

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

185,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



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

Anna M. De Leonardis, Maria Petrarulo,
Pasquale De Vita and Anna M. Mastrangelo
*CRA-Cereal Research Centre, Foggia
Italy*

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).

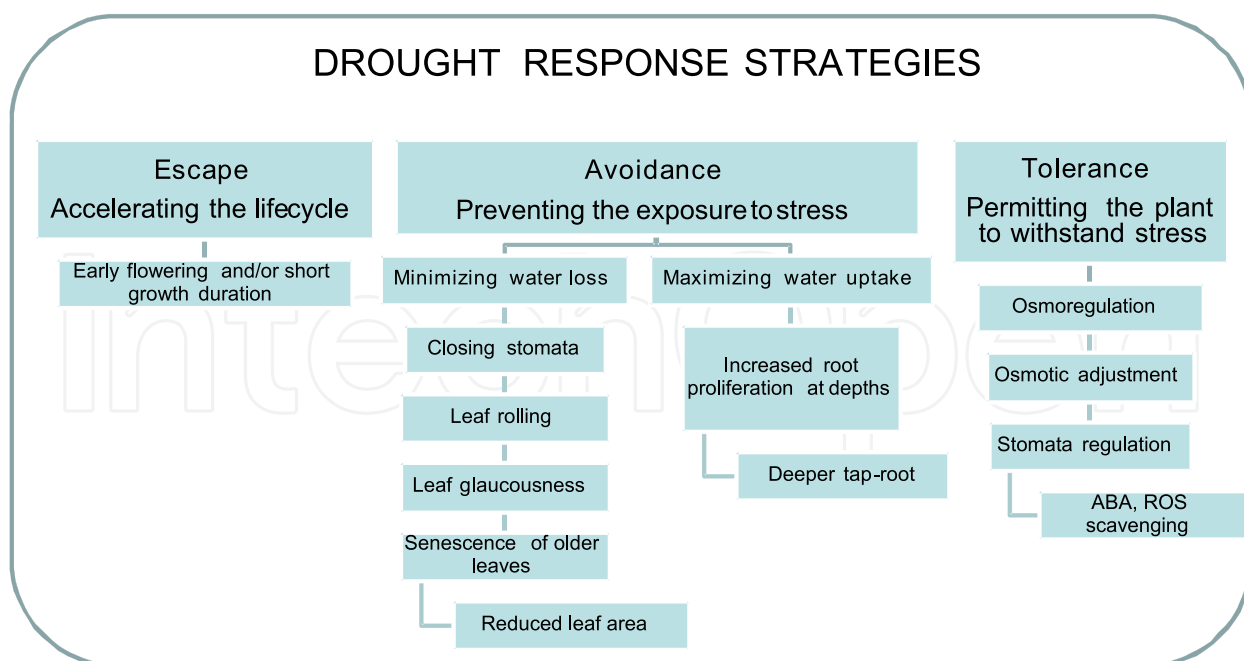


Fig. 1. Plant drought response mechanisms and main related traits.

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 CO₂ intake then results in reduced photosynthesis (Chaves et al., 2002). Nevertheless high yield requires high stomatal conductance to sustain a great CO₂ 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 CO₂ 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⁻¹ yr⁻¹) 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 (Δ) 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}C) and, as a result, in several C3 species, Δ is positively correlated with the ratio of internal leaf CO_2 concentration to ambient CO_2 concentration (C_i/C_a) and negatively associated with transpiration efficiency. Thus, a high C_i/C_a leads to a higher Δ 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⁺-ATPase and Ca²⁺-ATPase activities that trigger concerted changes of Ca²⁺ 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 toleracence (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	ERF	Sugarcane	overexpressed	Improved ABA, Salt and Woundig tolerance (Tobacco)	Trujillo et al., 2008
WXP1		Medicago	overexpressed	Improved Drought tolerance (Arabidopsis)	Zhang et al., 2007
GmERF3		Soybean	overexpressed	Improved Drought, salt and desease tolerance (Tobacco)	Zhang et al., 2009
RAP2.6		Arabidopsis	overexpressed	Hypersensitive to ABA, salt, osmotic and cold stress (Arabidopsis)	Zhu et al., 2010
DREB1C	DRE binding protein 1	Arabidopsis	overexpressed	Enhanced dessication tolerance (Arabidopsis)	Novillo et al., 2004
AtDREB1A		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	bZIP	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		Maize	overexpressed	Improved photosynthetic capacity under drought stress (Arabidopsis)	Zhang et al., 2008
SlAREB		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
OsbZIP23		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		Arabidopsis	overexpressed	Improved drought tolerance and enhanced sensitivity to ABA (Arabidopsis)	Ding et al., 2009
AtMYB41	R2R3 MYB	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		Arabidopsis	overexpressed	Improved drought and salt tolerance (Arabidopsis)	Tran et al., 2004
ONAC045	NAC	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 (Vågøfjalvi 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.

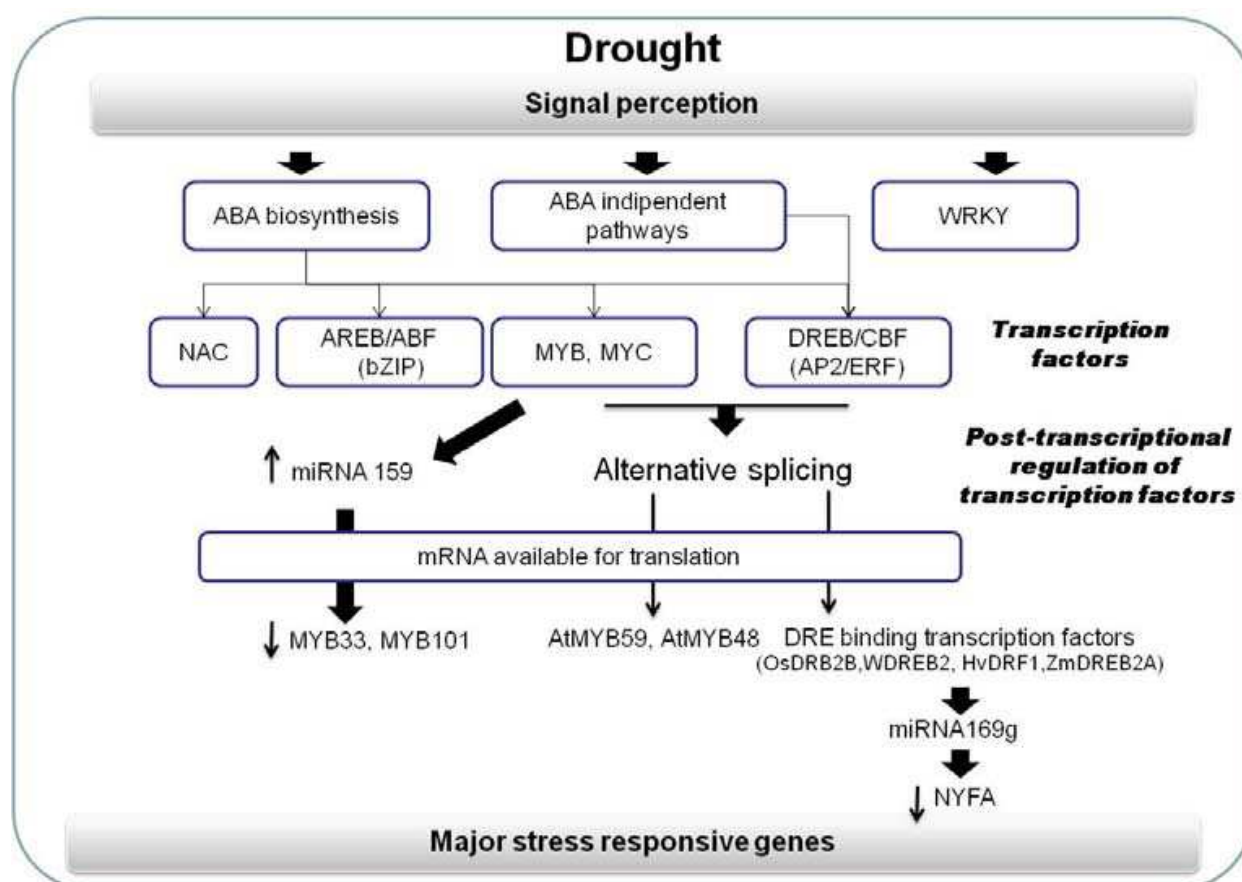


Fig. 2. ABA-dependent and independent pathways of response to drought in plants.

