Open Journal of Natural Science 自然科学, 2025, 13(3), 687-696
Published Online May 2025 in Hans. https://www.hanspub.org/journal/ojns
https://doi.org/10.12677/ojns.2025.133072

Hans汉斯

植物水杨酸功能与合成的研究进展

高　蓉

浙江师范大学生命科学学院，浙江　金华

收稿日期：2025年4月20日；录用日期：2025年5月22日；发布日期：2025年5月29日

摘　要

水杨酸(Salicylic Acid, SA)作为重要的植物激素，在植物生命活动中扮演关键角色。它广泛参与植物生长发育进程，如调控种子萌发，促使种子在适宜条件下打破休眠、启动萌发；影响根系生长，对根的形态建成和生长速率发挥调节作用；在开花诱导方面，参与植物从营养生长到生殖生长的转变过程，影响花期。同时，SA是植物应对生物和非生物胁迫的核心信号分子。在生物胁迫中，病原菌入侵时，SA能诱导植物产生局部和系统获得性抗性，增强植物对病原菌的防御能力；面对非生物胁迫，如干旱、低温、盐碱时，SA可通过调节植物体内的生理生化过程，提升植物的抗逆性。植物中SA的合成主要有两条途径。异分支酸合成酶(ICS)途径起始于叶绿体，分支酸在ICS1催化下形成异分支酸，经EDS5转运至细胞质，再由PBS3催化生成异分支酸－谷氨酸加合物，进而生成SA。苯丙氨酸解氨酶(PAL)途径则以苯丙氨酸为底物，经反式肉桂酸、苯甲酸等中间产物合成SA，但将苯甲酸转化为SA的部分基因尚未明确。不同植物中，这两条途径对SA合成的贡献存在差异。

关键词

水杨酸，功能，合成

Research Progress on the Function and Synthesis of Plant Salicylic Acid

Rong Gao

College of Life Sciences, Zhejiang Normal University, Jinhua Zhejiang

Received: Apr. 20th, 2025; accepted: May 22nd, 2025; published: May 29th, 2025

Abstract

Salicylic acid, as an important plant hormone, plays a key role in plant life activities. It is widely involved in plant growth and development, such as the regulation of seed germination, to promote the seeds to break dormancy and initiate germination under suitable conditions; affecting root

文章引用: 高蓉. 植物水杨酸功能与合成的研究进展[J]. 自然科学, 2025, 13(3): 687-696.
DOI: 10.12677/ojns.2025.133072

growth, and regulating the morphology and growth rate of roots; in the induction of flowering, it is involved in the transition from nutrient growth to reproductive growth, and affects the flowering period. Meanwhile, SA is a core signaling molecule for plants to cope with biotic and abiotic stresses. In biotic stress, when pathogenic bacteria invade, SA can induce local and systemic acquired resistance and enhance the defense ability of plants against pathogenic bacteria; in the face of abiotic stress, such as drought, low temperature, salinity and alkalinity, SA can enhance the plant's resilience by regulating the physiological and biochemical processes in the body of the plant. There are two main pathways for SA synthesis in plants. The isobranched acid synthase (ICS) pathway begins in chloroplasts, where branch acids are catalyzed by ICS1 to form isobranched acids, which are transported to the cytoplasm by EDS5 and then catalyzed by PBS3 to form isobranched acid-glutamic acid adducts, which in turn generate SA. The phenylalanine ammonia-lyase (PAL) pathway, on the other hand, synthesizes SA using phenylalanine as a substrate and intermediates, such as trans-cinnamic acid and benzoic acid, but some genes for the conversion of benzoic acid to SA have not yet been developed. The partial genes that convert benzoic acid to SA have not been identified. The contribution of these two pathways to SA synthesis varies among plants.

Keywords

Salicylic Acid, Function, Synthesis

1. 引言

水杨酸(Salicylic Acid, SA)及其衍生物，统称为水杨酸盐，几千年来一直被用于实现各类医疗目的[1]。1828 年，德国科学家 Johann Buchner 从柳树皮里成功提取出有效成分。鉴于白柳的拉丁文学名是 *Salix alba*，便将该成分命名为水杨苷(Salicyl glucoside, SAG)。1898 年，拜耳公司推出了乙酰水杨酸，商品名为阿司匹林，其迅速成为世界上最畅销的药物之一[2]。直到 20 世纪 90 年代初，人们才逐渐认识到 SA 在植物中的重要作用，并将其定义为植物激素[3]。

2. SA 的功能

在自然界中，植物为了克服各种各样的植物病原体和非生物胁迫，植物已经进化出复杂的防御机制[4]。在病原体感染或非生物胁迫期间，SA 在感染组织和全身组织中都被诱导和积累，包括编码病程相关蛋白(Pathogenesis-Related proteins，PR 蛋白)和参与氧化应激保护的酶等大量基因同时上调[5]。此外，SA 还与植物生长发育的各个方面密切相关[6]，包括光合作用、蒸腾作用、产热效应、衰老以及与其他激素的相互作用[7]，参与调控植物种子萌发、出芽、开花、坐果等过程[8]，随着对 SA 的深入研究，其在内质网胁迫和跨代记忆等方面的新功能也逐渐被发现[9]。

2.1. SA 与植物生长发育

SA 通过调控种子萌发、光合作用及器官发育等过程，在植物生长发育中发挥关键作用[10]。研究表明，外源 SA 处理可浓度依赖性地延缓拟南芥、大麦和玉米的种子萌发[11]-[13]。此外，SA 还通过调节气孔开度、叶绿体结构稳定性及光合酶活性等影响植物的光合效率[14] [15]。适宜浓度的 SA 可以刺激不同光周期条件下浮萍科植物的开花[16]。SA 还参与调节植物的衰老，受 SA 生物合成影响的拟南芥植物与野生型表现出衰老模式的改变，包括延迟变黄和减少坏死等现象[17]。除上述功能外，在拟南芥中，SA

