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Water Stress and Agriculture

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1. Introduction

Climate changes and water availability cause an important impact in agriculture, food disposal and consequently in human health. According to the U.S. Census Bureau, the total population of the World is now over 7,032 billion, and all growth projections for developed and undeveloped countries show that a total of 9 million of inhabitants will be reached before 2050. As a result, the demand for food and fuel will increase significantly. How agriculture will move on to guarantee continuous provision of food for all inhabitants of the planet?

As a consequence of the population growth the scenario has changed and an increase of urban areas has occurred in the last decades. From the 50th's urban population increased from 4 to 11% in Africa, 33 to 52% in Asia, 9 to 13% in Latin America, and decreased from 38 to 15% in Europe, from 15 to 6% in Northern America. Growth forecasts for 2050 are 54, 32.5 and 6.8% increase in Asia, Africa and Latin America respectively. Increasing urban areas make less cropland available for fuel and food production. Croplands are not expanding in the same rate as population in the last half a century and salinity and desertification have also contributed to the fact that less useful areas remain proper for agriculture. According to FAO about 12% of globe's land surface is used for crop production and most of remaining world agricultural land are covered by forest and protect by environmental laws. Brazil, Bolivia, Argentina, Colombia, Sudan and Democratic Republic of the Congo retain 90% of accessible agricultural land [1].

The climate changes in agriculture and human life can be considered under different aspects: the biological effects on crop yields; the resulting impacts on outcomes including prices, production and consumption and also the impact on per capita calorie consumption and

child malnutrition [2]. In other words their effects on agriculture will induce changes in production and prices, altering economic system, crop mix, production, food demand and consumption. Unfortunately those changes are already occurring and the projections on annual mean temperature for the next 20 to 30 years point to great economic losses due to decline in productivity for cereals like maize, wheat and rice as well. It is well known that most of our important crops will decrease yield with temperature above 30°C, as they grow faster in high temperature they have less time to accumulate carbohydrates, proteins and oil. Increasing temperature will perhaps make some areas available for agriculture, but will it be enough to replace the areas that will certainly be lost?

Recently, it was discussed the physical and economic consequences of climate changes considering temperature rising in Europe over four different factors such as agriculture, river floods, coastal systems and tourism [3]. Considering four different temperature increases from 2.5 to 5.1°C and five Europe regions (Southern, Central South, Central North, British Isle and Northern). Yield change (%) would affect Southern Europe (Portugal, Spain, Italy, Greece and Bulgaria) more than any other region with temperature increase. Northern Europe (Sweden, Finland, Estonia, Latvia, and Lithuania) instead would benefit from positive yield changes. River floods are natural disasters anywhere it happens, resulting in very large economic losses due to properties and agriculture damage. An increase on river flood is expected with global warming [4]. As a consequence of increasing temperature river floods would affect 250,000-400,000 additional people in Europe in the 2080s, specially Western Europe, British Isle and Central Europe regions. All the coastal systems across Europe would suffer with people flooded. Tourism in Europe would be impacted as well. According to bed night's percentage measures the effects will be a decrease in Southern Europe and an increase in all other areas such as Central and Northern Europe. But not only temperature would have importance to agriculture, fluctuation in seasonal precipitation is also extremely relevant and as well as increasing evaporation rates [3].

The effects of climate change on rainfed and irrigated crops for developing and developed countries were also discussed [2]. Percentage change in yield for irrigated and rainfed crops like maize, rice and wheat were analyzed using Decision Support System for Agrotechnology Transfer (DSSAT) crop-simulation model with and without CO₂ fertilization in 2050 scenario. The observed effects on rainfed were attributed to changes in temperature and precipitation index, while for irrigated areas the effects were only related to temperature variation. In general, yields in developed countries were less affected than those in developing countries, where for most crops without CO₂ fertilization the yield declines. The stress imposed by climate changes on agriculture will certainly intensify the disparities among regions.

Nevertheless, prices for major grain crops like rice, wheat, maize and soybean will increase up to 60 to 70 %, over the next few years, even without climate changes. Bearing in mind the predicted weather changes an additional of 32 to 37% for rice, 52 to 55% for maize, 94 to 111% for wheat and 11 to 14% for soybean can be expected [2].

2. Physiological aspects of water stress

It is well known that plant growth and development can be affected by abiotic agents such as salinity, high temperatures, radiation, flood and water deficit. Exacerbate action of those environmental conditions can led to great losses in productivity due to crop stress. When subjected to water deficit plants go through a cascade of metabolic alterations started with reduction in photosynthetic pigments concentration. Physiological mechanisms of plant response to water stress are summarized in Figure 1. Facing a water deficit situation plant responses can be species/genotype specific, under rehydration after a mild water deficit almost every plant can return to normal growth, but if the stress intensity was moderated or severe some will not recover at all.

