Molecular Mechanisms in Plant Abiotic Stress Response

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Introduction

Modern agriculture faces abiotic stresses, especially salinity and drought as major factors limiting crop productivity worldwide. Low temperatures, heat shock, heavy metals, UV-radiation and pesticides are also abiotic factors affecting crop yields (Bohnert et al. 1995, Tardieu & Tuberosa 2010). Climate changes with erratic rainfalls and prolonged drought out of the expected season have multiplicative effects on abiotic stress consequences and seriously threaten sustainable agricultural production. High salinity is not only a soil-type characteristic but can be also observed in arable, irrigated areas due to use of low quality water. In addition, soil salinity induces water deficit that leads to nutrient deficiencies. Abiotic stress is one primary cause of crop loss worldwide, causing average yield losses of more than 50% for major crops. Plants can resist abiotic stresses through different distinct mechanisms. Tolerance and susceptibility to abiotic stresses are very complex. Plant traits that are associated with resistance mechanisms are multigenic and thus difficult to control and engineer.

Drought induces mechanical stress on roots due to soil hardness, osmotic stress because of cell dehydration and removal of water in the extra-cellular space, and oxidative stress by the accumulation of reactive oxygen species (ROS) (Kovtun et al. 2000).

Plants respond to water stress through organ-compartmentalised changes. In roots, there is an enhanced capture of soil moisture (e.g. reaching deep soil moisture with longer roots), while in stem/leaves there is a reduction of water loss (e.g. stomatal closure, reduction of plant size and/or leaf area) retaining tissue hydration via osmotic adjustments (OA). A prolific and deep root system confers better growth and yield under terminal drought, especially for varieties showing either deep rooting features and a positive harvest index (number and size of seeds) (Chandra Babu et al. 2001). In the case of water scarcity or drought, plants improve their water use efficiency either by dehydration avoidance or through dehydration tolerance (Plaut et al. 2004, Thomas & Howarth 2000, Blum 2005).

Reduced growth duration (with early flowering) is also an important mechanism as the plant generally uses less water and can also avoid the end-of-season (terminal) stress. However, reduced or early flowering plants may lead to lower production rates and smaller seeds.
Stress-Responsive Gene Expression

Under abiotic stress (drought, salinity) plants respond with the activation of synthesis or inhibition of catabolism of osmolytes as sugars (saccharopine, trehalose, raffinose, galactinol, sorbitol, mannitol, fructans) (Cortina & Culianez-Macia 2005) and sugar alcohols (e.g. polyols), amino acids as branched chain aminoacids (BCA), proline and agmatin, quaternary ammonium compounds and small dipeptides as glycinebetaine (Holmstrom et al. 2000). Polyamines (i.e. putrescine) are involved in the increase of a wide range of plant processes including wounding (Groppa & Benavides 2008). Having a role in development and H₂O₂ production, amine oxidases are involved in the induction of expression of genes at the crossroad varieties with genotypes having enhanced or faster polyamines that mediate the stress responses.

There is a need to provide established or new varieties with genotypes having enhanced or faster rate of induction of expression of genes at the crossroad of permissive growth under stress condition. This group of permissive genes includes aquaporin isoforms able to optimise water fluxes (Javot et al. 2003). Several genes have been characterised for their role on stress protection. ERECTA is a gene regulating transpiration efficiency affecting stomatal closure, while the plant is able to maintain biomass production (Masle et al. 2005).

Other important regulatory proteins involved in drought stress are proton antiporters as TNHX1 and a proton pyrophosphatase TVP1 (Brini et al. 2005, Brini et al. 2007a) shown to improve salt and drought stress tolerance in Arabidopsis.

Dehydrin isoforms (LEA/DHN) of sizes 17 kDa, 30 kDa and 40 kDa, function as intracellular chaperones for other proteins and nucleic acids. One dehydrin (DHN-5) was shown to be involved in salt and drought resistant phenotypes of durum wheat (Brini et al. 2007b). Dehydrins accumulate to a high level in the mature embryos. The accumulation of DHN-5 was shown to have a role in preservation of cell integrity during late embryogenesis and desiccation (Brini et al. 2007b).