也在根毛形成[18]、根伸长和侧根形成[19]、根波状生长[20]和根分生组织形成[21]等方面也发挥重要功能。

与其他植物类似，SA 在水稻的生长发育进程中也发挥着重要作用。陈亮等人分离并鉴定了一个水稻顶端小穗败育突变体 *asa*，与野生型相比，该突变体产量降低，进一步结果显示，与 WT 植株相比，*asa* 幼穗的 SA 与 H_2O_2 含量增加。在 *asa* 与 *OsASA* 敲除株系中，SA 含量及与 SA 合成相关基因 *OsPAL3*、*OsPAL4*、*OsPAL6* 等均显著增加。这些结果表明，*OsASA* 通过影响 SA 生物合成来调节水稻顶穗的发育[22]。

此外，已有研究证明依赖于 OsAIM1 的 β 氧化途径参与水稻根中 SA 的合成。突变体 *osaim1* 根中 SA 合成受阻，导致根系变短[23] [24]。此外，SA 在水稻发芽、开花和成熟方面均发挥重要的调节作用。

2.2. SA 与植物免疫

SA 不仅调控植物的生长发育，还在免疫应答中发挥核心作用。高等植物拥有大量的细胞表面和细胞内免疫受体，以感知与病原体感染相关的各种免疫信号[25]。关于 SA 参与植物免疫的最早报告之一发表于半个世纪前[6]。White 等[26]发现经 SA 处理的烟草植株对烟草花叶病毒(TMV)的抗性增强。后续研究证实 SA 确实是调节植物免疫的关键植物激素，并在许多植物中都参与了植物抗病，如黄瓜、拟南芥和大豆等。例如，在大豆中，病原菌侵染诱导其体内 SA 积累及相关抗病基因表达上调，有助于大豆防御生物营养病原体[27]。另外，SA 在基础抗性中的关键作用在拟南芥 NahG (一种降解 SA 的水杨酸羟化酶)转基因植株上得到证实[28]。NahG 阻断 SA 积累导致拟南芥中细菌病原体的生长增加[29]。在苹果中，外源 SA 可以增加其体内 ROS 水平，使苹果叶片增强了对肾小球叶斑病的抗性[30]。

除此之外，SA 还可以激活植物免疫信号分子进而调控植物免疫。SA 水平升高通过促进 SA 受体 *NPR1* (Nonexpresser of Pathogenesis-related Genes 1，病程相关基因非表达子 1)的转录激活因子活性，并抑制 *NPR3/NPR4* 的转录抑制因子活性，从而诱导防御基因表达[31]，激发植物获得 SAR 并参与植物的 PTI 和 ETI [32] [33]。植物遭受病原物刺激后，SA 能促使叶片中木质素含量上升，增强机械保护作用，进而阻止病害的进一步侵染[34] [35]。同时，SA 会促进植物抗毒素(Phytoalexins, PAs)的产生。这类物质在植物组织中积累，能够对病原物产生毒性，抑制其生长或繁殖[36]。

2.3. SA 与植物非生物胁迫

在植物复杂的生长过程中，常常面临非生物胁迫的严峻挑战[37]。外源 SA 处理可通过诱导多种信号转导，导致 SAR 的激活，最终产生对胁迫的信号反应[38]。例如，当外源施加低剂量 SA 时，可显著改善拟南芥不同非生物胁迫条件下的种子萌发和幼苗生长[39]。在玉米中，外源 SA 促进高温下糯玉米胚乳发育及耐热性，通过提高籽粒最大灌浆速率、平均灌浆速率、延长籽粒灌浆持续时间，最终提高了玉米的穗粒数、粒重和产量[40]。此外，SA 处理通过改善光合性能、保持膜通透性、诱导胁迫蛋白和增强抗氧化酶的活性，有效改善了干旱胁迫对小麦的负面影响[41]。

在热胁迫下，水稻的结实率显著下降，严重影响水稻产量，生殖阶段的极端高温会显著降低 50%以上的粮食产量，甚至导致水稻植株完全丧失收成[42]。热胁迫引起的雄性不育是导致水稻减产的主要因素之一。减数分裂后的小孢子幼体对高温敏感，这一阶段发生的热应激使小孢子退化，绒毡层细胞肥大，最终导致雄性不育[43]-[45]。已有研究发现，SA 能逆转水稻热胁迫引起的花粉败育。在热胁迫下，SA 诱导花药中 H_2O_2 显著增加，从而增强花药的抗氧化能力，清除过量的 ROS，抑制花药中的 PCD，防止热应激引起的绒毡层降解，进而降低热胁迫下水稻产量的损失[46]。

除高温外，冷胁迫严重影响水稻幼苗的生长发育和产量。一些分子生物学研究已表明，SA 通过调节一系列与冷胁迫相关基因的表达，增强了植物的耐寒性[47]-[49]。在冷胁迫条件下，植物种子浸泡或喷洒

SA 显著提高了种子发芽率，促进了植物生长[50] [51]。此外，低温胁迫下施用 SA 可以增加水稻幼苗侧根数量，激活耐冷基因的表达，从而促进了水稻幼苗在冷胁迫条件下的生长[52]。

稳态气孔孔径是植物适应非生物胁迫的关键因素[53]-[55]。易可可等发现，高水平的 SA 是水稻通过 *OsWRKY45* 依赖途径调控稳态气孔孔径的必要条件[23]。水稻 *OsAIM1* 基因的功能缺失突变体地上部 SA 含量远低于野生型，使得其气孔开度增大、蒸腾作用增强，从而导致水稻地上部温度显著低于野生型。此结果表明 SA 通过 *OsWRKY45*-ROS 路径来调控气孔的开度，这一调控路径对水稻适应土壤盐和干旱胁迫起重要的作用。