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.

8. Acknowledgements

This study was supported by the Italian Ministry of Agriculture (MiPAAF), with the special grants AGRONANOTECH and MAPPA 5A, and by the Ministry of Education, University and Research (MIUR), with the special grant AGROGEN.

9. References

- Abeledo, L.G., Calderoni, D.F. & Slafer, G.A. (2002). Genetic improvement of barley yield potential and its physiological determinants in Argentina (1944–1998), *Euphytica* Vol.130: 325–334.
- Ambrosone, A., Costa, A., Leone, A. & Grillo, S. (2011). Beyond transcription: RNA-binding proteins as emerging regulators of plant response to environmental constraints, *Plant Science* doi: 10.1016/J.plantsci. 2011.02.004.
- Amir Hossain, M., Lee, Y., Cho, J.I., Ahn, C.H., Lee, S.K., Jeon, J.S., Kang, H., Lee, C.H., An, G. & Park, P.B. (2010), The bZIP transcription factor OsABF1 is an ABA responsive element binding factor that enhances abiotic stress signaling in rice, *Plant Molecular Biology* Vol.72: 557–566.
- Amudha, J., & Balasubramani, G. (2011). Recent molecular advances to combat abiotic stress tolerance in crop plants, *Biotechnology and Molecular Biology Review* Vol.6(No. 2): 31–58.
- Anderson, P. & Kedersha, N. (2009). RNA granules: post-transcriptional and epigenetic modulators of gene expression, *Natural Review Molecular Cell Biology* Vol.10: 430–436.
- Araus, J.L., Slafer, G.A., Reynolds, M.P. & Royo, C. (2002). Plant breeding and drought in C-3 cereals: what should we breed for?, *Annals of Botany* Vol.89: 925–940.
- Ashraf, M. (2010). Inducing drought tolerance in plants: recent advances, *Biotechnol Advances* Vol. 28(No.1): 169–183.
- Bahieldin, A., Mahfouz, H.T., Eissa, H.F., Saleh, O.M., Ramadan, A.M., Ahmed, I.A., Dyer, W.E., El-Itriby, H.A. & Madkour, M.A. (2005). Field evaluation of transgenic wheat

- plants stably expressing the HVA1 gene for drought tolerance, *Physiologia Plantarum* Vol. 123: 421-427.
- Bartels, D. & Souer, E. (2004). Molecular responses of higher plants to dehydration, in H. Hirt, K. Shinozaki (ed.), *Plant Responses to Abiotic Stress*, Springer Verlag, Berlin, Heidelberg, pp. 9-38.
- Bartel, D.P. (2004). MicroRNAs: Genomics, biogenesis, mechanism, and function, *Cell* Vol.116: 281-297.
- Beffagna, N., Buffoli, B. & Busi, C. (2005). Modulation of reactive oxygen species production during osmotic stress in *Arabidopsis thaliana* cultured cells: involvement of the plasma membrane Ca^{2+} -ATPase and H^{+} ATPase, *Plant Cell Physiology* Vol. 46 :1326-1339.
- Bengough, A.G., McKenzie, B.M., Hallett, P.D. & Valentine, T.A. (2011). Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits, *Journal of Experimental Botany* Vol.62 (No. 1). 59-68.
- Bolanos, J. & Edmeades, G.O. (1996). The importance of anthesis-silking interval in breeding for drought tolerance in tropical maize, *Field Crops Research* Vol.48(No. 1): 65-80.
- Borsani, O., Zhu, J., Verslues, P.E., Sunkar, R. & Zhu, J.-K. (2005). Endogenous siRNAs derived from a pair of natural cis-antisense transcripts regulate salt tolerance in *Arabidopsis*, *Cell* Vol.123: 1279-1291.
- Boudsocq, M. & Laurière, C. (2005). Osmotic signaling in plants: multiple pathways mediated by emerging kinase families, *Plant Physiology* Vol.138: 1185-1194.
- Bray, E.A. (2004). Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*, *Journal Experimental Botany* Vol.55: 2331-2341.
- Burd, C.G. & Dreyfuss, G. (1994). Conserved structures and diversity of functions of RNA-binding proteins, *Science* Vol.265: 615-621.
- Calderini, D.F. & Slafer, G.A. (1998). Changes in yield and yield stability in wheat during the 20th century, *Field Crops Research* Vol.57: 335-347.
- Camporeale, G., Oommen, A.M., Griffin, J.B., Sarath, G. & Zemleni, J. (2007). K12-biotinylated histone H4 marks heterochromatin in human lymphoblastoma cells, *The Journal of Nutritional Biochemistry* Vol. 18: 760-768.
- Cattivelli, L., Delogu, G., Terzi, V. & Stanca, A.M. (1994). Progress in barley breeding, in Slafer GA (ed.), *Genetic Improvement of Field Crops*, Marcel Dekker, Inc. New York, pp. 95-181.
- Cattivelli, L., Rizza, F., Badeck, F.-W., Mazzucotelli, E., Mastrangelo, A.M., Francia, E., Marè, C., Tondelli, A. & Stanca, A.M. (2008). Drought tolerance improvement in crop plants: an integrated view from breeding to genomics, *Field Crops Research* Vol.105: 1-14.
- Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osório, M.L., Carvalho, I., Faria, T. & Pinheiro, C. (2002). How Plants Cope with Water Stress in the Field? Photosynthesis and Growth, *Annals of Botany* Vol.89(No. 7): 907-916.
- Chen, X., Yang, R.-F., Li, W.-C. & Fu, F.-L. (2010). Identification of 21 microRNAs in maize and their differential expression under drought stress, *African Journal of Biotechnology* Vol. 9 (No. 30): 4741-4753.
- Chinnusamy, V., Schumaker, K. & Zhu, J.K. (2004). Molecular genetic perspectives on cross-talk and specificity in abiotic stress signalling in plants, *Jornal Experimental Botany* Vol.55: 225-236.

