene rapidly induced by abscisic acid, dehydration, high salt and cold treatments in *Arabidopsis thaliana*. *Plant Physiol.*, 113: 1203-1212.
- Hong, Z., K. Lakkineni, Z. Zhang and D.P.S. Verma, 2000. Removal of feedback inhibition of  $\Delta^1$ -pyrroline-5-carboxylate synthetase results in increased proline accumulation and protection of plants from osmotic stress. *Plant Physiol.*, 122: 1129-1136.
- Ingram, J. and D. Bartels, 1996. The molecular basis of dehydration tolerance in plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.*, 47: 377-403.
- Iturriaga, G., R. Suarez and B. Nova-Franco, 2009. Trehalose metabolism: from osmoprotection to signaling. *Int. J. Mol. Sci.*, 10: 3793-3810.

- Johansson, I., M. Karlsson, U. Johanson, C. Larsson and P. Kjellbom, 2000. The role of aquaporins in cellular and whole plant water balance. *Biochim. Biophys. Acta*, 1465: 324-342.
- Jonak, C., S. Kiegerl, W. Ligterink, P.J. Barker, N.S. Huskisson and H. Hirt, 1996. Stress signaling in plants: A mitogen-activated protein kinase pathway is activated by cold and drought. *Proc. Natl. Acad. Sci. USA.*, 93: 11274-11279.
- Kacperska, A., 2004. Sensor types in signal transduction pathways in plant cells responding to abiotic stressors: do they depend on stress intensity?. *Physiologia Plantarum*, 122: 159-168.
- Kamoshita, A., C.R. Babu, N.M. Boopathi and S. Fukai, 2008. Phenotypic and genotypic analysis of drought-resistance traits for development of rice cultivars adapted to rainfed environments. *Field Crops Res.*, 109: 1-23.
- Kang, J., J.U. Hwang, M. Lee, Y.Y. Kim, S.M. Assmann, E. Martinoia and Y. Lee, 2010. 2010. PDR-type ABC transporter mediates cellular uptake of the phytohormone abscisic acid. *Proc. Natl. Acad. Sci.*, 107: 2355-2360.
- Khush, G.S., 1999. Green revolution: preparing for the 21st century. *Genome*, 42: 646-655.
- Knight, H. and M.R. Knight, 2001. Abiotic stress signalling pathways: Specificity and cross-talk. *Trends Plant Sci.*, 6: 262-267.
- Koizumi, M., K. Yamaguchi-Shinozaki, H. Tsuji and K. Shinozaki, 1993. Structure and expression of two genes that encode distinct drought-inducible cysteine proteinases in *Arabidopsis thaliana*. *Gene*, 129: 175-182.
- Kranner, I., R.P. Beckett, S. Wornik, M. Zorn and H.W. Pfeifhofer, 2002. Revival of resurrection plant correlates with antioxidant status. *Plant J.*, 31: 13-24.
- Lafitte, H.R., A.H. Price and B. Courtois, 2004. Yield response to water deficit in an upland rice mapping population: associations among traits and genetic markers. *Theor. Applied Genet.*, 109: 1237-1246.
- Lam, E. and L. Meisel, 1999. Gene Switches and Stress Management: Modulation of Gene Expression by Transcription Factors. In: *Plant Responses to Environmental Stresses: from Phytohormones to Genome Reorganization*, Lerner, H.R. (Ed.). Marcel Dekker, New York, USA., pp: 51-70.
- Lambers, H., F. Stuart-Chapin III and T.L. Pons, 2000. *Plant Physiological Ecology*. Springer-Verlag, New York, USA., pp: 540.
- Lebreton, C., V. Lazi-Jani, A. Steed, A. Peki and S.A. Quarrie, 1995. Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. *J. Exp. Botany*, 46: 853-865.
- Lee, G.J., N. Pokala and E. Vierling, 1995. Structure and *in vitro* molecular chaperone activity of cytosolic small heat shock proteins from pea. *J. Biol. Chem.*, 270: 10432-10438.