Dehydrins are also known as late embryogenesis abundant (LEA) or early response to dehydration (ERD) proteins (Beck et al. 2007), so called because they also accompany seed formation. It has been shown that LEA/DHNs exert chaperone activity on proteins and also nucleic acids (Kovacs et al. 2008; Hara et al. 2009). DHN/LEAs lack a fixed three-dimensional structure, remarkably stable even at macromolecular crowding conditions, maintaining a disordered character under conditions (dehydration) in which unfolded states of several globular proteins would tend to collapse (Mouillon et al. 2008). Several LEA/DHN isoforms are regulated by abscisic acid (ABA) (Jimenez et al. 2008). While the size of induced DHNs was large, ranging between 14 kDa and 74 kDa, drought-tolerant bermudagrass varieties showed to induce preferentially the 31 kDa and 40 kDa isoforms (Hu et al. 2010).

Roots grow and recover their function after environmental stresses through specific genes that adapt root development to these restrictive conditions. The recovery of Medicago truncatula roots after a salt stress is mediated by regulatory networks depending on TFIIIA-like transcription factors, involved in the control of root adaptation to salt stress. Those conditions induced synthesis of a novel RNA-binding protein, a small G-protein homologous to ROP9, a receptor-like kinase, two TF IIIA-like and an AP2-like transcription factors (TF), MtZpt2-1, MtZpt2-2 and MtAp2, and a histidine kinase associated with cytokinin transduction pathways (Merchan et al. 2007).

Role of JA and ABA in Stress Signalling

The interplay of several plant hormones regulates the commitment of plants to growth or senescence under abiotic stress. The plant copes with a specific stress through complex signals circulating from roots to shoots and leaves (Fig. 1), and delivering hormones and signalling back to the roots, activating the expression of protective proteins or down-regulating unnecessary pathways. Plant hormones sustain signals at short distance, between cells, or in a systemic way in the case of transport systems. In this review, we will focus principally on the roles exerted by jasmonic acid (JA) and abscisic acid (ABA).

JA is the final product of the octodecanoic pathway which uses linoleic acid as substrate to produce oxylipins (Hughes et al. 2009). The octodecanoic pathway starts with the oxygenation of a polyunsaturated fatty acid (PUFA) by lipoxygenase (LOX), to form a fatty acid hydroperoxide. In plants, only the type-2 13-LOXs are believed to be associated with JA biosynthesis (De Domenico et al. 2007). In the biosynthesis of JA, the subsequent activities of 13-LOX, allene oxide synthase (AOS), allene oxide cyclase (AOC) lead to formation of cis-(-)-12-oxophytodienoic acid (OPDA), a JA precursor. JA can be methylated by a specific JA-methyltransferase. Methyl-Jasmonate (MeJA) is a volatile compound able to cross plasma membranes and exert its action at distance.

Another effector in the lipoxygenase biosynthesis pathway is jasmonate-conjugated isoleucin (JA-Ile) that may accumulate stored in organelles and
vacuoles. JA-Ile is able to translocate through membranes and move through xylem from roots to leaves and backward.

Once the hormone has arrived at its destination in the target cell (locally or at distance), the priming of jasmonate-inducible genes is regulated by convergent pathways, linked to phosphoinositide- and ABA-dependent signalling components.

1.1 JA Signalling in Root Response to Abiotic Stresses

Plant growth and development are largely dependent on the plant root system, due to its crucial role in water and mineral uptake. Abiotic below-ground stresses (e.g. drought, waterlogging, salt, nutrient soil status, physical soil properties) affect overall plant growth and architecture. This early signalling affects root growth regulation, resource acquisition and root-shoot communication under abiotic stress.

