Agrobiodiversity for Improving Nutrition, Health and Life Quality

Review

Phytohormones

Monika Ňorbová*, Alena Vollmannová, Judita Lidiková

Slovak University of Agriculture in Nitra, Institute of Food Science, Department of Chemistry, Slovakia

ORCID
Monika Ňorbová: https://orcid.org/0000-0002-2963-2189
Alena Vollmannova: https://orcid.org/0000-0001-7470-4500
Judita Lidiková: https://orcid.org/0000-0001-9922-4300

Article Details:
Received: 2021-07-08
Accepted: 2021-08-05
Available online: 2021-11-30

DOI: https://doi.org/10.15414/ainhlq.2021.0023

During evolution in plants, a sophisticated system of receptors and signaling pathways has emerged that allows for appropriate responses and responses to these signals. One of such signals is the plant hormone – phytohormone. Abscisic acid is a sesquiterpene, which has important roles in seed development and maturation, in the synthesis of proteins and compatible osmolytes, which enable plants to tolerate stresses due to environmental or biotic factors, and as a general inhibitor of growth and metabolic activities. Abscisic acid is essential for the initiation and maintenance of tuber dormancy. Its main antagonist is gibberellic acid, which affects carbohydrate metabolism, indicating the budding of tubers. Gibberellic acid is a naturally occurring plant hormone that is used as a plant growth regulator to stimulate both cell division and elongation that affects leaves and stems. Salicylic acid belongs to a group of plant phenols that play an important role in the regulation of plant growth, development, and interaction with other organisms. Salicylic acid (SA), a phytohormone, is a promising compound that can reduce the sensitivity of plants to environmental stresses through regulation of the antioxidant defense system, transpiration rates, stomatal movement, and photosynthetic rate. Phytohormones are essential regulators of plants in two physiological processes that coordinate growth, reproduction, and stress resistance. These molecules also show biological activities on human cells and animal models.

Keywords: phytohormones, abscisic acid, gibberellic acid, salicylic acid

Introduction

The first mention of plant hormones (phytohormones) dates back to the 19th century when the German botanist Julius Von Sachs predicted the existence of a cell messenger responsible for the formation and growth of plant organs (Taiz et al., 2014). According to this theory, the messenger is influenced by external influences, such as gravity. Although these views were not supported by any known chemicals, they later led to the discovery of phytohormones. Around the same time, Charles Darwin, along with his son Francis, observed the effect of light on the growth of the *Phalaris canariensis* (Darwin, 1880). In the case of lighting the coleoptiles on one side, there was bending and growth of the plant behind the light. However, this phenomenon did not occur when the tip was covered with a cap. Based on these results, Darwin formulated a hypothesis that assumes the existence of a certain signal arising at the peak of the growth peak and propagating to the site of bending (Christie

***Corresponding Author:** Monika Ňorbová, Slovak University of Agriculture in Nitra, Faculty of Biotechnology and Food Sciences, Institute of Food Science, Tr. A. Hlinku 2, 949 76 Nitra, Slovakia
xnorbova@uniag.sk

and Murphy, 2013). The term phytohormone was first defined in 1948 by the plant physiologist Thimann, to distinguish between animal and plant hormones (Went and Thimann, 1948).

Phytohormones (plant hormones) are chemical compounds produced in plants in very low concentrations, but able to regulate the most important developmental and growth processes of the plant cell. Phytohormone concentrations can vary considerably between organ types, for example in the roots compared to leaves (Ciura and Kruk, 2018). At the same time, they work as chemical messengers to communicate cellular processes in higher plants over longer distances, thereby mediating signaling between plant organs (Voß et al., 2014). Phytohormones play key roles and coordinate various signaling pathways during the response to abiotic stress. They regulate both external and internal stimuli (Kazan, 2015). Plant hormones determine the formation of flowers, stems, leaves, leaf fall, and the development and ripening of the fruit. They also shape the plant, affect seed growth, flowering time, sex of flowers, ageing of leaves and fruits. They are vital for plant growth, and without them, plants would only be a mass of undifferentiated cells (Procházka et al., 1998). The best-known groups of phytohormones include auxins, cytokinins (CK), gibberellins, ethylene, abscisic acid (ABA), and brassinosteroids (Kundan et al., 2015; Ciura and Kruk, 2018).

Abscisic acid

Abscisic acid (ABA) (Figure 1) is an optically active C15 carboxylic acid terpenoid. Its discovery dates back to the early 1960s when it was found to be involved in seed germination (Chen et al., 2019). According to the orientation of the carboxyl group on the second carbon, we can distinguish the cis and trans isomers of ABA. Thus, since ABA is optically active, it can exist as the R or S isomer. The S form is active naturally occurring, while the R form is inactive and occurs in plant vents (Taiz and Zeiger, 2010).

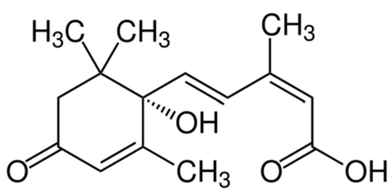

Figure 1 Abscisic acid (https://upload.wikimedia.org/wikipedia/commons/thumb/d/d9/Abscisic_acid_Structural_Formula_V1.svg/440px-Abscisic_acid_Structural_Formula_V1.svg.png)

The original name of abscisic acid was abscisin II and was first isolated from cotton (Humplík et al., 2017). ABA plays a vital role in many physiological processes during plant growth. Its important roles include fruit development, responses to biotic and abiotic stresses (Dong et al., 2015; Vishwakarma et al., 2017).