- Levi, A., L. Ovnat, A.H. Paterson and Y. Saranga, 2009. Photosynthesis of cotton near-isogenic lines introgresses with QTLs for productivity and drought related traits. *Plant Sci.*, 177: 88-96.
- Levine, A., 1999. Oxidative Stress as a Regulator of Environmental Responses in Plants. In: *Plant Responses to Environmental Stresses: from Phytohormones to Genome Reorganization*, Lerner, H.R. (Ed.). Marcel Dekker, New York, USA., pp: 247-264.
- Lin, M.K., H. Belanger, Y.J. Lee, E. Varkonyi-Gasic and K. Taoka *et al.*, 2007. Flowering locus T protein may act as the long-distance florigenic signal in the cucurbits. *Plant Cell*, 19: 1488-1506.

- Liu, Q., M. Kasuga, Y. Sakuma, H. Abe, S. Miura, K. Yamaguchi-Shinozaki and K. Shinozaki, 1998. Two transcription factors, *DREB1* and *DREB2*, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought and low-temperature-responsive gene expression, respectively, in *Arabidopsis*. *Plant Cell*, 10: 1391-1406.
- Lizana, C., M. Wentworth, J.P. Martinez, D. Villegas and R. Meneses *et al.*, 2006. Differential adaptation of two varieties of common bean to abiotic stress. Effects of drought on yield and photosynthesis. *J. Exp. Bot.*, 57: 685-697.
- Manavalan, L.P., S.K. Guttikonda, L.S. Tran and H.T. Nguyen, 2009. Physiological and molecular approaches to improve drought resistance in soybean. *Plant Cell Physiol.*, 50: 1260-1276.
- Mansour, M.M.F., 2000. Nitrogen containing compounds and adaptation of plants to salinity stress. *Biol. Plant*, 43: 491-500.
- Marcotte, W.R., S.H. Russell and R.S. Quatrano, 1989. Abscisic acid-responsive sequences from the Em gene of wheat. *Plant Cell*, 1: 969-976.
- Maurel, C. and M.J. Chrispeels, 2001. Aquaporins. A molecular entry into plant water relations. *Plant Physiol.*, 125: 135-138.
- McCouch, S., 2004. Diversifying selection in plant breeding. *PLoS Biol.*, 2: e347-e347.
- McCue, K.F. and A.D. Hanson, 1990. Drought and salt tolerance: Towards understanding and application. *Trends Biotechnol.*, 8: 358-362.
- McNaughton, S.J., 1991. Dryland Herbaceous Perennials. In: Response of Plants to Multiple Stresses, Mooney, H.A., W.E. Winner and E. Pell (Eds.). Academic Press, Inc., USA., pp: 307-328.
- Mittler, R. and E. Blumwald, 2010. Genetic engineering for modern agriculture: challenges and perspectives. *Annu. Rev. Plant Biol.*, 61: 443-462.
- Mizoguchi, T., K. Irie, T. Hirayama, N. Hayashida and K. Yamaguchi-Shinozaki *et al.*, 1996. A gene encoding a mitogen-activated protein kinase kinase kinase is induced simultaneously with genes for a mitogen-activated protein kinase and an S6 ribosomal protein kinase by touch, cold and water stress in *Arabidopsis Thaliana*. *Proc. Natl. Acad. Sci. USA.*, 93: 765-769.
- Monneveux, P. and E. Belhassen, 1996. The diversity of drought adaptation in the wide. *Plant Growth Regul.*, 20: 85-92.
- Montalvo-Hernández, L., E. Elías Piedra-Ibarra, L. Gómez-Silva, R. Lira-Carmona and J.A. Acosta-Gallegos *et al.*, 2008. Differential accumulation of mRNAs in drought-tolerant and susceptible common bean cultivars in response to water deficit. *New Phytol.*, 177: 102-113.
- Montero-Tavera, V., R. Ruiz-Medrano and B. Xoconostle-Cazares, 2008. Systemic nature of drought-tolerance in common bean. *Plant Signal. Behav.*, 3: 663-666.