2.4. SA 与其它植物激素相互作用

植物激素由植物自身代谢生成，属于有机信号分子，其浓度极低，却能触发显著的生理反应。除 SA 外，还有多种植物激素被深入研究，主要包括生长素(Auxins)、细胞分裂素(Cytokinins, CK)、赤霉素(Gibberellin, GA)、脱落酸(Abscisic acid, ABA)、乙烯(ethylene, ET)等。植物通过短距离和长距离运输激素来调节各种发育过程和对环境因素的反应[56]。此外，植物激素还参与植物对各种生物和非生物胁迫的反应，植物激素水平的改变导致防御相关基因表达的改变和防御反应的激活[57]。SA 可与其它植物激素产生串扰，互相协同或拮抗，共同维持植物稳态[58]。

在植物发育方面，SA 可以与其他植物激素和信号分子互作，参与复杂的信号通路系统[59]。例如 SA 可通过调节生长素运输调节植物根的发育[60]。在拟南芥中，SA 已被证明可以抑制 GA 介导的植物生长[61]；同时，SA 和 ET 协同促进拟南芥叶片衰老的新机制也已被报道[62]；此前也有研究表明，在调控植物免疫反应和顶端弯钩形成过程中，SA 和 ET 是相互拮抗的[63]，说明二者的互作关系会因植物生理过程不同而变化。

在植物免疫方面，SA 可以和 JA、ET、ABA 等激素共同调节，发挥免疫功能[64]，例如外源 0.1 mM SA 叶面喷施通过积累 ABA 减少小麦的冰冻胁迫[65]。在水稻中，超表达 *OsNPR1* 或 *OsWRKY45* 可以克服 ABA 诱导的稻瘟病病菌易感性，这表明 ABA 通过抑制 SA 诱导的水稻防御基因表达来抑制植物免疫[66]。同样的，JA 在植物免疫中也具有拮抗 SA 的作用[67]。

3. SA 的信号转导机制

SA 的信号感知涉及一个复杂的蛋白质网络，促进靶向防御反应的识别和转导[68]。SA 首先需要被相应的受体蛋白特异性识别和结合，进而启动下游信号级联反应来调控植物的生理过程。水杨酸结合蛋白(Salicylic acid binding proteins, SABPs)是最早与新合成的 SA 相互作用的蛋白之一[69]。其次，SA 的受体蛋白 NPR1/3/4 在 SA 信号转导过程中的功能也被逐步阐明。NPR1 是另一种众所周知的 SA 受体，在正常情况下以无活性低聚体状态存在于细胞质中，但在病原体攻击时转化为单体并易位到细胞核中发挥作用[70]。而 NPR3/4 承担和 NPR1 相反的功能并对其进行制约。此外，为防止 SA 信号过度激活导致植物生长受阻，存在许多转录因子促进或抑制 SA 下游基因表达，如 *TAG*，*WRKY* 等，将植物对 SA 的响应控制在合理范围内[71]。

4. SA 的生物合成

目前已知植物中存在两种 SA 的生物合成途径，即异分支酸合成酶途径(Isochorismate Synthase, ICS)和苯丙氨酸解氨酶途径(Phenylalanine Ammonia Lyase, PAL) [72]。

4.1. ICS 途径

借助于拟南芥突变体遗传分析和生物化学分析方法，SA 合成的 ICS 途径已被完全解析[6]。在异分

支酸途径中，分支酸(Chorismic acid, CA)在质体中通过异分支酸合酶(Iso-chorismate synthase, ICS)转化异分支酸(Isochorismate, IC)。异分支酸经 EDS5(Enhanced disease susceptibility 5)转运至细胞质，然后 PBS3 (AvrPphB susceptible 3)催化其与谷氨酸结合生成 IC-9-Glu (Isochorismate-9-glutamate，异分支酸-9-谷氨酸) [73]，随后 IC-9-Glu 自主分解或经 EPS1 催化加速分解最终产生 SA。

在拟南芥基因组中包含两个 *ICS* 基因，分别为 *ICS1* 和 *ICS2*，但只有 *ICS1* 会被病原体快速诱导[74]。*ICS1* 的缺失会消除病原体诱导的 SA 积累和 SAR [75]，而这两种 *ICS* 的缺失会导致 SA 水平进一步降低[76]，此外，有研究发现，在拟南芥中，苯丙氨酸(Phenylalanine, Phe)不能合成 SA (2-Hydroxybenzoic acid, 2-HBA)，而是合成 SA 的同分异构体 4-羟基苯甲酸(4-Hydroxybenzoic acid, 4-HBA) [77]。进一步证明了拟南芥中 SA 主要依赖 ICS 途径合成。ICS 途径在其它一些植物 SA 合成中也占主导地位，比如番茄[78]、玉米[79]等。与拟南芥相比，水稻中 *ICS* 是一个单拷贝基因，其体外和体内的酶活性都极低[80] [81]。*osics* 突变体呈现植株黄化、矮小且致死的表型，其株高、鲜重和叶绿素含量均显著降低，与光合作用相关的基因表达也受到影响。然而，与野生型相比，*osics* 突变体中 SA 的含量无显著变化[82]。猜测 OsWRKY6 激活 *OsICS* 基因导致 SA 积累[83]。然而，WRKY 调节多种防御相关基因，也可能导致 SA 增加[84]。

4.2. PAL 途径

在 PAL 途径中，分支酸经催化产生苯丙氨酸，苯丙氨酸进入细胞质后由 PALs 将其转化为反式肉桂酸(*t*-CA)。反式肉桂酸随后进入过氧化物酶体，可通过一系列酶促反应转化为苯甲酸(Benzoic acid, BA)。普渡大学 Natalia Dudareva 团队以矮牵牛花为研究对象，解析了从 CA 合成 BA 的关键酶[85]，主要包含肉桂酸：辅酶 A 连接酶(Cinnamate-CoA ligase, CNL) [86]、羟酰辅酶 A 水解酶(Hydroxyacyl-CoA hydrolyase, CHD)和 3-酮脂酰辅酶 A 硫解酶(3-ketoacyl-CoA thiolase, KAT) [87]-[90]。BA 再被转运至细胞质，然后通过假设的 BA-2-羟化酶(BA2H)将 BA 羟基化产生 SA [91]。

