EMPRO

Current Research in Pharmaceutical Sciences

Available online at www.crpsonline.com

ISSN: 2250-2688
Received: 01/01/2012
Revised: 16/03/2012
Accepted: 27/03/2012

Vinay Gupta
Uttarakhand Technical University, Dehradun (U.K), India.

Vikas Shrivastava, Gunjan Shrivastava
Arni University, Kangra (H.P), India

Nidhi Anand
National Centre of Fungal Taxonomy (NCFT), New Delhi, India.

Abhishek Mathur
dev bhoomi group of institutions (dbgi), dehradun (u.k), india.

Correspondence
Abhishek Mathur
Asst. Professor, Dept. of Biotechnology Dev Bhoomi Group of Institutions (DBGI) Dehradun (U.K), India
E-mail:
mathurabhishek37@yahoo.com

Study of the Relationship between Salt Concentration, ABA Production and Mangroves Species: A Review

Vinay Gupta, Vikas Shrivastava, Gunjan Shrivastava, Nidhi Anand, Abhishek Mathur

ABSTRACT

An attempt has been made to establish a correlation between salt concentration, ABA production and Mangroves species. Mangroves are salt tolerant (halophytic) species that allows them to live under high salt conditions. Vivipary is the common feature found is Mangroves. It is revealed that drought and salt stresses induces ABA biosynthesis through transcriptional regulation of ABA biosynthetic genes thus can be able to convert vivipary to nonvivipary in Mangroves. The study may lead to the significant outcome of the proposed work. Further the work can act as a basis to screen viviparous and non viviparous varieties of mangroves in different pharmacological aspects.

Keywords: Vivipary, salt stress, ABA, Mangroves, salt tolerant, transcriptional regulation.

1. INTRODUCTION

Mangroves are plants living in the tidal coastal areas between sea and land[1]. They are able to tolerate partial submersion in high salinity water, and poor oxygen content in the ground where their roots penetrate. Different kinds of mangrove trees have evolved different ways of dealing with these two limiting factors but all true mangrove trees must deal with them to survive. Mangroves grow only in the tropics. The richest mangrove communities occur is areas where the day time temperature is greater than 75^0F and the annual rainfall exceed 40 inches (100 centimeters).

To deal with salt, many mangroves stop the salt from entering their tissues by filtering it out at root level. Some mangrove plants can exclude about 90% of the salt in the salt water they absorb with a special filter in the roots[2].

The Major plant species forming the mangrove tangle have aerial roots, commonly prop roots or stilt roots (Examples: red mangrove and its root tip). These serve, of course, to anchor the plants, but also are important in aeration, because the mangrove mud tends to be anaerobic. Special vertical roots called pneumatophores, form from lateral roots in the mud, often projecting above water (*Avicennia).* These are particularly well developed in species of Avicennia, Sonneratia, less so in Laguncularia, and as knee-like structures in *Xylocarpus mekongensis, Bruguiera*, and *Ceriops*[3].

Probably because mangrove plants can only thrive in a narrow range of conditions, many species have developed fascinating techniques of reproduction. While the dispersal of live, germinated seeds (known as vivipary) is very rare in most plants, many species of mangrove plants utilize this technique[4].

Several species of viviparous mangrove plants produce seeds which have a buoyant outer coating. The seed floats until it reaches favored water salinity (not too fresh). When the salinity is right, the coating peels off, and the seed sinks to the bottom. With luck it will take hold and grow[5]. Other species produces seedlings which stay attached to the mangrove plant while stay attached to the mangrove plant while a steam and the some roots grow out of either side of the seed. After the seed has developed its "starter" root and stem, it falls into the water. In the buoyancy of salt into the water, the whole seedling floats horizontally on the tides and currents. But when the seeding reaches brackish coastal water less buoyant root sinks, flipping the whole seedling to a vertical position where the root can hopefully touch bottom and take hold. While not all mangrove trees utilize vivipary, they all seem to produce large seeds or fruits which can survive a long time, suggesting that sometimes these seeds or fruits float for quite a while in "suspended animation" until they find a suitable place to germinate**.**

Regulation Of Absicisic Acid Biosynthesis

Plant growth and development are regulated by internal signals and by external environmental conditions. One important regulator that coordinates growth and development with responses to the environment is the sesquiterpenoid hormone abscisic acid (ABA). ABA plays important roles in many cellular processes including seed development, dormancy, germination, vegetative growth, and environmental stress responses. These diverse functions of ABA involve complex regulatory mechanisms that control its production, degradation, signal perception, and transduction. Because of the key role of ABA in plant stress responses, understanding these regulatory mechanisms will help devise rational strategies to breed or genetically engineer crop plants with increased tolerance to adverse environmental conditions.