- Choi, H., Hong, J., Ha, J., Kang, J. & Kim, S.Y. (2000). ABFs, a family of ABA-responsive element binding factors, *Journal of Biological Chemistry* Vol. 275:1723-1730.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J. et al. (2005). *Europe-wide reduction in primary productivity caused by the heat and drought in 2003*, *Nature* Vol.472: 529-533.
- Cominelli E., Galbiati M., Vavasseur A., Conti L., Sala T., Vuylsteke M., Leonhardt N., Dellaporta S. & Tonelli C. (2005). A guard-cell-specific MYB transcription factor regulates stomatal movements and plant drought tolerance, *Current Biology* Vol.15:1196-1200.
- Cook, K.B., Kazan, H., Zuberi, K., Morris, Q. & Hughes, T.R. (2010). RBPDB: a database of RNA-binding specificities, *Nucleic Acids Research* Vol.39(suppl.1): 301-308.
- Courtois, B., Ahmadi, N., Khowaja, F., Price, A.H., Rami, J.F., Frouin, J., Hamelin, C. & Ruiz, M. (2009). Rice Root Genetic Architecture: Meta-analysis from a Drought QTL Database, *Rice* Vol.2: 115-128.
- Covarrubiales, A.A. & Reyes, J.L. (2010). Post-transcriptional gene regulation of salinity and drought responses by plant microRNAs, *Plant Cell and Environment* Vol.33: 481-489.
- de Dorlodot, S., Forster, B., Pagè, L., Price, A., Tuberosa, R. & Draye, X. (2007). Root system architecture: opportunities and constraints for genetic improvement of crops, *Trends in Plant Science* Vol.12: 474-481.
- De Leonardis, A. M., Marone, D., Mazzucotelli, E., Neffar, F., Rizza, F., Di Fonzo, N., Cattivelli, L. & Mastrangelo, A.M. (2007). Durum wheat genes up-regulated in the early phases of cold stress are modulated by drought in a developmental and genotype dependent manner, *Plant Science* Vol.172: 1005-1016.
- De Vita, P., Mastrangelo, A.M., Matteu, L., Mazzucotelli, E., Virzi, N., Palumbo, M., Lo Storto, M., Rizza, F. & Cattivelli, L. (2010). Genetic improvement effects on yield stability in durum wheat genotypes grown in Italy, *Field Crops Research* Vol.119: 68-77.
- Delseny, M., Han, B. & Hsing, Y.I. (2010). High throughput DNA sequencing: The new sequencing revolution, *Plant Science* Vol. 179: 407-422.
- Dichio, B., Xiloyannis, C., Sofo, A. & Montanaro, G. (2006). Osmotic regulation in leaves and roots of olive tree (*Olea europaea* L.) during water deficit and rewatering. *Tree Physiology*, Vol. 26: 179-185.
- Ding, Z., Li, S., An, X., Liu, X., Qin, H., & Wang, D. (2009). Transgenic expression of MYB15 confers enhanced sensitivity to abscisic acid and improved drought tolerance in *Arabidopsis thaliana*, *Journal of Genetics & Genomics* Vol.36: 17-29.
- Dong, C.H., Agarwal, M., Zhang, Y., Xie, Q. & Zhu, J.K. (2006). The negative regulator of plant cold responses, HOS1, is a RING E3 ligase that mediates the ubiquitination and degradation of ICE1, *Proc. Natl. Acad. Sci. U.S.A.* Vol.103: 8281-8286.
- Downes, B. & Vierstra, R.D. (2005). Post-translational regulation in plants employing a diverse set of polypeptide tags, *Biochemical Society Transaction* Vol.33: 393-399.
- Dreyfuss, G., Kim, V.N. & Kataoka, N. (2002). Messenger-RNA-binding proteins and the messages they carry, *Nature Reviews Molecular Cell Biology* Vol.3: 195-205.
- Duan, K., Luo, Y.-H., Luo, D., Xu, Z.-H. & Xue, H.-W. (2005). New insights into the complex and coordinated transcriptional regulation networks underlying rice seed development through cDNA chip-based analysis, *Plant Molecular Biology* Vol.57: 785-804.
- Dyachenko, O.V., Zakharchenko, N.S., Shevchuk, T.V., Bohnert, H.J., Cushman, J.C. & Buryanov, Y.I. (2006). Effect of hypermethylation of CCWGG sequences in DNA of *Mesembryanthemum crystallinum* plants on their adaptation to salt stress, *Biochemistry (Moscow)* Vol.71: 461-465.

- Eapen, D., Barroso, M.L., Ponce, G., Campos, M.E. & Cassab, G.I. (2005). Hydrotropism: Root growth responses to water, *Trends in Plant Science* Vol.10: 44–50.
- Fang, Y., You, J., Xie, K., Xie, W. & Xiong, L. (2008). Systematic sequence analysis and identification of tissue-specific or stress-responsive genes of NAC transcription factor family in rice, *Molecular Genetics & Genomics* Vol.280: 547–563.
- Farquhar, G.D. & Richards, R.A. (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes, *Australian Journal of Plant Physiology* Vol.11: 539–552.
- Fischer, R.A., Rees, D., Sayre, K.D., Lu, Z.-M., Condon, A.G. & Larque Saavedra, A. (1998). Wheat Yield Progress Associated with Higher Stomatal Conductance and Photosynthetic Rate, and Cooler Canopies, *Crop Science* Vol. 38 (No. 6): 1467–1475.
- Fitzgerald, J.N., Lehti-Shui, M.D., Ingram, P.A., Deak, K.I., Biesiada, T. & Malamy, J.E. (2006). Identification of quantitative trait loci that regulate Arabidopsis root system size and plasticity, *Genetics* Vol.172: 485–498.
- Francia, E., Barabaschi, D., Tondelli, A., Laidò, G. Rizza, F., Stanca, A.M., Busconi, M. & Fogher, C. (2007). Fine mapping of a HvCBF gene cluster at the frost resistance locus Fr-H2 in barley, *Theoretical and Applied Genetics* Vol.115: 1083–1091.
- Fu, W., Wu, K. & Duan, J. (2007). Sequence and expression analysis of histone deacetylases in rice, *Biochemical and Biophysical Research Communication* Vol.356: 843–850.
- Fujita, M., Fujita, Y., Maruyama, K., Seki, M., Hiratsu, K., Ohme-Takagi, M., Tran, L.S.P., Yamaguchi-Shinozaki, K. & Shinozaki, K. (2004). A dehydration-induced NAC protein, RD26, is involved in a novel ABA-dependent stress-signaling pathway *The Plant Journal* Vol.39: 863–876.
- Fujita, Y., Fujita, M., Satoh, R., Maruyama, K., Parvez, M., Seki, M., Hiratsu, K., Ohme-Takagi, M., Shinozaki, K. & Yamaguchi-Shinozaki, K. (2005). AREB1 is a transcriptional activator of novel ABRE dependent ABA signaling that enhances drought stress tolerance in Arabidopsis, *Plant Cell* Vol.17: 3470–3488.
- Garrity, D.P. & O'Toole, J.C. (1994). Screening rice for drought resistance at the reproductive phase, *Field Crops Research* Vol.39: 99–110.
- Giuliani, S., Sanguineti, M.C., Tuberosa, R., Bellotti, M., Salvi, S. & Landi, P. (2005). Root-ABA1, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes, *Journal of Experimental Botany* Vol.56: 3061–3070.
- Gong, Z., Dong, C.H., Lee, H., Zhu, J., Xiong, L., Gong, D., Stevenson, B. & Zhu, J.K. (2005). A DEAD box RNA helicase is essential for mRNA export and important for development and stress responses in Arabidopsis, *Plant Cell* Vol.17: 256–267.
- Gong, Z., Lee, H., Xiong, L., Jagendorf, A., Stevenson, B. & Zhu, J.K. (2002). RNA helicase-like protein as an early regulator of transcription factors for plant chilling and freezing tolerance, *Proc. Natl Acad. Sci. USA* Vol.99: 11507–11512.
- Granot, G., Sikron-Persi, N., Gaspan, O., Florentin, A., Talwara, S., Paul, L.K., Morgenstern, Y., Granot, Y. & Grafi, G. (2009). Histone modifications associated with drought tolerance in the desert plant *Zygophyllum dumosum* Boiss, *Planta* Vol.231: 27–34.
- Gupta, P., Langridge, P. & Mir, R.R. (2010). Marker-assisted wheat breeding: present status and future possibilities, *Molecular Breeding* Vol.26: 145–161.
- Haake, V., Cook, D., Riechmann, J.L., Pineda, O., Thomashow, M.F. & Zhang J.Z. (2002). Transcription factor CBF4 is a regulator of drought adaptation in Arabidopsis, *Plant Physiology* Vol.130: 639–648.