Many plants develop mutualistic interactions with arbuscular mycorrhizal (AM) fungi and with nitrogen-fixing bacteria. AM interaction is widely distributed among most of the land plants, while actinorhiza and rhizobia interactions are restricted to species of ten plant families, including the legumes. Fungi of the phylum *Glomeromycota* exist in a symbiotic association with vascular plants (Schüssler et al. 2006). As for the actinorhiza, the symbiosis occurs between actinobacteria of the genus *Frankia* and plants of *Fagales, Cucurbitales* and *Rosales* (Pawlowski & Sirrenberg 2003). On the other hand, the legume-rhizobia symbiosis (LRS) occurs between *Rhizobium* species and legumes (Kistner & Parniske 2002). Both types of nodule symbioses are characterized by the intracellular uptake of bacteria and the formation of specialized organs, the root nodules.

A phytohormone involved in the regulation of interactions between root and bacteria is JA and its conjugated form (MeJA) which cross the membrane barrier functioning as a long-distance signal (Hause & Schaarschmidt 2009). MeJA has been detected in high levels in germinating
soybeans and in root tips (Mason et al. 1992, Oldroyd 2009). Jasmonates directly induce nod gene expression in rhizobia, and indirectly promote bacterial Nod factor production by nod gene expression in rhizobia, and indirectly promote bacterial Nod factor production by inducing (iso)flavonoid biosynthesis genes in the plant (Zhang et al. 2007). As a negative feedback, Nod factor causes Ca^{2+} spiking in root hairs (Oldroyd 2009).

Regulation of the redistribution of nutrients might be the most important role of jasmonates in AM roots. In plants such as *M. truncatula* and barley, developing a mutualistic symbiosis which ultimately leads to a promoted growth, jasmonates might help to regulate the nutrient exchange between both partners. However, root JA and Me-Ja are important also in plants devoid of symbiotic relationships.

1.2 JA Receptors and Downstream Signal Transduction in Distant Signalling and Abiotic Stress Response

There is an intense communication between different organs through the phloem sap, the system of delivery of nutrients and solutes, and through the xylem, the water channels which move soluble compounds from roots to leaves. How these signals move, using the xylem or the phloem way, upward or downward, and which compounds (conjugated phytohormones, proteins, RNAs) is mostly unknown and under investigation, but several findings show a significant role of certain hormones and signals (Lough & Lucas 2006).

JA-related compounds have been identified in plants with mutations in components of the ubiquitin proteasome system (Tiryaki & Staswick 2002, Lorenzo & Solano 2005, Moon et al. 2007). Recent developments include the identification of COI1 as a receptor for jasmonates. COI1 is an F-box protein taking part of an Skp1-Cullin-F-box (SCF) complex, closely related to the auxin receptor revealed that formation of the ternary complex COI1-JA-Ile-JAZ is an ordered process (Balbi and Devoto 2008). JA-Ile promotes the interaction between the ubiquitin ligase complex SCF(COI1) and JAZ proteins, resulting in their degradation by the 26S proteasome, thereby liberating AtMYC2 from repression according to the prevailing model.

Two jasmonate-responsive promoter sequences are known. The GCC motif, commonly found in promoters activated synergistically by jasmonate and ethylene, and the G-box, found in promoters activated by jasmonates and repressed by ethylene. Important transcription factors conferring jasmonate-responsive gene expression in *Arabidopsis* are ORA59 and AtMYC2. ORA59 interacts with the GCC motif and controls the expression of genes that are synergistically induced by jasmonates and ethylene, whereas AtMYC2 interacts with the G-box and related sequences, and controls genes activated by jasmonate alone (Geller et al. 2010).

1.3 Early Stress Sensing in Roots and Associated Bacteria and Fungi

Once the soil derived signals (mechanical and osmotic stress, and signals originated from the stressed ectomycorrhiza) are sensed by root, they are rapidly translated into specific signals. The relevance of an early and immediate response in stress tolerant varieties is utmost, while in unresponsive varieties there is a delayed and reduced response (Schachtman & Goosder 2008).

