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# Genetic and Molecular Aspects of Plant Response to Drought in Annual Crop Species

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## 1. Introduction

Stress is defined as any soil and climatic conditions or combination of both that hinders the full realization of genetic potential of a plant, limiting their growth, development and reproduction. These effects in plants of agricultural interest have a major impact on productivity and quality and thus represent, together with biotic stress, the cause of the gap between yield potential and actual production (Ciais et al., 2005). Stressful environmental conditions are extreme air temperature, drought, excessive presence of salts, anoxia and hypoxia, ozone and heavy metals. Among these factors, heavy damages on agricultural production in Mediterranean environments are exerted by drought, salt stress and early spring low temperatures. The changes in climate forecasted for the near future are expected to exacerbate the onset and magnitude of events of stress due to increased drought and erratic rainfall and rise of evapotranspiration rates due to growing temperatures.

Responses to drought are species specific and often genotype specific (De Leonardis et al., 2007). Moreover, the nature of drought response of plants is influenced by the duration and severity of water loss (Pinheiro & Chaves, 2011), the age and stage of development at the point of drought exposure (De Leonardis et al., 2007), as well as the organ and cell type experiencing water deficits (Pastori & Foyer, 2002).

Plants use various mechanisms to cope with drought stress including their morphology, physiology and metabolism at organ and cellular levels (Levitt, 1972). The Figure 1 shows the drought response strategies which include i) escape, ii) avoidance, and iii) tolerance. Escaping strategy, via a short life cycle or developmental plasticity (Araus et al., 2002), allows the plant to complete its life cycle during the period of sufficient water supply before the onset of drought. The drought avoidance mechanism, via enhanced water uptake and reduced water loss (Chaves et al., 2002), involves strategies which help the plant to maintain high water status during periods of stress, either by a more efficient water absorption from roots or by reducing evapotranspiration from aerial parts. Drought tolerance, via osmotic adjustment, enhanced antioxidative capacity and physical desiccation tolerance of the organs, allows to withstand water deficit with low tissue water potential (Ingram & Bartels, 1996). The osmotic compounds synthesized include proteins and aminoacids (like proline, aspartic acid and glutamic acid), methylated quaternary ammonium compounds (e.g. glycine betaine, alanine betaine), hydrophilic proteins (e.g. late embryogenesis abundant (LEA), carbohydrates (like fructan and sucrose) and cyclitols (e.g. D-pinitol, mannitol).

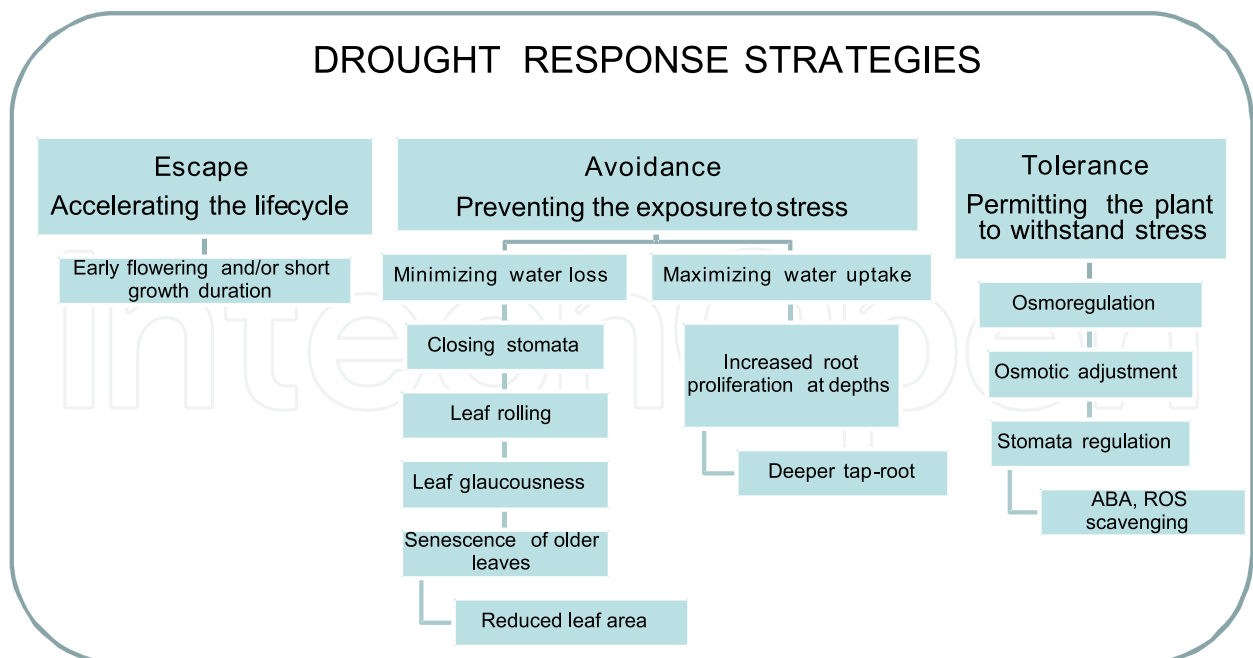


Fig. 1. Plant drought response mechanisms and main related traits.

Recent research has uncovered physiological-, biochemical- and molecular-based mechanisms involved in the drought response in plants (Amudha & Balasubramani, 2011).

More research into how plants respond to drought conditions is needed and will become more important in the future based on climate change predictions of an increase in arid areas (Petit et al., 1999). Understanding plant responses to drought is of great importance in order to select plants more tolerant to stress (Reddy et al., 2004). Advances in the understanding of these processes may lead to genetically modified drought tolerant crop plants.

This chapter focuses on the most recent findings on water stress response in plants. Both morpho-physiological traits and molecular changes contribute to promote stress resistance. In particular, the future perspectives of breeding for drought tolerance are viewed as resulting from the integration of genomic approaches based on the identification of genomic regions involved in the control of stress-related traits and a deep knowledge of the molecular mechanisms acting at cellular level in response to drought stress.

## 2. Morpho-physiological traits involved in the response to water stress

As the damage exerted by water stress is translated into important loss in amount and quality of crop yield, the improvement of drought tolerance represented and still represents one of the major objectives of plant breeding. At this purpose, a very important task consists of the identification of the main phenotypic features for plant to cope with drought, and therefore the formulation of the drought-tolerant ideotype. Physiological traits relevant for the responses to water deficits and/or modified by water deficits span a wide range of vital processes.

Morphological traits as early plant vigour, wider leaves and a more prostrate growth habit can sustain a rapid ground cover thus avoiding loss of water by soil evaporation and suppressing

weed competition for water, with a clear advantage on maintaining a favourable plant water status in order to sustain transpiration and yield (Mastrangelo et al., 2011a).

Plant phenology (escape) represents an important aspect for selecting drought tolerant crops, as it allows the alignment of plant life cycle to the features of the target drought environment. In this regard, the genetic improvement of crops has to take into account the modality of drought stress occurrence in the various environments, and in particular the stress timing, frequency and intensity. As an example, earliness is an effective breeding strategy for enhancing yield stability in Mediterranean environments where crops are exposed to terminal drought stress, even if an extreme earliness leads to yield penalty (Cattivelli et al., 1994). Nevertheless, in the case of cereal species in environments in which the drought stress is experienced in early season during the initial vegetative stage, late flowering, followed by a short grain-filling period, can lead to higher yield (van Ginkel et al., 1998). However, early-flowering varieties will escape terminal drought, but they are not necessarily considered drought-resistant.