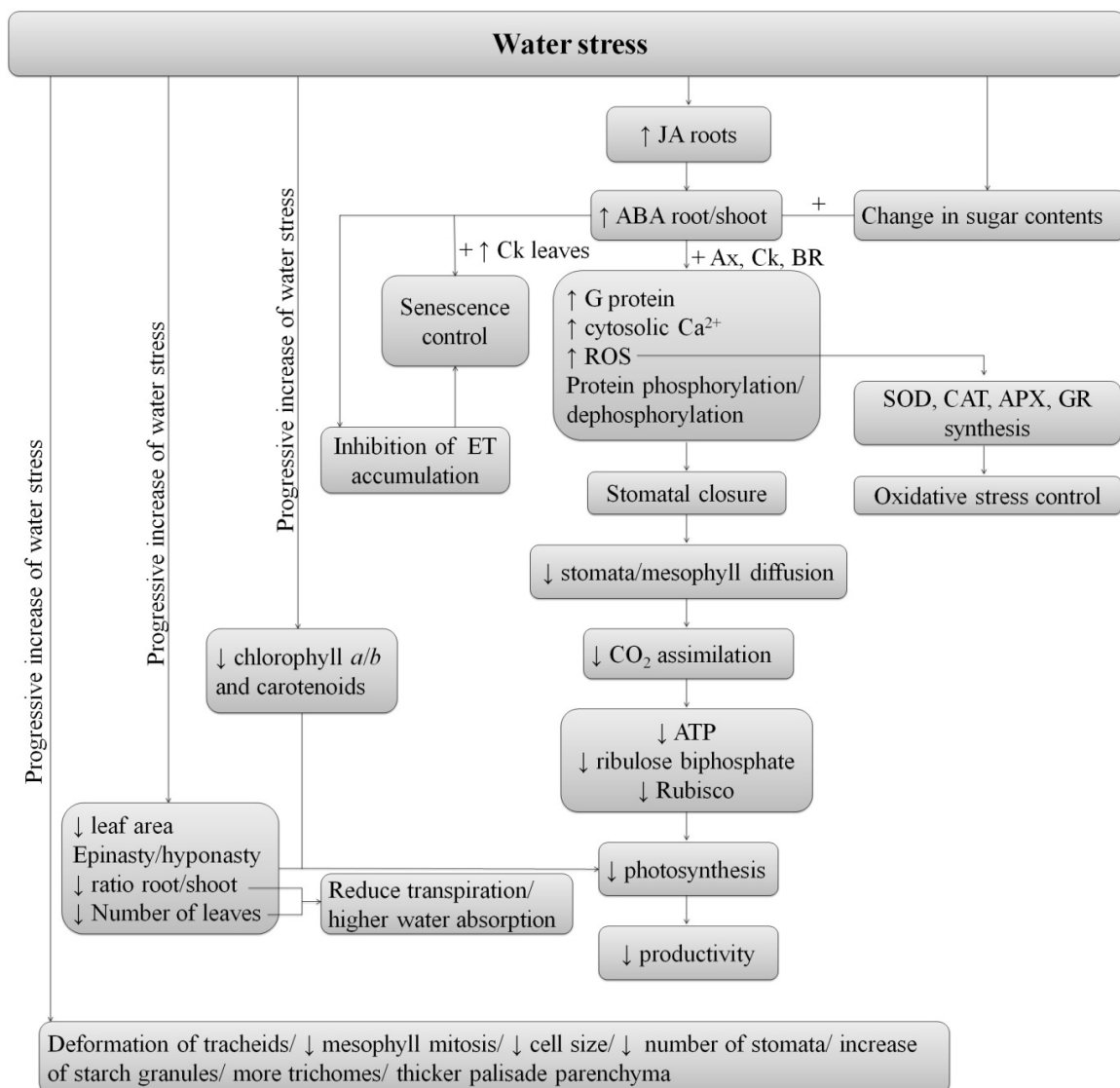


Figure 1. Physiological mechanisms induced by water stress.

2.1. Photosynthetic responses

One of the significant alterations responsible for reduction in crop productivity is low photosynthetic ability. The water stress may cause decrease in CO₂ assimilation in the leaves, the amount of ATP and the level of ribulose biphosphate [5-8]. Stomatal closure limiting diffusion through stomata and mesophyll is one of the first events in plants response under water deficit situation with consequent increase of the Rubisco enzyme, responsible for CO₂ fixation, in order to overcome the low conductance [9-13]. However, some species (*Gossypium barbadense*, *Hypericum balearicum*) show, instead, a decrease in Rubisco activity [13-15]. Furthermore the decrease in CO₂ concentration will induce a reduction in the dynamic of the carboxylation process [8].

The electron transport in thylakoids and the use of trioses phosphates are also reduced in the stress biochemical control therefore, the net photosynthetic rate tends to be lower. It has been proved that in plants subjected to water stress the photochemical efficiency of photosystem II (PSII) and quantum generation is reduced [6, 15-17]. Alterations in the level of photosynthetic pigment were also detected in water stressed plants; showing reduced or even no pigmentation. Both chlorophyll *a* and *b* declines in stressed plants and this directly affect plant biomass production. The reduction of photosynthetic pigments will drive a cut down in energy consumption and carbon demand for chlorophyll synthesis [8, 11, 17, 18]. Other pigments such as carotenoids, which play essential role in the antioxidant defense system under stress conditions, can function as an accessory pigment for photosynthesis although, their concentration can also be reduced as part of plant response [8, 17, 19, 20].

2.2. Sugar and Reactive Oxygen Species (ROS) protection

Changes in the content of carbohydrates such as sucrose and raffinose, together with the unbalanced of plant hormones function as a signal that plant response to stress should be initiated [21]. Raffinose has been correlated to a plant tolerance to desiccation, possibly involved in the protection against ROS that are responsible for loss of membrane integrity and cellular death [22, 23]. Moreover, induction of sugar accumulation, i. e, sucrose, fructose, maltose and inositol is relevant for the osmoprotection process and has been associated to plant tolerance to water stress [22].