ABA can act as a promoter but also as an inhibitor. Its main effects and functions include regulating the water regime of plants, closing, and opening vents, inhibiting elongation growth, regulating dormancy (Vishwakarma et al., 2017). ABA reduces the growth rate of growing tissues and organs, so it is an auxin antagonist in this effect. This effect is accompanied by a reorientation of the microtubules longitudinally in the direction of growth. However, if the concentration of ABA is low, prolonged growth will not be affected (Procházka et al., 1998).

The most important function of the ABA is to regulate the water regime of plants. If the plant is deficient in water, the ABA will cause the vents to close. When there is a lack of water, there is a rapid increase in ABA in roots and leaves. In dehydration, if ABA levels are high, there is a positive stimulation of root growth and, conversely, inhibition of shoot growth (Vishwakarma et al., 2017). When there is a lack of water in the leaves, the ABA is transferred from the mesophyll to the epidermis, where it causes the airways to close and restrict transpiration. Thus, abscisic acid is considered to be a defense mechanism of the plant against stress, it reduces the negative effect not only in insufficient hydration of the plant but also at low temperature or salinity and can adapt the plant to these conditions (Procházka et al., 1998; Nambara, 2017).

Abscisic acid exists naturally in plants as both the anionic form (ABA−) and the protonated form (ABAH). ABAH can diffuse passively across the plasma membrane, and ABA diffusion decreases significantly with cytoplasmic alkalization, which increases during osmotic stress (Chen et al., 2019).

Biosynthesis of ABA

Two ABA biosynthesis pathways have been proposed. In the forward pathway (sesquiterpenoid pathway), ABA is derived from farnesyl diphosphate (FDP) (Chen et al., 2019). In the indirect pathway (carotenoid pathway), ABA is formed by the cleavage of carotenoids (Nambara, 2017). This pathway has been proposed due to the structural similarity between ABA and xanthoxin (a carotenoid degradation product). It has been confirmed by several biochemical studies and is therefore thought to be synthesized by ABA in higher