尽管这两种 SA 生物合成途径在进化上具有保守性，但是不同植物在病原体感染后会启动不同的 SA 合成途径。拟南芥具有较低的内源 SA 水平，当拟南芥受到病原菌侵染时，新合成的 SA 主要通过 ICS 途径合成，仅有 10%通过 PAL 途径合成；在 TMV 感染烟草叶片，或烟草遭受其它胁迫如臭氧时，SA 则主要是通过 PAL 途径合成[92]。与拟南芥和烟草不同，大豆中 PAL 和 ICS 途径对于病原体诱导的 SA 生物合成同等重要[93]。而在水稻中，病原菌诱导的 SA 主要由 PAL 途径合成[23]。

5. 总结与展望

水杨酸作为植物体内重要的激素，在植物的生长发育以及应对各种胁迫过程中都具有不可忽视的作用。在生长发育方面，其对种子萌发、根系发育、开花等进程均有调控；在生物胁迫下，能诱导植物产生局部和系统获得性抗性来抵御病原菌侵害，非生物胁迫时，可调节生理生化过程增强植物抗逆性。合成途径上，主要有 ICS 和 PAL 两条，且不同植物中两条途径贡献有别。随着全球气候变化的加剧，植物与环境的互作关系变得越来越重要。SA 作为一种重要的植物激素，在植物对环境变化的响应中可能发挥着关键作用。未来的研究可以深入探讨 SA 在植物对气候变化的适应性中的作用机制，以及 SA 如何调节植物与微生物群落的相互作用，从而提高植物的生态适应性。

参考文献

[1] Klessig, D.F., Choi, H.W. and Dempsey, D.A. (2018) Systemic Acquired Resistance and Salicylic Acid: Past, Present, and Future. *Molecular Plant-Microbe Interactions*®, **31**, 871-888. https://doi.org/10.1094/mpmi-03-18-0067-cr

[2] Sneader, W. (2000) The Discovery of Aspirin: A Reappraisal. *BMJ*, **321**, 1591-1594. https://doi.org/10.1136/bmj.321.7276.1591

[3] Raskin, I. (1992) Salicylate, a New Plant Hormone. *Plant Physiology*, **99**, 799-803. https://doi.org/10.1104/pp.99.3.799

[4] Jones, J.D.G., Staskawicz, B.J. and Dangl, J.L. (2024) The Plant Immune System: From Discovery to Deployment. *Cell*, **187**, 2095-2116. https://doi.org/10.1016/j.cell.2024.03.045

[5] Kachroo, P., Liu, H. and Kachroo, A. (2020) Salicylic Acid: Transport and Long-Distance Immune Signaling. *Current Opinion in Virology*, **42**, 53-57. https://doi.org/10.1016/j.coviro.2020.05.008

[6] Peng, Y., Yang, J., Li, X. and Zhang, Y. (2021) Salicylic Acid: Biosynthesis and Signaling. *Annual Review of Plant Biology*, **72**, 761-791. https://doi.org/10.1146/annurev-arplant-081320-092855

[7] Jia, X., Wang, L., Zhao, H., Zhang, Y., Chen, Z., Xu, L., *et al.* (2024) The Origin and Evolution of Salicylic Acid Signaling and Biosynthesis in Plants. *Molecular Plant*, **16**, 245-259. https://doi.org/10.1016/j.molp.2022.12.002

[8] Koo, Y.M., Heo, A.Y. and Choi, H.W. (2020) Salicylic Acid as a Safe Plant Protector and Growth Regulator. *The Plant Pathology Journal*, **36**, 1-10. https://doi.org/10.5423/ppj.rw.12.2019.0295

[9] Liu, X., Rockett, K.S., Kørner, C.J. and Pajerowska-Mukhtar, K.M. (2015) Salicylic Acid Signalling: New Insights and Prospects at a Quarter-Century Milestone. *Essays in Biochemistry*, **58**, 101-113. https://doi.org/10.1042/bse0580101

[10] Rivas-San Vicente, M. and Plasencia, J. (2011) Salicylic Acid Beyond Defence: Its Role in Plant Growth and Development. *Journal of Experimental Botany*, **62**, 3321-3338. https://doi.org/10.1093/jxb/err031

[11] Rajjou, L., Belghazi, M., Huguet, R., Robin, C., Moreau, A., Job, C., *et al.* (2006) Proteomic Investigation of the Effect of Salicylic Acid on Arabidopsis Seed Germination and Establishment of Early Defense Mechanisms. *Plant Physiology*, **141**, 910-923. https://doi.org/10.1104/pp.106.082057

[12] Xie, Z., Zhang, Z., Hanzlik, S., Cook, E. and Shen, Q.J. (2007) Salicylic Acid Inhibits Gibberellin-Induced Alpha-Amylase Expression and Seed Germination via a Pathway Involving an Abscisic-Acid-Inducible *WRKY* Gene. *Plant Molecular Biology*, **64**, 293-303. https://doi.org/10.1007/s11103-007-9152-0

[13] Guan, L. and Scandalios, J.G. (1995) Developmentally Related Responses of Maize Catalase Genes to Salicylic Acid. *Proceedings of the National Academy of Sciences*, **92**, 5930-5934. https://doi.org/10.1073/pnas.92.13.5930

[14] Melotto, M., Underwood, W., Koczan, J., Nomura, K. and He, S.Y. (2006) Plant Stomata Function in Innate Immunity against Bacterial Invasion. *Cell*, **126**, 969-980. https://doi.org/10.1016/j.cell.2006.06.054