One basic mechanism for reducing the impact of drought is early stomatal closure at the beginning of a period of water deficit. Stomatal closure reduces water loss, but also reduces the gas exchange between the plant and the ambient air. The reduced CO<sub>2</sub> intake then results in reduced photosynthesis (Chaves et al., 2002). Nevertheless high yield requires high stomatal conductance to sustain a great CO<sub>2</sub> fixation. Some leaf traits, such as stomatal number/density and leaf mesophyll structure can be important in increasing the water use efficiency. In particular, studies carried out in wheat suggest that the high-yielding modern varieties are “opportunistic”, that is they have high rates of stomatal conductance with optimal soil moisture, but markedly reduce stomatal conductance when soil moisture is limiting (Siddique et al., 1990; Rizza et al., 2011). Maximal rates of photosynthesis were also positively correlated with increased yields of advanced varieties, while leaf temperatures were negatively correlated (Fischer et al., 1998). Leaf permeability is another crucial trait, as leaves can lose water through cuticle, increasing crop transpiration without an associated benefit in CO<sub>2</sub> fixation. Glauousness, which is caused by the presence of epicuticular wax, can prevent these losses (Kerstiens, 2006).

At cellular level, osmotic adjustment is an adaptive mechanism in which the accumulation of solutes helps to maintain a favourable gradient of water potential in the soil-plant-air system. It allows to maintain a sufficient water absorption from a relatively dry soil for sustaining photosynthetic and transpiration activity, and cell expansion for root growth (Mastrangelo et al., 2011a; Dichio et al., 2006). Regarding the importance of this trait in improving grain yield in water stressed environment, a positive correlation between osmotic adjustment and yield increases has been found in particular in conditions of severe water stress (Serraj & Sinclair, 2002).

Besides above-ground traits of plant, deep rooted cultivars have demonstrated a clear yield advantage under water stress conditions. An increased root development in presence of water stress represents a complementary strategy to stomatal closure regulation. The influence of root architecture on yield and other agronomic traits, especially under stress conditions, has been widely reported in all major crops (Tuberosa et al., 2002a; de Dorlodot et al., 2007).

A deep and expanded root system should permit to explore a greater soil volume and extract more water. The information available on the genetic control of root traits in the field and their

relationships with yield is limited, mainly due to difficulty of measuring root characteristics in a large number of genotypes. Moreover, field studies on roots often require destructive approaches and are complicated by heterogeneity in soil profile, structure, and composition. The acquisition and analysis of root parameters such as total root length are tedious, time-consuming, and often inaccurate (Zoon & Van Tienderen, 1990). Furthermore, environmental effects on root development have been documented by a number of researcher. Many of the root characteristics, such as length, average diameter, surface area, and mass have been used to assess the quantity of roots and the functional fraction of the root system. Total root mass is usually viewed as easier to measure than root length or surface area and has frequently been used to compare root systems. However, total root mass alone cannot describe many root functions adequately involved in plant-soil relationship.

In the case of annual crops capture of water, at sowing for establishment and late in the season for grain filling, may be the most important target for root system traits. The location and the timing of these water sources within the soil profile depend on the soil type and its water holding capacity, the preceding crop and its water use, the soil water content at sowing and the pattern of rainfall during and after the crop growing season. Modelling can estimate when and where valuable water is likely to be present in the soil profile for targeting root traits (Lilley & Kirkegaard, 2007; Sadras & Rodriguez, 2007). Late-season water, for example, may be located mid-profile, or at the bottom of the root zone. This suggests that it would be beneficial to combine root vigour with other root characteristics to favour resource capture.

The other characteristics may include weak root gravitropism to promote a more wide-spreading root system for shallower water uptake, or a strong gravitropism to promote deeper root penetration and deep-water uptake (Ho et al., 2005; Manschadi et al., 2006), faster extension towards moisture (hydrotropism) (Eapen et al., 2005) and more or less nodal and seminal root axes (Hochholdinger et al., 2004). Root growth in soil can be limited by physical, chemical, and biological properties of the soil. Despite the intense work carried out on these topics, there is still insufficient understanding upon the soil factors which limit root growth, and the influence of time period and weather conditions on them. Without this information, it is difficult to manage soil to maximize crop production. In terms of physical limitations to root growth, water stress (too little water for root growth), hypoxia or anoxia (too little oxygen), and mechanical impedance (soil that is too hard for roots to penetrate rapidly) are the major causes of poor root system growth and development. In particular, there is a strong interplay between the strength and water content of soil. As soils dry, capillary forces make matric potential more negative, often causing strength to increase rapidly (Whitmore & Whalley, 2009). A review from Bengough et al. (2011) describes selectively both old and new literature on root elongation in drying soil and the role of water stress, mechanical impedance, and their likely interactions.

### **3. Breeding for drought tolerance improvement**

Drought tolerance has been historically one of the major targets of genetic improvement of crops, and some relevant results have been obtained during the last century despite the low heritability, due to a high genotype  $\times$  environment ( $G \times E$ ) interaction, of this trait. Consistent genetic gains (from 10 to 50 kg ha<sup>-1</sup> yr<sup>-1</sup>) have been registered for cereals and legumes over the last century in all countries, including those characterized by vast drought-prone regions (Calderini & Slafer, 1998; Abeledo et al., 2002). Many studies

suggest that cultivars selected for high yield in stress free environments are also adapted to stress prone environments (Cattivelli et al., 2008). In different field experiments modern durum wheat genotypes outperformed the old ones in all test environments including those with moderate drought stress and showed a stronger responsiveness to improved fertility (De Vita et al., 2010). Moderate drought stress is defined physiologically as reduced cell turgor that generally results in reduced stomatal conductance (reduced water loss from the leaf), and lower cellular water potential, which allows the tissue to hold onto the water that is in the leaf more tenaciously (Levitt 1972). This suggests that some of the traits selected to improve potential yield can still sustain yield at least in mild to moderate drought conditions ensuring yield stability (Slafer et al., 2005; Tambussi et al., 2005). A possible explanation is that the main targets of selection (high harvest index in wheat and barley, stay green in maize and sorghum, resistance to pests and diseases, nitrogen use efficiency) are equally useful under dry and wet conditions and, often, the best performances for these traits were overriding the differences in drought adaptability (Mastrangelo et al., 2011a).

In some cases adaptive traits were shown to contribute significantly to performance under drought. Retrospective studies on maize showed that most of the genetic yield improvement for hybrids bred in the second half of the last century could be attributed to traits related to tolerance to stress, like high plant population density, weed interference, low night temperatures during the grain-filling period, low soil moisture, and low soil N (Cattivelli et al., 2008; Tollenaar & Wu, 1999; Tollenaar & Lee, 2002).