ISSN 2585-8246

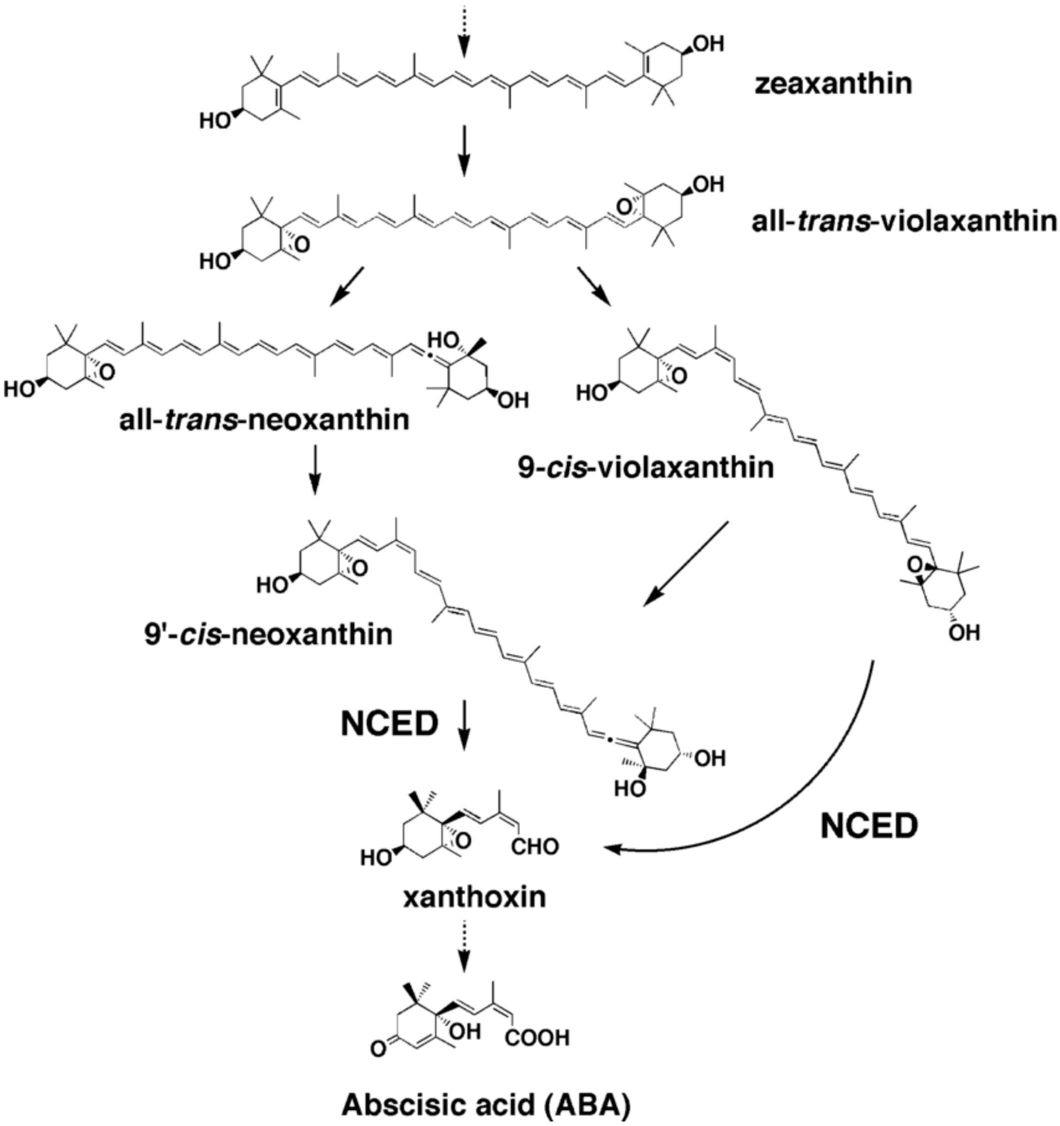

Figure 2 Biosynthesis pathway of ABA (https://www.researchgate.net/profile/Kazuo-Nakashima/publication/8462646/figure/fig1/AS:601693926486046@1520466419599/ABA-biosynthesis-pathway-in-higher-plants-ABA-is-derived-from-C-40-carotenoids-such-as.png)

plants through the carotenoid pathway (Ruiz-Sola and Rodrígeuz-Concepción, 2012).

This pathway begins from the precursor isopentenyl diphosphate (IPP), which is synthesized in plastids from glyceraldehyde-3-phosphate and pyruvate via methylerythritol phosphate (Nambara and Marion-Poll, 2005). This is followed by the synthesis of violaxanthin catalyzed by zeaxanthin epoxidase (ZEP). Violoxanthine is converted to 9-*cis*-neoxanthin, which is subsequently cleaved to xanthoxal by the enzyme 9-*cis*-epoxycarotenoid dioxygenase (NCED). The final steps in biosynthesis are the oxidation of xanthoxal to ABA-aldehyde and then to ABA catalyzed by aldehyde oxidases (Nambara, 2017).

Gibberellins

After the discovery of auxin, scientists attributed all regulation of developmental phenomena in plants to auxin for about 20 years, until the second group of hormones, gibberellins, was characterized in 1950 (Taiz and Zeiger, 2010). Gibberellins (GA) are phytohormones that primarily determine the height of plants. The first gibberellin was isolated in Japan from the fungus *Giberella fujikuroi*, after which they were named (Kwon and Paek, 2016; Binenbaum et al., 2018).

All gibberellins are native. They are isoprenoids from the group of diterpenes. Gibberellins are a large group of similar substances and some of them are precursors of active hormones (Gupta and Chakrabarty, 2013; Camara et al., 2018).

Unlike active auxin, gibberellins retain activity in the plant and also do not cause toxicity, i.e. they are not harmful to the plant even in higher concentrations. There is no particular enzymatic mechanism for degrading gibberellins in plants, but they can be converted to inactive forms that form conjugates with carbohydrates. The biogenesis of gibberellins is affected by light and controlled by phytochrome (Rodrigues et al., 2011).

It is proven that their synthesis takes place in the root tips or is transported to them, later distributed by basipetal movement, especially by the transpiration current (Brestič and Olšovská, 2001).

Transport takes place by wood and varnish. Transport can also take place acropetally, non-polar. Their movement is often oriented, regardless of polarity, behind the IAA source (Binenbaum et al., 2018).

Gibberellins are probably produced in all plant organs. The highest concentrations are in sites of active growth and emerging organs (Gupta and Chakrabarty, 2013). The regulatory effects of gibberellins include the enhancement of apical dominance along with abscisic acid. With ABA, they also induce parthenocarpy in seedless vine varieties (*Vitis vinifera*) and enlarge berries. They indicate the formation of flowers in photo periodically sensitive plants, thus accelerating their flowering and enlarging the flowers. They suppress the development of female flowers and support the development of male flowers. They also prevent the ageing of leaves and fruits and stimulate seed germination (Rodrigues et al., 2011; Cheng et al., 2017).

Gibberellic acid (GA3) (Figure 3) is a diterpenoid carboxylic acid that belongs to the gibberellin family and acts as a natural plant growth hormone. It is produced by plants and some microorganisms, such as fungi and bacteria. GA3 has a promising application in the agro-industrial sector due to its properties related to plant development. GA3 is applied to crops, orchards, and ornamental plants, where it plays a role in seed germination, response to abiotic stress, enhanced fruit growth, stem elongation, flowering, barley malting, and other physiological effects that occur in its interaction with other phytohormones (Camara et al., 2018).

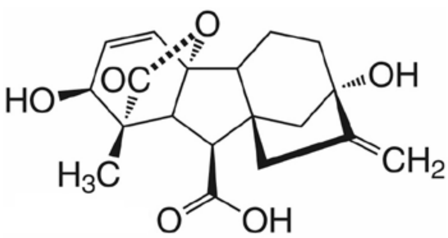

Figure 3 Gibberellic acid (https://img.p-lab.cz/userimages/product_main/1770/2007_656dde6c4fa997a1fce-c59a522ddeb5d_large.jpg)

