Journal of Plant Physiology 171 (2014) 486–496

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Molecular Biology

Abscisic acid and abiotic stress tolerance – Different tiers of regulation

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ARTICLE INFO

Article history:
Received 10 August 2013
Received in revised form
12 December 2013
Accepted 13 December 2013

Keywords:
ABA signaling
Abiotic stress
Abscisic acid
ACGT *cis* element
Protein phosphatase 2C

SUMMARY

Abiotic stresses affect plant growth, metabolism and sustainability in a significant way and hinder plant productivity. Plants combat these stresses in myriad ways. The analysis of the mechanisms underlying abiotic stress tolerance has led to the identification of a highly complex, yet tightly regulated signal transduction pathway consisting of phosphatases, kinases, transcription factors and other regulatory elements. It is becoming increasingly clear that also epigenetic processes cooperate in a concerted manner with ABA-mediated gene expression in combating stress conditions. Dynamic stress-induced mechanisms, involving changes in the apoplastic pool of ABA, are transmitted by a chain of phosphatases and kinases, resulting in the expression of stress inducible genes. Processes involving DNA methylation and chromatin modification as well as post transcriptional, post translational and epigenetic control mechanisms, forming multiple tiers of regulation, regulate this gene expression. With recent advances in transgenic technology, it has now become possible to engineer plants expressing stress-inducible genes under the control of an inducible promoter, enhancing their ability to withstand adverse conditions. This review briefly discusses the synthesis of ABA, components of the ABA signal transduction pathway and the plants' responses at the genetic and epigenetic levels. It further focuses on the role of RNAs in regulating stress responses and various approaches to develop stress-tolerant transgenic plants.

Introduction

Plants, though continuously exposed and challenged by environmental cues, are capable of surviving by means of adaptations at the molecular, cellular and chromatin level of organization (Kim et al., 2010). Drought, salinity and temperature variations are among the major abiotic stresses, which hamper plant growth and productivity and often cause a series of morphological, physiological and biochemical changes. One such example can be seen in plants adapted to cold conditions, which show up-regulation of genes involved in the synthesis of unsaturated fatty acids, while those exposed to drought show a decrease in the number and surface area of leaves and an increase in root length (Shinozaki et al., 2003). Abscisic acid (ABA) is a widely studied phytohormone, and its role in ameliorating abiotic stress in plants is well established. In plants, ABA is of paramount significance as it plays an important role in mediating host responses to both biotic and abiotic stresses. It not only helps in seed maturation and seed dormancy but also gives desiccation tolerance to the cells during dehydration stress and is hence aptly called as a stress hormone.

ABA: evolutionary significance, synthesis and stress regulatory mechanisms

ABA: ubiquitous presence across different lineages

ABA is present in cyanobacteria, algae, bryophytes, fungi, lichens and higher plants. Out of eleven species of cyanobacteria tested for ABA synthesis under varied stress conditions, four species showed an increase in the level of ABA when subjected to salt stress (reviewed in Wolfram, 2010). Even though the majority of bacterial species does not exhibit ABA synthesis, a study has reported the presence of ABA in endophytic bacteria, which are present in the roots of *Helianthus annuus* under water stress conditions (Forchetti et al., 2007). In the cyanobacterium *Anacystis nidulans*, exogenous ABA has been shown to increase growth (Ahmad et al., 1978;Wolfram, 2010). ABA is believed to have protective functions

Abbreviations: PP2C, protein phosphatase 2C; SNF, sucrose non-fermenting; SnRK2, SNF1-related protein kinase 2.

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http://dx.doi.org/10.1016/j.jplph.2013.12.007