Since the discovery of ABA in the early 1960s, much effort has been devoted to understanding how ABA is synthesized. Through genetic and biochemical studies, the pathway for ABA biosynthesis in higher plants is now understood in great detail. Recently, all the major genes for the enzymes in the biosynthesis pathway have been identified[6]. The new challenge is to understand how these biosynthesis genes, and the biosynthetic pathway as a whole, are regulated. Although much remains to be learned about the regulatory mechanism, evidence thus far indicates that ABA biosynthesis is subject to complex regulation during plant development and in response to environmental stresses. In this Update, we first present a brief overview of the functions of ABA and the biosynthesis pathway. We then focus on the regulation of ABA production and attempt to provide some future directions in ABA biosynthesis studies.

Biological Functions of ABA

Under non-stressful conditions, ABA in plant cells is maintained at low levels. Some low levels of ABA is may be required for normal plant growth, as evidenced by reduced vigor observed in ABA-deficient mutant plants that can be restored to the wild-type level of growth by exogenous ABA[7]. Because all ABA-deficient mutants still have certain basal levels of ABA that are not dramatically lower than those in the wild type under normal growth conditions, it is difficult to uncover the cellular processes that require a very small amount of ABA. As a consequence, our knowledge of ABA functions has been gained mainly from observations with ABA at elevated levels, either from endogenous or exogenous sources. ABA levels can increase dramatically during seed maturation and in response to environmental stresses. Thus, ABA functions have been most extensively studied in these two processes.

During seed development, ABA is known to initiate the following programs: embryo maturation, synthesis of storage reserves and late embryogenesis abundant (LEA) proteins, and initiation of seed dormancy, although ABA is not the sole regulator of these processes. In particular, the induction of LEA protein synthesis to preserve the viability of embryos the role of ABA in promoting synthesis of LEA like proteins in vegetative tissues to tolerate dehydration stress. Embryos from ABA antibody-expressing plants lose their viability as a result of desiccation intolerance[8].

In vegetative tissues, ABA levels increase when plants encounter adverse environmental conditions such as drought, salt, and to a lesser extent, low temperature. Although a higher level of exogenous ABA inhibits plant growth under non-stressful conditions, an increased ABA content is beneficial for plants under environmental stress as a result of ABA induced changes at the cellular and whole-plant leaves. ABA promotes the closure of stomata to minimize transpiration water loss. It also mitigates stress damage through the activation of many stress responsive genes that encode enzymes for the biosynthesis of compatible osmolytes and LEA-like proteins, which collectively increase plant stress tolerance[9]. Plant mutants defective in ABA biosynthesis are more susceptible to the environmental stresses and have been isolated in stress sensitivity screens[10]. ABA biosynthesis genes provide an effective means to increase plant stress resistance**.**

The ABA Biosynthesis Pathway

ABA deficient mutants have been instrumental for revealing the pathway of ABA biosynthesis. By virtue of their precious germination of seeds and the witty appearance of the plants, mutants defective in ABA biosynthesis were isolated from a number of plant species including maize (*Zea mays*), tomato (Lyc*opersicum esculentum*), tobacco (*Nicotiana tobacum*), potato (*Solanum tubersoum*), barley (*Hordeum vulgare*) and Arabidopsis,

Before the molecular identities of the affected genes were known, a major route for ABA biosynthesis was revealed by profiling ABA biosynthetic intermediates in combination with feeding assays using these mutants. These studies suggested that ABA in higher plants is synthesized from an "indirect" pathway through the cleavage of a C_{40} carotenoid precursor, followed by a two-step conversion of the intermediate xanthoxin to ABA via ABA aldehyde[6, 11-13].