Biosynthesis of gibberellins

The biosynthetic pathway occurs through certain intermediates. The synthesis of GA is carried out via terpenes from geranylgeranyl diphosphate by plants and fungi. The four isoprenoid molecules are linked together to form a linear molecule of 20 carbon atoms, known as geranylgeranyl diphosphate (GGPP). This molecule is transformed into *ent*-copalyl diphosphate by the action of *ent*-copalyl diphosphate synthase (CPS), which in turn is converted to a tetracyclic compound known as *ent*-kaurene by the action of *ent*-kaurene synthase (KS). *Ent*-kauren oxidase (KO) in plants and P450-4 in fungi catalyze the gradual oxidation of *ent*-kauren to C-19 to form *ent*-kaurenic acid, which is subsequently affected by kaurenic acid oxidase (KAO) in plants and P450-1 in fungi converts to GA12-aldehyde. In plants, GA12-aldehyde is first converted to GA12 and then converted to GA9 by the action of GA20-oxidase, which is responsible for the production of C19-GA. In a parallel pathway, GA12 is also 13-hydroxylated to produce GA53, which is converted to GA20 by C20-oxidase. Then, GA3-oxidase converts GA20 and GA9 by adding a 3β-hydroxyl group to GA1 and GA4, respectively. GA3 is synthesized by converting GA20 to GA5 using GA3-oxidase. This stage varies between species and depends on environmental conditions (Gupta and Chakrabarty, 2013; Camara et al., 2018; Hedden, 2020).

In fungi, GA12-aldehyde is 3β-hydroxylated to GA14-aldehyde, which is oxidized to form GA14. The latter is again converted to GA4 by oxidation with C20. GA4 is the first bioactive molecule to be formed and desaturated to form GA7, which is then converted to GA3 by 13-hydroxylation. GA1 is formed by 13-hydroxylation of GA4 (Camara et al., 2018; Hedden, 2020).

The pathways of biosynthesis in plants and fungi during the conversion of geranylgeranyl diphosphate to *ent*-kaurene and subsequent conversion to GA12-aldehyde are similar. The pathways differ from the stage at which GA12-aldehyde is converted to other GA, in the order in which the 3β-hydroxylation and 13-hydroxylation steps occur in plants and fungi. Plant and fungal GA biosynthetic pathways are described in Figure 4 (Camara et al., 2018).