Because of the complex nature of drought tolerance, conventional breeding has obtained little success in this regard. Successful cases of genetic improvement for yield in drought-prone environments have been obtained by selecting for secondary traits related to drought tolerance. In maize the silk-tassel interval was identified as a highly indicative secondary trait for drought-resistant breeding (Bolanos & Edmeades, 1996). Spikelet fertility can be visually estimated under field conditions and has been used as an indirect index for drought screening in rice (Garrity & O'Toole, 1994). Another example is based on the use of carbon isotope discrimination ( $\Delta$ ) as a surrogate for water use efficiency to select wheat lines with high water use efficiency in drought-prone environments (Rebetzke et al., 2002). During photosynthesis plants discriminate against the heavy isotope of carbon ( $^{13}\text{C}$ ) and, as a result, in several  $\text{C}_3$  species,  $\Delta$  is positively correlated with the ratio of internal leaf  $\text{CO}_2$  concentration to ambient  $\text{CO}_2$  concentration ( $C_i/C_a$ ) and negatively associated with transpiration efficiency. Thus, a high  $C_i/C_a$  leads to a higher  $\Delta$  and a lower transpiration efficiency (Farquhar & Richards, 1984).

In the last years a great effort has been devoted to the identification of genomic regions involved in the control of traits related to drought stress tolerance. Once the region has been mapped, closely linked molecular markers are identified, which can be used in breeding programs based on MAS (Marked Assisted Selection). The wide range of physiological and biochemical mechanisms involved in dehydration response explains the complexity of plant response to drought, for which a high number of quantitative trait loci (QTLs) widespread on many chromosomes have been found (Cattivelli et al., 2008).

As an example, Yang et al., (2007) reported several QTLs for accumulation and remobilization of water-soluble carbohydrates in wheat stems. Depending on cultivars and

environments, stem water-soluble carbohydrates accumulated before flowering, and during the early periods after flowering, contributed up to 70% or more of the grain weight under terminal drought conditions (Yang et al., 2001). Major genomic regions controlling productivity and related traits (Carbon isotope ratio, osmotic potential, chlorophyll content, flag leaf rolling index) were identified on chromosomes 2B, 4A, 5A and 7B by Peleg et al., (2009) in durum wheat. QTLs for productivity were associated with QTLs for drought-adaptive traits, suggesting the involvement of several strategies in wheat adaptation to drought stress. Sixteen QTLs were identified in durum wheat by Maccaferri et al. (2008), including two major QTLs on chromosome arms 2BL and 3BS that affected grain yield and showed significant effects in multiple environments (rainfed and irrigated).

Five QTLs for anther-silking interval were identified in the maize drought tolerant line Ac7643 and transferred to the susceptible line CML247 by marker-assisted backcross. Hybrid lines were obtained that performed better than controls in well watered and mild drought condition in terms of grain yield (Ribaut & Ragot, 2007).

The identification of markers or genes associated with root growth and architecture would be particularly useful for breeding programmes to improve root traits by molecular marker-assisted selection. Few papers have described work on the identification of QTLs for root traits in wheat.

Root system architecture (RSA), the spatial configuration of a root system in the soil, is used to describe the shape and structure of root systems. Its importance in plant productivity lies in the fact that major soil resources are heterogeneously distributed in the soil, so that the spatial development of roots will determine the ability of plant to secure edaphic resources (Lynch, 1995). The search for QTLs has been a major research avenue in investigating the genetic variation of RSA, a task that is complicated by the strong responses of RSA to environmental conditions. In several instances overlap of QTLs for root features with those for productivity (yield, water use o capture) has suggested the possible role of the former in determining the latter (Tuberosa et al., 2002a; 2002b; Steele et al., 2007). Although there are few examples of QTLs that individually explained up to 30% of phenotypic variation for root traits in rice (Price & Tomos, 1997) and in maize (Giuliani et al., 2005) and for the response of RSA to environmental factors, root morphology is in most cases regulated by a suite of small-effect loci that interact with the environment (de Dorlodot et al., 2007). This is one of the constrains that limit progress from QTL discovery to the release of new varieties.

Some recent papers have reviewed in details the QTLs identified for traits related to drought stress tolerance (Maccaferri et al., 2009; Ashraf, 2010), furthermore, for many crop plants information on drought-related QTL findings have been collected in open source databases, such as GRAMENE (<http://www.gramene.org/>) or GRAINGENES (<http://wheat.pw.usda.gov/GG2/quickquery.shtml#qtls>). In particular, Courtois et al. (2009) extracted information from about sixty papers published between 1995 and 2007 and compiled a database containing QTLs for drought tolerance traits and for 29 root parameters. The data describe 2137 root and drought QTLs, out of which 675 for root traits detected in 12 mapping populations.

In rice, several QTLs for root deepness were transferred from the japonica upland cultivar "Azucena", adapted to rainfed conditions, to the lowland indica variety "IR64". MAS selected lines showed a greater root mass in low rainfall trials and higher grain yield (Steele

et al., 2007). Following these studies, a highly drought tolerant variety, Birsa Vikas Dhan 111 was released in India, characterized by early maturity, high drought tolerance and high grain yield with good grain quality (Steele, 2009).

Linked molecular markers were identified for resistance to cereal cyst nematode (CCN) root disease and the root tolerance to the toxic element Al and are currently used by commercial breeding companies.

Combining, or pyramiding, a number of root characteristics for a target environment can be achieved by phenotype selection in the short term. In future, molecular markers may be available for these characteristics since a gene regulating hydrotropism has been identified in *Arabidopsis* (Kobayashi et al., 2007); a gene regulating specific root types, including seminal versus nodal roots, has been identified in maize (Taramino et al., 2007); and a significant QTL associated with large root system size was identified in *Arabidopsis* growing in agar under high osmotic stress (Fitzgerald et al., 2006).

Over the past few years there have been several mapping studies that have targeted drought tolerance and other abiotic stress tolerance loci associated with performance in low yielding environments. However, despite this substantial research effort the only markers that have found their way into practical plant breeding programmes are those for boron and aluminium tolerance (Gupta et al., 2010).

#### 4. Molecular bases of plant response to water stress

Molecular and biochemical response of plant to water stress is a very complex task depending on multiple factors (Rizhsky et al., 2002; Bartels & Souer, 2004). Changes in membrane integrity and modulation of lipid synthesis are key factors in the primary sensing of abiotic stress (Kader & Lindberg, 2010). Secondary, osmotic stress-induced signalling involves changes in plasma membrane H<sup>+</sup>-ATPase and Ca<sup>2+</sup>-ATPase activities that trigger concerted changes of Ca<sup>2+</sup> influx, cytoplasmic pH, and apoplastic production of ROS (Beffagna et al., 2005).

Transcription factors represent the first level of regulation of mRNA metabolism, controlling the synthesis of pre-mRNA. These molecules are then subject to a splicing process that produces mature mRNA. A well studied phenomenon, with a clear role in regulation of gene expression in stress conditions, is alternative splicing, in which different mRNAs can be produced starting from the same pre-mRNA molecule (Mastrangelo et al., 2011b). The amount of mRNAs in the cell can also be controlled by mechanisms affecting their stability. Not only proteins but also small non-coding RNA molecules are involved in the regulation of these processes, and they have been recognized as important regulators of gene expression and genome integrity (Ambrosone et al., 2011). Epigenetic regulation, which comprises histone variants and post-translational modifications, DNA methylation and certain small-interfering RNA (siRNA) pathways, controls chromatin structure which can be modified in response to stress. Finally, availability of mRNAs for translation affects the synthesis of the corresponding proteins. In the last years, a new mechanism of post-transcriptional regulation of gene expression was identified in the sequestration of mRNAs in the cytoplasm to generate Stress Granules (SG). SG, produced as result of stress condition, were represented by a subset of mRNAs aggregated with specific proteins, allowing physical separation of these mRNAs from the translational machinery and resulting in transient translational repression (Anderson & Kedersha, 2009).