Plant-growth-promoting (PGP) fungi (Pennisi 2006, White & Torres 2010) and plant-growth-promoting rhizobacteria (PGPR) (Liu et al. 2007) augment plant productivity and immunity through an increase in the antioxidative state. PGP endophytes induce root biomass, counteract salt-induced increase in heat efflux, produce changes in fatty acids composition, reduce lipid peroxidation in leaves, increase antioxidant enzyme activities and enable roots to maintain ascorbate in its reduced state under salt stress (Baltrushat et al. 2008). Certain bacteria promote plant growth through the activity of several genes, coding for putative proteins involved in survival in the rhizosphere (to cope with oxidative stress or uptake of nutrients released by plant roots), root adhesion (pili, adhesion, hemagglutinin, cellulose biosynthesis), colonization/establishment inside the plant (chemotaxis, flagella, cellulose phosphorylase), plant protection against fungal and bacterial infections (siderophore production and synthesis of the antimicrobial compounds 4-hydroxybenzoate and 2-phenylethanol), and improved growth and development through the production of the phytohormones indole acetic acid, acetoin, and 2,3-butanediol (Taghavi et al. 2010).
PGPR also elicit the ‘induced systemic tolerance’ to salt and drought. Even in the non-ectosymbiotic population of bacteria, there are positive influences on the plant hosts. The *Pseudomonas syringae* phytotoxin coronatine mimics jasmonoyl-isoleucine (JA-Ile), which is a crucial plant signalling molecule for regulating plant defence responses (Weiler et al. 1994, Bender et al. 1999). During water stress, the nodules sense drought and respond by activating defence mechanisms (Luo et al. 2009). In this way, Ectomycorrhizas (EMs) and rhizobia alleviate and improve also stress tolerance of host plants (Yang et al. 2009). It is worthy to note that arbuscular mycorrhizal fungi host endosymbiotic bacteria providing beneficial properties such as heat tolerance and protection from pests (Naumann et al. 2010).

Bacteria possess a nitric-oxide-synthase involved in stress resistance. NO is a mobile gaseous second messenger that is sensed at root level. In legumes, globin NO binding proteins, called leghemoglobins, accumulate in symbiosomes (root nodules) of various legumes. Non-symbiotic *hb* genes are expressed in specific plant tissues, and over-expressed in organs of stressed plants. These observations suggest that nsHbs function as additional to O(2)-transporters, such as to modulate levels of ATP and NO (avoiding protein nitrosylation). Non-symbiotic haemoglobins are a key enzymatic system for NO scavenging in plants, indicating that the primordial function of haemoglobins may be linked to the protection against nitrosative stress (Perazzolli et al. 2006, Smagghe et al. 2009).

*P. fluorescens* WCS417r bacteria and beta-aminobutyric acid can induce disease resistance in *Arabidopsis*, priming specific defence mechanisms. Both WCS417r and beta-aminobutyric acid prime enhanced deposition of callose-rich papillae after infection by the oomycete *Hyaloperonospora arabidopsi* (Van der Ent et al. 2009).

### 2.1 Abscisic Acid in Abiotic Stresses

Abscisic acid (ABA) is a phytohormone involved in senescence, seed dormancy, plant development, drought tolerance and stress response, synthesised in the xylem and in the aerial parts of the plant, where it regulates stomatal movement and the activity of shoot meristems. ABA can flow in the root cortex across apoplastic barriers and play an important role in the regulation of signal intensity. The abscisic acid glucose ester (ABA-GE) is a long-distance stress signal, stored in microsomes, and released by activated beta-glucosidases, both in the apoplast and the cytosol of the mesophyll cells. ABA-GE transporters located on plasma membrane of the xylem parenchyma cells influence ABA mobility. When discussing the intensity of the ABA signal in the xylem, internal and external sources of ABA have to be considered. External ABA originates from root exudation and from ABA-producing soil organisms (predominantly fungi), whereas internal ABA comes from its biosynthesis at root shoots level and phloem import (Sauter & Hartung 2000, Sauter et al. 2001). It was shown that conjugated ABA (ABA-GE) also occurs in the soil, often in higher concentrations than ABA. The Casparian bands of the exodermis and endodermis are perfect barriers for ABA-GE. When an exodermis is absent (*Fabaceae* and hydroponically cultivated plants), external ABA-GE enters into the apoplast of the root cortex. Apoplastic β-glucosidases can cleave the conjugated form and release free ABA, which is distributed to the symplast and/or transported across the endodermis into the xylem (Hartung et al. 2002).