ISSN 2585-8246

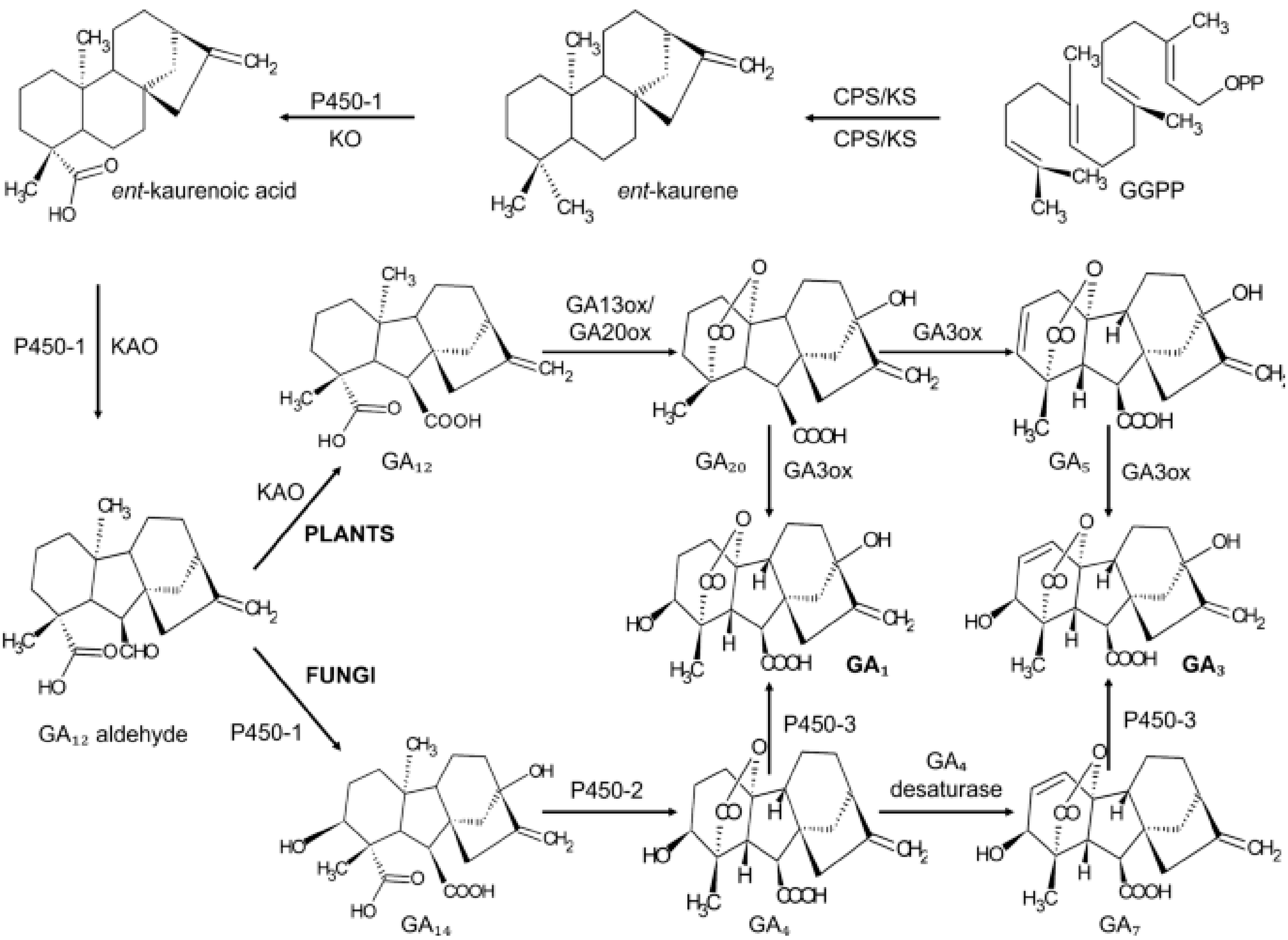

Figure 4 Biosynthesis of gibberellins in plants and fungi (https://media.springernature.com/lw685/springer-static/image/art%3A10.1007%2Fs00425-018-2959-x/MediaObjects/425_2018_2959_Fig3_HTML.png?as=webp)

Salicylic acid

Several centuries ago, the ancient Greeks used willow leaves and bark to alleviate pain and fever. Johann Buchner successfully isolated a small amount of salicin (glycoside salicyl alcohol) in 1828, which was identified as the major salicylate in willow bark (Maruri-López et al., 2019; Arif et al., 2020).

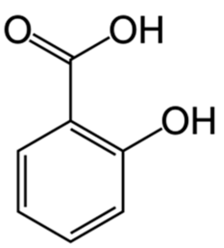

Figure 5 Salicylic acid (https://upload.wikimedia.org/wikipedia/commons/thumb/8/8e/Salicylic-acid-skeletal.svg/220px-Salicylic-acid-skeletal.svg.png)

Salicylic acid (Figure 5) or ortho-hydroxybenzoic acid belongs to a diverse group of plant phenols, which are substances bearing an aromatic ring to which a hydroxyl group or a functional derivative thereof is attached. Plant phenols are often classified as secondary metabolites, which play an important role in the regulation of plant growth, development, and interaction with other organisms (Maruri-López et al., 2019).

Free salicylic acid is a crystalline white powder having a melting point of about 157–159 °C. It is moderately soluble in water and very soluble in polar organic solvents. The saturated aqueous salicylic acid solution has a pH of 2.4. Salicylic acid fluoresces at 412 nm, while its excitation wavelength is at 301 nm, allowing it to be detected using a more sensitive fluorescence detector (Hayat and Ahmad, 2007).

Salicylic acid is produced by plants as protection against stress and disease (Metwaly and El-Shatoury, 2017).