[15] Mateo, A., Mühlenbock, P., Rustérucci, C., Chang, C.C., Miszalski, Z., Karpinska, B., *et al*. (2004) *LESION SIMULATING DISEASE 1* Is Required for Acclimation to Conditions That Promote Excess Excitation Energy. *Plant Physiology*, **136**, 2818-2830. https://doi.org/10.1104/pp.104.043646

[16] Khurana, J.P. and Cleland, C.F. (1992) Role of Salicylic Acid and Benzoic Acid in Flowering of a Photoperiod-Insensitive Strain, *Lemna paucicostata* LP6. *Plant Physiology*, **100**, 1541-1546. https://doi.org/10.1104/pp.100.3.1541

[17] Morris, K., -Mackerness, S.A.-H., Page, T., John, C.F., Murphy, A.M., Carr, J.P., *et al*. (2000) Salicylic Acid Has a Role in Regulating Gene Expression during Leaf Senescence. *The Plant Journal*, **23**, 677-685. https://doi.org/10.1046/j.1365-313x.2000.00836.x

[18] García-Sánchez, S., Bernales, I. and Cristobal, S. (2015) Early Response to Nanoparticles in the *Arabidopsis* Transcriptome Compromises Plant Defence and Root-Hair Development through Salicylic Acid Signalling. *BMC Genomics*, **16**, Article No. 341. https://doi.org/10.1186/s12864-015-1530-4

[19] Kim, T., Kunz, H., Bhattacharjee, S., Hauser, F., Park, J., Engineer, C., *et al*. (2012) Natural Variation in Small Molecule-Induced TIR-NB-LRR Signaling Induces Root Growth Arrest via EDS1- and PAD4-Complexed R Protein VICTR in *Arabidopsis*. *The Plant Cell*, **24**, 5177-5192. https://doi.org/10.1105/tpc.112.107235

[20] Zhao, X., Wang, J., Yuan, J., Wang, X., Zhao, Q., Kong, P., *et al.* (2015) NITRIC OXIDE-ASSOCIATED PROTEIN1 (ATNOA1) Is Essential for Salicylic Acid-Induced Root Waving in *Arabidopsis thaliana*. *New Phytologist*, **207**, 211-224. https://doi.org/10.1111/nph.13327

[21] Pasternak, T., Groot, E.P., Kazantsev, F.V., Teale, W., Omelyanchuk, N., Kovrizhnykh, V., *et al.* (2019) Salicylic Acid Affects Root Meristem Patterning via Auxin Distribution in a Concentration-Dependent Manner. *Plant Physiology*, **180**, 1725-1739. https://doi.org/10.1104/pp.19.00130

[22] Zhou, D., Shen, W., Cui, Y., Liu, Y., Zheng, X., Li, Y., *et al.* (2021) APICAL SPIKELET ABORTION (ASA) Controls Apical Panicle Development in Rice by Regulating Salicylic Acid Biosynthesis. *Frontiers in Plant Science*, **12**, Article 636877. https://doi.org/10.3389/fpls.2021.636877

[23] Xu, L., Zhao, H., Wang, J., Wang, X., Jia, X., Wang, L., *et al.* (2023) AIM1-Dependent High Basal Salicylic Acid Accumulation Modulates Stomatal Aperture in Rice. *New Phytologist*, **238**, 1420-1430. https://doi.org/10.1111/nph.18842

[24] Xu, Z., Jia, X., Li, R., Wang, L., Xu, L. and Yi, K. (2025) The Basal Level of Salicylic Acid Represses the PRT6 N-Degron Pathway to Modulate Root Growth and Stress Response in Rice. *Plant Communications*, **6**, Article 101239. https://doi.org/10.1016/j.xplc.2025.101239

[25] Kourelis, J. and van der Hoorn, R.A.L. (2018) Defended to the Nines: 25 Years of Resistance Gene Cloning Identifies Nine Mechanisms for R Protein Function. *The Plant Cell*, **30**, 285-299. https://doi.org/10.1105/tpc.17.00579

[26] White, R.F. (1979) Acetylsalicylic Acid (Aspirin) Induces Resistance to Tobacco Mosaic Virus in Tobacco. *Virology*, **99**, 410-412. https://doi.org/10.1016/0042-6822(79)90019-9

[27] Shine, M.B., Yang, J., El-Habbak, M., Nagyabhyru, P., Fu, D., Navarre, D., *et al*. (2016) Cooperative Functioning between Phenylalanine Ammonia Lyase and Isochorismate Synthase Activities Contributes to Salicylic Acid Biosynthesis in Soybean. *New Phytologist*, **212**, 627-636. https://doi.org/10.1111/nph.14078

[28] Gaffney, T., Friedrich, L., Vernooij, B., Negrotto, D., Nye, G., Uknes, S., *et al*. (1993) Requirement of Salicylic Acid for the Induction of Systemic Acquired Resistance. *Science*, **261**, 754-756. https://doi.org/10.1126/science.261.5122.754

[29] Delaney, T.P., Uknes, S., Vernooij, B., Friedrich, L., Weymann, K., Negrotto, D., *et al*. (1994) A Central Role of Salicylic Acid in Plant Disease Resistance. *Science*, **266**, 1247-1250. https://doi.org/10.1126/science.266.5188.1247

[30] Zhang, Y., Shi, X., Li, B., Zhang, Q., Liang, W. and Wang, C. (2016) Salicylic Acid Confers Enhanced Resistance to Glomerella Leaf Spot in Apple. *Plant Physiology and Biochemistry*, **106**, 64-72. https://doi.org/10.1016/j.plaphy.2016.04.047

[31] Ding, Y., Sun, T., Ao, K., Peng, Y., Zhang, Y., Li, X., *et al*. (2018) Opposite Roles of Salicylic Acid Receptors NPR1 and NPR3/NPR4 in Transcriptional Regulation of Plant Immunity. *Cell*, **173**, 1454-1467.E15. https://doi.org/10.1016/j.cell.2018.03.044

