

Biochemistry of Plant Hormone ABA (Abscisic Acid)

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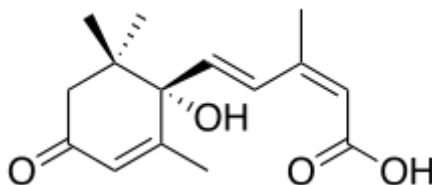
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ABSTRACT: Abscisic acid (ABA) is a plant hormone which has important functions in the control of abscission, dormancy and germination. Further, applications of ABA can inhibit growth and promote senescence in a large variety of experimental materials. The broad spectrum of responses to ABA and its wide distribution in plants suggest that it may be one of the more important hormonal factors in the control of plant behaviour, and has stimulated numerous investigations of the chemistry and biochemistry of the physiological action of ABA.

KEYWORDS: Abscisic Acid, dormancy, germination, senescence, hormonal, behavior, inhibit

I. INTRODUCTION

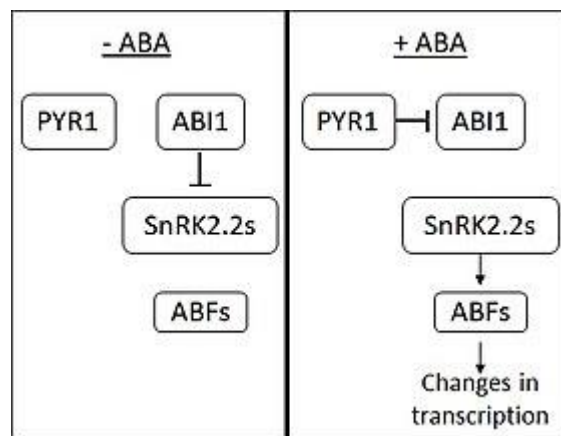
Abscisic acid (ABA) is a plant hormone. ABA functions in many plant developmental processes, including seed and bud dormancy, the control of organ size and stomatal closure. It is especially important for plants in the response to environmental stresses, including drought, soil salinity, cold tolerance, freezing tolerance, ¹heat stress and heavy metal ion tolerance. ABA was originally believed to be involved in abscission, which is how it received its name. This is now known to be the case only in a small number of plants. ABA-mediated signaling also plays an important part in plant responses to environmental stress and plant pathogens. The plant genes for ABA biosynthesis and sequence of the pathway have been elucidated. ABA is also produced by some plant pathogenic fungi via a biosynthetic route different from ABA biosynthesis in plants.²



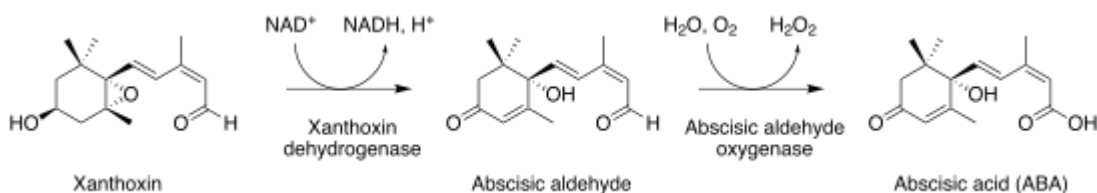
In preparation for winter, ABA is produced in terminal buds. This slows plant growth and directs leaf primordia to develop scales to protect the dormant buds during the cold season. ABA also inhibits the division of cells in the vascular cambium, adjusting to cold conditions in the winter by suspending primary and secondary growth.³

Abscisic acid is also produced in the roots in response to decreased soil water potential (which is associated with dry soil) and other situations in which the plant may be under stress. ABA then translocates to the leaves, where it rapidly alters the osmotic potential of stomatal guard cells, causing them to shrink and stomata to close. The ABA-induced stomatal closure reduces transpiration (evaporation of water out of the stomata), thus preventing further water loss from the leaves in times of low water availability. A close linear correlation was found between the ABA content of the leaves and their conductance (stomatal resistance) on a leaf area basis.⁴

Seed germination is inhibited by ABA in antagonism with gibberellin. ABA also prevents loss of seed dormancy. Several ABA-mutant *Arabidopsis thaliana* plants have been identified and are available from the Nottingham *Arabidopsis* Stock Centre - both those deficient in ABA production and those with altered sensitivity to its action. Plants that are hypersensitive or insensitive to ABA show phenotypes in seed dormancy, germination, stomatal regulation, and some mutants show stunted growth and brown/yellow leaves⁵