2.3. Hormonal regulation

It is well known that hormones play a special role in plant reaction to water stress conditions. The abscisic acid (ABA) is the main hormone correlated to water stress. Plants exposed to drought substantially increase the level of ABA in shoots and roots [24-26], and the ABA positive regulators induce plant response as G protein activation, ROS production, increase in cytosolic Ca²⁺, protein phosphorylation and dephosphorylation events and immediate stomatal closure [27, 28]. Actually the balance of positive and negative ABA regulators actions command the resistance or sensitivity to water scarcity situation. However, the regulation of stomatal closure occurs not only due the action of ABA, but by the integrated hormonal balance between ABA, Auxin (Ax) and Cytokinin (Ck) [21]. Along with Ck, ABA

plays a role in controlling senescence [29, 30]. The high concentration of ABA possibly prevents excessive accumulation of ethylene (ET), thus indirectly maintaining the growth of roots and shoots [31, 32].

ABA seems to be also involved in remobilize carbon to accelerate grains filling in rice and wheat [29, 30, 33]. The ABA increased level also induce ROS production and in order to prevent the oxidative stress, antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) are immediately activated [34, 35]. The importance of regulating ABA contents as a stress signaling was also observed in rice leaves when, after a water stress period, plants were rehydrated; decreasing ABA content occurred a reduction on ROS, CAT and SOD [36].

Wheat and maize plants submitted to a moderate water deficit exhibit an increase in ET concentration [27, 37] that would be partly responsible for decreasing growth rates. In contrast for beans, cotton and miniature rose it has been shown that the rate of ethylene production is not affected during progressive drought [27]. ET is also involved in ROS production and antioxidant enzymes synthesis [23].

Cytokinins are generally involved in root and shoot development, but it has been shown an increased cytokinin concentration in leaves, from roots translocation, in plants submitted to water deficit [24, 29, 38]. Bentgrass transgenic plants expressing the enzyme adenine isopen-tenyl phosphotransferase for Ck synthesis ligated to a senescence-activated promoter (SAG12), resulted in increases in Ck accumulation in the leaves and roots and in the overall plant tolerance to water stress [39].

The gibberellins (GA), Ax and brassinosteroids (BR) do not seem to have a direct involvement with water stress, however, the accumulation of GA in some dicots has been reported and also the BR along with ABA regulate the development and function of stomata [27]. In contrast in monocots such as maize, there is a decrease in the levels of GA in leaves [25, 27]. The Ax content in plants seems to decrease in roots and leaves under stress, but the importance of auxin in water stress response remains inconclusive [24, 25, 27, 40].

The JA instead seems to play a role in the biosynthesis of ABA in water stress. In citrus plants, for example, drought causes an increase of JA concentration in roots with subsequent increase in the concentration of ABA. One can conclude that JA is possibly the precursor in the signal transduction cascade in case of drought stress, providing increased levels of ABA which, in turn, induce later responses [41].

2.4. Morphological and anatomical modifications

All the known morphological changes that occur in plants under water deficit can be associated to hormone actions. Plants develop more roots in order to access more water, increasing the ratio root/shoot, reduce leaf number and leaf area to lower transpiration rates what leads, unfortunately, to a decrease in photosynthetic rates and biomass production [20, 26, 42] and develop the epinasty/hyponasty effects [43]. The increase of apoplastic pH in the elongation of leaf area could be the responsible for the foliar reduction [44]. The number of lateral seedling roots [17] as well as the stem length can also be affected [20].

The deformation of tracheids in the xylem due to the decrease in osmotic potential [45], the reduction of mitotic activity of mesophyll cells [46], the increase of starch granules in chloroplasts [17, 47] and trichome production, as well as the decrease in cell size and number of stomata per leaf, the thickness of palisade parenchyma are anatomical changes resulting from water stress [7].

2.5. C₃ and C₄ responses

The response to water deficit may vary from species C₃ i.e. *Triticum aestivum* and *Panicum bisulcatum* and C₄ i.e. *Zuloagaea bulbosa* and *Zea mays*. Although in the oxidative stress the production of hydrogen peroxide seems to be higher in C₃ plants, the C₄ plants are much more sensitive to water stress mainly due to stomatal closure and non-stomatal factors such as decreased activity of photosynthesis enzymes, the induction of premature senescence and changes in leaf anatomy [48-50].

3. Plant biochemical mechanisms to face water stress

Drought stress and its detrimental effects on plants in both natural and agricultural environments are receiving increasing attention in order to discover alternative solutions to enhance plant vigor and high tolerance; to maintaining crop yields under adverse or extreme climate conditions overcoming economic losses.

3.1. Drought effects: Two sides of the coin

Contrasting with the negative environmental aspects caused by water stress, the adverse effects on agriculture affecting plant growth and crop productivity can be mitigated by metabolic changes which invigorate the plant biosynthesis of natural products with widespread use by the pharmaceutical, energy and food industries.

3.2. Protective role of secondary metabolites in the plant response and tolerance to water stress

Plant defense response and tolerance to drought and salinity involves the perception of signal stress by receptors at the membrane level followed by signaling transduction in the cell, inducing a multiplicity of biochemical mechanisms involved in the protective role of secondary metabolites. Water stress reduces plant growth, so the carbon fixed during photosynthesis could be used to form secondary metabolites as established in several studies. Restrictions of water supply to plant bring about the production of a complex variety of secondary metabolites which level can be modulated through biochemical and genetic manipulation. Water stress induce the accumulation of reactive oxygen species (ROS), resulting in oxidative stress in the plant cells. Thus, antioxidant secondary metabolites, able to scavenger and detoxify ROS by the availability of –OH, –NH₂, and –SH groupings, as well as aromatic nuclei and unsaturated aliphatic chains,

can play important role in protecting plant species against oxidative stress caused by water deficit. It is well known that terpenoids possess antioxidative properties. Volatile isoprenoids accumulated in *Hevea brasiliensis* were thought to be involved in scavenging ROS and potentially in protecting this species against oxidative stress [51].

