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# Abscisic acid biosynthesis, regulation and physiological response

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**Abstract**
ABA (Abscisic acid) is a central hormone in plants, which plays a key role in the regulation of several important processes. The pathways for ABA biosynthesis contains three main steps: Phase I. Biosynthesis of Isopentenyl pyrophosphate (IPP) from precursors. Phase II. Biosynthesis of Zeaxanthin (XAN) from IPP. Phase III. Biosynthesis of ABA. ABA level responses rapidly to a number of *in vitro* stresses including heat, drought, cold, salinity and chemical herbicide. ABA plays a lot of vital functions in plants in embryo development, seeds germination, fruit ripening. etc. This review elaborates the biosynthesis of ABA and its physiological functions in plants.

**Keywords:** abscisic acid, isopentenyl pyrophosphate, biosynthesis of zeaxanthin

## Introduction
Abscisic acid (ABA) is a type of plant hormone responding to stresses. It plays a vital role in resisting environmental stresses, e.x., heat, drought, cold, salinity and chemical herbicide (Grossmann *et al.*, 1996) [16]. The ABA level also changes in plant embryo development, seeds germination, and fruit ripen (Sagi *et al*., 1999; Chernys and Zeevaart, 2000) [34, 5]. ABA was discovered to function in plant wilt and stomata closure (Wright and Hiron, 1969, Mittelheuser and Van Steveninck, 1969) [40, 26]. ABA promotes the closure and inhibits the opening of stomata in response to the drought stress (Schreoder *et al*., 2001) [35].

ABA biosynthesis in higher plants usually has two pathways: $C_{15}$ direct pathway and $C_{40}$ pathway. $C_{15}$ direct pathway starts with mevalonate (MVA) as the precursor to form $C_{15}$ ABA through $C_{15}$ Farnesyl pyrophosphate (FPP). The main pathway of ABA biosynthesis is $C_{40}$ pathway, which comprises three phases: Phase I. Small phosphorylated intermediates are assembled in early reactions as precursors. Phase II. Uncyclized $C_{40}$ carotenoid phytoene was formed at the begining and 9-cis-neoxanthin was cleaved in the end in a series of intermediate interactions. Phase III. Xanthoxal as the skeleton of $C_{15}$ ABA was formed (Finkelstein and Rock, 2002) [12].

In the biosynthesis of ABA, apart from the inducement from environment, some *in vivo* factors like enzyme or coenzyme are also important in regulation. In enzyme regulated biosynthesis, zeaxanthin cyclooxygenase (ZE), 9-cis-epoxy-carotenoid dioxygenase (NCED), and aldehyde oxidase (AO) are likely to play major roles (Sagi *et al*., 1999; Chernys and Zeevaart, 2000) [34, 5]. Secondly, some enzymes related to isopentenyl pyrophosphate (IPP) biosynthesis, some isomerase, some co-factors like MoCo and MCSU, and some membrane steroid can all regulate ABA biosynthesis (Xiong *et al*., 2001) [41].

Previously, it was believed plant leaves, especially old leaves are the major organs for ABA biosynthesis. New evidence, however, has shown in excised roots, especially root tip, can also synthesis ABA in slow dehydration. In somatic roots, ABA can also be synthesized in stress and delivered to leaves to induce stomata closure (Davies and Zhang, 1991; Zeevart and Greenlman, 1988) [8, 43]. Other organs, especially flower, fruits and seeds, can also syntheses ABA.

ABA in plant leaves concentrates in chloroplasts. Immunogold electron microscopy localization showed ABA is largely distributed in chloroplasts in leaves of *Vicia faba* and *Lavandula stoechas.* Gold particles can also be found in the cytoplasm and nucleus, but not in vacuole or cell walls (Pastors *et al*., 1995) [27]. In tomato seedlings root cap cells, ABA is mainly distributed in plastids, cytoplasmic capsule, amyloplast, which are likely to be the main subcellular position for ABA biosynthesis (Benhamou *et al*., 1989) [3].