#### 2.2 Timing of ABA Synthesis and Mobilisation

NaCl causes a rapid increase in ABA level in the transpiring portion of growing leaves. Within 10 min following salt addition, ABA levels show a 6-fold increase in the distal portion of the leaf elongation zone whereas it accumulate later in the proximal portion. In the portion of the growing blade, ABA increases 3-fold and remains elevated during the following 20 min. This precedes the decrease in transpiration and stomatal conductivity. Twenty hours following salt addition, ABA concentration returned to the pre-stress level. Leaf elongation velocity was still reduced. An ATP-Binding Cassette (ABC) transporter, AtABCG25, expressed mainly in vascular tissues such as roots and leaf veins, localized in the outer cell membranes (Kuromori et al. 2010) was identified as the gene involved in a plant mutant hypersensitive to ABA at the germination and seedling stages. Plants genetically engineered to over express AtABCG25 had higher leaf temperature compared to normal plants and decreased water loss from isolated leaves. Thus, facilitated ABA movements may affect distant targets such as guard cells.

#### 2.3 Salt Stress and Phosphate Deficiency Increase ABA Formation in the Roots

Strong ABA synthesis and accumulation in the roots can be observed in plants affected by...
hemiparasites such as *Rhinanthus minor* (Jiang et al. 2004). ABA biosynthesis in the roots was 12-fold higher after attack, resulting in 14-fold higher ABA flows in the xylem.

Plants regulate inorganic phosphate (Pi) homeostasis to adapt to environmental changes in Pi availability. Some degree of cross-talk between ABA and other signalling pathways was reported in phosphate limitation conditions. This mechanism involves phosphate uptake increase from the soil and phosphate mobilization from the leaf. Upon Pi starvation, upregulated miR399 cleaves its target gene, PHO2, in *A. thaliana*, an ubiquitin-conjugating E2 enzyme, thereby releasing several protein targets from ubiquitin-pathway dependent degradation and increasing Pi content in the shoots (Franco-Zorrilla et al. 2007).

### 2.4 Correlation between Xylem ABA Concentration and Leaf Conductance

ABA signalling can be intensified in many crops, for instance grapevine, by applying modern irrigation techniques, such as partial root drying (PRD). PRD is an irrigation technique where water is distributed unevenly to the root system divided into irrigated and dry compartments. Applying PRD to grape cultivation (Stoll et al. 2000), ABA signalling was found to be reduced after prolonged drying of one compartment. To sustain PRD effects, it was necessary to alternate wet and dry parts regularly (PRD-A). PRD-A was shown to intensify ABA signalling with positive consequences for water saving and improvement of the quality of the crops (Dodd et al. 2008). The factors that regulate the intensity of the ABA signal in the xylem, on its route from the root to the target cells, are therefore of particular interest.

### 2.5 Role of ABA in JA Signalling

Recent findings have suggested an interaction between jasmonic acid and ABA in plants under drought stress (Mahouachi et al. 2007). The pattern of accumulation of JA is compatible with a triggering signal upstream ABA. The phytohormone ABA acts in all adaptive responses to environmental stresses. The phytohormones gibberellin (GA) and ABA play essential and often antagonistic roles in regulating plant growth, development and stress responses. The transduction of their signal occurs through several types of receptors (Razem et al. 2006). Soil water stress elicits a hydraulic response in the shoot, which precedes ABA signalling and stomatal closure (Christmann et al. 2007). ABA biosynthesis in leaves is increased significantly only when turgor approaches zero. The location of ABA release and the tissue-specific expression of ABA receptor types are signals for that particular tissue (seeds, leaves) to reorganize and reprogram, through epigenetic control, differential gene expression of an ABA-directed cluster of genes (Seki et al. 2007).

### 2.6 ABA Receptors and Downstream Signal Transduction

The Arabidopsis ABA receptor FLOWERING TIME CONTROL LOCUS A (FCA), the GA receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1) and the nuclear-located auxin receptor show an important activity as plant hormone receptors within the cell nucleus. GID1, FCA and TRANSPORT INHIBITOR RESPONSE1 (TIR1) receptors reveal a novel signalling mechanism that appears to be short, to be independent of relay intermediates, and to involve only protein–protein interactions that are affected by receptor-hormone binding.