- Harb, A., Krishnan, A., Ambavaram, M.M.R. & Pereira, A. (2011). Molecular and Physiological Analysis of Drought Stress in Arabidopsis Reveals Early Responses Leading to Acclimation in Plant Growth, *Plant Physiology* Vol.154: 1254–1271.
- Hay, R.T. (2005). SUMO: a history of modification, *Molecular Cell* Vol.18: 1–12.
- Hicke, L. (2001). Protein regulation by monoubiquitin, *Nature Reviews Molecular Cell Biology* Vol.2: 195–201.
- Hirayama, T. & Kazuo Shinozaki, K.(2010). Research on plant abiotic stress responses in the post-genome era: past, present and future, *The Plant Journal* Vol.61: 1041–1052.
- Ho, M.D., Rosas, J.C., Brown, K.M. & Lynch, J.P. (2005). Root architectural tradeoffs for water and phosphorus acquisition, *Functional Plant Biology* Vol.32: 737–748.
- Hochholdinger, F., Park, W.J., Sauer, M. & Woll, K. (2004). From weeds to crops: Genetic analysis of root development in cereals, *Trends in Plant Science* Vol.9: 42–48.
- Hsieh, T.H., Li, C.W., Su, R.C., Cheng, C.P., Sanjaya, T. et al., (2010). A tomato bZIP transcription factor, SlAREB, is involved in water deficit and salt stress response, *Planta* Vol.231: 1459–1473.
- Hugouvieux, V., Kwak, J.M. & Schroeder, J.I. (2001). An mRNA cap binding protein, ABH1, modulates early abscisic acid signal transduction in Arabidopsis, *Cell* Vol.106: 477–487.
- Hussain, S.S., Kayani, M.A. & Amjad, M. (2011). Transcription Factors as Tools to Engineer Enhanced Drought Stress Tolerance in Plants, *American Institute of Chemical Engineers February* Vol.7: 297–306.
- Ingram, J. & Bartels D. (1996). The molecular basis of dehydration tolerance in plants. *Annual Reviews Plant Physiology Plant Molecular Biology* Vol.47: 377–403.
- Ishitani, M., Xiong, L., Lee, H., Stevenson, B. & Zhu, J.K. (1998). HOS1, a genetic locus involved in cold-responsive gene expression in Arabidopsis, *Plant Cell* Vol.10: 1151–1162.
- Ito, Y., Katsura, K., Maruyama, K., Taji, T., Kobayashi, M., Seki, M., Shinozaki, K. & Yamaguchi-Shinozaki, K. (2006). Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice, *Plant Cell Physiology* Vol.47: 141–153.
- Ito, H., Gaubert, H., Bucher, E., Mirouze, M., Vaillant, I. & Paszkowski, J. (2011). An siRNA pathway prevents transgenerational retrotransposition in plants subjected to stress, *Nature* Vol.472: 115–119.
- Jen, C.-H., Michalopoulos, I., Westhead, D.R. & Meyer, P. (2005). Natural antisense transcripts with coding capacity in Arabidopsis may have a regulatory role that is not linked to double-stranded RNA degradation, *Genome Biology* Vol.6: R51.
- Jeong, J.S., Kim, Y.S., Baek, K.H., Jung, H., Ha, S.H., Do Choi, Y., Kim, M., Reuzeau, C. & Kim, J.K. (2010). Root-specific expression of Os-NAC10 improves drought tolerance and grain yield in rice under field drought conditions, *Plant Physiology* Vol.153: 185–197.
- Jiang, Y. & Deyholos. M.K. (2009). Functional characterization of Arabidopsis NaCl-inducible WRKY25 and WRKY33 transcription factors in abiotic stresses, *Plant Molecular Biology* Vol.69: 91–105.
- Jones-Rhoades, M.W. & Bartel, D.P. (2004). Computational identification of plant microRNAs and their targets, including a stress-induced miRNA, *Molecular Cell* Vol.14: 787–799.

- Jones-Rhoades, M.W., Bartel, D.P. & Bartel, B. (2006). MicroRNAs and their regulatory roles in plants, *Annual Review of Plant Biology* Vol. 57: 19–53.
- Jung, C., Seo, J.S., Han, S.W., Koo, Y.J., Kim, C.H., Song, S.I., Nahm, B.H., Choi, Y.D. & Cheong, J.J. (2008). Overexpression of AtMYB44 enhances stomatal closure to confer abiotic stress tolerance in transgenic Arabidopsis, *Plant Physiology* Vol.146: 623–635.
- Kader, M.A. & Lindberg, S. (2010). Cytosolic calcium and pH signaling in plants under salinity stress, *Plant Signaling & Behaviour* Vol. 5: 233–238.
- Kaldenhoff, R., Ribas-Carbo, M., Flexas Sans, J., Lovisolo, C., Heckwolf, M. & Uehlein, N. (2008). Aquaporins and plant water balance, *Plant, Cell and Environment* Vol.31: 658–666.
- Kang, J., Choi, H., Im, M. & Kim, S.Y. (2002). Arabidopsis basic leucine zipper proteins that mediate stress-responsive abscisic acid signalling, *Plant Cell* Vol.14: 343–357.
- Kapazoglou, A., Tondelli, A., Papaefthimiou, D., Ampatzidou, H., Francia, E., Stanca, M.A., Bladenopoulos, K. & Tsaftaris, A.S. (2010). Epigenetic chromatin modifiers in barley: IV. The study of barley polycomb group (PcG) genes during seed development and in response to external ABA, *BMC Plant Biology* Vol.10: 73.
- Karlson, D., Nakaminami, K., Toyomasu, T. & Imai, R. (2002). A cold-regulated nucleic acid-binding protein of winter wheat shares a domain with bacterial cold shock proteins, *The Journal of Biological chemistry* Vol.277: 35248–35256.
- Kasuga, M., Miura, S. & Yamaguchi-Shinozaki, K. (2004). A combination of the Arabidopsis DREB1A gene and stress inducible rd29A promoter improved drought and low temperature stress tolerance in tobacco by gene transfer, *Plant Cell Physiology* Vol.45: 346–350.
- Kerstiens, G. (2006). Water transport in plant cuticles: an update, *Journal of Experimental Botany* Vol. 57(No. 11): 2493–2499.
- Kim, Y.O., Pan, S.O., Jung, C.H. & Kang, H. (2007). A zinc finger-containing glycine-rich RNA-binding protein, atRZ-1a, has a negative impact on seed germination and seedling growth of Arabidopsis thaliana under salt or drought stress conditions, *Plant Cell Physiology* Vol.48: 1170–1181.
- Kobayashi, A., Takahashi, A., Kakimoto, Y., Miyazawa, Y., Fujii, N., Higashitani, A. & Takahashi, H. (2007). A gene essential for hydrotropism in roots, *Proc. Natl. Acad. Sci. U.S.A.* Vol.104: 4724–4729.
- Kuhn, J.M. & Schroeder, J.I. (2003). Impacts of altered RNA metabolism on abscisic acid signaling, *Current Opinion in Plant Biology* Vol.6: 463–469.
- Lan, L., Li, M., Lai, Y., Xu, W., Kong, Z., Ying, K., Han, B. & Xue, Y. (2005). Microarray analysis reveals similarities and variations in genetic programs controlling pollination/fertilization and stress responses in rice (*Oryza sativa* L.), *Plant Molecular Biology* Vol.59: 151–164.
- Lareau, L.F., Green, R.E., Bhatnagar, R.S. & Brenner, S.E. (2004). The evolving roles of alternative splicing, *Current Opinion in Cell Biology* Vol.14: 273–282.
- Levitt (1972). Responses of plants to environmental stresses. Academic Press, New York.
- Li, J., Li, X., Guo, L., Lu, F., Feng, X., He, K., Wei, L., Chen, Z., Qu, L. J. & Gu, H. (2006). A subgroup of MYB transcription factor genes undergoes highly conserved alternative splicing in Arabidopsis and rice, *Journal of Experimental Botany* Vol. 57: 1263–1273.
- Li, W.X., Oono, Y., Zhu, J., He, X.J., Wu, J.M., Iida, K., Lu, X.Y., Cui, X., Jin, H. & Zhu, J.K. (2008). The Arabidopsis NFYA5 transcription factor is regulated transcriptionally and posttranscriptionally to promote drought resistance, *The Plant Cell* Vol.20: 2238–2251.