[32] Zhou, J. and Zhang, Y. (2020) Plant Immunity: Danger Perception and Signaling. *Cell*, **181**, 978-989. https://doi.org/10.1016/j.cell.2020.04.028

[33] Zhang, Y. and 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

[34] Liu, X., Dai, H., Zhang, F., Wang, J., Shi, J., Chen, J., *et al*. (2024) The *miR7125-MdARF1* Module Enhances the Resistance of Apple to *colletotrichum Gloeosporioides* by Promoting Lignin Synthesis in Response to Salicylic Acid Signalling. *Plant Biotechnology Journal*, **22**, 2741-2755. https://doi.org/10.1111/pbi.14401

[35] Liu, N., Wang, Y., Li, K., Li, C., Liu, B., Zhao, L., *et al*. (2023) Transcriptional Analysis of Tea Plants (*Camellia sinensis*) in Response to Salicylic Acid Treatment. *Journal of Agricultural and Food Chemistry*, **71**, 2377-2389. https://doi.org/10.1021/acs.jafc.2c07046

[36] Liu, A., Wang, M., Dong, J., Yan, Z., Wang, X., Li, J., *et al*. (2024) Foliar Application of Exogenous Salicylic Acid Mitigates the Detrimental Effects Caused by Salt Stress in Sunflower Seedlings. *Industrial Crops and Products*, **222**, Article 119854. https://doi.org/10.1016/j.indcrop.2024.119854

[37] Abdelrahman, M., Selim, M.E., ElSayed, M.A., Ammar, M.H., Hussein, F.A., ElKholy, N.K., *et al*. (2021) Developing Novel Rice Genotypes Harboring Specific QTL Alleles Associated with High Grain Yield under Water Shortage Stress. *Plants*, **10**, Article 2219. https://doi.org/10.3390/plants10102219

[38] Elsisi, M., Elshiekh, M., Sabry, N., Aziz, M., Attia, K., Islam, F., *et al*. (2024) The Genetic Orchestra of Salicylic Acid in Plant Resilience to Climate Change Induced Abiotic Stress: Critical Review. *Stress Biology*, **4**, Article No. 31. https://doi.org/10.1007/s44154-024-00160-2

[39] Alonso-Ramírez, A., Rodríguez, D., Reyes, D., Jiménez, J.A., Nicolás, G., López-Climent, M., *et al*. (2009) Evidence for a Role of Gibberellins in Salicylic Acid-Modulated Early Plant Responses to Abiotic Stress in Arabidopsis Seeds. *Plant Physiology*, **150**, 1335-1344. https://doi.org/10.1104/pp.109.139352

[40] Guo, J., Wang, Z., Li, J., Qu, L., Chen, Y., Li, G., *et al*. (2024) Salicylic Acid Promotes Endosperm Development and Heat-Tolerance of Waxy Maize (*Zea mays* L. var. *ceratina Kulesh*) under Heat Stress. *Plant Stress*, **14**, Article 100684. https://doi.org/10.1016/j.stress.2024.100684

[41] Khalvandi, M., Siosemardeh, A., Roohi, E. and Keramati, S. (2021) Salicylic Acid Alleviated the Effect of Drought Stress on Photosynthetic Characteristics and Leaf Protein Pattern in Winter Wheat. *Heliyon*, **7**, e05908. https://doi.org/10.1016/j.heliyon.2021.e05908

[42] Fu, G., Song, J., Xiong, J., Liao, X., Zhang, X., Wang, X., *et al*. (2012) Thermal Resistance of Common Rice Maintainer and Restorer Lines to High Temperature during Flowering and Early Grain Filling Stages. *Rice Science*, **19**, 309-314. https://doi.org/10.1016/s1672-6308(12)60055-9

[43] Sakata, T., Oshino, T., Miura, S., Tomabechi, M., Tsunaga, Y., Higashitani, N., *et al*. (2010) Auxins Reverse Plant Male Sterility Caused by High Temperatures. *Proceedings of the National Academy of Sciences*, **107**, 8569-8574. https://doi.org/10.1073/pnas.1000869107

[44] Smith, A.R. and Zhao, D. (2016) Sterility Caused by Floral Organ Degeneration and Abiotic Stresses in *Arabidopsis* and Cereal Grains. *Frontiers in Plant Science*, **7**, Article 1503. https://doi.org/10.3389/fpls.2016.01503

[45] Deng, Y., Srivastava, R., Quilichini, T.D., Dong, H., Bao, Y., Horner, H.T., *et al*. (2016) IRE1, a Component of the

Unfolded Protein Response Signaling Pathway, Protects Pollen Development in Arabidopsis from Heat Stress. *The Plant Journal*, **88**, 193-204. https://doi.org/10.1111/tpj.13239

[46] Feng, B., Zhang, C., Chen, T., Zhang, X., Tao, L. and Fu, G. (2018) Salicylic Acid Reverses Pollen Abortion of Rice Caused by Heat Stress. *BMC Plant Biology*, **18**, Article No. 245. https://doi.org/10.1186/s12870-018-1472-5

[47] Gondor, O.K., Pál, M., Janda, T. and Szalai, G. (2022) The Role of Methyl Salicylate in Plant Growth under Stress Conditions. *Journal of Plant Physiology*, **277**, Article 153809. https://doi.org/10.1016/j.jplph.2022.153809

[48] Fung, R.W.M., Wang, C.Y., Smith, D.L., Gross, K.C. and Tian, M. (2004) MeSA and MeJA Increase Steady-State Transcript Levels of Alternative Oxidase and Resistance against Chilling Injury in Sweet Peppers (*Capsicum annuum* L.). *Plant Science*, **166**, 711-719. https://doi.org/10.1016/j.plantsci.2003.11.009

[49] Arif, Y., Sami, F., Siddiqui, H., Bajguz, A. and Hayat, S. (2020) Salicylic Acid in Relation to Other Phytohormones in Plant: A Study Towards Physiology and Signal Transduction under Challenging Environment. *Environmental and Experimental Botany*, **175**, Article 104040. https://doi.org/10.1016/j.envexpbot.2020.104040