#### 4.1 Transcriptional factors influencing the expression of genes in response to environmental signals

Plant transcription factors are involved in the response to environmental stresses as critical regulators of the expression of stress-related genes. More than 1,500 genes coding for transcription factors have been annotated in Arabidopsis, and they are classified into several families based on the structure of their DNA-binding domains (Ratcliffe & Riechmann, 2002 – <http://datf.cbi.pku.edu.cn/>). In particular, members of the MYB, MYC, ERF, bZIP, and WRKY transcription factor families have been implicated in the regulation of plant stress responses (Hussain et al., 2011).

Studies carried out in the model species Arabidopsis allowed to identify different stress signal transduction pathways leading to the activation of members of the above mentioned transcription factor families. These pathways can be either dependent or not by the plant hormone ABA (Hirayama and Shinozaki, 2010).

Among transcription factors depending on ABA, bZIPs are a large family of transcription factors with 75 members annotated in the Arabidopsis genome. Regarding water stress response, the ABRE-binding factor (ABF)/ABA-responsive-element-binding (AREB) proteins respond at the transcriptional and post-transcriptional level to drought and salt stress (Choi et al., 2000; Uno et al., 2000), increasing drought stress tolerance (Table 1).

MYC and MYB proteins have a role in late stages of stress response and are also activated following accumulation of endogenous ABA. They generally promote water stress tolerance by acting as positive regulators (Table 1), even if a different mechanism was described for the AtMYB60 and AtMYB44 genes, that are involved in stomatal movements, and function as transcriptional repressors (Cominelli et al., 2005; Jung et al., 2008).

More than 100 members of the NAC gene family have been identified in both Arabidopsis and rice (Fang et al., 2008; Ooka et al., 2003). Members of this family are involved in drought and salinity stress response, as well as in diverse processes as developmental programs, and biotic stress responses (Olsen et al., 2005). RD26, a dehydration-induced NAC protein induced by drought, high salinity, ABA, and JA treatments, represents a key factor in mediating cross-talk between ABA signalling and JA signalling during drought and wounding stress responses (Fujita et al., 2004).

An example of ABA-independent transcription factors acting in drought response are zinc finger homeodomain (ZFHD) proteins. Arabidopsis ZFHD1 binds the ZFHDR motif in the promoter of ERD1 gene, which is also regulated by NAC proteins (Hirayama & Shinozaki, 2010).

Ethylene responsive factors (ERFs) represent a class of genes which function in both ABA-dependent and independent pathways. They are a transcription factor superfamily that is unique to plants, with 124 members in Arabidopsis (Riechmann et al., 2000). ERF proteins share a conserved 58–59 amino-acid domain (the ERF domain) that binds to two similar cis-elements: the GCC box, which is found in several PR (Pathogenesis-Related) gene promoters where it confers ethylene responsiveness, and the C-repeat (CRT)/dehydration-responsive element (DRE) motif, which is involved in the expression of dehydration- and low-temperature-responsive genes.

Gene	Gene family	Species	Gene expression	Phenotype of transgenic or mutant plants	Reference
SodERF3		Sugarcane	overexpressed	Improved ABA, Salt and Wounding tolerance (Tobacco)	Trujillo et al., 2008
WXP1	ERF	Medicago	overexpressed	Improved Drought tolerance (Arabidopsis)	Zhang et al., 2007
GmERF3		Soybean	overexpressed	Improved Drought, salt and disease tolerance (Tobacco)	Zhang et al., 2009
RAP2.6		Arabidopsis	overexpressed	Hypersensitive to ABA, salt, osmotic and cold stress (Arabidopsis)	Zhu et al., 2010
DREB1C		Arabidopsis	overexpressed	Enhanced desiccation tolerance (Arabidopsis)	Novillo et al., 2004
AtDREB1A	DRE binding protein 1	Wheat	overexpressed	Delayed wilting under drought stress (Wheat)	Pellegrineschi et al., 2004
AtDREB1A		Tobacco	overexpressed	Improved Drought and cold tolerance (Tobacco)	Kasuga et al., 2004
AtDREB1A		Rice	overexpressed	Improved Drought and salt tolerance (Rice)	Oh et al., 2005
AtCBF4		Arabidopsis	overexpressed	Improved Drought and freezing tolerance (Arabidopsis)	Haake et al., 2002
OsDREB1		Rice	overexpressed	Improved Drought, Salt and freezing tolerance (Rice)	Ito et al., 2006
HvCBF4		Barley	overexpressed	Increased Drought, Salt and freezing tolerance (Rice)	Oh et al., 2007
AREB1		Arabidopsis	overexpressed	Improved Dehydration survival (Arabidopsis)	Fujita et al., 2005
ABF3/ABF4		Arabidopsis	overexpressed	Improved Drought tolerance (Arabidopsis)	Kang et al., 2002
AREB1		Arabidopsis	knock-out mutant	Reduced Drought tolerance (Arabidopsis)	Yoshida et al., 2010
ABP9	bZIP	Maize	overexpressed	Improved photosynthetic capacity under drought stress (Arabidopsis)	Zhang et al., 2008
SIAREB		Tomato	overexpressed	Improved Drought and Salt tolerance (Arabidopsis and Tomato)	Hsieh et al., 2010
OsABF1-1, OsABF1-2		Rice	mutant	More sensitive to drought and salinity treatments (Rice)	Amir Hossain et al., 2010
OsZIP23		Rice	overexpressed	Improved Drought and Salt stress tolerance (Rice)	Xiang et al., 2008
WRKY25, WRKY 33		Arabidopsis	overexpressed	Increased sensitivity to ABA and improved salt tolerance (Arabidopsis)	Jiang & Deyholos, 2009
WRKY63	WRKY	Arabidopsis	knock out mutant	Decreased drought tolerance and hypersensitive to ABA (Arabidopsis)	Ren et al., 2010
OsWRKY45		Rice	overexpressed	Improved drought tolerance and enhanced disease resistance (Arabidopsis)	Qiu et al., 2009
AtMYB60	TF involved in stomatal movements	Arabidopsis	null mutation	Decreased wilting under water stress conditions (Arabidopsis)	Cominelli et al., 2005
AtMYB44		Arabidopsis	overexpressed	Improved drought and salt tolerance (Arabidopsis)	Jung et al., 2008
AtMYB15	R2R3 MYB	Arabidopsis	overexpressed	Improved drought tolerance and enhanced sensitivity to ABA (Arabidopsis)	Ding et al., 2009
AtMYB41		Arabidopsis	overexpressed	Negative regulation of transcriptional responses to osmotic stress (Arabidopsis)	Lippold et al., 2009
AtRD26		Arabidopsis	overexpressed	Enhanced sensitivity to ABA (Arabidopsis)	Fujita et al., 2004
ANAC019, ANAC055, ANAC072	NAC	Arabidopsis	overexpressed	Improved drought and salt tolerance (Arabidopsis)	Tran et al., 2004
ONAC045		Rice	overexpressed	Improved drought and salt tolerance (Rice)	Zheng et al., 2009
OsNAC10		Rice	overexpressed	Improved drought tolerance and grain yield (Rice)	Jeong et al., 2010

Table 1. Examples of transcription factors regulating drought tolerance in plants.