- Lilley, J.M. & Kirkegaard, J.A. (2007). Seasonal variation in the value of subsoil water to wheat: Simulation studies in southern New South Wales, *Australian Journal of Agricultural Research* Vol.58: 1115–1128.
- Lin, W.-Y., Matsuoka, D., Sasayama, D. & Nanmori, T. (2010). A splice variant of Arabidopsis mitogen-activated protein kinase and its regulatory function in the MKK6–MPK13 pathway, *Plant Science* Vol.178: 245–250.
- Lippold, F., Sanchez, D.H., Musialak, M., Schlereth, A., Scheible, W.R., Hinch, D.K. & Udvardi, M.K. (2009). AtMyb41 regulates transcriptional and metabolic responses to osmotic stress in Arabidopsis, *Plant Physiology* Vol.149: 1761–1772.
- Lira-Medeiros, C.F., Parisod, C., Fernandes, R.A., Mata, C.S., Cardoso, M.A. & Ferreira, P.C. (2010). Epigenetic variation in mangrove plants occurring in contrasting natural environment, *PLoS One* Vol.5: e10326.
- Lister, R., O'Malley, R.C., Tonti-Filippini, J., Gregory, B.D., Berry, C.C., et al. (2008). Highly integrated single base resolution maps of the epigenome in Arabidopsis, *Cell* Vol.133: 523–536.
- Lorkovic, Z.J. (2009). Role of plant RNA-binding proteins in development, stress response and genome organization, *Trends Plant Science* Vol.14: 229–236.
- Lu, X.-Y & Huang, X.-L. (2008). Plant miRNAs and abiotic stress responses, *Biochemical and Biophysical Research Communications* Vol.368: 458–462.
- Lynch, J. (1995). Root architecture and plant productivity, *Plant Physiology* Vol.109: 7–13.
- Maccaferri, M., Sanguineti, M.C., Corneti, S., Araus Ortega, J.L., Ben Salern, M. et al. (2008). Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* Desf.) across a wide range of water availability, *Genetics* Vol.178: 489–511.
- Maccaferri, M., Sanguineti, M.C., Giuliani, S. & Tuberosa, R. (2009). Genomics of Tolerance to Abiotic Stress in the Triticeae. In: Feuillet C, Muehlbauer G (eds) *Plant Genetics and Genomics: Crops and Models*, Vol. 7 Genetics and Genomics of the Triticeae, Springer, pp. 481–558.
- Manschadi, A.M., Christopher, J., Devoil, P. & Hammer, G.L. (2006). The role of root architectural traits in adaptation of wheat to water-limited environments, *Functional Plant Biology* Vol.33: 823–837.
- Masle, J., Gilmore, S.R. & Farquhar, G.D. (2005). The ERECTA gene regulates plant transpiration efficiency in Arabidopsis, *Nature* Vol.436: 866–870.
- Mastrangelo, A.M., Belloni, S., Barilli, S., Reperti, B., Di Fonzo, N., Stanca, A.M. & Cattivelli, L. (2005). Low temperature promotes intron retention in two e-cor genes of durum wheat, *Planta* Vol.221: 705–715.
- Mastrangelo, A.M., Mazzucotelli, E., Guerra, D., De Vita, P. & Cattivelli, L. (2011a). Improvement of drought resistance in crops: from conventional breeding to genomic selection In “Crop Stress and its Management: Perspectives and Strategies” Arun K. Shanker eds, DOI 10.1007/978-94-007-2220-0_7.
- Mastrangelo, A.M., Marone, D., Laidò, G., De Leonardi, A.M. & De Vita, P. (2011b). Alternative splicing: Enhancing ability to cope with stress via transcriptome plasticity, *Plant Science* doi:10.1016/j.plantsci.2011.09.006
- Matsukura, S., Mizoi, J., Yoshida, T., Todaka, D., Ito, Y., Maruyama, K., Shinozaki, k. & Yamaguchi-Shinozaki, K. (2010). Comprehensive analysis of rice DREB2-type genes that encode transcription factors involved in the expression of abiotic stress-responsive genes, *Molecular Genetics & Genomics* Vol.283: 185–196.

- Mazzucotelli, E., Mastrangelo, A.M., Crosatti, C., Guerra, D., Stanca, A.M. & Cattivelli, L. (2008). Abiotic stress response in plants: when post-transcriptional and post-translational regulations control transcription, *Plant Science* Vol.174:420–431.
- McGuire, A.M., Pearson, M.D., Neafsey, D.E. & Galagan, J.E. (2008). Cross-kingdom patterns of alternative splicing and splice recognition, *Genome Biology* Vol.9: R50.
- Meuwissen, T., Hayes, B.J. & Goddard, M.E. (2001). Prediction of total genetic value using genome-wide dense marker maps, *Genetics* Vol.157: 1819–1829.
- Miller, G., Shulaev, V. & Mittler, R. (2008). Reactive oxygen signaling and abiotic stress, *Physiologia Plantarum* Vol.133: 481–489.
- Mirouze, M., Reinders, J., Bucher, E., Nishimura, T., Schneeberger, K., Ossowski, S., Cao, J., Weigel, D., Paszkowski, J. & Mathieu, O. (2009). Selective epigenetic control of retrotransposition in *Arabidopsis*, *Nature* Vol.461: 427–430.
- Miura, K., Jin, J.B. & Hasegawa, P.M. (2007). Sumoylation, a post-translational regulatory process in plants, *Current Opinion in Plant Biology* Vol.10: 495–502.
- Mlynarova, L., Nap, J.P. & Bisseling, T. (2007). The SWI/SNF chromatinremodeling gene *AtCHR12* mediates temporary growth arrest in *Arabidopsis thaliana* upon perceiving environmental stress, *Plant Journal* Vol.51: 874–885.
- Mohammadi, M., Nat, N.V.K. & Deyholoso, M.K. (2007). Transcriptional profiling of hexaploid wheat (*Triticum aestivum* L.) roots identifies novel dehydration-responsive genes, *Plant Cell Environ* Vol.30: 630–645.
- Nathan D., Ingvarsdottir K., Sterner D.E., Bylebyl G.R., Dokmanovic M., Dorsey J.A., Whelan K.A., Krsmanovic M., Lane W.S., Meluh P.B. et al. (2006). Histone sumoylation is a negative regulator in *Saccharomyces cerevisiae* and shows dynamic interplay with positive-acting histone modifications, *Genes Development* Vol.20: 966–976.
- Ner-Gaon, H. & Fluhr, R. (2006). Whole-genome microarray in *Arabidopsis* facilitates global analysis of retained introns, *DNA Research* Vol.13: 111–121.
- Nobuta, K., Venu, R.C., Lu, C., Belo, A., Vemaraju, K., et al. (2007). An expression atlas of rice mRNAs and small RNAs, *Nature Biotechnology* Vol 25: 473–77.
- Novillo, F., Alonso, J.M., Ecker, J.R. & Salinas, J. (2004). CBF2/DREB1C is a negative regulator of CBF1/DREB1B and CBF3/DREB1A expression and plays a central role in stress tolerance in *Arabidopsis*, *Proc. Natl. Acad. Sci. U.S.A.* Vol.101: 3985–3990.
- Ogura, Y., Ihara, N., Komatsu, A., Tokioka, Y., Nishioka, M., Takase, T. & Kiyosue, T. (2008). Gene expression, localization, and protein-protein interaction of *Arabidopsis* SKP1-like (ASK) 20A and 20B, *Plant Science* Vol.174: 485–495.
- Oh S.J., Song S.I., Kim Y.S., Jang H.J., Kim M. & Kim Y.K. (2005). *Arabidopsis* CBF3/DREB1A and ABF3 in transgenic rice increased tolerance to abiotic stress without stunting growth, *Plant Physiology* Vol.138: 341–351.
- Oh, S.J., Kwon, C.W., Choi, D.W., Song S.I.K. & Kim, J.K. (2007). Expression of barley HvCBF4 enhances tolerance to abiotic stress in transgenic rice, *Journal of Plant Biotechnology* Vol.5: 646–656.
- Olsen, A.N., Ernst, H.A., Leggio, L.L. & Skriver, K. (2005). NAC transcription factors: structurally distinct, functionally diverse, *Trends in Plant Sciences* Vol.10: 79–87.
- Ooka, H., Satoh, K., Doi, K., Nagata, T., Otomo, Y., Marukami, K., Matsubara, K., Osato, N., Kawai, J., Carninci, P., Hayashizaki, Y., Suzuki, K., Kojima, K., Takahara, Y., Yamamoto, K. & Kikuchi, S. (2003). Comprehensive analysis of NAC family genes in *Oryza sativa* and *Arabidopsis thaliana*, *DNA Research* Vol.10: 239–247.