By now, major ABA- deficient mutant, genes, and enzymes have been characterized in Arabidopsis[6]. The information from Arabidopsis is applicable to other plant species because the pathway and the angiosperms. To avoid confusion, in this update, genes are named after their products instead of the respective genetic loci.

The first step that is more specific to the ABA biosynthesis pathway is the epoxidation of zeaxanthin and antheraxanthin to violaxanthin, which occurs in plastids. This step is catalyzed by a zeazanthin epoxidase (ZEP), whose molecular identity was first revealed in tobacco[13]. After a series of structural modifications, violaxanthin by the 9-cis-epoxycarotenoid. Oxidative cleavage of major epoxycarotenoid 9-cis-neoxanthin by the 9-cis-epoxycarotenoid dioxygenase (NCED) yields a C_{15} intermediate, xanthoxin[13]. This step was considered pathway the first committed step in ABA biosynthesis. The *ZmNCED* gene was isolated using the maize mutant[14]. The product xanthoxin is then exported to the cytosol, where it is converted to ABA through a two step reaction via ABA- aldehyde. A short- chain alcohol dehydrogenase / reductase (SDR), encoded by the *AtABA2* italics gene[15-17] catalyzes the first step of this reaction and generates ABA aldehyde. ABA aldehyde oxidase (AAO) then catalyzes the last step in the biosynthesis pathway. A mutation in either the aldehyde oxidase apoprotein or molybdenum cofactor (MoCo) synthase (e.g. AtABA3) gene encodes a MoCo sulfurase that catalyzes the sulfurylation of a dioxo form of MoCo to a sulfurylated mono-oxo form[18, 19]. This form of MoCo is required by aldehyde oxidase and xanthine dehydrogenase for their activities. The summarization of steps of ABA Biosynthesis is included in figure 1

Developmental Regulation Of ABA Biosynthesis

Seed maturation and germination expose the young embryo to dramatic osmotic stresses. ABA is the major factor that is required to escort the embryo upon entering and exiting its quiescent state. ABA in developing seeds can either-be derived from maternal tissues or be synthesized de novo in the embryo[20]. The first one occurs about halfway during seed development (approximately 10 day after pollination). This ABA is likely to be derived from maternal tissues because in reciprocal crosses, the peak only occurred when the wild type but not ABA- deficient mutants were used as the female. ABA at this stage promotes the synthesis of storage proteins. Embryos from ABA antibody expressing plants either did not accumulate or accumulated a much lower level of storage proteins relative to the wild-type embryos[8]. The second peak with less significant ABA accumulation (about one-third of the first peak) is from biosynthesis in the embryo an may activate the synthesis of LEA proteins that prepare the embryo for dormancy. ABA levels fall rapidly in the later stage of seed maturation and are very low in dry seeds. During seed inhibition, de novo ABA biosynthesis in the embryo is a determinant of seed dormancy[21, 22]. ABA at this stage also maintains, within a narrow time window, the imbibed embryo in a reversible state window, the imbibed embryo in a reversible state between dormancy and germination by regulating the basic Leu Zip transcription factor AB15[23]. These important roles of ABA and its dynamics of accumulation in the embryo suggest that ABA biosynthesis is under tight developmental regulation in the embryo.

Transcripts for all the ABA biosynthetic genes are detected in embryos /developing seeds, although more detailed analysis of the expression of individual genes during seed development has not been reported except for *AtZEP1*. In situ hybridization deleted AtZEP expression in the embryo from globular to desiccation states[24] which medicals that the ZEP gene was expressed during embryogenesis before the first peak of ABA accumulation in developing seeds. In addition to suggesting a potential role of low-level ABA in embryogenesis, it also raises an interesting question regarding which signal (s) activities ZEP (and other ABA biosynthetic genes) in developing embryos. Although the possibility of a unique developmental signal that induces one or more of the ABA biosynthetic genes cannot be reeled out, current experimental evidence implies that soluble sugars, osmotic stress, and ABA itself are likely to be the signals that activate ABA biosynthesis in developing seeds.