Therefore, these proteins can have a role in both biotic and abiotic stress responses, as demonstrated for soybean *GmERF3* and the the Arabidopsis ABA-responsive *RAP2.6* genes (Zhang et al., 2009; Zhu et al., 2010). In Arabidopsis, two distinct gene families of DRE/CRT

binding proteins (*CBF/DREB1* and *DREB2*) were described as two distinct targets of cold and drought ABA-independent signalling transduction pathways, respectively (Shinozaki & Yamaguchi-Shinozaki, 2000). Nevertheless *CBF4*, a member of *CBF/DREB1* family, was described as an ABA-dependent regulator of drought adaptation in *Arabidopsis* (Haake et al., 2002). *CBF/DREB1* and *DREB2* represent therefore a point of integration of different signal transduction pathways in response to abiotic stresses. The importance of *CBF/DREB* genes for tolerance to abiotic stresses has been well established in particular in cereals, with evidences at level of phenotypic evaluation of over-expressing plants, and co-segregation of *CBF* genes with QTLs for frost tolerance (Vågüfalvi et al., 2005).

Finally, *WRKY* proteins contain either one or two *WRKY* domains, 60-amino-acid regions that contain the sequence *WRKYGQK*, and a zinc-finger-like-motif. They are involved in the regulation of diverse plant processes including development, response to various biotic and abiotic stresses, and hormone-mediated pathways (Ramamoorthy et al., 2008). *A. thaliana* *WRKY25* and *WRKY33* genes are responsive to osmotic stress but they also are regulated by oxidative stress (Miller et al., 2008). Down-stream regulated target genes of *WRKY33* include transcripts with function in ROS detoxification as peroxidases and glutathione-S-transferases (Jiang & Deyholos, 2009).

#### 4.2 Stress related transcripts from alternative splicing events

Alternative splicing is a process which generates two or more different transcripts from the same pre-mRNA molecule by using different splice sites. The rate of plant genes subject to alternative splicing is comprised between 20 and 70%, depending on the species considered (Mastrangelo et al., 2011b). Alternative splicing events do not randomly affect mRNA of all genes, rather they seem to occur preferentially to mRNAs of certain classes of genes commonly involved in signal transduction, or encoding enzymes, receptors and transcription factors (Ner-Gaon & Fluhr, 2006; Lareau et al., 2004). Four main types of alternative splicing have been described: exon skipping, alternative 5' and 3' splice sites and intron retention. The last one is the most common alternative splicing type in plants and fungi (>50% McGuire et al., 2008).

Alternative splicing has been proposed as one of the regulatory mechanisms amplifying the number of proteins that can be produced from a single coding unit. Nevertheless, alternative transcripts containing in frame stop codons, often resulting from retained introns, can be targeted to degradation by nonsense-mediated decay. This mechanism contributes to the fine regulation of the amount of functional protein that will be produced in stressed conditions. Otherwise, truncated polypeptides can be produced, which are not necessarily functionless forms of the full length protein. An example is a stress-related transcript of the *MPK13* gene, encoding a protein kinase. This transcript is translated into a truncated protein that has no protein kinase activity, but enhances the *MKK6*-dependent activation of the *MPK13* full-length protein (Lin et al., 2010).

Many of the above described stress-related transcription factors are regulated by alternative splicing. In *Arabidopsis*, the *AtMYB59* and *AtMYB48* genes were found to code for alternative proteins differing for their *MYB* repeats and probably for their binding affinities to gene promoters (Li et al., 2006; Fig. 2). A stress-dependent alternative splicing mechanism was described for the *OsDREB2B* gene and its homologs in different species (Mastrangelo et al., 2011b). A transcript containing a shorter ORF (*OsDREB2B1*) accumulated in non stress

conditions, and was rapidly converted in the full length transcript (*OsDREB2B2*) by removal of an exon carrying an in frame stop codon in response to stress exposure. This mechanism is probably aimed to finely and rapidly regulate the amount of functional protein. Moreover, this mechanism can keep the transcription of *OsDREB2B* constitutively active without affecting plant growth (Matsukura et al., 2010).

The serine/arginine proteins are a class of RNA binding proteins involved in splicing regulation. Twenty genes encoding serine/arginine proteins have been identified in *Arabidopsis* up to now, and most of their mRNAs undergo alternative splicing following developmental and environmental stimuli producing nearly 100 different transcripts (Palusa et al., 2007). They can promote alternative splicing of their own transcripts as well as of other gene products in response to a number of abiotic stresses (Wang & Brendel, 2006). A similar behavior has been shown for some glycine-rich RNA-binding proteins as AtGRP7 and AtGRP8, which are able to auto-regulate their own splicing and cross-regulate with each other in a negative feed-back loop (Schoning et al., 2008). Alternative splicing regulation of genes producing transcripts that alter the splicing of other genes in turn might considerably enhance and amplify the signal-transduction cascade in response to stress stimuli.

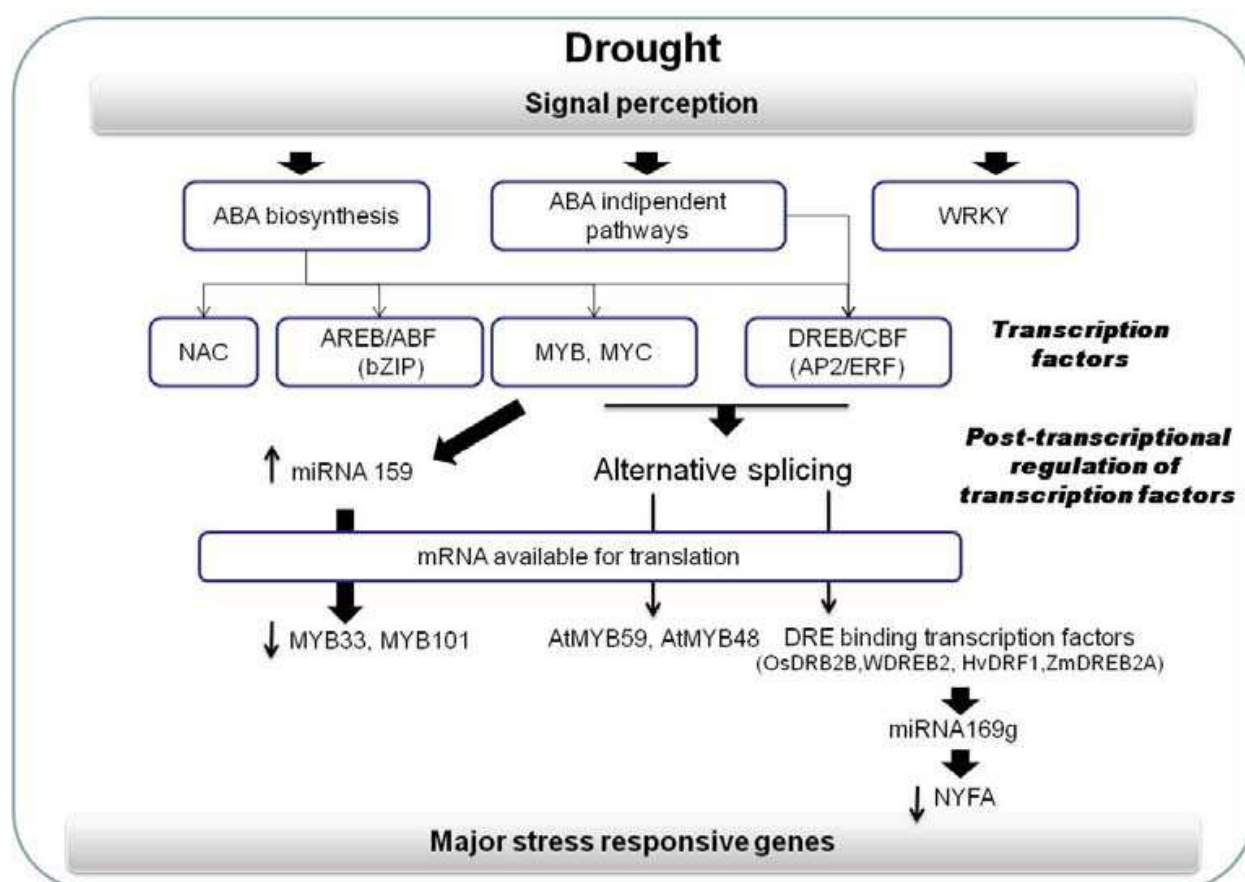


Fig. 2. ABA-dependent and independent pathways of response to drought in plants.