- Murphy, R. and J.K.E. Ortega, 1995. A new pressure probe method to determine the average volumetric elastic-modulus of cells in plant tissue. *Plant Physiol.*, 107: 995-1005.
- NOAA, 2003. All about droughts: National weather service. National Oceanic and Atmospheric Administration. <http://www.nws.noaa.gov>.
- Oono, Y., M. Seki, T. Nanjo, M. Narusaka and M. Fujita *et al.*, 2003. Monitoring expression profiles of *Arabidopsis* gene expression during rehydration process after dehydration using ca. 7000 full-length cDNA microarray. *Plant J.*, 34: 868-887.
- Osakabe, Y., K. Maruyama, M. Seki, M. Satou, K. Shinozaki and K. Yamaguchi-Shinozaki, 2005. Leucine-rich repeat receptor-like kinase1 is a key membrane-bound regulator of abscisic acid early signaling in *Arabidopsis*. *Plant Cell*, 17: 1105-1119.

- Ozturk, Z.N., V. Talame, M. Deyhols, C.B. Michalowski and D.W. Galbraith *et al.*, 2002. Monitoring large-scale changes in transcript abundance in drought and salt-stressed barley. *Plant Mol. Biol.*, 48: 551-573.
- Padgett, S.R., K.H. Kolacz, X. Delannay, D.B. Re and B.J. LaVallee *et al.*, 1995. Development, identification and characterization of a glyphosate-tolerant soybean line. *Crop Sci.*, 35: 1451-1461.
- Passioura, J.B., 1996. Drought and drought tolerance. *Plant Growth Regul.*, 20: 79-83.
- Peng, Z., Q. Lu and D.P. Verma, 1996. Reciprocal regulation of D1-pyrroline-5-carboxylate synthetase and proline dehydrogenase genes controls proline levels during and after osmotic stress in plants. *Mol. Gen. Genet.*, 253: 334-341.
- Phillips, J.R., M.J. Oliver and D. Bartels, 2002. Molecular Genetics of Desiccation and Tolerant Systems. In: CAB International Desiccation and Survival in Plants: Drying without Dying, Black, M. and H. Pritchard (Eds.). CAB International, New York, pp: 319-341.
- Quan, R., M. Shang, H. Zhang, Y. Zhao and J. Zhang, 2004. Engineering of enhanced glycinebetaine synthesis improves drought tolerance in maize. *Plant Biotechnol. J.*, 2: 477-486.
- Quarrie, S.A., M. Gulli, C. Calestani, A. Steed and N. Marmioli, 1994. Localization of drought-induced abscisic acid production on the long arm of chromosome 5 A of wheat. *Theor. Applied Genet.*, 89: 794-800.
- Raghavendra, A.S., V.K. Gonugunta, A. Christmann and E. Grill, 2010. ABA perception and signalling. *Trends Plant Sci.*, 15: 395-401.
- Rajaram, S., 2005. Role of conventional plant breeding and biotechnology in future wheat production. *Turk. J. Agric. For.*, 29: 105-111.
- Ramanjulu, S. and D. Bartels, 2002. Drought- and desiccation-induced modulation of gene expression in plants. *Plant Cell Environ.*, 25: 141-151.
- Ribaut, J.M. and M. Ragot, 2007. Marker-assisted selection to improve drought adaptation in maize: The backcross approach, perspectives, limitations and alternatives. *J. Exp. Bot.*, 58: 351-360.
- Rodríguez-Uribe, L. and M.A. O'Connell, 2006. A root-specific bZIP transcription factor is responsive to water deficit stress in tepary bean (*Phaseolus acutifolius*) and common bean (*P. vulgaris*). *J. Exp. Bot.*, 57: 1391-1398.
- Rovere, L., M. Sudarshan, D. John, A.M. Pedro, G. Kamala, P.H. Dave and F.V. Dagoberto, 2009. Economic and livelihood impacts of maize research in hill regions in Mexico and Nepal: Including a method for collecting and analyzing spatial data using Google Earth. <http://ideas.repec.org/p/ags/cimmis/56090.html>.