Maternal ABA has been shown to be required for the first peak accumulation of ABA in developing seeds, yet it is not clear whether the ABA in developing seeds, yet it is not clear whether the ABA was directly derived from maternal tissues or rather that maternal ABA serves only as a signal for de novo synthesis of ABA in developing embryos. This question is relevant because ZEP, SDR, AAO, and MCSU genes are all induced by sugar to various extents[25], sugar levels may regulate ABA biosynthesis in the embryo. This mechanism is perhaps more important for SDRI because SDR is not induced by either osmotic stress or ABA. At the onset of seed maturation, osmotic stress may become more important in activating *de novo* ABA biosynthesis, which is responsible for embryo desiccation tolerance and dormancy.

The activation of individual genes in seeds may eventually be responsible for ABA biosynthesis and accumulation in seeds. For instance, the expression of NtZEP reached ABA

accumulation during this period[25]. Likewise, seeds from plants over showed enhanced dormancy[23], suggesting that NtZEP may regulate ABA biosynthesis in seeds and during seed germination. Similarly, in tomato, NCED may also regulate ABA levels in the seeds. Over expression of the *LeNCEDI* gene increased ABA levels in imbibed seeds and extended seed dormancy [26, 27]. These experimental records suggest that ABA biosynthesis in developing an inspiring seeds may be regulated at multiple steps.

Abiotic Stress Regulation Of ABA Biosynthesis

Certain environmental signals such as light have been suggested to regulate ABA biosynthesis directly or indirectly. The environmental conditions that most dramatically activate ABA biosynthesis, however, are drought and salt stress. Increased ABA levels under these abiotic stresses result mainly from increased de novo biosynthesis. The degradation of ABA appears to be suppressed by stress and activated by ABA and stress relief. Drought and salt stresses induce ABA biosynthesis largely through transcriptional regulation of ABA biosynthetic genes because blocking transcription by using transcription inhibitors impairs stress induced ABA biosynthesis. Therefore, transcriptional regulation of ABA biosynthetic genes holds the key to understanding how ABA biosynthesis is regulated, although regulation of the specific activities of ABA biosynthesis enzymes also exists.

ZEP was the first gene in the ABA biosynthesis pathway to be cloned, and its expression and regulation have been scrutinized in a number of plant species. ZEP genes were expressed ubiquitously in every plant part with a higher basal expression in leaves[25, 28]. It was thought that ZEP does not limit ABA biosynthesis in photosynthetic tissues because on a molar basis, the amount of 9-cis-epoxycarotenoid (precursor down-stream of the ZEP- catalyzed reaction) in photosynthetic tissues such as leaves is several times higher than the amount of ABA produced during stress. In tobacco and tomato plants, the transcript levels of ZEP genes in leaves were also not regulated by drought stress but were found to be regulated diurnally with high transcript levels in the day, which may reflect regulation by the circadian rhythm[25, 26].

The cleavage step is rate limiting in ABA biosynthesis, the expression of NCED gene(s) has received particular attentions drought stress treatments were shown to induce NCED expression in maize[14], tomato[16]. Significant increases in NCED transcript levels can be detected within 15 to 30 minutes after leaf detachment or dehydration treatment[26] indicating that the activation of NCED genes can be fairly quick.

In fact, with the exception of At SDR, whose expression appears not to be regulated by stress[17], all the other ABA biosynthetic genes are up-regulated by drought and salt stresses increase after the transcript levels of these genes increase after the transcript levels, as was seen with the NCED gene.

In contrast to the clear regulation of these genes by drought and salt stress, the expression of AtZEP[28], NCED and AtMCSU[10] was not obviously up-regulated by cold. This is consistent with the observation that the magnitude of increase in ABA contents in plants subjected to cold treatment[29] was much less than that in drought- stressed plants.