## ABA Biosynthesis
ABA biosynthesis in higher plant include three phases as described above. Phase I is the biosynthesis of isopentenyl pyrophosphate (IPP). There are two pathways for IPP biosynthesis, in cytoplasm and plastid respectively. In cytoplasm mevalonate (MVA) is the precursor for ABA biosynthesis. In plants, MVA is the precursor of carotenoid and other tetraterpenes, and later it was discovered that mevinlonin, which prohibit the synthesis of MVA, does not affect the synthesis of carotenoid (Bach and Lichtenthaler, 1982) [2]. $^{13}CO_2$ is incorporated into the leaf terpenoids efficiently but very slowly into steroids made in cytoplasm (McCaskill and Croteau, 1995; Lereto *et al*., 1996) [23, 20]. Therefore, the synthesis of IPP may have little to do with MVA pathway. IPP was believed by (Rohmer, 1999) [31] to be synthesized from the MEP pathway in the chloroplasts. Two carbon atoms of pyruvate were condensed with glyceraldehyde phosphate to synthesize 1-deoxyxylulose-5-P (Romher *et al*., 1993; Schwender *et al*., 1996; Lichtenthaler *et al*., 1997) [32, 36, 22], forming IPP with the participant of cytidine triphosphate (CTP) (Rohmer, 1999; Rohdich *et al*., 1999) [31, 29]. The formed IPP must rely on a carrier to penetrate the plastid membrane to enter plastid (Soler *et al*., 1993) [37].

The second phase for ABA biosynthesis is the synthesis of zeaxanthin (XAN). No matter synthesized from MVA in cytoplasm and entered plastids or synthesized in plastids, IPP can then be transformed XAN. Zeaxanthin is synthesized from

IPP through the intermediate TPP (farnesyl pyrophosphate). Zeaxanthin will then be cyclized into epoxy zeaxanthin with the catalysis of epoxy zeaxanthin cyclase. Violaxanthin and neoxanthin can be oxidative cleaved into xanthoxin with the catalysis of 9-cis-epoxy-carotenoid dioxygenase (NCED). The identification of NCED was from the study of maize (*Zea mays*) mutant vp14 (*viviparous 14*) mutant (Tan *et al*., 1997) [38].

The *loci* and process to form ABA from XAN are still in dispute. (Li and Walton, 1987) [21] claimed that XAN was converted to ABA in cytosol rather than in chloroplasts, however, (Milborrow and Lee, 1988) [25] claimed the whole convert of IPP to ABA can occur in chloroplasts. There are three possible pathways for the conversion of XAN to ABA: through abscisic aldehyde, xanthoxic acid or abscisic alcohol. The *ABA2* gene isolated from Arabidopsis was shown to play a crucial role in catalyze XAN to abscisic aldehyde (Rook *et al*., 2001) [33]. Arabidopsis *ABA3* gene was cloned and recombinant *ABA3* gene was shown to have Moco sulfrase activity (Bittner *et al*., 2001) [4]. In summary, xanthoxin is converted to abscisic aldehyde by the enzyme encoded by *ABA2* gene at the beginning and then oxidased by aldehyde oxidase (AO) to form ABA (Fig.1).