- Salekdeh, G.H., M. Reynolds, J. Bennett and J. Boyer, 2009. Conceptual framework for drought phenotyping during molecular breeding. *Trends Plant Sci.*, 14: 488-496.
- Sanchez, A.C., P.K. Subudhi, D.T. Rosenow and H.T. Nguyen, 2002. Mapping QTLs associated with drought resistance in sorghum (*Sorghum bicolor* L. Moench). *J. Plant Mol. Biol.*, 48: 713-726.
- Sang, Y., S. Xheng, W. Li, B. Huang and X. Wang, 2001. Regulation of plant water loss by manipulating the expression of phospholipase D $\alpha$ . *Plant J.*, 28: 135-144.
- Saranga, Y., M. Menz, C.X. Jiang, R.J. Wright, D. Yakir and A.H. Paterson, 2001. Genomic dissection of genotype x environment interactions conferring adaptation of cotton to arid conditions. *Genome Res.*, 11: 1988-1995.
- Sari-Gorla, M., P. Krajewski, N. Di Fonzo, M. Villa and C. Frova, 1999. Genetic analysis of drought-tolerance in maize by molecular markers. II. Plant height and flowering. *TAG Theoretical Applied Genet.*, 99: 289-295.

- Schroeder, J.I., J.M. Kwak and G.J. Allen, 2001. Guard cell abscisic acid signalling and engineering drought hardiness in plants. *Nature*, 410: 327-330.
- Sekhar, K., B. Priyanka, V.D. Reddy and K.V. Rao, 2010. Isolation and characterization of a pigeonpea cyclophilin (CcCYP) gene, and its over-expression in *Arabidopsis* confers multiple abiotic stress tolerance. *Plant Cell Environ.*, 33: 1324-1338.
- Seki, M., M. Narusaka, H. Abe, M. Kasuga and K. Yamaguchi-Shinozaki *et al.*, 2001. Monitoring the expression pattern of 1300 *Arabidopsis* genes under drought and cold stresses by using a full-length cDNA microarray. *Plant Cell*, 13: 61-72.
- Seki, M., M. Narusaka, J. Ishida, T. Nanji and M. Fujita *et al.*, 2002. Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. *Plant J.*, 31: 279-292.
- Shinozaki, K. and K. Yamaguchi-Shinozaki, 2000. Molecular responses to dehydration and low temperature: Differences and cross-talk between two stress signaling pathways. *Curr. Opin. Plant Biol.*, 3: 217-223.
- Smirnoff, N. and Q.J. Cumbes, 1989. Hydroxyl radical scavenging activity of compatible solutes. *Phytochemistry*, 28: 1057-1060.
- Smirnoff, N., 1998. Plant resistance to environmental stress. *Curr. Opin. Biotechnol.*, 9: 214-219.
- Steele, K., 2009. Novel upland rice variety bred using marker-assisted selection and client-oriented breeding released in Jharkhand India. *Plant Breed. News*,
- Stockinger, E.J., S.J. Gilmour and M.F. Thomashow, 1997. *Arabidopsis thaliana CBF1* encodes an AP2 domain-containing transcriptional activator that binds to the C-repeat/DRE, a cis-acting DNA regulatory element that stimulates transcription in response to low temperature and water deficit. *Proc Natl. Acad. Sci. USA.*, 94: 1035-1040.
- Taiz, L. and E. Zeiger, 1998. *Plant Physiology*. 1st Edn., Sinauer Associates Inc., Massachusetts, London.
- Tari, I., D. Camen, G. Coradini, J. Csiszár and E. Fediuc *et al.*, 2008. Changes in chlorophyll fluorescence parameters and oxidative stress responses of bush bean genotypes for selecting contrasting acclimation strategies under water stress. *Acta Biol. Hung.*, 59: 335-345.