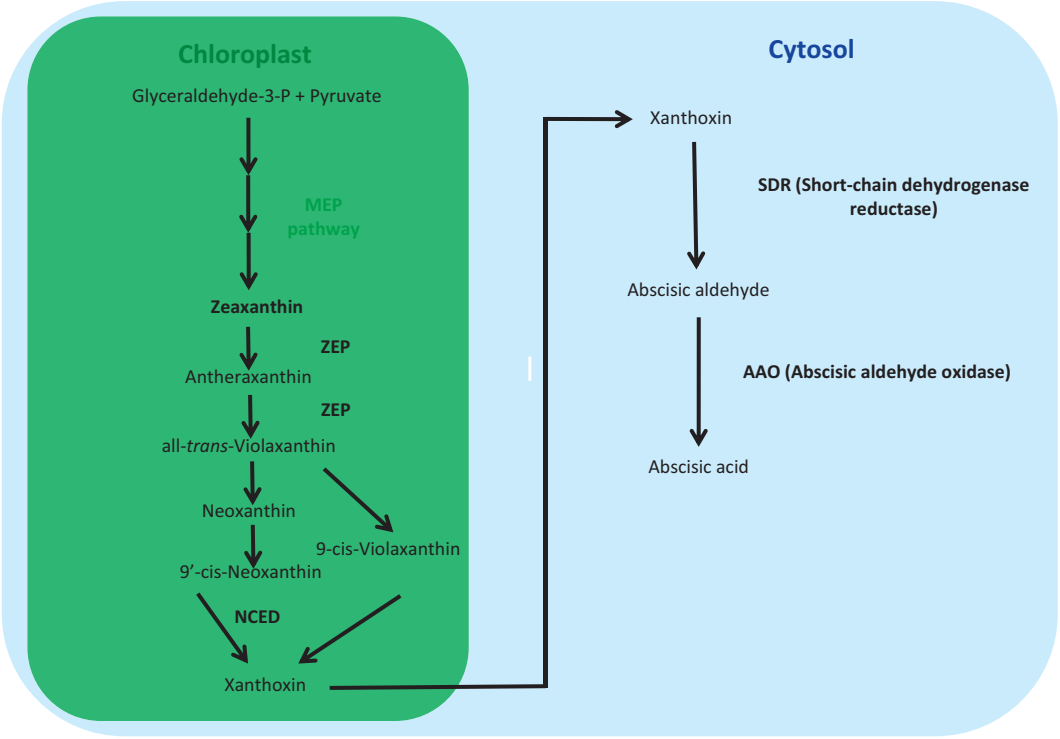

Fig. 1. Cellular synthesis of abscisic acid: ABA biosynthesis occurs partly in chloroplasts, and partly in the cytoplasm. The preliminary steps involve generation of zeathanxin from carotenoids via the MEP pathway. ABA synthesis starts from the breakdown of zeaxanthin to all-*trans* violaxanthin under the catalysis of zeaxanthin epoxidase (ZEP). The all-*trans* violaxanthin, an intermediate product, is catalyzed to xanthoxin in the presence of 9-*cis* epoxycarotenoid dioxygenase (NCED) in the chloroplast which is transported to the cytoplasm. In the cytoplasm, xanthoxin is first converted to abscisic aldehyde by short chain dehydrogenase reductase (SDR) and finally abscisic aldehyde is converted to ABA by the action of abscisic aldehyde oxidase (AAO).

in lower plants as it shields *Chlamydomonas reinhardtii* cells from photoinhibition and oxidative damage caused by salt and osmotic stress (Saradhi et al., 2000). ABA has also been found to regulate opening and closing of stomata in mosses and sporophytes of hornworts elucidating yet another function. More than 100 species of algae have also been reported for the presence of ABA though different algae respond differently to the applied stress (reviewed by Wolfram, 2010). With the evolution of liverworts, mosses and ferns, the endogenous levels of ABA have been observed to rise. However, the quantity of ABA has been shown to be very low in lower classes of plants.

ABA biosynthesis

ABA biosynthesis occurs via the mevalonic-acid independent pathway in plastids ABA, the 15-carbon isoprenoid plant hormone, is synthesized in plastids via the mevalonic acid-independent pathway called the 2-C-methyl-d-erythritol-4-phosphate (MEP) pathway. The 15 carbon atoms of ABA are derived from the cleavage of C_{40} carotenoids originating from the MEP pathway (Nambara and Marion-Poll, 2005). The biosynthesis of ABA starts in the plastids from the C_{40} carotenoid zeaxanthin and ends in the cytosol with the formation of abscisic aldehyde, which in turn, is oxidized into ABA (Seo and Koshiba, 2002). The mechanism of ABA biosynthesis is shown in Fig. 1.

In the plastid: from zeaxanthin to xanthoxin

The first step of the ABA-biosynthetic pathway is the conversion of zeaxanthin to all-*trans*-violaxanthin, catalyzed by zeaxanthin epoxidase (ZEP). Antheraxanthin is formed as an intermediate in this reaction. Thereafter, the conversion of all-*trans*-violaxanthin to 9-*cis*-violaxanthin or 9′-*cis*-neoxanthin occurs. The enzyme(s) involved in this reaction are not known (Seiler et al., 2011). The oxidative cleavage of 9-*cis*-violaxanthin and/or 9-*cis*-neoxanthin, catalyzed by 9-*cis*-epoxy carotenoid dioxygenase (*NCED*), leads to the formation of a C_{15} product, xanthoxin, and a C_{25} metabolite. This reaction is considered to be the rate-limiting step, and *NCED* is the key enzyme in ABA biosynthesis (Tan et al., 1997).

In the cytosol: from xanthoxin to ABA

Xanthoxin is transferred to the cytosol where it is converted to ABA via two enzymatic reactions. In the first step, xanthoxin is converted to abscisic aldehyde by an enzyme belonging to short-chain dehydrogenase/reductase (SDR) family. The gene responsible for this has been identified in *Arabidopsis thaliana*, named *AtABA2* (Gonzalez-Guzman et al., 2002). The final step of ABA biosynthesis is the oxidation of abscisic aldehyde to ABA. This reaction is catalyzed by an abscisic aldehyde oxidase (AAO).

ABA transport

ABA transport is both passive and mediated by ABA transporters

The level of endogenous ABA is maintained by interaction between anabolic and catabolic pathways. The catabolic products like ABA glucosyl ester and phaseic acid are stored in the vacuole or apoplast pool. Under drought stress, ABA is released from its conjugate form, which is facilitated by β-glucosidase, and is transported to guard cells where its accumulation leads to stomatal closure. One such enzyme, AtBG1, a type of β-glucosidase, has been reported in *A. thaliana* (Lee et al., 2006a).

It is not clear if specific transporters facilitate the movement of ABA between cells. It has been shown that ABA transport to the outside of cells in response to pH changes can occur without a specific transporter (Seo and Koshiba, 2011). Similarly, at the site of action, ABA uptake into cells could be mediated by diffusion or by