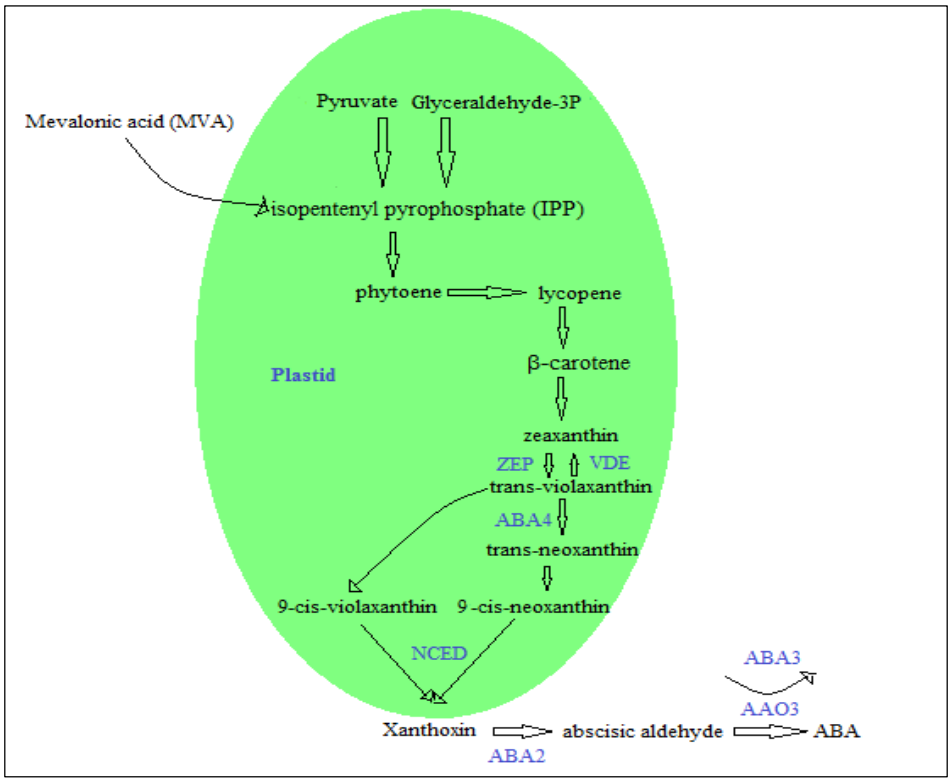


**Fig 1:** ABA biosynthesis pathway. Isopentenyl pyrophosphate (IPP) is produced in the plastids as the precursor for ABA biosynthesis. ABA can be translocated from the cytosol to the plastids as indicated. The conversion of zeaxanthin to all-trans-violanxanthin is catalyzed by zeaxanthin epoxidse (ZEP). A reversible reaction happens in chloroplasts under intensive light. Violaxanthin de-epoxidase (VDE) catalyzes this reaction. ABA4 protein is evolved in neoxanthin formation. 9-cis-epoxycarotenoid dioxygenases (NCED) catalyzes carotenoid cleavage to form neoxanthin.

Another pathway to form ABA from zeaxanthin is xanthoxic acid (Milborrow, 2001; Cowan, 2000) [24, 6]. In ripening avocado fruits, inhibition of aldyhyde oxidase (AO) activity results in accumulation of zeaxanthin, implying that zeaxanthin is the substrate of AO (Lee and Milborrow, 1997) [19]. The third pathway to synthesize ABA is via abscisic alcohol. In *flacca* and *sitiens* tomato mutants, exogenously supplied abscisic aldehyde is converted to abscisic alcohol, indicating the process from abscisic aldehyde to abscisic alcohol and to ABA. The third pathway might be a minor source for ABA synthesis in wild-type plants but a major pathway in mutants which lack the ability to oxidase abscisic aldehyde to ABA directly (Rock *et al*., 1991) [30].

**Regulation of ABA Biosynthesis**

The synthesis of carotenoid contributes to the regulation of ABA biosynthesis. Recent studies showed a potential connect in between the early and late stage of ABA synthesis. The expression level of DXS changes according to the level of endogenous isoprenoid content in the form of chlorophylls, tocopherols or carotenoids. These phenomenon implies a role of DXS in the regulation of isoprenoids biosynthesis (Estévez *et al*., 2001) [11]. Endogenous ABA levels are also influenced by DXS expression. These suggest early ABA synthesis steps, especially the forming of DXP, might participate in the regulation of ABA biosynthesis.

The existence of large amount of ABA deficient mutants has clearly shown the ABA biosynthesis is regulated by genes. Genetic mutations will prohibit the generation of ABA synthase. Gene expression is largely controlled by plant development condition and environmental condition. In young leaves, the genes in control of ABA biosynthesis are usually in non-expression status, hence, the ability of young leaves to synthesize ABA is much weaker than old leaves. Several

adverse environments, like drought, cold, heat, salinity, waterlogging, anoxia, nutrient deficiency, ammonium poisoning and pathogens infection can all stimulate ABA synthesis (Giraudat *et al*., 1994; Zeevaart and Greenlman, 1988; Davies and Zhang, 1991) [13, 43 8]. But it is still in dispute about how the environmental stresses initiate ABA biosynthesis.

Recent studies showed protein transcription and translation inhibitors actinomycin-D and cycloheximide can inhibit ABA biosynthesis in adverse environment, indicating that inducing ABA biosynthesis needs gene expression and new protein synthesis (Zeevaart and Greenlman, 1988) [43]. Proteinase inhibitor can also significantly inhibit the waterlogging induced ABA biosynthesis. Hence, protein phosphorylation participated in ABA biosynthesis. (Richardson and Cowan, 1996) [28] found from the exocarp cell-free system from *Citrus sinensis* that NADH, NADPH, DTT and Amo-1618 all promote $^{14}$C-MVA and $^{14}$C-IPP to generate $^{14}$C-ABA, molybdenum and NADH can enhance the effect when function together. Cytochrome oxidase P-450 catalyzes ABA aldehyde into ABA with the assistance of molybdenum cofactor. Also, reduction of MVA biosynthesis inhibitors mevinolin, carotenoid biosynthesis inhibitor fluridone can all inhibit the accumulation of abscisic acid (Zeevaart and Greenlman, 1988) [43]. Carotenoid is a ROS scavenger, and ROS takes part in ABA biosynthesis. (Ederli *et al*., 1997) [10] found $O_3$ can increase ABA level in tobacco leaves 3.5-9 times in 4 hours, (Koboyashi *et al*., 1997) [18] also believed endogenous ROS participates in ABA biosynthesis inducement from drought stresses.