- Teulat, B., P. Monneveux, J. Wery, C. Borries, I. Souyris, A. Charrier and D. This, 1997. Relationships between relative water content and growth parameters in barley: a QTL study. *New Phytol.*, 137: 99-107.
- Tsonev, S., E. Todorovska, V. Avramova, S. Kolev; N. Abu-Mhadi and N.K. Christov, 2009. Genomics assisted improvement of drought tolerance in maize: QTL approaches. *Biotechnol. Biotechnol. Eq.*, 23: 1410-1413.
- Umezawa, T., M. Fujita, Y. Fujita, K. Yamaguchi-Shinozaki and K. Shinozaki, 2006. Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. *Curr. Opin. Biotechnol.*, 17: 113-122.
- Urao, T., B. Yakubov, R. Satoh, K. Yamaguchi-Shinozaki, M. Seki, T. Hirayama and K. Shinozaki, 1999. A transmembrane hybrid-type histidine kinase in *Arabidopsis* functions as an osmosensor. *Plant Cell*, 11: 1743-1754.
- Valkoun, J.J., 2001. Wheat pre-breeding using wild progenitors. *Euphytica*, 119: 17-23.
- Van Berloo, R., A. Zhu, R. Ursem, H. Varbakel, G. Gort and F.A. van Eeuwijk, 2008. Diversity and linkage disequilibrium analysis within a selected set of cultivated tomatoes. *Theor. Applied Genet.*, 117: 89-101.
- Verslues, P.E., M. Agarwal, S. Katiyar-Agarwal, J. Zhu and J.K. Zhu, 2006. Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *Plant J.*, 45: 523-539.



- Wang, W.X., B. Vinocur, O. Shoseyov and A. Altman, 2004. Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends Plant Sci.*, 9: 244-252.
- Way, H., S. Chapman, L. McIntyre, R. Casu, G.P. Xue, J. Manners and R. Shorter, 2005. Identification of differentially expressed genes in wheat undergoing gradual water deficit stress using a subtractive hybridization approach. *Plant Sci.*, 168: 661-670.
- Wu, R. and A. Garg, 2003. Engineering rice plants with trehalose-producing genes improves tolerance to drought, salt and low temperature. ISB News Report. <http://www.isb.vt.edu/news/2003/news03.mar.html>.
- Xiao, B., Y Huang, N. Tang and L. Xiong, 2007. Overexpression of LEA gene in rice improves drought resistance under field conditions. *Theoretical Applied Genet.*, 115: 35-46.
- Yadav, R.S., C.T. Hash, F.R. Bidinger, K.M. Devos and C.J. Howarth, 2004. Genomic regions associated with grain yield and aspects of postflowering drought tolerance in pearl millet across stress environments and testers background. *Euphytica*, 136: 265-277.
- Yamaguchi-Shinozaki, K. and K. Shinozaki, 1994. A novel cis-acting element in an Arabidopsis gene is involved in responsiveness to drought, low-temperature, or high-salt stress. *Plant Cell*, 6: 251-264.
- Yancey, P.H., M.E. Clark, S.C. Hand, R.D. Bowlus and G.N. Somero, 1982. Living with water stress: Evolution of osmolyte systems. *Science*, 217: 1214-1222.
- Yang, L., B. Zheng, C. Mao, X. Qi, F. Liu and P. Wu, 2004. Analysis of transcripts that are differentially expressed in three sectors of the rice root system under water deficit. *Mol. Genet. Genomics*, 272: 433-442.
- Zheng, J., J. Fu, M. Gou, J. Huai and Y. Liu *et al.*, 2010. Genome-wide transcriptome analysis of two maize inbred lines under drought stress. *Plant Mol. Biol.*, 72: 407-421.
- Zhu, J.K., 2001. Cell signaling under salt, water and cold stresses. *Curr. Opin. Plant Biol.*, 4: 401-406.
- Zhu, X.G., S.P. Long and D.R. Ort, 2008. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass?. *Curr. Opin. Biotechnol.*, 19: 153-159.