Finally, alternative splicing events also have been described for proteins acting in the regulation of gene expression at post-translational level. E3 ubiquitin ligases represent a very large and complex gene family involved in regulation of protein half life by spliceosome-mediated protein degradation. Alternative splicing events were described for two *Arabidopsis*

E3 genes (*At4g39140* and *At2g21500*) and for the durum wheat homolog 6G2, whose mRNA retained the last 3'UTR-located intron following exposure to dehydration and cold stress (Mastrangelo et al., 2005). The same stresses induced the accumulation of an alternative transcript for the Arabidopsis SKP1-like 20 (ASK20) gene (Ogura et al., 2008).

#### 4.3 Regulatory proteins affecting mRNA availability and activity

Transport, initiation of translation and degradation by RNA interference have been shown to regulate mRNA levels of genes in response to water stress. Many of these processes are mediated by RNA-binding proteins (RBP), a variety of heterogeneous proteins involved in diverse aspects of post-transcriptional regulation by direct interaction with single/double strand RNA molecules. The processes in which they are involved comprise mRNA maturation events such as splicing, capping, polyadenylation and export from the nucleus. At level of the cytoplasm, they can regulate mRNA localization, stability, decay and translation (Burd & Dreyfuss, 1994; Dreyfuss et al., 2002). RBPs are characterized by conserved RNA-binding motifs, such as RNA recognition, K homology, glycine-rich, arginine-rich, zinc finger (mainly CCCH type - C-x8-C-x5-C-x3-H), and double-stranded RNA-binding motifs. RRM motifs in particular are involved in RNA recognition and in protein-protein interactions, leading to the formation of heterogeneous ribonucleoprotein (RNP) complexes. More than 200 putative RBP genes have been identified in the Arabidopsis and rice genomes, and many of them seem to be unique to plants, suggesting that they might serve plant specific functions (Lorkovic, 2009; Cook et al., 2010).

Expression and/or activity of a number of RBPs were found to be regulated in response to environmental variables, including water deficit, temperature, light and low-oxygen stresses (Park et al., 2009; Sachetto-Martins et al., 2000; Sahi et al., 2007). Several RBPs resulted also to be ABA-regulated, supporting the regulatory role of ABA in the control of post-transcriptional RNA metabolism (Kuhn & Schroeder, 2003).

The role of RBPs in response to drought stress was also demonstrated by using plant mutants. The supersensitive to ABA and drought 1 (*sad1*) mutant line was isolated in Arabidopsis and exhibited enhanced responses to ABA and drought (Xiong et al., 2001). The ABA hypersensitive 1 (*abh1*) mutant showed ABA hypersensitive stomatal closing and reduced wilting during drought treatment (Hugouvieux et al., 2001). *SAD1* encodes an Sm-like protein possibly involved in RNA transport, splicing or degradation, while *ABH1* encodes a mRNA cap binding protein which can effectively control ABA signalling components at the RNA level (Covarrubiales & Reyes, 2010). These two genes have been identified as negative regulators of ABA-dependent germination and drought tolerance, together with *CBP20* (Cap-Binding Protein 20) and *HYL1* (Hyponastic Leaves 1) which codes for a double stranded RNA-binding factor necessary for the biogenesis of miRNAs and crucial for the precise and efficient cleavage of several primary-miRNAs (Vazquez et al., 2004; Szarzynska et al., 2009; Kuhn & Schroeder, 2003).

Some glycine-rich proteins, containing a dispersed CCHC-type zinc finger at the C-terminus (Karlson et al., 2002), have been identified in plants as cold shock domain protein (CSDP) (Verslues et al., 2006). Arabidopsis AtRZ-1a is a cold shock domain protein and has a negative impact on seed germination and seedling growth of Arabidopsis under salt or dehydration stress conditions (Kim et al., 2007).

Not only the sequence information, but also the secondary and tertiary structures of RNA molecules contribute to their biological activity. RNA helicases are RBPs that catalyze RNA secondary structure rearrangements, and are potentially required in any cellular process involving RNA maturation (Tanner & Linder, 2001; Rocak & Linder, 2004). The majority of RNA helicases belong to the superfamily 2 (SF2) composed of three subfamilies, termed DEAD, DEAH and DExH/D (Tanner & Linder, 2001). Amino acid sequences outside a common core (Asp-Glu-Ala-Asp) are not conserved and are believed to provide helicase specificity for target RNAs or protein-protein interactions. RNA helicases are associated with a diverse range of biotic cellular functions and are involved in cellular response to abiotic stress. Recently, a temperature-regulated RNA helicase, *LOS4*, has been linked with developmental processes including flowering and vernalization in *Arabidopsis* (Gong et al., 2002; 2005). These processes also involve ABA, to which the *los4* mutants are sensitive (Gong et al., 2005).

Two DEAD-box-related helicases, *DNA Helicase 47 (PDH47)* and *PDH45* are induced by a variety of abiotic stresses in pea (Chinnusamy et al., 2004; Sanan-Mishra et al., 2005; Vashisht et al., 2005). The expression of *PDH47* in particular is regulated in a tissue specific manner: the gene is induced by cold and salinity stress in shoots and roots, and by heat and ABA treatment only in roots (Chinnusamy et al., 2004).

Finally, evidences have been reported that helicases can be regulated by the stress-induced alteration of subcellular localization, and by phosphorylation, which provides the opportunity to directly link helicase activity with environmental sensing-signal transduction phosphorylation cascades (Owttrim, 2006).

#### 4.4 Degradation of stress related transcript by siRNAs and miRNAs

MicroRNAs (miRNAs) and siRNAs are small noncoding RNAs that have recently emerged as important regulators of mRNA degradation, translational repression, and chromatin modification.

miRNAs form an abundant class of tiny RNAs characterized by a high level of conservation across species, suggesting a common evolutionary basis. They act in regulating the expression of protein-coding genes in multicellular eukaryotes (Bartel, 2004). Plant miRNAs participate in numerous processes, including development, pattern formation, flowering time, hormone regulation, nutrient limitation, response to stress, and even self-regulation of the miRNA biogenesis pathway (Jones-Rhoades et al., 2006). Regarding their involvement in stress response, abiotic stresses like cold, dehydration, salt stress and nutrient starvation regulate the expression of different plant miRNAs (Lu & Huang, 2008). An example is the *Arabidopsis* miR393, that is up-regulated by cold, dehydration, high salinity, and abscisic acid (ABA) treatments (Sunkar & Zhu, 2004). In maize 21 miRNA differentially expressed under drought stress were identified (Chen et al., 2010).