Some plant growth regulators also affect the ABA biosynthesis, like zeatin, iso-pentene adenine, adenosine, ancymidol and CPPU will all deduct the ABA accumulation (Richardson and Cowan, 1996; Cowan *et al*., 1999) [28, 7]. CPPU and ancymidol mainly prohibit the XAN to transform to ABA (Cowan *et al*., 1999) [7]. Tungstate can also weaken the ABA biosynthesis (Hays *et al*., 1999) [17]. Amo-1618 promotes ABA biosynthesis through inhibition of activity of kauriene oxidase A and squalene oxide cyclase, and hamper the generation of GA and parts of steroids. Stigmasterol is the important steroid component of of cytoplasm membrane. It prohibits ABA biosynthesis from β-carotenoids at the concentration of 50-100 mM (Richardson and Cowan, 1996) [28]. Jasmonic acid is a type of sterols plant growth regulator, shares similar physiological effect with ABA, in fact, jasmonic acid can also significant reduce the ABA level in rapeseed (Hays *et al*., 1999) [17].

**Functions of ABA in plants**

ABA plays a crucial role in seed maturation as well as establishment and maintenance of dormancy. It was reported that ABA can induce dormancy during the late stages of seed maturation. During seed development, the endogenous ABA level correlates with the expression of *NpZEP*, which peaks during the middle phase of seed development (Audran *et al*., 1998) [1]. Transgenic plants with over-expressed *NpZEP* cDNA accumulate ABA in seeds, therefore, the dormancy is enhanced (Frey *et al*., 1999) [14]. The relevance of ABA synthesis in imbibed seeds for dormancy maintaining has been recently reported. ABA level increase when dormant tobacco seeds imbibe. Fluridone inhibits the increase of ABA level (Grappin *et al*., 2000) [15]. Heat treatment prohibits germination of lettuce seeds (Yoshioka *et al*., 1998) [42]. In normal germination conditions, ABA level decreases fastly in lettuce seeds. But at heat imbibition hampers significant changes in ABA level. When the seeds are imbibed, ABA level decreases, therefore, the seeds show weaker ability of dormancy and stronger ability to germinate.

Xanthophylls are taking part in protecting the photosynthetic apparatus from photo-oxidative damage (Demmig-Adams and Adams, 1996) [9]. ZEP transforms zeaxanthin to violaxanthin under low light. Violaxanthin can be reversely converted to zeaxanthin with the catalysis of violaxanthin de-epoxidase under excessive light. So the expression of ZEP is influenced by light intensity but independent from ABA level. In tobacco and tomato, ZEP expression varies with a diurnal curve consisting of light and dark periods (Audran *et al*., 1998; Thompson *et al*., 2000) [1, 39]. The diurnal oscillation of ZEP expression in tobacco and tomato leaves is related to its role in xanthophyll cycle. The diurnal oscillation of *LeNECD1* expression was surprisingly found in tomato leaves as NCED is supposed to be a main regulator in leaves (Thompson *et al*., 2000) [39]. The peak of *NCED* expression is at the end of the light period, whilst the peak of *ZEP* expression is at the middle of the light period. The impact of the diurnal fluctuation of *NCED* on the rate of ABA synthesis needs to be further studied.

**Prospects**

The biosynthesis is ABA involves many biochemical processes including polymerization, cyclization, isomerization, and oxidation. A lot of synthesis details are still not clear yet, and the study about its regulation is far from maturation. The discovery of a large amount of ABA deficient mutants has been a great promotion in ABA biosynthesis study. Biochemical studies have identified several key enzymes responsible for ABA biosynthesis and regulation. The expression level of several of these enzymes changes in response to ABA level, resulting in ABA regulation. ABA also promotes the generation of degradation enzymes. ABA regulates development events like embryo maturation. As the development of novel research technologies and protocols, studies about ABA responses to environmental stresses, ABA signal transduction, protein synthesis and regulation will be further revealed.

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