ISSN 2585-8246

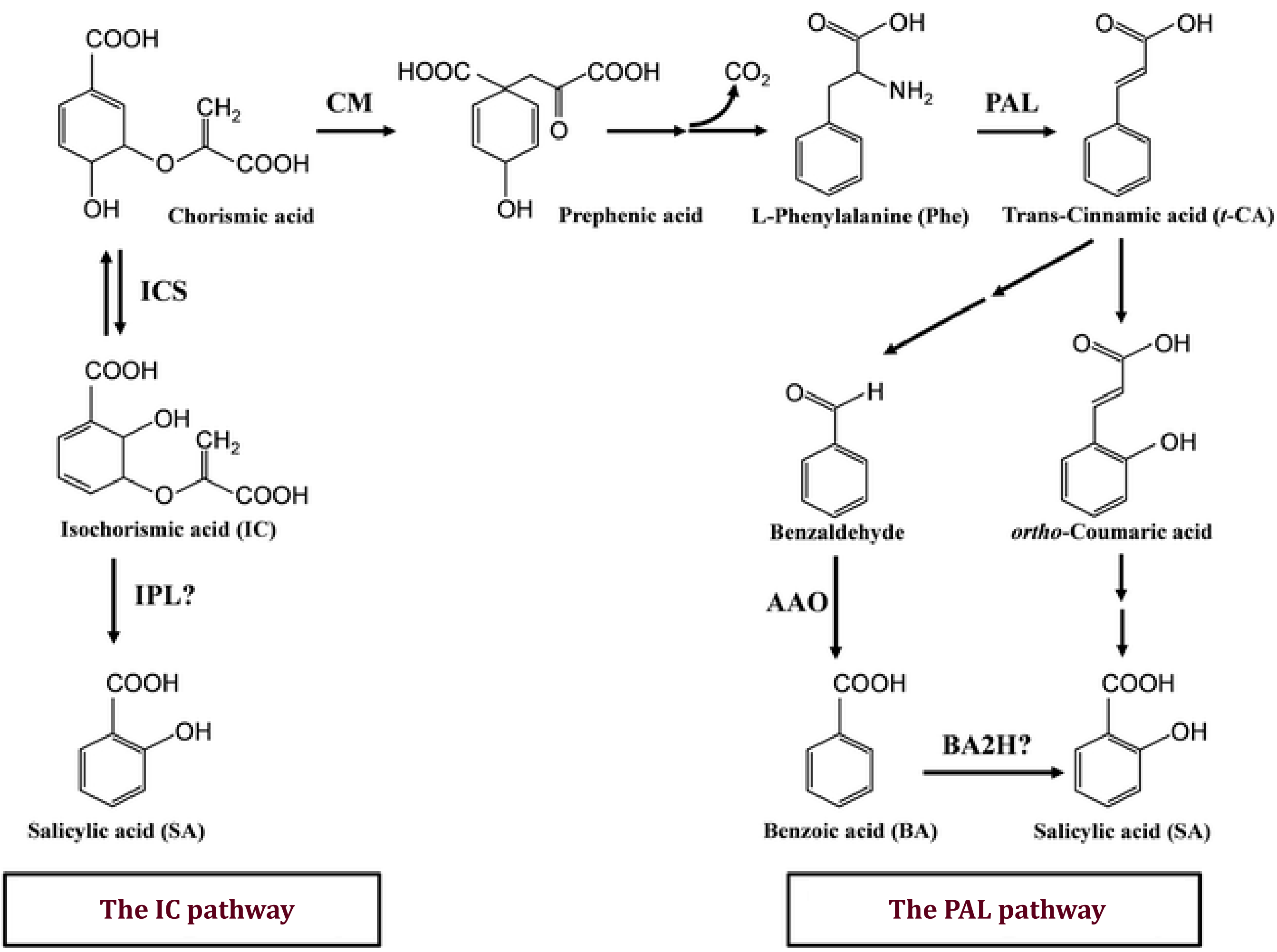

Figure 6 Biosynthesis pathways of salicylic acid (https://media.springernature.com/full/springer-static/image/art%3A10.1186%2Fs12915-017-0364-8/MediaObjects/12915_2017_364_Fig1_HTML.gif)

This can then serve as an explanation for its higher content in organically grown vegetables without the use of pesticides. John Paterson and his team from the University of Strathclyde found that soups made from organically grown vegetables contained six times more salicylic acid than soups made from vegetables grown in a conventional way (Klimeková and Lehocká, 2021).

Salicylic acid (SA) is a naturally occurring hormone that functions as an important signaling molecule. It affects various biochemical and physiological functions and has a different effect on tolerance to both biotic and abiotic stress (Li et al., 2019; Maruri-López et al., 2019). Thus, it is a key phytohormone that regulates defense against both biotrophic and hemibiotrophic pathogens and is often the primary chemical signal induced during the resistant response. This small molecule plays a crucial role in stimulating the plant's immune response. Usually, SA affects seed germination, seedling establishment, cell growth, respiration, ventricular closure, gene expression associated with ageing, responses to abiotic stress, basal thermotolerance, nodulation in legumes, and crop fertility (Vlot et al., 2009; Maruri-López et al., 2019). It further activates universal transcriptional reprogramming and resistance to a wide range of pathogens (Fu et al., 2012).

Biosynthesis of salicylic acid

Salicylic acid is a natural derivative of cinnamic acid, an intermediate of the shikimate metabolic pathway, and it is a starting material for the synthesis of many phenolic compounds. Its biosynthesis probably proceeds in two different ways (Figure 6) (Zhang and Li, 2019).

The first synthetic route proposes the formation of salicylic acid by decarboxylation of the cinnamic acid side chain to benzoic acid, which subsequently undergoes hydroxylation at the C-2 position. An enzyme catalyzing the β-oxidation of cinnamic acid to

ISSN 2585-8246

benzoic acid has been identified in the summer oak (*Quercus robur*), but other enzymes responsible for the conversion of benzoic acid to salicylic acid have not yet been identified. The second route describes the hydroxylation of cinnamic acid to o-coumaric acid, from which salicylic acid is formed by subsequent decarboxylation. The conversion of cinnamic acid to o-coumaric acid is catalyzed by the enzyme *trans*-cinnamate-4-hydroxylase, which was first discovered in pea seedlings, but enzymes that activate the conversion of o-coumaric acid to salicylic acid have not yet been characterized. When radioactive 14C-benzoic acid or 14C-cinnamic acid was involved, labeled salicylic acid was formed in *Gaultheria procumbens*, which supported the theory of salicylic acid synthesis from cinnamic acid via benzoic acid as an intermediate. In higher plants, both synthetic pathways are involved in salicylic acid formation (Zhang and Li, 2019; Arif et al., 2020).

Conclusions

Phytohormones are essential regulators of plants in two physiological processes that coordinate growth, reproduction, and stress resistance. These molecules also show biological activities on human cells and animal models. Importantly, these phytohormones are not plant-specific and have even been shown to be endogenously produced in the human body or human cell cultures. When we are constantly exposed to this molecular, they are no strangers to human physiology. This means that they are likely to be involved in various physiological processes. In addition, several phytohormones may also be produced by microbes, and such compounds produced in our intestines are likely to have physiological effects (Kim et al., 2020).

Some phytohormones are anti-inflammatory compounds that inhibit several inflammatory diseases. For example, the treatment of ABA in humans and animal models requires beneficial effects against a wide range of inflammatory diseases such as type 2 diabetes, colitis, atherosclerosis, glioma, and depression. Salicylates have pharmacological properties in cardiovascular disease, colon cancer, and diabetes. Administered citokinins or its derivatives lead to attenuated oxidative stress in mammalian cells and anti-cytotoxicity in neoplastic cells. High IAA production has been shown to attenuate liver damage caused by a high-fat diet, relying on the aryl hydrogen receptor. Phytohormones that are not endogenously produced can also have physiological effects and have anti-inflammatory effect. For example, gibberellins (GA) induce the anti-inflammatory protein A20 in filter epithelial cells that could protect against asthma (Chanclud and Lacombe, 2017; Kim et al., 2020).

Conflicts of interest

The authors declare no conflict of interest.