These mutants reflect the importance of ABA in seed germination and early embryo development. Pyrabactin (a pyridyl containing ABA activator) is a naphthalene sulfonamide hypocotyl cell expansion inhibitor, which is an agonist of the seed ABA signaling pathway⁶. It is the first agonist of the ABA pathway that is not structurally related to ABA. Abscisic acid (ABA) is an isoprenoid plant hormone, which is synthesized in the plastidal 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway; unlike the structurally related sesquiterpenes, which are formed from the mevalonic acid-derived precursor farnesyl diphosphate (FDP), the C₁₅ backbone of ABA is formed after cleavage of C₄₀ carotenoids in MEP. Zeaxanthin is the first committed ABA precursor; a series of enzyme-catalyzed epoxidations and isomerizations via violaxanthin, and final cleavage of the C₄₀ carotenoid by a dioxygenation reaction yields the proximal ABA precursor, xanthoxin, which is then further oxidized to ABA via abscisic aldehyde.⁷



Abamine has been designed, synthesized, developed and then patented as the first specific ABA biosynthesis inhibitor, which makes it possible to regulate endogenous levels of ABA.

- Synthesized in nearly all plant tissues, e.g., roots, flowers, leaves and stems
- Stored in mesophyll (chlorenchyma) cells where it is conjugated to glucose via uridine diphosphate-glucosyltransferase resulting in the inactivated form, ABA-glucose-ester
- Activated and released from the chlorenchyma in response to environmental stress, such as heat stress, water stress, salt stress⁸
- Released during desiccation of the vegetative tissues and when roots encounter soil compaction.
- Synthesized in green fruits at the beginning of the winter period
- Synthesized in maturing seeds, establishing dormancy
- Mobile within the leaf and can be rapidly translocated from the leaves to the roots (opposite of previous belief) in the phloem
- Accumulation in the roots modifies lateral root development, improving the stress response
- ABA is synthesized in almost all cells that contain chloroplasts or amyloplasts⁹

III. DISCUSSION

ABA can be catabolized to phaseic acid via CYP707A (a group of P450 enzymes) or inactivated by glucose conjugation (ABA-glucose ester) via the enzyme uridine diphosphate-glucosyltransferase (UDP-glucosyltransferase). Catabolism via the CYP707As is very important for ABA homeostasis, and mutants in those genes generally accumulate higher levels of ABA than lines overexpressing ABA biosynthetic genes. In soil bacteria, an alternative catabolic pathway leading to dehydrovomifoliol via the enzyme vomifoliol dehydrogenase has been reported.¹⁰

- Antitranspirant - Induces stomatal closure, decreasing transpiration to prevent water loss.
- Inhibits fruit ripening
- Responsible for seed dormancy by inhibiting cell growth – inhibits seed germination
- Inhibits the synthesis of Kinetin nucleotide
- Downregulates enzymes needed for photosynthesis.
- Acts on endodermis to prevent growth of roots when exposed to salty conditions¹¹

In the absence of ABA, the phosphatase ABI1-INSENSITIVE1 (ABI1) inhibits the action of SNF1-related protein kinases (subfamily 2) (SnRK2s). ABA is perceived by the PYRABACTIN RESISTANCE 1 (PYR1) and PYR1-like membrane proteins. On ABA binding, PYR1 binds to and inhibits ABI1. When SnRK2s are released from inhibition, they activate several transcription factors from the ABA RESPONSIVE ELEMENT-BINDING FACTOR (ABF) family. ABFs then go on to cause changes in the expression of a large number of genes. Around 10% of plant genes are thought to be regulated by ABA. Like plants, some fungal species (for example *Cercospora roscicola*, *Botrytis cinerea* & *Magnaporthe oryzae*) have an endogenous biosynthesis pathway for ABA. In fungi, it seems to be the MVA biosynthetic pathway that is predominant (rather than the MEP pathway that is responsible for ABA biosynthesis in plants). One role of ABA produced by these pathogens seems to be to suppress the plant immune responses.¹²