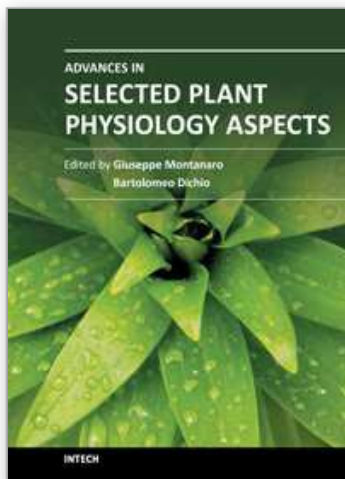
- Owtttrim, G.W. (2006). RNA helicases and abiotic stress, *Nucleic Acids Research* Vol. 34(No. 11): 3220-3230.
- Ozturk, Z.N., Talame, V., Deyholos, M., Michalowski, C.B., Galbraith, D.W., Gozukirmizi, N., Tuberosa, R. & Bohnert, H.J. (2002). Monitoring large-scale changes in transcript abundance in drought- and salt stressed barley, *Plant Molecular Biology* Vol.48: 551-573.
- Palusa, G.S. Ali, G.S. & Reddy, A.S.N. (2007). Alternative splicing of pre-mRNAs of Arabidopsis serine/arginine-rich proteins: regulation by hormones and stresses, *Plant Journal* Vol.49: 1091-1107.
- Park, H.Y., Kang, I.S., Han, J.S., Lee, C.H., An, G. & Moon, Y.H. (2009). OsDEG10 encoding a small RNA-binding protein is involved in abiotic stress signaling, *Biochemical and Biophysical Research Communication* Vol.380: 597-602.
- Pastori, G.M. & Foyer, C.H. (2002). Common components, networks and pathways of cross-tolerance to stress. The central role of 'redox' and abscisic-acid-mediated controls, *Plant Physiology* Vol.129: 460-468.
- Peleg, Z., Fahima, T., Krugman, T., Abbo, S., Yakir, D., Korol, A.B. & Saranga, Y. (2009). Genomic dissection of drought resistance in durum wheatxwild emmer wheat recombinant inbred line population. *Plant, Cell and Environment* Vol.32: 758-779.
- Pellegrineschi, A., Reynolds, M., Pacheco, M., Brito, R.M., Almeraya, R., Yamaguchi-Shinozaki, K. & Hoisington, D. (2004). Stress induced expression in wheat of the Arabidopsis thaliana DREB1A gene delays water stress symptoms under greenhouse conditions. *Genome* Vol.47: 493-500.
- Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davisk, M. et al. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, *Nature* Vol. 399: 429-436.
- Pinheiro, C. & Chaves, M.M. (2011). Photosynthesis and drought: can we make metabolic connections from available data?, *Journal of Experimental Botany* Vol.62(No. 3): 869-882.
- Price, A.H. & Tomos, A.D. (1997). Genetic dissection of root growth in rice (*Oryza sativa* L.). 2 mapping quantitative trait loci using molecular markers, *Theoretical and Applied Genetics* Vol.95: 143-152.
- Qiu, Y. & Yu, D. (2009). Over-expression of the stress-induced OsWRKY45 enhances disease resistance and drought tolerance in Arabidopsis, *Environment and Experimental Botany* Vol.65: 35-47.
- Ramamoorthy, R., Jiang, S.Y., Kumar, N., Venkatesh, P.N. & Ramachandran, S. (2008). A comprehensive transcriptional profiling of the WRKY gene family in rice under various abiotic and phytohormone treatments, *Plant Cell Physiology* Vol.49: 865-879.
- Ratcliffe, O.J. & Riechmann, J.L. (2002). Arabidopsis transcription factors and the regulation of flowering time: a genomic perspective, *Current Issues in Molecular Biology* Vol.4: 77-91.
- Rebetzke, G.J., Condon, A.G., Richards, R.A. & Farquhar, G.D. (2002). Selection for reduced carbon-isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat, *Crop Science* Vol. 42: 739-745.
- Reddy, A.R., Chaitanya, K.V. & Vivekanandan, M. (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants, *Journal of Plant Physiology* Vol.161: 1189-1202.
- Reinders, J., Wulff, B.B.H., Mirouze, M., Mari-Ordóñez, A., Dapp, M., Rozhon, W., Bucher, E., Theiler, G. & Paszkowski, J. (2009). Compromised stability of DNA methylation

- and transposon immobilization in mosaic Arabidopsis epigenomes, *Genes Development* Vol.23: 939-950.
- Ren, X., Chen, Z., Liu, Y., Zhang, H., Zhang, M., Liu, Q., Hong, X., Zhu, J.K. & Gong, Z. (2010). ABO3, a WRKY transcription factor, mediates plant responses to abscisic acid and drought tolerance in Arabidopsis, *Plant Journal* Vol.63: 417-429.
- Reyes, J.L. & Chua, N.H. (2007). ABA induction of miR159 controls transcript levels of two MYB factors during Arabidopsis seed germination, *The Plant Journal* Vol.49: 592-606.
- Rhoades, M.W., Reinhart, B.J., Lim, L.P., Burge, C.P., Bartel, B. & Bartel, D.P. (2002). Prediction of plant microRNA targets, *Cell* Vol.110: 513-520.
- Ribaut, J.M. & Ragot, M. (2007). Marker-assisted selection to improve drought adaptation in maize: the backcross approach, perspectives, limitations, and alternatives, *Journal of Exp Botany* Vol.58: 351-360.
- Riechmann, J.L., Heard, J., Martin, G., Reuber, L., Jiang, C., Keddie, J., Adam, L., Pineda, O., Ratcliffe, O.J. & Samaha, R.R., Creelman, R., Pilgrim, M., Broun, P., Zhang, J.Z., Ghandehari, D., Sherman, B.K. & Yu, B.K. (2000). Arabidopsis transcription factors: genome-wide comparative analysis among eukaryotes, *Science* Vol.290: 2105-2110.
- Rios, G., Gagate, A.P., Castillo, J., Berbel, A., Franco, L. & Rodrigo, M.I. (2007). Abscisic acid and desiccation-dependent expression of a novel putative SNF5-type chromatin-remodeling gene in *Pisum sativum*, *Plant Physiology and Biochemistry* Vol.45: 427-435.
- Rizhsky, L., Liang, H. & Mittler, R. (2002). The combined effect of drought stress and heat shock on gene expression in tobacco, *Plant Physiology* Vol.130: 1143-1151.
- Rizza, F., Ghashghaie, J., Meyer, S., Matteu, L., Mastrangelo, A.M. & Badeck, F.-W. (2011). Constitutive differences in water use efficiency between two durum wheat cultivars, *Fields Crops Research* doi: 10.1016/J.fcr.2011.09.001.
- Rocak, S. & Linder, P. (2004). DEAD-box proteins: the driving forces behind RNA metabolism. *Nature Review Molecular Cell Biology* Vol.5: 232-241.
- Sachetto-Martins, G., Franco, L.O. & deOliveira, D.E. (2000). Plant glycine-rich proteins: a family or just proteins with a common motif?, *Biochimica et Biophysica Acta* Vol.1492: 1-14.
- Sade, N., Vinocur, B.J., Diber, A., Shatil, A., Ronen, G., Nissan, H., Wallach, R., Karchi, H. & Moshelion, M. (2009). Improving plant stress tolerance and yield production: is the tonoplast aquaporin SLTIP2;2 a key to isohydric to anisohydric conversion?, *New Phytologist* Vol.181: 651-661.
- Sadras, V.O., & Rodriguez, D. (2007). The limit to wheat water use efficiency in eastern Australia. II. Influence of rainfall patterns, *Australian Journal of Agricultural Research* Vol.58: 657-669.
- Sahi, C., Agarwal, M., Singh, A. & Grover, A. (2007). Molecular characterization of a novel isoform of rice (*Oryza sativa* L.) glycine rich-RNA binding protein and evidence for its involvement in high temperature stress response, *Plant Science* Vol.173(No. 2): 144-155.
- Sanan-Mishra, N., Pham, X.H., Sopory, S.K. & Tuteja, N. (2005). Pea DNA helicase 45 overexpression in tobacco confers high salinity tolerance without affecting yield, *Proc. Natl Acad. Sci. USA* Vol.102: 509-514.
- Sarnowski, T.J., Rios, G., Jasik, J., Swiezewski, S., Kaczanowski, S., Li, Y., Kwiatkowska, A., Pawlikowska, K., Kozbial, M., Kozbial, P. et al. (2005). SWI3 subunits of putative SWI/SNF chromatin-remodeling complexes play distinct roles during Arabidopsis development, *Plant Cell* Vol.17: 2454-2472.