FCA is a plant-specific RNA-binding protein, possesses two RNA-recognition motifs (RRM) in addition to a tryptophan-tryptophan (WW) protein-interaction domain. FCA shares sequence homology at the C-terminus with the ABA-binding protein (ABAP1) associated with the plasma membranes of barley aleurone cells. FCA ABA receptor affects RNA metabolism by binding directly to a RNA binding protein (Simpson et al. 2003).

Although ABAP1 does not possess the common RRM to bind RNA, it does possess a WW interaction domain that harbours residues homologous to the Prp40 splicing factor and there is substantial evidence to link nuclear WW-containing proteins to both transcription and RNA splicing. ABA–ABAP1 binding results in changes in ABAP1 protein conformation, the subsequent dissociation from an interacting protein in the plasma membrane, and the appearance of ABAP1 in cytosolic and nuclear compartments. In either instance, if the proteins that interact with characterized (FCA) or putative (ABAP1) receptors are restricted in their subcellular localization, then the mobility of ABA hormone receptors might have particular relevance for covering the entire suite of non-genomic and genomic responses encompassed by ABA (Hugouvieux et al. 2001).

PYR/PYL/RCAR proteins function as ABA receptors that, following ABA binding, inhibit...
the activity of known negative regulators of ABA signalling (the type 2C protein phosphatases (PP2Cs) AB11, AB12, HAB1, HAB2 and PP2CA) in both seeds and vegetative tissues. In the presence of ABA, PYR/PYL/RCARs bind to PP2Cs and induce the release of SNRK2 Ser/Thr kinases from PP2Cs, which would otherwise keep SNRK2s in an inactive state. The association of kinases from PP2Cs, which would otherwise keep PP2Cs and induce the release of SNRK2 Ser/Thr phosphorylation of downstream substrates, including ABA responsive element-binding protein (ABF) and ABA responsive element-binding factor (ABF) bZIP transcription factors activates ABA-responsive genes and ABA-related responses (Yin et al. 2009).

Another transcription factors activated by ABA signalling is R2R3MYB that translates ABA effects through differential gene expression (Abuqamar et al. 2009).

GPCR-type G proteins (GTG1 and GTG2) bind ABA specifically and interact with the Arabidopsis G protein alpha subunit, GPA1, but also have intrinsic GTP-binding and GTPase activity (Pandey et al. 2009).

Epigenetic processes are an integral part of ABA-regulated processes. Epigenetic mechanisms, namely, histone modifications and cytosine DNA methylation-induced modification of genome give rise to epigenomes (Chinnusamy et al. 2008). Abiotic stress-induced ABA regulates stomatal response and stress responsive gene expression through HDACs and HOS15-dependent histone deacetylation, as well as through the ATP-dependent SWITCH/SUCROSE NONFERMENTING CRC. ABA also probably regulates the abiotic stress response through DNA methylation and short interfering RNA pathways. Further studies on ABA-regulated epigenome will be of immense use to understand the plant development, stress adaptation and stress memory.

2.7 ABA and Abiotic Stress Memory

Abiotic stress-induced genomic changes are necessary for stress memory. UV-C radiation or flagellin (a plant defence elicitor) stress-induced changes in the genome have shown to be a dominant trait and transmitted through both the maternal and the paternal crossing partner in Arabidopsis (Molinier et al. 2006). Progeny of tobacco mosaic virus (TMV) infected plants showed enhanced frequency of the somatic and meiotic recombination rates at certain loci due to DNA hypomethylation. Thus, stress memory appears to be inherited through epigenetic changes (Boyko et al. 2007). ABA may be involved also in the somatic recombination frequency (Boyko et al. 2006) and induces chromatin remodelling, which regulates transcription, recombination, replication and genome organization. It is also likely that ABA might regulate DNA methylation through DML3 and siRNAs. Under abiotic stresses ABA mediates reduction in plant growth. One of the mechanisms of abiotic stress-induced growth arrest is regulated by chromatin remodelling (Mlynarova et al. 2007). Abiotic stress-induced inheritable epigenetic state might have an adaptive advantage but also a negative effect on the yield of crops, as stress memory can inhibit the expression of full potential of crops. There is a great interest to understand the role of ABA in abiotic stress memory to exploit it in agricultural practices.