In order to understand the mechanisms by which they exert a role in stress protection, it is important to characterize their target mRNAs. At this regard, an interesting feature of miRNAs is the fact that their targets are often regulatory genes (Jones-Rhoades & Bartel, 2004; Rhoades et al., 2002; Zhang et al., 2006). The level of miR159 increased in *Arabidopsis* seedlings water stressed. In *Arabidopsis* transgenic plants the over-expression of miRNA159 reduced the level of *MYB33* and *MYB101* transcripts, and a hyposensitive phenotype to ABA was observed (Reyes & Chua, 2007; Fig. 2).

Sunkar and Zhu (2004) reported other ABA induced miRNAs (miR397b and miR402) but also cases of miRNA down-regulated by this hormone (miR389a).

Two members of the miR169 gene family, miR169a and miR169c, are repressed following drought treatments in Arabidopsis. As their target is the nuclear factor Y transcription factor *NFYA5*, the abundance of this transcript increases and promotes stress response in mature plants (Li et al., 2008). Nevertheless, even if the same conserved miRNA family regulates homologous targets in two different plant species, the effects of this regulation can be different. Members of the miR169 family in rice, miR169g and miR169n/o are induced by salt (Zhao et al., 2009) and drought (Zhao et al., 2007) and differences in levels of induction can be observed in different tissues, being more prominent in roots than in shoots. Interestingly, miR-169g, that acts reducing the expression of *NFYA*, may be regulated directly by DREB transcriptional factors (Zhao et al., 2009).

Ten percent of Arabidopsis genes are in convergent overlapping gene pairs, also known as natural cis-antisense gene pairs and overlapping transcripts in antisense orientation could form double-stranded RNAs that may be processed into small RNAs (Jen et al., 2005; Wang et al., 2005). These nat-siRNAs (natural antisense transcripts-generated siRNAs) have recently emerged as important players in plant stress responses. A study in Arabidopsis demonstrated the involvement of nat-siRNA in the accumulation of proline during response to stress. As an example, the Arabidopsis *P5CDH* gene, involved in proline catabolism, is down-regulated in response to salt stress following the induction of *SRO5*, a gene of unknown function. The two genes form an antisense overlapping gene pair that generates two siRNAs (Borsani et al., 2005).

#### 4.5 Epigenetic contribution to water stress response in plants

Epigenetic regulation is emerging as an important mechanism in response to stress. Drought induced linker histone variant H1-S was shown to be involved in the negative regulation of stomatal conductance based on the phenotypic analysis of antisense transgenic H1-S tomato plants (Scippa et al., 2004). Several histone deacetylases (HDACs) are induced by ABA in rice (Fu et al., 2007) and Arabidopsis (Sridha et al., 2006). Transgenic Arabidopsis plants overexpressing AtHD2C exhibited enhanced expression of ABA-responsive genes and greater salt and drought tolerance than the WT plants (Sridha et al., 2006).

Besides acetylation and de-acetylation, other post-translational mechanisms can regulate the abundance and activity of histones. In particular, histone phosphorylation and ubiquitination showed a role in enhancing gene transcription (Sridhar et al., 2007; Zhang et al., 2007), while biotinylation and sumoylation repress gene expression (Nathan et al., 2006; Camporeale et al., 2007). In the desert shrub *Zygophyllum dumosum* methylation level of histone H3 was higher in presence of water than under dry growth conditions indicating post-translational regulation of gene expression activity (Granot et al., 2009).

ABA-mediated pathways also are involved in epigenetic modifications, as suggested by the ABA-dependent regulation of barley Polycomb proteins expression, with a role in histone methylation control (Kapazoglou et al., 2010).

Studies on Arabidopsis over-expressing or knock out lines for the SNF2/ BRAHMA-type chromatin remodeling gene *AtCHR12* indicated a role of this gene in regulation of growth, in particular under drought and heat stresses (Mlynarova et al., 2007). In *Pisum sativum* ABA

and drought stress induced the expression of the chromatin remodelling *PsSNF5* gene. PsSNF5 protein interacts with Arabidopsis SWI3-like proteins (SWI3A and SWI3B), which in turn interact with FCA, a protein involved in the regulation of flowering (Sarnowski et al., 2005; Rios et al., 2007). This is a clear example in which stress response and plant development are co-ordinately regulated through chromatin remodeling.

Direct DNA methylation can also be involved in plant stress response. Drought and salt stresses induced a switch in photosynthesis mode from C3 to CAM in the facultative halophyte *Mesembryanthemum crystallinum* L. This metabolic change was associated with stress-induced-specific CpHpG-hypermethylation of satellite DNA (Dyachenko et al., 2006). In natural populations of mangroves DNA was hypomethylated when grown under saline conditions in contrast to populations from non-saline sites (Lira-Medeiros et al., 2010).

Although global analysis in plants such as Arabidopsis and rice suggests that the vast majority of transposons are inactive, methylated, and targeted by siRNAs (Nobuta et al., 2007; Lister et al., 2008), the induction of alternative epigenetic states not only triggers the formation of novel epialleles but also promotes the movement of DNA transposons and retroelements that are very abundant in plant genomes (Reinders et al., 2009; Mirouze et al., 2009). A lot of examples of environmentally induced transposon activities were reported (Slotkin & Martienssen, 2007), as the family of copia retrotransposon, named Onsen, activated by heat stress in Arabidopsis (Ito et al., 2011). In natural populations, stress may play a role in transposon amplification. An example is the copy number of BARE-1 retrotransposons in barley, which varies in natural populations depending on aridity of growth environment (Vicent et al., 1999). These evidences indicate that plant populations living in stressed environments may carry inherited memories of stress adaptation and transfer this epigenetically to next generations.

## **5. The molecular response of plants to water stress: A complex frame resulting from integration of multiple regulation layers**

The plant response mechanisms to water deficit strictly depend on plant developmental stage, stress intensity and stress duration (Bartels & Souer 2004; De Leonardis et al., 2007). A study on 325 rice transcription factors demonstrated that many of them have a tissue or developmental stage specific expression (Duan et al., 2005). In a genome wide study, Bray (2004) compared three independent array experiments dedicated to the Arabidopsis water stress response. The experiments differed for plants age, substrate of growth and stress applications. Only a small set of genes were commonly induced or repressed. Similar results were obtained in wheat, barley and rice (Ozturk et al., 2002; Lan et al., 2005; Mohammadi et al., 2007). In Arabidopsis the *Nine-Cisepoxycarotenoid Dioxygenase 3* (*NCED3*), *DREB2A* and *RD29B* genes were expressed with different levels and timing following two different kinds of stress imposition (Harb et al., 2011). These differences observed following a rapid or gradual water stress are probably due to the need of plants to optimally react to a stress event as it occurs in field conditions. Therefore, many internal and external stimuli have to be integrated into common signalling pathways.

Moreover, plants usually are exposed in field to different kinds of stress simultaneously, and the effect of the combined stresses in terms of gene expression is not simply the sum of the effects produced by the stresses applied separately (Rizhsky et al., 2002).



The superimposed complexity levels in the response to environmental changes, are therefore aimed to ensure temporally and spatially appropriate patterns of downstream stress-related gene expression.