- Schoning, J.C., Streitner, C., Meyer, I.M., Gao, Y. & Staiger, D. (2008). Reciprocal regulation of glycine-rich RNA-binding proteins via an interlocked feedback loop coupling alternative splicing to non sense-mediated decay in *Arabidopsis*, *Nucleic Acids Research* Vol.36: 6977–6987.
- Scippa, G.S., Di Michele, M., Onelli, E., Patrignani, G., Chiatante, D. & Bray, E.A. (2004). The histone-like protein H1-S and the response of tomato leaves to water deficit, *Journal of Experimental Botany* Vol.55: 99-109.
- Serraj, R. & Sinclair, T.R. (2002). Osmolyte accumulation: can it really increase crop yield under drought conditions?, *Plant Cell and Environment* Vol.25: 333-341.
- Shinozahi, Z.K. & Yamaguchi-Shinozaki K. (2000). Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signalling pathways, *Current Opinion in Plant Biology* Vol. 3: 217–223.
- Siddique, K.H.M., Tennant, D., Perry, M.W. & Belford, R.K. (1990). Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment, *Australian Journal of Agricultural Research* Vol.41(No. 3): 431 – 447.
- Slafer, G.A., Araus, J.L., Royo, C. & Del Moral, L.F.G. (2005). Promising ecophysiological traits for genetic improvement of cereal yields in Mediterranean environments, *Annals of Applied Biology* Vol.146: 61-70.
- Slotkin, R.K. & Martienssen, R.A. (2007). Transposable elements and the epigenetic regulation of the genome, *Nature Reviews Genetics* Vol.8: 272-285.
- Sridha, S. & Wu, K. (2006). Identification of AtHD2C as a novel regulator of abscisic acid responses in *Arabidopsis*, *Plant Journal* Vol.46: 124-133.
- Sridhar, V.V., Kapoor, A., Zhang, K., Zhu, J., Zhou, T., Hasegawa, P.M., Bressan, R.A. & Zhu, J.K. (2007). Control of DNA methylation and heterochromatic silencing by histone H2B deubiquitination, *Nature* Vol.447: 735-738.
- Steele, K. (2009). Novel upland rice variety bred using marker-assisted selection and client-oriented breeding released in Jharkhand. India: Bangor University.
- Steele, K.A., Virk, D.S., Kumar, R., Prasad, S.C. & Witcombe, J.R. (2007). Field evaluation of upland rice lines selected for QTLs controlling root traits, *Field Crops Research* Vol.101: 180–186.
- Stone, S.L. & Callis, J. (2007). Ubiquitin ligases mediate growth and development by promoting protein death, *Current Opinion in Plant Biology* Vol.10: 624–632.
- Sunkar, R. & Zhu, R.-K. (2004). Novel and stress-regulated microRNAs and other small RNAs from *Arabidopsis*, *Plant Cell* Vol.16: 2001–2019.
- Szarzynska, B., Sobkowiak, L., Pant, B.D., Balazadeh, S., Scheible, W., Mueller-Roeber, B., Jarmolowski, A. & Szweykowska-Kulinska, Z. (2009). Gene structures and processing of *Arabidopsis thaliana* HYL 1-dependent pri-miRNAs, *Nucleic Acids Research* Vol.37: 3083–3093.
- Tambussi, E.A., Nogues, S., Ferrio, P., Voltas, J. & Araus, J.L. (2005). Does higher yield potential improve barley performance in Mediterranean conditions? A case of study, *Field Crop Research* Vol.91: 149-160.
- Tanner, N.K. & Linder, P. (2001). DExD/H box RNA helicases: from generic motors to specific dissociation functions, *Molecular Cell* Vol.8: 251–262.
- Taramino, G., Sauer, M., Stauffer, J.L., Multani, D., Niu, X., Sakai, H. & Hoccholding, F. (2007). The maize (*Zea mays* L.) RTCS gene encodes a LOB domain protein that is a key regulator of embryonic seminal and post-embryonic shoot-borne root initiation, *Plant Journal* Vol.50: 649–659.