Ethical statement

This article does not contain any studies that would require an ethical statement.

References

Arif, Y., Sami, F., Siddiqui, H., Bajguz, A., & Hayat, S. (2020). Salicylic acid in relation to other phytohormones in plant: A study towards physiology and signal transduction under challenging enviroment. *Enviromental and Experiental Botany, 175*, 104040. https://doi.org/10.1016/j.envexpbot.2020.104040

Binenbaum, J., Weinstain, R., & Shani, E. (2018). Gibberellin Localization and Transport in Plants. *Trends in Plant Science, 23*(5), 410–421. https://doi.org/10.1016/j.tplants.2018.02.005

Brestič, M., & Olšovská, K. (2001). Plant *water stress: causes, consequences, perspectives*. Nitra: Slovak University of Agriculture. ISBN 80-7137-902-6.

Camara, M.C., Vandenberghe, L.P.S., Rodrigues, C., Oliveira, J., Faulds, C., Bertrand, E., & Soccol, C.R. (2018). Current advances in gibberellic acid (GA3) production, patented technologies and potential applications. *Planta, 248*, 1049–1062. https://doi.org/10.1007/s00425-018-2959-x

Ciura, J., & Kruk, J. (2018). Phytohormones as targets for improving plant productivity and stress tolerance. *Journal of Plant Physiology, 229*, 32–40. https://doi.org/10.1016/j.jplph.2018.06.013

Darwin, C. (1880). *The power of movement in plants. London*: John Murray Publishers. https://doi.org/10.1017/CBO9780511693670

Dong, T., Park, Y., & Hwang, I. (2015). Abscisic acid: biosynthesis, inactivation, homeostasis and signalling. *Essays in Biochemistry, 58*, 29–48. https://doi.org/10.1042/bse0580029

Fu, Z.Q., Yan, S., Saleh, A., Wang, W., Ruble, J., Oka, N., Mohan, R., Spoel, S.H., Tada, Y., Zheng, N., & Dong, X. (2012). NPR3 and NPR4 are receptors for the immune signal salicylic acid in plants. *Nature, 486*, 228–232. https://doi.org/10.1038/nature11162

Gupta, R., & Chakrabarty, S.K. (2013). Gibberellic acid in plant. *Plant Signaling & Behavior, 8*(9), e25504. https://doi.org/10.4161/psb.25504

Hayat, S., & Ahmad, A. (2007). *Salicylic acid-a plant hormone* [online]. Dordrecht: Springer, 400 s. ISBN 1-4020-5184-0. Available at: https://books.google.sk/books?hl=sk&lr=&id=9XMWWDhLXJMC&oi=fnd&pg=PR11&dq=salicylic+acid&ots=YrcmIPUI08&sig=ZK74q28hrtGrU2Cagxj5Xi-uKYWI&redir_esc=y#v=onepage&q=salicylic%20acid&f=false

Hedden, P. (2020). The Current status of research on gibberellin biosynthesis. *Plant and Cell Physiology, 61*(11), 1832–1849. https://doi.org/10.1093/pcp/pcaa092

https://upload.wikimedia.org/wikipedia/commons/thumb/d/d9/Abscisic_acid_Structural_Formula_V1.svg/440px-Abscisic_acid_Structural_Formula_V1.svg.png

https://www.researchgate.net/profile/Kazuo-Nakashima/publication/8462646/figure/fig1/AS:601693926486046@1520466419599/ABA-biosynthesis-pathway-in-higher-plants-ABA-is-derived-from-C-40-carotenoids-such-as.png

https://img.p-lab.cz/userimages/product_main/1770/2007_656dde6c4fa997a1fcec59a522dde-b5d_large.jpg

https://media.springernature.com/lw685/springer-static/image/art%3A10.1007%2Fs00425-018-2959-x/MediaObjects/425_2018_2959_Fig3_HTML.png?as=webp

https://upload.wikimedia.org/wikipedia/commons/thumb/8/8e/Salicylic-acid-skeletal.svg/220px-Salicylic-acid-skeletal.svg.png

https://media.springernature.com/full/springer-static/image/art%3A10.1186%2Fs12915-017-0364-8/MediaObjects/12915_2017_364_Fig1_HTML.gif

Humplík, J.F., Bergougnoux, V., & Van Volkenburgh, E. (2017). To Stimulate or inhibit? that is the qustion for the function of abscisic acid. *Trends in Plant Science, 22*(10), 830–841. https://doi.org/10.1016/j.tplants.2017.07.009

Chanclud, E., & Lacombe, B. (2017). Plant hormones: key players in gut microbiota and human diseases? *Trends in Plant Science, 22*(9), 754–758. https://doi.org/10.1016/j.tplants.2017.07.003

Chen, K., Li, G.J., Bressan, R.A., Song, Ch. P., Zhu, J.K., & Zhao, Y. (2019). Abscisic acid dynamics, signaling, and functions in plants. *Journal of Integrative Plant Biology, 62*(1), 25–54. https://doi.org/10.1111/jipb.12899

Cheng, L., Wang, Y., Liu, Y., Zhang, Q., Gao, H., & Zhang, F. (2017). Comparative proteomics illustrates the molecular mechanism of potato (*Solanum tuberosum* L.) tuberization inhibited by exogenous gibberellins *in vitro*. *Physiologia Plantarum, 163*(1), 103–123. https://doi.org/10.1111/ppl.12670