ABA might restrict its own accumulation by activating its degradation, at least under non-stressful conditions. The NCED gene product has been suggested to catalyze the rate-limiting step in the ABA biosynthesis pathway, whether or not this gene is regulated by ABA is very relevant to the question of whether ABA can auto regulate its own biosynthesis. In tomato plants, it was found that the NCED gene was not induced by exogenous ABA[26]. These observations would support the idea that ABA may stimulate its own degradation but not its production However, when the expression of ABA biosynthetic genes was examined across wide genetic back grounds, a different picture emerged. To our surprise, we have found that *ZEP*, *AAO*, and *MCSU* in Arabidopsis are all up-regulated by ABA, in addition to being regulated by expression of these significantly enhanced the expression of these genes[10, 19, 28]

2. CONCLUSION

The expression of the gene (s) involved in ABA biosynthesis can be determined and screened.

When these gene (s) are over expressed, ABA biosynthesis occurs and the production of ABA results as feedback stimulation of ABA, thus inhibiting the vivipary[19]. Thus regulation of ABA biosynthesis is of great importance in controlling ABA level and thus reducing the chances of conversion of viviparous to non-viviparous species. Although there is further a detailed study to be done to inhibit/reduce the expression of ABA genes so that ABA biosynthesis is deteriorated but according to the past researches done on other plants to inhibit the expression of genes involved in ABA biosynthesis the following points must be considered:

- Minimum saline conditions must be provided to the growing plant so that expression of genes of ABA biosynthesis gets reduced[30].
- Freezing conditions must be provided to the growing seed so that ABA biosynthesis gets reduced by following the expression of NCED gene[29].

- Exogenous ABA can inhibit the expression of NCED gene in tomato plants[26, 27].

REFERENCES

1. Audran C, Biotenberg S, Gonneau M, North H, Frey A, Tap – Waksman K, Vartanian N, Mario-Poll A. Localization and expression of zeaxanthin epoxidase mRNA in Arabidopsis in response to drought stress and during seed development. Aust. J. Plant Physiol. 2001; 28: 1161-1173.
2. Cutler A, Krochko I. Formation and breakdown of ABA. Trends Plant Sci. 1999; 4: 472- 478.
3. Rolland F, Moore B, Sheen J. Sugar sensing and signaling in plants. Plant Cell. 2002; 14: 5185-205.
4. Rook F, Corke F, Card R, Munz G, Smith C, Bevan MW. Impaired sucrose-induction mutants reveal the modulation of sugar-induced starch biosynthetic gene expression by abscisic acid signaling. Plant J. 2001; 26:421-433.
5. Huguuvieus V, Kwak JM, Schroeder JI. An mRNA cap binding protein. ABHI modulates early abscisic acid signal transduction. Cell. 2001; 106: 477 487.
6. Schwartz SH, Qin X, Zeevaart JAD. Elucidation of the indirect pathway of abscisic acid biosynthesis by mutants, genes, and enzymes. Plant Physiol. 2003; 131:1591-1601.
7. Taylor IB, Burbidage A, Thompson AJ. Control of abscisic acid synthesis. J Exp Bot. 2000; 51: 1563-1574.
8. Phillips J, Artsaenko O, Fiedler U, Horstmann C, Mock HP, Murntz K, Conrad U. Seed-specific immunomodulation of abscisic acid activity induces a developmental switch. The EMBO Journal.1997; 16: 4489–96.
9. Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. Annual Rev. Plant Mol Plant Physiol. 2000; 51:161 199.
10. Xiong L, Ishitani M, Lee H, Zhu JK. The Arabidopsis LO55/ABA3 locus encodes a molybdenum cofactor sulfurase and modulates cold osmotic stress-responsive gene expression. Plant Cell. 2000; 13: 2063-2083.
11. Seo M, Koiwa H, Akaba S, Komano T, Oritani T, Kamiya Y, Koshiba T. Abscisic acid aldehyde oxidase of *Arabidopisis thaliamaa* Plant J. 2000a; 23: 481-488.
12. Seo M, Peeeters AJM, Koiwai H, Oritani T, Marion-Poll A, Zeevart JAD, Koorneef M, Kamiya YK, Koshiba T. The Arabidopsis aldehyde oxidase 3 (AAO3) gene product catalyzes the final step in abscisic acid biosynthesis in leaves. Proc. Nat. Acad. Sci. USA. 2006b; 97:12908-12913.
13. Schwartz SH, Tan BC, Gage DA, Zeevaart JAD, McCarty DR. Specific oxidative cleavage of cartenoid by VP14 of maize. Science. 1997; 276: 1872-1874.
14. Tan BC, Schwartz SH, Zeevaart JAD, McCarty DR. Genetic control of abscisic acid biosynthesis in maize. Proc Natl Acad Sci USA. 1997; 94: 12235- 12240.
15. Ghassemian M, Nambara, E, Cutler S. Kawaide H, Kamiya Y, McCourt P. Regulation of abscisic acid signaling by the ethylene response pathway in Arabidopsis. Plant Cell. 2000; 12:1117-1126
16. Burbidge A, Grieve IM, Jackson A, Thompson, A, McCarty DR, Taylor IB. Characterization of the ABA- deficient tomato mutant *notabills* and its relationship with maize ep 14. Plant J. 1999; 17: 427-431.
17. Cheng WH, Endo A, Zhou I., Penney J, Chen HC, Arroyo A, Leo P, Nambara E. Asami T, Seo M. A unique short – chain dehydrogenase/ radio phase in Arabidopsis glucose signaling and abscisic acid biosynthesis in avocado. Plant Physiol.2002; 124:343-353.
18. Bittner F, Oreb M, Mendel RR. ABA3 is a molybdenum cofactor sulfurase required for activation of aldehyde oxidase and xanthine dehydrogenase in *Arabidopsis thaliana.* J Biol Chem. 2001; 276: 40381-40384
19. Xiong L, Gong Z, Rock C, Subramanian S, Guo Y, Xu W, Galbraith D, Zhu JK. Modulation of abscisic acid signal transduction and biosynthesis by a Sm-like protein in Arabidopsis. Dev Cell. 2001; 1: 771-781
20. Finkelstein KR and Rock CD. Abscisic acid biosynthesis and response. In CR Somersville, EM Meyerowitz ed., The Arabidopsis Book. American Society of Plant Biologists, Rockville, MD (2002) 1-52.
21. Uknes SJ, Ho THD. Mode of action of action of abscisic acid in barley aleurone layers. Abscisic acid induces its own conversion to phaseic acid. Plant Physiol. 1984; 75:1126-1132.
22. Bentsink I and Koornneef M. Seed dormancy and germination. In CR Somerville, em Meyerowitz ed., The Arabidopsis Book. American Society of Plant Biologist, Rockville, MD (2002) 1-17.
23. Frey A. Audram C, Marin E, Sotta B, Marion-Poll A. Engineering seed chorman by the modification of zeaxanthin epoxidase gene expression. Plant Mol Biol. 1999; 39:1267-1274.