- Tollenaar, M. & Wu, J. (1999). Yield in temperate maize is attributable to greater stress tolerance, *Crop Science* Vol.39: 1597-1604.
- Tollenaar, M. & Lee, E.A. (2002). Yield stability and stress tolerance in maize, *Field Crop Research* Vol.75: 161-169.
- Tran, L.S., Nakashima, K., Sakuma, Y., Simpson, S.D., Fujita, Y., Maruyama, K., Fujita, M., Seki, M., Shinozaki, K. & Yamaguchi-Shinozaki, K. (2004). Isolation and functional analysis of Arabidopsis stress inducible NAC transcription factors that bind to a drought responsive cis-element in the early responsive to dehydration stress 1 promoter, *Plant Cell* Vol.16: 2481-2498.
- Trujillo, L.E., Sotolongo, M., Menendez, C., Ochogava, M.E., Coll, Y., Hernandez, I., Borrás-Hidalgo, O., Thomma, B.P.H.J., Vera, P. & Hernandez, L. (2008). SodERF3, a novel sugarcane ethylene responsive factor (ERF), enhances salt and drought tolerance when over-expressed in tobacco plants, *Plant Cell Physiology* Vol.49: 512-515.
- Tuberosa, R., Sanguineti, M.C., Landi, P., Giuliani, M.M., Salvi, S. & Conti, S. (2002a). Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes, *Plant Molecular Biology* Vol.48: 697-712.
- Tuberosa, R., Salvi, S., Sanguineti, M.C., Landi, P., Maccaferri, M. & Conti, S. (2002b). Mapping QTLs regulating morphophysiological traits and yield: case studies, shortcomings and perspectives in drought stressed maize, *Annals of Botany* Vol.89: 941-963.
- Uno, Y., Furihata, T., Abe, H., Yoshida, R., Shinozaki, K. & Yamaguchi-Shinozaki, K. (2000). Arabidopsis basic leucine zipper transcription factors involved in an abscisic acid-dependent signal transduction pathway under drought and high-salinity conditions, *Proc Natl Acad Sci USA* Vol. 97: 11632-11637.
- Vågøfjalvi, A., Aprile, A., Miller, A., Dubcovsky, J., Delugu, G., Galiba, G. & Cattivelli, L. (2005). The expression of several Cbf genes at the Fr-A2 locus is linked to frost resistance in wheat, *Molecular Genetics & Genomics* Vol.274: 506-514.
- van Ginkel, M., Calhoun, D.S., Gebeyehu, G., Miranda, A., Tian-you, C., Pargas Lara, R., Trethowan, R.M., Sayre, K., Crossa, J. & Rajaram, S. (1998). Plant traits related to yield of wheat in early, late, or continuous drought conditions, *Euphytica* Vol.100: 109-121.
- Vashisht, A.A., Pradhan, A., Tuteja, R. & Tuteja, N. (2005). Cold- and salinity stress-induced bipolar pea DNA helicase 47 is involved in protein synthesis and stimulated by phosphorylation with protein kinase C, *Plant Journal* Vol.44: 76-87.
- Vazquez, F., Gasciolli, V., Crété, P. & Vaucheret, H. (2004). The nuclear dsRNA binding protein HYL1 is required for microRNA accumulation and plant development, but not post-transcriptional transgene silencing, *Current Biology* Vol.14: 346-351.
- Verslues, P.E., Agarwal, M., Katiyar-Agarwal, S., Zhu, J. & Zhu, J.K. (2006). Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status, *Plant Journal* Vol.45: 523-539.
- Vicient, C.M., Suoniemi, A., Ananthawat-Jonsson, K., Tanskanen, J., Beharav, A. et al. (1999). Retrotransposon BARE-1 and its role in genome evolution in the genus *Hordeum*, *Plant Cell* Vol.11: 1769-1784.
- Wang, X.-J., Gaasterland, T. & Chua, N.-H. (2005). Genome-wide prediction and identification of cis-natural antisense transcripts in *Arabidopsis thaliana*, *Genome Biology* Vol.6: R30.
- Wang, B.B. & Brendel, V. (2006). Genome wide comparative analysis of alternative splicing in plants, *Proc. Natl. Acad. Sci. USA* Vol. 103: 7175-7180.

- Whitmore, A.P. & Whalley, W.R. (2009). Physical effects of soil drying on roots and crop growth, *Journal of Experimental Botany* Vol.60: 2845–2857.
- Xiang, Y., Tang, N., Du, H., Ye, H. & Xiong, L. (2008). Characterization of Osb-ZIP23 as a key player of the basic leucine zipper transcription factor family for conferring abscisic acid sensitivity and salinity and drought tolerance in rice, *Plant Physiology* Vol.148: 1938–1952.
- Xiong, L., Gong, Z., Rock, C.D., Subramanian, S., Guo, Y., Xu, W., Galbraith, D. & Zhu, J.K. (2001). Modulation of abscisic acid signal transduction and biosynthesis by an Sm-like protein in Arabidopsis, *Developmental Cell* Vol.1: 771–781.
- Yang, K.Y., Liu, Y. & Zhang, S. (2001). Activation of a mitogen-activated protein kinase pathway is involved in disease resistance in tobacco, *Proc. Natl. Acad. Sci. U.S.A.* Vol.98: 741–746.
- Yang, D.L., Jing, R.L., Chang, X.P. & Li, W. (2007). Identification of quantitative trait loci and environmental interactions for accumulation and remobilization of water-soluble carbohydrates in wheat (*Triticum aestivum* L.) stems, *Genetics* Vol.176: 571–584.
- Yoshida, T., Fujita, Y., Salama, H., Kidokoro, S., Maruyama, K., Mizoi, J., Shinozaki, K. & Yamaguchi-Shinozaki, K. (2010). AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and require ABA for full activation, *Plant Journal* Vol.61: 672–685.
- Zhang, B., Pan, X., Cannon, C.H., Cobb, G.P. & Anderson, T.A. (2006). Conservation and divergence of plant microRNA genes, *Plant Journal* Vol.46: 243–259.
- Zhang, K., Sridhar, V.V., Zhu, J., Kapoor, A. & Zhu, J.K. (2007). Distinctive core histone post-translational modification patterns in Arabidopsis thaliana, *PLoS ONE* Vol.11: e1210.
- Zhang, X., Wollenweber, B., Jiang, D., Liu, F. & Zhao, J. (2008). Water deficit and heat shock effects on photosynthesis of a transgenic Arabidopsis thaliana constitutively expressing ABP9, a bZIP transcription factor, *Journal of Experimental Botany* Vol. 59: 839–848.
- Zhang, G., Chen, M., Li, L., Xu, Z., Chen, X., Guo, J. & Ma, Y. (2009). Overexpression of the soybean GmERF3 gene, an AP2/ERF type transcription factor for increased tolerances to salt, drought, and diseases in transgenic tobacco, *Journal of Experimental Botany* Vol.60(No. 13): 3781–3796.
- Zhao, B.T., Liang, R.Q., Ge, L.F., Li, W., Xiao, H.S., Lin, H.X., Ruan, K.C. & Jin, Y.X. (2007). Identification of drought-induced microRNAs in rice, *Biochemical and Biophysical Research Communication* Vol.354: 585–590.
- Zhao, B., Ge, L., Liang, R., Li, W., Ruan, K., Lin, H. & Jin, Y. (2009). Members of miR-169 family are induced by high salinity and transiently inhibit the NF-YA transcription factor, *BMC Molecular Biology* Vol.10: 29.
- Zheng, X., Chen, B., Lu, G. & Han, B. (2009). Overexpression of a NAC transcription factor enhances rice drought and salt tolerance, *Biochemical and Biophysical Research Communication* Vol.379: 985–989.
- Zhu, Q., Zhang, J., Gao, X., Tong, J., Xiao, L., Li, W. & Zhang, H. (2010). The Arabidopsis AP2/ERF transcription factor RAP2.6 participates in ABA, salt and osmotic stress responses, *Gene* Vol.457: 1–12.
- Zoon, F.C. & Van, Tienderen P.H. (1990). A rapid quantitative measurement of root length and root branching by microcomputer image analysis, *Plant Soil* Vol.126: 301–308.



Advances in Selected Plant Physiology Aspects

Edited by Dr. Giuseppe Montanaro

ISBN 978-953-51-0557-2

Hard cover, 388 pages

Publisher InTech

Published online 25, April, 2012

Published in print edition April, 2012

The book provides general principles and new insights of some plant physiology aspects covering abiotic stress, plant water relations, mineral nutrition and reproduction. Plant response to reduced water availability and other abiotic stress (e.g. metals) have been analysed through changes in water absorption and transport mechanisms, as well as by molecular and genetic approach. A relatively new aspects of fruit nutrition are presented in order to provide the basis for the improvement of some fruit quality traits. The involvement of hormones, nutritional and proteomic plant profiles together with some structure/function of sexual components have also been addressed. Written by leading scientists from around the world it may serve as source of methods, theories, ideas and tools for students, researchers and experts in that areas of plant physiology.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Anna M. De Leonardis, Maria Petrarulo, Pasquale De Vita and Anna M. Mastrangelo (2012). Genetic and Molecular Aspects of Plant Response to Drought in Annual Crop Species, *Advances in Selected Plant Physiology Aspects*, Dr. Giuseppe Montanaro (Ed.), ISBN: 978-953-51-0557-2, InTech, Available from: <http://www.intechopen.com/books/advances-in-selected-plant-physiology-aspects/genetic-and-molecular-aspects-of-plant-response-to-drought-stress>

INTECH
open science | open minds

InTech Europe

University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
www.intechopen.com

InTech China

Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

© 2012 The Author(s). Licensee IntechOpen. This is an open access article distributed under the terms of the [Creative Commons Attribution 3.0 License](https://creativecommons.org/licenses/by/3.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

IntechOpen

IntechOpen