Similarly, drought stress markedly enhanced the total concentrations of monoterpenes and resin acids in the main stem wood of Scots Pine and Norway Spruce Seedlings [52]. Results of investigations conducted on the effect of water deficit imposed to potted *Prunella vulgaris* L. a Chinese plant of medicinal and industrial importance, demonstrated increased levels of the phenolic triterpenes rosmarinic acid, ursolic acid and oleanolic acid [53]. Drought also caused increased accumulation of phenolic compounds (ferulic acid) in the leaves of triticale seedlings [54] and enhancement of total phenolic contents of *Trachyspermum ammi* leaves [55]. Investigation conducted with water-stressed cucumber (*Cucumis sativus* L.) demonstrated that adverse effects of water stress can be minimized by the application of melatonin which promotes activities of the ROS scavenging enzymes, i.e., superoxide dismutase, peroxidase, and catalase; significantly reduced chlorophyll degradation and stimulates root generation and vitality [17].

Polyamines (PAs) are low molecular weight polycations that have been implicated in a wide range of biological processes in plant growth and development, including environmental stress. The major PAs occurring in plant cells are the diamine putrescine (PUT), triamine spermidine (SPD) and tetramine spermine (SPM). Among the important roles attributed to those plant polyamines are: membrane stabilization and free radicals scavenger action. Polyamine mediated regulation of the water deficit stress response of soybean seedlings was investigated using exogenous applications of polyamines and their biosynthetic inhibitors. The exogenous supply of PUT, SPD and SPM to soybean seedlings resulted in reduction of the stress injury in roots which showed increased length and water content over non-treated stressed controls. Moreover, up to 40% increase of shoot growth was observed in seedlings supplemented PUT, SPD and SPM in comparison with controls. In contrast, in the presence of polyamines inhibitors the stress injury intensified, growth was severely inhibited, and water content of roots was significantly decreased. Overall results suggested that polyamines are potentially useful to overcome the detrimental effects of drought [56].

Water stress is also known to increase the secondary metabolite production in a variety of medicinal plants. Increase of hypericin and betulinic acid levels upon *Hypericum brasiliense* Choisy exposure to drought represents an antioxidant response to ROS production [57, 58]. *Artemisia annua* plants tolerate well water deficit treatments showing increased accumulation of artemisinin, a potent anti-parasitic drug, as proved in greenhouse experiments. The authors suggested that artemisinin could be part of *A. annua* chemical system of defense against water deficit [59]. Pharmacologically active terpene indole alkaloids production is stimulated in Apocynaceae species in response to water deficit. Comparing *Catharanthus roseus* drought stress plants with well watered controls it was observed significant enrichment in the antihypertensive drug ajmalicine suggesting that the production of this class of secondary metabolite can be upgraded during drought stress *C. roseus* plants [60].

The main physiological and biochemical known mechanisms triggered by water stressed plants are illustrated in Figure 2.

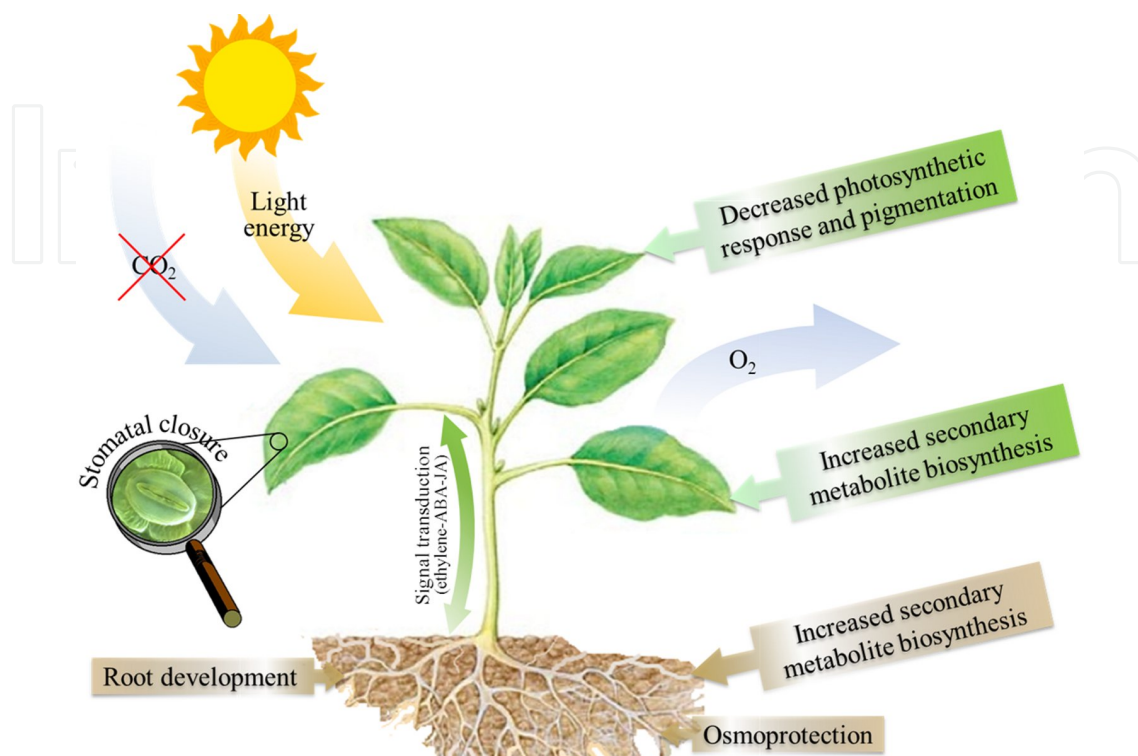


Figure 2. Plant global response to cope with water deficit, high temperature and salinity.