24. Bray EA. Abscisic acid regulation of gene expression during water-deficit stress in the era of the Arabidopsis genome. Plant Cell Environ. 2002; 25:153-161.

25. Audran C, Borel C, Frey A, Sotta B, Meyer C, Simoneau T, Marion-Poll A. Expression studies of the zeazanthin epoxidase gene in *Nicotiana plumbaginifotin*. Plant Physiol. 1998; 118:1021-1028.

26. Thompson AJ, Jackson AC, Parker RA, Morpeth DR, Burbidge A, Taylor IB. Abscisic acid biosynthesis in tomato: regulation of zeaxanthin epoxidase and 9-cis-epoxycarotenoid dioxygenase mRNAs by light/dark cycles, water stress and abscisic acid. Plant Mol Biol. 2000a; 42:833-845.

27. Thompson AJ, Jackson AC, Symonds RC, Multholland BJ, Dadswell AR, Black PS, Burbidge A, Taylor IB. Ectopic expression of a tomato 9-cis epoxycarotenoid dioxygenase gene causes over-production of abscisic acid. Plant J. 2000b; 23:363-1132.

28. Xiong L, Lee H, Ishitani M, Zhu JK. Regulation of osmotic stress responsive gene expression by the LO56/ABA1 locus in Arabidopsis. J Biol Chem. 2002; 277: 8588-8596.

29. Thomashow MF. Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. Ann. Rev. Plant Physiol. Plant Mol Biol. 1999; 50: 571-599.

30. Sharp RE. Interaction with ethylene: Changing views on the role of abscisic acid in root and shoot growth responses to water stress. Plant Cell Environ. 2002; 25:211-222.