ABA has also been found to be present in metazoans, from sponges up to mammals including humans. Currently, its biosynthesis and biological role in animals is poorly known. ABA has recently been shown to elicit potent anti-inflammatory and anti-diabetic effects in mouse models of diabetes/obesity, inflammatory bowel disease, atherosclerosis and influenza infection. Many biological effects in animals have been studied using ABA as a nutraceutical or pharmacognostic drug, but ABA is also generated endogenously by some cells (like macrophages) when stimulated. There are also conflicting conclusions from different studies, where some claim that ABA is essential for pro-inflammatory responses whereas other show anti-inflammatory effects. Like with many natural substances with medical properties, ABA has become popular also in naturopathy.¹³ While ABA clearly has beneficial biological activities and many naturopathic remedies will contain high levels of ABA (such as wheatgrass juice, fruits and vegetables), some of the health claims made may be exaggerated or overly optimistic. In mammalian cells ABA targets a protein known as lanthionine synthetase C-like 2 (LANCL2), triggering an alternative mechanism of activation of peroxisome proliferator-activated receptor gamma (PPAR gamma). LANCL2 is conserved in plants and was originally suggested to be an ABA receptor also in plants,¹⁴ which was later challenged. Several methods can help to quantify the concentration of abscisic acid in a variety of plant tissue. The quantitative methods used are based on HPLC and ELISA. Recently, 2 independent FRET probes have been developed that can measure intracellular ABA concentrations in real time in vivo¹⁵

IV. RESULTS

Abscisic acid (ABA) is a plant hormone that regulates numerous aspects of plant growth, development, and stress responses. ABA-deficient mutants from various plant species display reduced seed dormancy and wilted phenotypes, highlighting that these crucial ABA functions are conserved in the plant kingdom. ABA is a sesquiterpene (C₁₅) synthesized from carotenoids (C₄₀) via oxidative cleavage. ABA catabolism is initiated by several modifications such as oxidation and conjugation. Several types of ABA receptors have been reported and, among them, PYR/PYL/RCAR receptors play a crucial role in ABA signaling. In the presence of ABA, PYR/PYL/RCAR

receptors inhibit the activity of Group A Protein Phosphatase 2C (PP2C), the repressors of ABA signaling.¹⁶ ABA is a mobile signal, and its movement is mediated by influx and efflux carrier proteins. Movement of ABA is an important mechanism of plant responses to drought stress. ABA is synthesized in roots in response to stress and transported to the leaves but leaves are also capable of producing ABA. Both intra- and extracellular ABA receptors have been proposed. However, extracellular but not microinjected, intracellular ABA, inhibits stomatal opening in *Commelina* and functions as an antagonist in gibberellic acid induced gene expression in barley aleurone protoplasts. However, microinjection of ABA or caged ABA in guard cells lead to stomatal closure and to expression of the Em gene in barley aleurone. This suggests the existence of an intracellular ABA receptor.¹⁶ The pH dependence of ABA action points to both extra- and intracellular receptors as an ABA target. Despite the evidence for several ABA receptors none has been cloned. It is thought that desiccation and other stresses leading to low water potential result in cell wall loosening. This in turn induces a signalling cascade that includes synthesis of ABA, through a pathway that requires protein synthesis. In plants the mRNA level of the zeaxanthin epoxidase is low in roots. In leaves, it is high at the beginning of the light period, then decreases and is undetectable in the dark. The induction in light probably reflects the protective role of zeaxanthin on the photosynthetic apparatus rather than regulation of ABA levels. This reinforces the possibility that a step downstream of all-trans-violaxanthin is the regulatory step in ABA biosynthesis.¹⁷

V. CONCLUSIONS

ABA is produced under drought-stress conditions de novo, which requires protein biosynthesis. As mentioned above, this process is important for drought-inducible gene expression. ABA is synthesized from β -carotene via zeaxanthin, neoxanthin, xanthoxin, and ABA-aldehyde (C40 pathway), and the step of conversion of neoxanthin to xanthoin is rate-limiting in the ABA biosynthesis under drought stress.¹⁸ Genetic evidence supports the C40 pathway, and biochemical studies suggest that the cleavage of neoxanthin is a key regulatory step in ABA biosynthesis. Many ABA-deficient mutants that do not produce ABA have been isolated in various plants. Based on genetic analysis of ABA-deficient mutants, most of the enzymes involved in ABA biosynthesis have been identified, such as zeaxanthin epoxidase (ZEP; ABA1/LOS6 in *Arabidopsis*, ABA2 in tobacco (*Nicotiana tabacum*)), 9-cis-epoxycarotenoid dioxygenase (NCED; VP14 in corn (*Zea mays*; maize),¹⁹ ABA aldehyde oxidase (AAO in *Arabidopsis*), molybdenum cofactor sulfurase (MCSU; ABA3/LOS5 in *Arabidopsis*). In various plants,²⁰ NCED genes are significantly induced by drought stress but not by cold stress, which suggests that ABA mainly functions in osmotic stress responses. Transgenic plants that overexpress NCEDs accumulate ABA and are tolerant to drought stress. This also indicated a key role of NCED in ABA biosynthesis.²¹

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