3.3. Sustainable exploitation of cultured drought-resistant plants

3.3.1. Oilseed crops: Biofuel production

Recently, considerable attention has been given to biofuels as an alternative to fossil fuels and the challenge is to find oil bearing plants that produce non-edible oils as the feedstock for biodiesel production. *Jatropha* (*Jatropha curcas* L.) popularly known in Brazil as “pinhão manso” is a drought resistant perennial tree widespread in arid, semi-arid and tropical regions of the world and requires a minimum rainfall of 250 mm [61]. Native grown in marginal and waste lands is one of the potential plant species to be exploited as a new source of oil for biodiesel production. *Jatropha* represents great promise to the energy economy of developing, as well as developed countries. It has been reported that new and large markets for biodiesel demand are expected to emerge in China, India and Brazil [62]. In those countries farmers have started to produce *Jatropha* for biodiesel production. The *Jatropha* seed is particularly suitable for biodiesel production because it can be harvested in the third year of plantation five or six times annually. Diesel consumption in Brazil is about 40 billion liters per year, providing huge opportunities for biodiesel production, and it is estimated that by 2013 the biodiesel market will be approximately 2 billion liters [63].

Besides the oil production, *Jatropha* species are source of jatrophone and jatropholone, macrocyclic diterpenoids, secondary metabolites that display varied pharmacological activities [64, 65].

3.3.2. Quinoa

Based on the high quality of the oil, and on the fact that some varieties show oil concentrations of up to 9.5%, quinoa could be considered as a potentially valuable new oil crop [66].

Quinoa is currently grown for its grain in the South American countries of Peru, Bolivia, Ecuador, Argentina, Chile and Colombia. Quinoa populations display a high degree of genetic distancing, and variable tolerance to salinity. Cultivars of quinoa can be adapted to growth from sea level to an altitude of 4,000 m, from 40°S to 2°N latitude, and from the cold highland climate to subtropical conditions, i.e. quinoa plant is cold and drought tolerant. The plasticity of quinoa biochemical response to a wide range of environmental conditions makes it possible to select, adapt, and breed cultivars [67]. Studies have shown that quinoa is a very good source of antioxidants and it can be a substitute for common cereals [68, 69]. The content of total phenolic compounds and the correlated radical scavenging activity of quinoa varieties have been analyzed. There were significant differences between the varieties and the content of total polyphenols [70]. Moreover, the saponins obtained as a by-product in the processing of quinoa grain can be utilized by the cosmetics and pharmaceutical industries.

3.3.3. Cotton

Polyphenols and carotenoids compounds with reactive oxygen species (ROS)-scavenging ability biosynthesized in drought tolerance Cotton genotypes were correlated to the drought tolerance of this important crop [71].

4. What have been done?

In order to cope with the major environmental problems that affect crops such as drought, salinity, cold and heat shock, genetic engineering and breeding techniques have become fundamental tools, as they have been for decades regarding biotic stresses, pests and diseases resistance. It is well known that very often an adversity results in another unfavorable condition for the development of a crop, for example high temperatures provoke water deficit reducing soil moisture resulting in salinity problems and desertification.

Biotechnological approaches focused on secondary metabolism pathways induction or repression at the transcriptional level are now being conducted to significantly improve plant tolerance to water deficit, extreme temperatures and ion imbalance.

4.1. Breeding crops

Considering all climate changes that the planet is going through it is vital the development of crops with high efficiency in water recovery and consequently tolerance to water stress,

higher temperatures, salinity and desertification. Through conventional breeding methods and selection based in progeny tests it was possible to obtain stress resistant varieties [72], but it has to be considered that instability of genotypes in different environments may affect the cultivars agronomic performance.

Researchers consider that genetic improvement for stress tolerance can be achieved in two ways: directly, through the evaluation of primary features in the target environment, i.e. as productivity (empirical breeding); or indirectly (analytical breeding), through secondary characteristics related to stress adaptation observed in crops growing in limiting environment. Over the past 50 years genetic improvement have been carried out empirically, however, this type of traditional selection has not presented significant efficiency in terms of productivity, requiring the support of indirect selection [73]. The selection of genotypes with promising agronomic characteristics and tolerant to abiotic stresses demands successive seasonal evaluations of field cultures conducted in different locations, and under influence of stress agents, requesting arduous and extensive work.

Furthermore, it is important to highlight that the low heritability of complex traits have limited the development of tolerant cultivars due to significant $G \times E$ interaction and the QTL-by-environment interaction ($QTL \times E$), and the trivial understanding of the physiological parameters related to the genetic yield potential in dry environments [73]. Biotechnology plays an important role for managing abiotic stress, allowing the exploitation of large germplasm collections with no need of experimental procedures under unfavorable environmental conditions [74].

4.2. Which genes are involved in plant responses?

Lately, much has been done to identify and isolate drought-induced genes in order to investigate the role those gene products play and the paths for induction of those genes [75, 76]. Gene expression in response to water stress can enhance the plant's ability to respond appropriately to the deleterious effect of drought, stimulating its aptitude to survive desertification [77]. In general, the stress-induced gene products can be classified in two ways: genes that directly protect the plant against stress and genes that regulate the expression of other genes [78, 79].