[50] Li, Z., Xu, J., Gao, Y., Wang, C., Guo, G., Luo, Y., *et al*. (2017) The Synergistic Priming Effect of Exogenous Salicylic Acid and H_2O_2 on Chilling Tolerance Enhancement during Maize (*Zea mays* L.) Seed Germination. *Frontiers in Plant Science*, **8**, Article 1153. https://doi.org/10.3389/fpls.2017.01153

[51] Guan, Y., Li, Z., He, F., Huang, Y., Song, W. and Hu, J. (2015) "On-Off" Thermoresponsive Coating Agent Containing Salicylic Acid Applied to Maize Seeds for Chilling Tolerance. *PLOS ONE*, **10**, e0120695. https://doi.org/10.1371/journal.pone.0120695

[52] Xu, Q., Yan, Y., Wei, Q., Wang, H., Chi, C., Pan, L., *et al*. (2025) Salicylic Acid Alleviates Cold Stress in Rice via Regulating Nutrient Absorption, Osmotic Material Content, Antioxidation System, and Expression of Cold Tolerance Genes. *Journal of Plant Growth Regulation*. https://doi.org/10.1007/s00344-024-11615-1

[53] Cui, L., Shan, J., Shi, M., Gao, J. and Lin, H. (2015) DCA1 Acts as a Transcriptional Co-Activator of DST and Contributes to Drought and Salt Tolerance in Rice. *PLOS Genetics*, **11**, e1005617. https://doi.org/10.1371/journal.pgen.1005617

[54] Murata, Y., Mori, I.C. and Munemasa, S. (2015) Diverse Stomatal Signaling and the Signal Integration Mechanism. *Annual Review of Plant Biology*, **66**, 369-392. https://doi.org/10.1146/annurev-arplant-043014-114707

[55] Sukiran, N.A., Steel, P.G. and Knight, M.R. (2020) Basal Stomatal Aperture Is Regulated by GA-DELLAs in Arabidopsis. *Journal of Plant Physiology*, **250**, Article 153182. https://doi.org/10.1016/j.jplph.2020.153182

[56] Zhang, Y., Berman, A. and Shani, E. (2023) Plant Hormone Transport and Localization: Signaling Molecules on the Move. *Annual Review of Plant Biology*, **74**, 453-479. https://doi.org/10.1146/annurev-arplant-070722-015329

[57] Bari, R. and Jones, J.D.G. (2009) Role of Plant Hormones in Plant Defence Responses. *Plant Molecular Biology*, **69**, 473-488. https://doi.org/10.1007/s11103-008-9435-0

[58] Tian, H., Xu, L., Li, X. and Zhang, Y. (2024) Salicylic Acid: The Roles in Plant Immunity and Crosstalk with Other Hormones. *Journal of Integrative Plant Biology*, **67**, 773-785. https://doi.org/10.1111/jipb.13820

[59] Kaya, C., Ugurlar, F., Ashraf, M. and Ahmad, P. (2023) Salicylic Acid Interacts with Other Plant Growth Regulators and Signal Molecules in Response to Stressful Environments in Plants. *Plant Physiology and Biochemistry*, **196**, 431-443. https://doi.org/10.1016/j.plaphy.2023.02.006

[60] Tan, S., Abas, M., Verstraeten, I., Glanc, M., Molnár, G., Hajný, J., *et al*. (2020) Salicylic Acid Targets Protein Phosphatase 2A to Attenuate Growth in Plants. *Current Biology*, **30**, 381-395.e8. https://doi.org/10.1016/j.cub.2019.11.058

[61] Yu, X., Cui, X., Wu, C., Shi, S. and Yan, S. (2022) Salicylic Acid Inhibits Gibberellin Signaling through Receptor Interactions. *Molecular Plant*, **15**, 1759-1771. https://doi.org/10.1016/j.molp.2022.10.001

[62] Yu, X., Xu, Y. and Yan, S. (2021) Salicylic Acid and Ethylene Coordinately Promote Leaf Senescence. *Journal of Integrative Plant Biology*, **63**, 823-827. https://doi.org/10.1111/jipb.13074

[63] Bertoni, G. (2020) Ethylene versus Salicylic Acid in Apical Hook Formation. *The Plant Cell*, **32**, 531-531. https://doi.org/10.1105/tpc.20.00031

[64] Aerts, N., Pereira Mendes, M. and Van Wees, S.C.M. (2020) Multiple Levels of Crosstalk in Hormone Networks Regulating Plant Defense. *The Plant Journal*, **105**, 489-504. https://doi.org/10.1111/tpj.15124

[65] Wang, W., Wang, X., Huang, M., Cai, J., Zhou, Q., Dai, T., *et al*. (2018) Hydrogen Peroxide and Abscisic Acid Mediate Salicylic Acid-Induced Freezing Tolerance in Wheat. *Frontiers in Plant Science*, **9**, Article 1137. https://doi.org/10.3389/fpls.2018.01137

[66] Jiang, C., Shimono, M., Sugano, S., Kojima, M., Yazawa, K., Yoshida, R., *et al*. (2010) Abscisic Acid Interacts Antagonistically with Salicylic Acid Signaling Pathway in Rice-*Magnaporthe grisea* Interaction. *Molecular Plant-Microbe Interactions*®, **23**, 791-798. https://doi.org/10.1094/mpmi-23-6-0791

[67] Hou, S. and Tsuda, K. (2022) Salicylic Acid and Jasmonic Acid Crosstalk in Plant Immunity. *Essays in Biochemistry*,