Christie, J.M., & Murphy, A.S. (2013). Shoot phototropism in higher plants: New light through old concepts. *Americal Journal of Botany, 100*(1), 35–46. https://doi.org/10.3732/ajb.1200340

Kazan, K. (2015). Diverse roles of jasmonates and ethylene in abiotic stress tolerance. *Trends in Plant Science, 20*(4), 219–229. https://doi.org/10.1016/j.tplants.2015.02.001

Kim, S.W., Goossens, A., Libert, C., Van Immerseel, F., Staal, J., & Beyaert, R. (2020). Phytohormones: Multifunctional nutraceuticals against metabolic syndrome and comorbid diseases. *Biochemical Pharmacology, 175*, 113866. https://doi.org/10.1016/j.bcp.2020.113866

Klimeková, M., & Lehocká, Z. (2021). Quality in organic farming – myth or reality? *Agricultural advisory system* [online], [cit. 2021-03-21]. Available at: http://www.agroporadenstvo.sk/ep/kvalita_ep.pdf

Kundan, R., Pant, G., Jadon, N., & Agrawal, P.K. (2015). Plant Growth Promoting Rhizobacteria: Mechanism And Current Prospective. *Journal of Fertilizers & Pesticides, 6*, 1–9.

Kwon, C.T., & Paek, N.C. (2016). Gibberellic acid: A key phytohormone for spikelet fertility in rice grain production. *International Journal of Molecular Sciences, 17*(5), 794.

Li, Q., Wang, G., Wang, Y., Yang, D., Guan, Ch., & Li, J. (2019). Foliar application of salicylic acid alleviate the cadmium toxicity by modulation the reactive oxygen species in potato. *Ecotoxicology and Environmental Safety, 172*, 317–325. https://doi.org/10.1016/j.ecoenv.2019.01.078

Maruri-López, I., Aviles-Baltazar, N. Y., Buchala, A., & Serrano, M. (2019). Intra and extracellular journey of the phytohormone salicylic acid. *Frontiers in Plant Science, 10*, 423. https://doi.org/10.3389/fpls.2019.00423

Metwaly, E.E., & El-Shatoury, R.S. (2017). Impact of foliar application with salicylic acid on growth and yield of potato (*Solanum tuberosum* L.) under different irrigation water quantity. *Jounal of Plant Production, 8*(10), 969–977. https://doi.org/10.21608/jpp.2017.41052

Nambara, E. (2017). Abscisic acid. *Encyclopedia of Applied Plant Sciences, 1*, 361–366. [cit. 2021-03-11], Available at: https://www.sciencedirect.com/science/article/pii/B9780123948076000988?via%3Dihub

Nambara, E., & Marion-Poll, A. (2005). Abscisic acid biosynthesis and catabolism. *Annual Review of Plant Biology, 56*, 165–185. https://doi.org/10.1146/annurev.arplant.56.032604.144046

Procházka, S., Macháčková, I., Krekule, J., & Šebánek, J. (1998). *Plant physiology*. Praha : Academia. ISBN 80-200-0586-2.

Rodrigues, C., Vandenberghe, L.P., De S., De Oliveira, J., & Soccol, C. R. (2011). New perspectives of gibberellic acid production: a review. *Critical Reviews in Biotechnology, 32*(3), 263–273. https://doi.org/10.3109/07388551.2011.615297

Ruiz-Sola, M.Á., & Rodríguez-Concepción, M. (2012). Carotenoid biosynthesis in *Arabidopsis*: a colorful pathway. *Arabidopsis Book, 10*, e0158. https://doi.org/10.1199/tab.0158

Taiz, L., & Zeiger, E. (2010). *Plant Physiology*. Sunderland – Massachusetts: Sinauer Associates. ISBN 978-0878938667.

Taiz, L., Zeiger, E., Moller, I. M., & Murphy, A. (2014). *Plant physiology and development – Signals and signal transduction*. Sunderland – Massachusetts: Sinauer Associates. ISBN 0878938664.

ISSN 2585-8246

Vishwakarma, K., Upadhyay, N., Kumar, N., Yadav, G., Singh, J., Mishra, R. K., Kumar, V., Verma, R., Upadhyay, R. G., Pandey, M., & Sharma, S. (2017). Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. *Frontiers in Plant Science, 8*, 161. https://doi.org/10.3389/fpls.2017.00161

Vlot, A.C., Dempsey, D.A., & Klessig, D.F. (2009). Salicylic acid, a multifaceted hormone to combat disease. *Annual Review of Phytopathology, 47*, 177–206. https://doi.org/10.1146/annurev.phyto.050908.135202

Voß, U., Bishopp, A., Farcot, E., & Bennett, M.J. (2014). Modelling hormonal response and development. *Trends in Plant Science, 19*(5), 311–319. https://doi.org/10.1016/j.tplants.2014.02.004

Went, F.W., Thimann K.V. (1948). *Phytohormones* [online]. New York: The Macmillan Company [cit. 2021-02-03]. 294 s. Available at: https://www.biodiversitylibrary.org/item/26595#page/310/mode/1up

Zhang, Y., & Li, X. (2019). Salicylic acid: biosynthesis, perception, and contributions to plant immunity. *Current Opinion in Plant Biology, 50*, 29–36. https://doi.org/10.1016/j.pbi.2019.02.004