Through analysis of transcripts it was observed that the genes exhibit distinct expression profiles, being that stress-induced gene decrease mRNA levels when the plants are freed from stress conditions. However, the expression patterns of those genes are complex, with some genes responding very quickly to water deficit while others answer very slowly after the accumulation of ABA (abscisic acid) [80].

The differential gene expression analysis of two sugar cane cultivars, tolerant and sensitive to drought, showed that the number of genes expressed in the sensitive cultivar increased with the severity of the drought. Comparing the gene expression profiles 91 common genes were found among both cultivars, most of them drought-induced genes that are still unknown. Moreover, genes of important pathways related to drought stress were suppressed in sensitive plants. It was evidenced that plants submitted to the same water conditions re-

sponded differently to stress. Morphological changes occurred, but some genes may represent the difference between tolerance and sensitivity, as the S-adenosylmethionine decarboxylase (SAMDC) and induced cinnamoyl-CoA reductase (CCR) in resistant cultivars or lipid transfer protein that have been repressed, as well as other genes [81].

The expression of some sugarcane water-stress related genes and their association with sucrose accumulation was also investigated and a group of stress-induced genes that could be associated with sucrose accumulation were identified, showing that genes associated with the synthesis of proline are associated with stress and sucrose accumulation. Stress-related transcription factors and sugar transporter also play a role in sucrose accumulation [82].

For better understanding the processes and genes involved in water deficit tolerance it is required a full knowledge of the molecular principles that regulate plant responses to stress conditions. Thus, studies with model plants stand for and will continue to represent a relevant strategy for the elucidation of signaling and transcription processes using molecular genetics techniques [79, 83].

Genes isolated from several cultured species have been the focus of researches using gene expression in model plants with the objective of elucidating their direct effect on abiotic stress tolerance. Genetic transformation of plants in order to increase resistance is often based on the manipulation of genes to preserve the function and structure of cellular components [84]. In this context, the genetic engineering techniques for pest and herbicide resistance differ from the procedures for abiotic stress tolerance, since the first is a monogenic trait, more easily manipulated. In contrast, tolerance to environmental stresses may associate more than one of the genes involved in different signaling pathways.

The expression of *SPCP2* that encodes the putative papain-like cysteine protease isolated from senescent leaves of sweet potato has been studied in transgenic *Arabidopsis* plants subjected to stress conditions and has shown very interesting results. Firstly, changes in phenotypic characteristics were noted, such as alterations in the development of seeds and silique resulting in greater incompatibility and lower production and seed germination. Furthermore, *SPCP2* gene expression caused early transition from vegetative to reproductive stage and foliar senescence, indicating that the gene is associated with senescence. Results also indicated that the gene expression was induced by darkness, ethephon, abiscisc acid (ABA) and jasmonic acid (JA). However, tolerance to salinity and drought stress was increased [85].

4.2.1. Signaling genes

Many of these genes encode proteins involved in signaling pathways, including protein kinases mitogen-activated (MAPKs), histidine kinases, protein kinase Ca^{2+} dependent (CDPKs), family SOS3 sensors Ca^{2+} as well as transcription factors [86, 87].

The association of three genes *SRK2D*, *SRK2E* and *SRK2I* in ABA signaling and in water stress tolerance, since their gene products were found to be involved in ABRE-protein phosphorylation (ABA responsive element) and ABA signaling during germination and root development and at stomatal level was reported [88]. Genetic transformation and genetic

crosses carried out to obtain double and triple mutants of *Arabidopsis* plants subsequently subjected to drought tolerance bioassay, showed that only the triple mutant plants (srk2d/e/i) died after seven days of water suppression, while all other mutants and wild type plants survived to maturity after rehydration. Obtained results suggest that the triple mutation completely blocks the ABA signaling and greatly affect the expression of various ABA/stress-responsive genes previously identified. Moreover, many osmotic stress marker genes (*KIN2*, *RD20*, and *COR15A RD29B*) are regulated by transcription factors that are controlled by protein kinases SRK2D/E/I that can act on ABA dependent and independent pathways in response to water stress.

Transgenic sugarcane plants overexpressing heterologous *P5CS* genes, responsible for the production of proline a protein commonly induced under stress conditions, revealed tolerance to severe water deficit, not as a mediator of osmotic adjustment, but as a component of the antioxidant defense system [89].

In the same way, after detecting the up-regulated expression of two maize putatives PIS in response to drought, one of them, the *ZmPIS* gene was over-expressed in tobacco plants showing to enhance drought tolerance, since it increased the membrane integrity and decreased the solute loss. The PIS gene is involved on the synthesis of phosphatidylinositol, an important lipid that functions as a key membrane constituent [90].

Remarkable results were observed with the *Arabidopsis* vacuolar pyrophosphatase gene (*AVP1*) over-expressed in cotton, which improved drought and salt tolerance in greenhouse conditions, and also increased fiber yield in dry land field conditions. Moreover, it was observed larger root systems and enhanced shoot biomass compared to controls when cultured under saline or reduced irrigation conditions [91].

4.2.2. Transcriptional factors genes

Transcription factors (TFs) have been extensively studied and have shown to be important in the regulation of stress tolerance in plants. The TFs are proteins that play a role in physiological and biological processes such as growth, development and responses to environmental stresses acting as key regulators involved in early stages of expression, gene regulation, signal transduction [92].

The TF *MYB15*, a member of the *Arabidopsis* *R2R3 MYB* family showed interesting results in studies carried out with *Arabidopsis* transgenic plants over-expressing the gene. It was found that the *MYB15* positively regulated tolerance to drought and salinity, inversely to what was observed in studies of freezing tolerance. Furthermore, the *MYB15* gene was found to be induced by treatment with ABA and salinity and drought conditions [83].