2.8 Regulatory Metabolic Networks in Drought Stress Responses

Localised delivery of paracrine hormones, long distance signalling and a second wave of tissue specific hormone signals regulate the intensity of ABA signals (Jiang & Hartung 2008).

In higher plants, a number of physiological processes are regulated by systemic RNA signalling molecules. This phloem-mediated remote-control system provides specific and efficient regulation to fine-tune many plant developmental programs. In phloem, several endogenous RNA-binding proteins have been identified. In addition, viral RNA-binding proteins can counterbalance the plant RNA silencing effectors synthesised to block viral RNA (Lakatos et al. 2004). CmPP16 protein from Cucurbita maxima was shown to possess properties similar to those of viral movement proteins (Xoconostle-Cázares et al. 1999). Messenger RNAs have been shown to travel at long distance in the phloem. Four mRNAs (BEL5, LeT6, KNOTTED1 and GAI) are able to move for long distances in Arabidopsis and potato (Haywood et al. 2005, Banerjee et al. 2006). GAI RNA is the mRNA for gibberellin acid insensitive (GAI), a DELLA protein of Arabidopsis and potato (Haywood et al. 2005, Banerjee et al. 2006). GAI RNA is the mRNA for gibberellin acid insensitive (GAI), a DELLA protein of GRAS transcription factors (Pysh et al. 1999). DELLA proteins interact and block the activity of GA-responsive transcription factors (Huang & Yu 2009). The RNA–protein complexes are subsequently transported into sieve elements through plasmodesmata (Lucas et al. 2009). Non-coding RNAs (small RNAs as miRNAs, and long RNAs as antisense RNA, dsRNA, and long RNA species) have many roles, functioning as regulators of other mRNAs, at transcriptional
and post-transcriptional level, and controlling protein ubiquitination and degradation. Several microRNAs has been shown to move through the phloem to exert their activity at distance. MIR172 as well as MIR399, which is induced upon phosphate starvation, is present in small RNA libraries made from phloem exudates indicating that they are part of a long distance signalling network (Chuck & O’Connor 2010). Phloem specific small RNAs travel to inform the roots of the nutrient status of the shoot, such as miR319 (Zhang et al. 2009) which targets a subset of the TCP family of transcription factors. LOX2 expression may be dependent on TCP4, due to the presence of a promoter motif important for the direct regulation of LOX2 by TCP4 (Schommer et al. 2008).

Conclusions

The molecular analysis of stress-induced signalling pathways that lead to plant adaptation or to cell death constitutes a major research area in the abiotic stress field. The crossroad between stress adaptation and cell death and the determinant events leading to one or the other direction represent a challenging research area in the next future.

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Molekularni mehanizmi odgovora biljaka na abiotički stres

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Izvodi: Poboljšane sorte ratarskih useva so potrebne za održevanje zaliha hrane, borbu proti klimatskih promenam, nedostatka vode, povečanja temperature in visoke varijabilnosti padavin. Variabilnosti suše in porast zaslanjenosti zemljišta imajo nepovoljan uticaj na rast biljaka, a abiotički stres ozbiljno ugrožava održljiv poljoprivredni proizvodnjo. Kako bi se prevazišlo uviraču abiotičnega stresa, javlja se potreba za novimi, tolerantnimi sortami in signalni putevi regulisani biljnim hormonoma. U žiži mnogih skupin vodnih rastlin posebej se streča znanstvenikov svet, ker morajo napraviti sistem za obdrževanje biljnih organa v stresu.

Ključne reči: abscisinska kiselina (ABA), jasmonat (JA), osmotsko prilagojanje (OP), transkripcioni faktor (TF)