After the translation, many post-translational mechanisms can target proteins modifying their activity, sub-cellular localization and half-life (Downes & Vierstra, 2005). Phosphorylation is one of the best known mechanism that plays a key role in many biological processes, as phosphorylation/de-phosphorylation cascades commonly translate extracellular stimuli into the activation of specific responses (Boudsocq & Laurière, 2005).

Among the polypeptides, ubiquitin and SUMO conjugations are emerging as major post-translational regulatory processes in all eukaryotes (Stone & Callis, 2007; Miura et al., 2007). The covalent binding of poly-ubiquitin usually targets proteins for proteolysis. Conversely, monoubiquitination regulate the location and activity of proteins, affecting various cellular processes from transcriptional regulation to membrane transport (Hicke, 2001). Similar effects are produced by the covalent conjugation of the SUMO (Small Ubiquitin-like Modifier) peptide (Hay et al., 2005). Both ubiquitination and sumoylation are involved in the promotion of stress tolerance in plants, and they offer a very clear example of multiple layer control of key regulators of the stress response. Along this chapter DREB/CBF proteins have been described as transcription factors with a pivotal role in plant tolerance to cold and drought stress. Their expression has shown to be modulated at transcriptional level, but also by alternative splicing (Matsukura et al., 2010). Furthermore, the HOS1 protein, corresponding to an E3 ubiquitin ligase, mediates the ubiquitination of the master regulator for the response to cold, the transcription factor Inducer of CBF Expression 1, ICE1, and repressor of *MYB15* expression. This leads to its proteasome-mediated degradation during exposure to cold (Dong et al., 2006). ICE1 protein, in turn, is stabilized by sumoylation that therefore acts in this pathway with an antagonistic role with respect to ubiquitination (Ishitani et al., 1998). Finally, DREB transcriptional factors can down-regulate the expression of *NFYA* through activation of miRNAs (Zhao et al., 2009).

The great complexity of the pathway of regulation of gene expression in plant response to water stress makes the analysis of transcriptome in different conditions not suitable alone to draw a clear picture of tolerance mechanisms. Variations at level of proteins and ultimately of metabolites have to be investigated to achieve a more complete evaluation. In this light, recent advances in profiling of plant proteome and metabolome in water stress conditions have provided chances to integrate data from gene expression and protein activities studies. Outcomes indicate an important role of post-transcriptional and post-translational mechanisms in coordinating the plant molecular response to water stress (Mazzucotelli et al., 2008).

## **6. The contribution of genetic and molecular knowledge to the improvement of drought tolerance in field**

A very complex network of gene interactions in response to water stress has been described in the last years, and a high number of QTLs, widespread in the genome, have been identified for tolerance, each of them controlling a low percentage of explained phenotypic variability. In some cases the molecular basis of resistance QTLs has been explained. Genes having a role in stress tolerance were shown to co-localize with tolerance QTLs in mapping

populations. This is the case of DREB/CBF genes, for which a large gene cluster has been mapped in correspondence of QTLs for frost and drought tolerance in barley and wheat (Vàgùjfalvi et al., 2005; Francia et al., 2007). On the other side, many efforts are in course to isolate the gene(s) behind tolerance QTLs, in order to have access to the transgenic approach, or to design perfect molecular markers to pyramid different QTLs into the same genotype through MAS without the risk of losing association due to recombination. The Arabidopsis *ERECTA* gene was cloned, as the sequence beyond a QTL for transpiration efficiency (Masle et al., 2005).

Even if the molecular basis of QTLs is not known, some examples are available in which the transfer of some tolerance QTLs in MAS programs has contributed to increase grain yield in water stress conditions (see paragraph n. 3).

Anyway, the investigation of molecular mechanisms which concur in regulating the water stress response in plant allows the identification of genes/processes with a key role in determining tolerance. The expression of these genes can be altered in transgenic plants in order to obtain a tolerant phenotype. Besides the genes reported in Table 1, in some cases this approach has been successful in increasing agronomic performance of plants in the field. An example is represented by transgenic wheat constitutively expressing the barley *HVA1* gene, encoding a member of the group 3 late embryogenesis abundant (LEA) proteins. Results of nine field experiments over six cropping seasons, showed that the *HVA1* protein confers a significant protection from water stress (Bahieldin et al., 2005). Aquaporins mediate most of the symplastic water transport in plants, which represents a limiting factor for plant growth and vigor in particular under unfavorable growth conditions and abiotic stress. Differential expression of genes that encode different aquaporin isoforms during plant development has been shown to be associated with various physiological processes. Such processes include stomatal closure and opening, organ movement, cell elongation, and cell division (Kaldenhoff et al., 2008). The *SITIP2* gene coding for an aquaporin was particularly effective in improving water stress resistance of tomato plants (Sade et al., 2009). Another successful gene is *OsNAC10*, introduced in field-tested rice plants under the control of the constitutive promoter *GOS2* and the root-specific promoter *RCc3* (Jeong et al., 2010).

## 7. Perspectives

Two different but complementary approaches have been presented in this chapter for the improvement of water stress tolerance. In the first one, the phenotypic and molecular evaluation of suitable genetic materials leads to the identification of genomic regions involved in the control of tolerance. At the same time, closely linked molecular markers are found, which can be used in MAS programs to transfer useful alleles for tolerance. In the second one, the molecular study of the water stress response in plant leads to the identification of genes/processes with a key role in determining tolerance.

In the last years, strong technical advances have been realized, in the frame of the “omic” technologies, which make the study of genomes, transcriptomes, proteomes, metabolomes and phenomes more rapid and precise. Methods for a more fine phenotypic evaluation of a high number of individuals, in both controlled and field conditions, are needed for an accurate genetic analysis on segregating populations or germplasm collections.

The development in particular of new DNA sequencing technologies rapidly is producing huge amounts of sequence information with a number of applications including genome resequencing and polymorphism detection, mutation mapping, DNA methylation and histone modification studies, transcriptome sequencing, gene discovery, alternative splicing identification, small RNA profiling and DNA-protein interactions (Lister et al., 2008; Delseny et al., 2010). Thanks to these advancements, new perspectives are open for the investigation of genetic and molecular basis of water stress tolerance. Sequencing of entire genomes of crop species is expected to provide a huge opportunity to clone QTLs for drought-related traits in the near future. Moreover, sequence analysis on a genome-wide scale allows the fast and low-cost development of extremely high number of molecular markers. The availability in particular of large SNP (Single Nucleotide Polymorphism) panels for crops will accelerate the QTL discovery and transfer in MAS programs already in course for single marker-trait associations. Furthermore, it will be possible to apply a new method called genomic selection (Meuwissen et al., 2001), which predicts breeding values using data deriving from all molecular markers covering the whole genome at the same time. In this way, breeders now have an opportunity to integrate classical phenotype-based selection with selection on the basis of genotype. In particular, they will have the possibility to follow genomic variations associated to many traits of interest at the same time.

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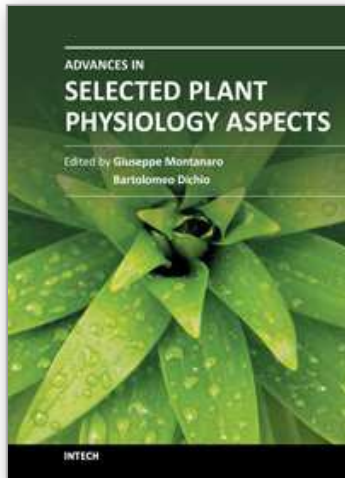
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