In *Oriza sativa* [93] reported that the gene *TSRF1* TF, a protein ERF (ethylene-responsive factor), when overexpressed increased drought and osmotic tolerance of transgenic rice plants, without affecting plant development. It also increased the sensitivity to ABA treatment, increased the content of proline and soluble sugars and the expression of genes related to responses to stress and photosynthesis. Curiously, in previous studies, the authors observed

that *TSRF1* increased resistance to pathogens in tomato and tobacco plants, but reduced osmotic tolerance in tobacco.

The *sodERF3* another sugarcane TF, was also characterized, after *in silico* analyses of sugarcane cDNA sequence and the similarity of its 201 aa encoded proteins of the superfamily of ERF transcription factors was confirmed. A bioassay revealed that transgenic tobacco plants expressing the gene *sodERF3* showed to be tolerant to drought and osmotic stress. Furthermore, it was observed the gene induction in response to salt stress injuries and treatment with ABA [94].

Additionally, the soybean *GmERF3* TF from the AP2/ERF family was evaluated in transgenic tobacco plants and promoted tolerance to drought, salinity and disease. Furthermore, the gene expression was induced by salinity, desertification and treatments with salicylic acid (AS), ethylene (ET), JA and ABA. However, the cold stress did not affect gene expression. Thus, it is possible to assume that the *GmERF3* transcription factor plays a role in the responses to biotic and abiotic stresses [95].

It is evident the relevance of studying and elucidating the role of genes putatively related to water stress tolerance. In this context the molecular biology and the plant biotechnology comprise an efficient and helpful tool to achieve cultivars tolerant to environmental stresses that are gradually responsible for production losses all over the world.

4.2.3. Genetic modified crops using genetic engineering

Currently private companies have invested heavily in biotechnological programs for liberation of cultivars tolerant to insects, herbicides and drought. GMOs have been commercially cultivated since the 90's, tolerance to herbicides and insects are the main features of GM crops, including maize, soybean, cotton, canola, rice, tomato, etc. Some crops that has been transformed using genetic engineering technology to receive genes which metabolic function are related to water stress response are listed in Table 1. Genes involved in osmoprotection, ABA responsive elements and Transcription factors have been used to generate more resistant plants. Soybean, maize, rice, cotton and tomato are the most denoted transgenic crops.

Gene	Gene function	Metabolic Functions	Specie	References
<i>adc</i>	Arginine decarboxylase	Reduced chlorophyll loss under drought stress	<i>Oryza sativa</i>	[96]
<i>Adc</i>	Polyamine synthesis	Drought resistance	<i>Oryza sativa</i>	[97]
<i>badh-1</i>	Betaine aldehyde dehydrogenase	Maintenance of osmotic potential	<i>Solanum lycopersicum</i>	[98]
<i>badh-1</i>	Betaine aldehyde dehydrogenase	Salinity tolerance	<i>Daucus carota</i>	[99]

Gene	Gene function	Metabolic Functions	Specie	References
<i>betA</i>	Choline dehydrogenase (glycinebetaine synthesis)	Drought resistance at seedling stage and high yield after drought	<i>Zea mays</i>	[100]
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	Tolerance to stress induced photo inhibition	<i>Brassica juncea</i>	[101]
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	Increased tolerance to salinity and cold	<i>Oryza sativa</i>	[102]
<i>codA</i>	Choline oxidase (glycine betaine synthesis)	Recovery from a week long salt stress	<i>Oryza sativa</i>	[103]
<i>cox</i>	Choline oxidase (glycine betaine synthesis)	Salt and stress tolerance	<i>Oryza sativa</i>	[104]
<i>gs2</i>	Chloroplastic glutamine synthetase	Increased salinity resistance and chilling tolerance	<i>Oryza sativa</i>	[105]
<i>mt1D and GutD</i>	Mannitol-1-phosphate dehydrogenase & glucitol-6-phosphate dehydrogenase	High salt tolerance due to mannitol and glucitol accumulation	<i>Pinus taeda</i>	[106]
<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase (mannitol synthesis)	Drought and salinity tolerance of calli and plants	<i>Triticum vulgare</i>	[107]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Osmotic adjustment and drought Resistance	<i>Citrus</i>	[108]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Salinity tolerance	<i>Solanum tuberosum</i>	[109]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Increased biomass production under drought and salinity stress	<i>Oryza sativa</i>	[110]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Reduced oxidative stress under osmotic stress	<i>Oryza sativa</i>	[111]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Drought resistance, high RWC, high proline	<i>Glycine max</i>	[112]
<i>p5cs</i>	Pyrroline carboxylate synthase (proline synthesis)	Drought resistance via antioxidant role of proline	<i>Saccharum spp.</i>	[89]

Gene	Gene function	Metabolic Functions	Specie	References
<i>sst/fft</i>	Fructan accumulation	Reduced proline accumulation at low water status	<i>Solanum tuberosum</i>	[113]
<i>tpsp</i>	Trehalose synthesis	Drought, salt and cold tolerance	<i>Oryza sativa</i>	[114]
<i>tps1</i>	Trehalose synthesis	Drought, salt and oxidative stress Tolerance	<i>Solanum lycopersicum</i>	[115]
<i>hva1</i>	Group 3 LEA protein gene	Delayed wilting under drought stress	<i>Avena sativa</i>	[116]
<i>hva1</i>	Group 3 LEA protein gene	Salinity tolerance in yield/ plant	<i>Avena sativa</i>	[117]
<i>hva1</i>	Group 3 LEA protein gene	Dehydration avoidance and cell membrane Stability	<i>Oryza sativa</i>	[118]
<i>hva1</i>	Group 3 LEA protein gene	Drought and salinity tolerance	<i>Oryza sativa</i>	[119]
<i>hva1</i>	Group 3 LEA protein gene	Increased biomass and WUE under stress	<i>Triticum vulgare</i>	[120]
<i>hva1</i>	Group 3 LEA protein gene	Improved plant water status and yield under field drought conditions	<i>Triticum vulgare</i>	[121]
<i>OsLEA3-1</i>	Lea protein	Drought resistance for yield in the field	<i>Oryza sativa</i>	[122]
<i>rwc3</i>	Aquaporin overexpression	Maintenance of leaf water potential and transpiration under 10 h PEG stress	<i>Oryza sativa</i>	[123]
<i>atnhx1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Salt tolerance in photosynthesis and yield	<i>Gossypium hirsutum</i>	[124]
<i>atnhx1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Salt tolerance, growth, fruit yield	<i>Solanum lycopersicum</i>	[125]
<i>atnhx1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	Salt tolerance for grain yield in the field	<i>Triticum vulgare</i>	[126]
<i>hkt1</i>	Potassium transporter	Salt tolerance in growth and improved K ⁺ /Na ⁺ ratio	<i>Triticum vulgare</i>	[127]
<i>abf3</i>	Transcription factor	Drought resistance	<i>Oryza sativa</i>	[128]
<i>adc</i>	Arginine decarboxylase overexpression	Polyamine accumulation and salt resistance in biomass accumulation	<i>Oryza sativa</i>	[129]

Gene	Gene function	Metabolic Functions	Specie	References
<i>dreb1 or osdreb1</i>	Transcription factor	Drought, salt and cold tolerance with reduced growth under non-stress	<i>Oryza sativa</i>	[130]
<i>dreb1a</i>	Transcription factor	Delayed wilting under drought stress	<i>Triticum vulgare</i>	[131]
<i>sp12 and sp5</i>	ABA overproduction	High water-use efficiency, low transpiration and greater root hydraulic conductance	<i>Solanum lycopersicum</i>	[132]
<i>tos1</i>	Increased ABA sensitivity	Hypersensitive to osmotic stress and exogenous ABA	<i>Solanum lycopersicum</i>	[133]
<i>ZmACS6</i>	Ethylene synthesis	Non-functional mutant expressed drought induced Senescence	<i>Zea mays</i>	[134]
<i>spcp2</i>	putative papain-like cysteine protease	related to protein degradation for nutrient remobilization during leaf senescence	<i>Ipoema batatas</i>	[85]
<i>srk2d, srk2e, srk2i</i>	ABA signaling (ABA responsive element)	ABRE protein phosphorylation	<i>Arabidopsis thaliana</i>	[88]
<i>zmpis</i>	Phosphatidylinositol synthesis	Membrane protection	<i>Nicotiana tabacum</i>	[90]
<i>avp1</i>	Vacuolar pyrophosphatase gene	Proton pump activity	<i>Gossypium hirsutum</i>	[91]
<i>myb15</i>	Transcription factor (R2R3 MYB family member)	ABA responses, salinity and drought conditions tolerance	<i>Arabidopsis thaliana</i>	[83]
<i>tsrf1</i>	Protein ERF (ethylene-responsive factor)	ABA responses , accumulation of proline and soluble sugars content, induction of genes related to responses to stress and photosynthesis	<i>Oryza sativa</i>	[93]
<i>soderf3</i>	Sugarcane ERF transcription factors	Drought, osmotic stress, salt stress injuries and treatment with ABA	<i>Nicotiana tabacum</i>	[94]
<i>ap2/erf</i>	Soybean transcription factor family	Responses against biotic and abiotic stresses	<i>Nicotiana tabacum</i>	[95]

LEA Later embryogenesis abundant proteins

Table 1. Genes, gene function, metabolic function and transgenic.

5. Concluding remarks

The global warming is a reality that we have to face and in order to provide food to the growing population some actions have to be taken by government and researchers. The development of new cultivars more resistant to the environmental conditions, for every crop, must be a priority, in order to guarantee food demand security. To avoid yield reductions from floods, droughts and rising temperatures agribusiness will have to be reconsidered, investments have to be done, researchers will have to focus on ways to improve food quality, nutritional composition and increase yield using less land for farming. Crops will have to grow under a different scenario including less water and high temperature.

As it was discussed in this chapter changes in climate conditions will require several plant adaptations in order to minimize decreases in crop yield and to maintain food accessibility. Genetic breeding has been used over the last decades to improve yield and food quality. But how much can we still get from traditional plant breeding programs regarding to improve plants to face water scarcity? It is time to adopt new technologies as genetic engineering to help breeders in generating more adapted plants to survive water stress. For several years researchers have been spending time to understand how plants adapt to different situations, understanding the physiological parameters and their role in plants response to water stress specially hormones and transcriptional factors can help the development of new cultivars more resistant to stress conditions. All this knowledge allied to molecular biology techniques and genetic engineering can promote the development of transgenic plants with higher product quality, better storage conditions, easier processing, more efficient and more resistant to extreme conditions.

Nowadays, transgenic crops are cultivated all over the world, but there are some remains questions: How much are farmers dependent on biotechnology companies? Which economic and cultural losses transgenic cultures will bring about? These subjects are still extensively debated and researchers do not know for sure what is ahead. In the specific case of drought tolerance, much has been discussed about genetic engineering and experts consider the biotechnology relevant in developing higher genotypes.

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