66, 647-656. https://doi.org/10.1042/ebc20210090

[68] Roychowdhury, R., Mishra, S., Anand, G., Dalal, D., Gupta, R., Kumar, A., *et al*. (2024) Decoding the Molecular Mechanism Underlying Salicylic Acid (SA)-Mediated Plant Immunity: An Integrated Overview from Its Biosynthesis to the Mode of Action. *Physiologia Plantarum*, **176**, e14399. https://doi.org/10.1111/ppl.14399

[69] Loake, G. and Grant, M. (2007) Salicylic Acid in Plant Defence—The Players and Protagonists. *Current Opinion in Plant Biology*, **10**, 466-472. https://doi.org/10.1016/j.pbi.2007.08.008

[70] Zhou, J., Trifa, Y., Silva, H., Pontier, D., Lam, E., Shah, J., *et al*. (2000) NPR1 Differentially Interacts with Members of the TGA/OBF Family of *Transcription* Factors That Bind an Element of the *Pr-1* Gene Required for Induction by Salicylic Acid. *Molecular Plant-Microbe Interactions®*, **13**, 191-202. https://doi.org/10.1094/mpmi.2000.13.2.191

[71] Xu, G., Yuan, M., Ai, C., Liu, L., Zhuang, E., Karapetyan, S., *et al*. (2017) uORF-Mediated Translation Allows Engineered Plant Disease Resistance without Fitness Costs. *Nature*, **545**, 491-494. https://doi.org/10.1038/nature22372

[72] Lefevere, H., Bauters, L. and Gheysen, G. (2020) Salicylic Acid Biosynthesis in Plants. *Frontiers in Plant Science*, **11**, Article 2655. https://doi.org/10.3389/fpls.2020.00338

[73] Nawrath, C., Heck, S., Parinthawong, N. and Métraux, J. (2002) EDS5, an Essential Component of Salicylic Acid-Dependent Signaling for Disease Resistance in Arabidopsis, Is a Member of the MATE Transporter Family. *The Plant Cell*, **14**, 275-286. https://doi.org/10.1105/tpc.010376

[74] Mishra, A. and Baek, K. (2021) Salicylic Acid Biosynthesis and Metabolism: A Divergent Pathway for Plants and Bacteria. *Biomolecules*, **11**, Article 705. https://doi.org/10.3390/biom11050705

[75] Nawrath, C. and Métraux, J. (1999) Salicylic Acid Induction-Deficient Mutants of Arabidopsis Express *PR-2* and *Pr-5* and Accumulate High Levels of Camalexin after Pathogen Inoculation. *The Plant Cell*, **11**, 1393-1404. https://doi.org/10.1105/tpc.11.8.1393

[76] Garcion, C., Lohmann, A., Lamodière, E., Catinot, J., Buchala, A., Doermann, P., *et al*. (2008) Characterization and Biological Function of the *ISOCHORISMATE SYNTHASE2* Gene of Arabidopsis. *Plant Physiology*, **147**, 1279-1287. https://doi.org/10.1104/pp.108.119420

[77] Wu, J., Zhu, W. and Zhao, Q. (2023) Salicylic Acid Biosynthesis Is Not from Phenylalanine in *Arabidopsis*. *Journal of Integrative Plant Biology*, **65**, 881-887. https://doi.org/10.1111/jipb.13410

[78] Uppalapati, S.R., Ishiga, Y., Wangdi, T., Kunkel, B.N., Anand, A., Mysore, K.S., *et al*. (2007) The Phytotoxin Coronatine Contributes to Pathogen Fitness and Is Required for Suppression of Salicylic Acid Accumulation in Tomato Inoculated with *Pseudomonas syringae* Pv. *tomato* Dc3000. *Molecular Plant-Microbe Interactions®*, **20**, 955-965. https://doi.org/10.1094/mpmi-20-8-0955

[79] Djamei, A., Schipper, K., Rabe, F., Ghosh, A., Vincon, V., Kahnt, J., *et al*. (2011) Metabolic Priming by a Secreted Fungal Effector. *Nature*, **478**, 395-398. https://doi.org/10.1038/nature10454

[80] Yokoo, S., Inoue, S., Suzuki, N., Amakawa, N., Matsui, H., Nakagami, H., *et al*. (2018) Comparative Analysis of Plant Isochorismate Synthases Reveals Structural Mechanisms Underlying Their Distinct Biochemical Properties. *Bioscience Reports*, **38**, BSR20171457. https://doi.org/10.1042/bsr20171457

[81] Su, Z., Niu, C., Zhou, S., Xu, G., Zhu, P., Fu, Q., *et al*. (2024) Structural Basis of Chorismate Isomerization by *Arabidopsis* ISOCHORISMATE SYNTHASE1. *Plant Physiology*, **196**, 773-787. https://doi.org/10.1093/plphys/kiae260

[82] Wang, Z., Yang, G., Zhang, D., Li, G., Qiu, J. and Wu, J. (2024) Isochorismate Synthase Is Required for Phylloquinone, but Not Salicylic Acid Biosynthesis in Rice. *aBIOTECH*, **5**, 488-496. https://doi.org/10.1007/s42994-024-00166-4

[83] Choi, C., Hwang, S., Fang, I.R., Kwon, S.I., Park, S.R., Ahn, I., *et al*. (2015) Molecular Characterization of *Oryza sativa* wrky6, Which Binds to W-Box-Like Element 1 of the *Oryza sativa Pathogenesis-Related* (*PR*) *10a* Promoter and Confers Reduced Susceptibility to Pathogens. *New Phytologist*, **208**, 846-859. https://doi.org/10.1111/nph.13516

[84] Liu, Q., Li, X., Yan, S., Yu, T., Yang, J., Dong, J., *et al*. (2018) *OsWRKY67* Positively Regulates Blast and Bacteria Blight Resistance by Direct Activation of PR Genes in Rice. *BMC Plant Biology*, **18**, Article No. 257. https://doi.org/10.1186/s12870-018-1479-y

[85] Widhalm, J.R. and Dudareva, N. (2015) A Familiar Ring to It: Biosynthesis of Plant Benzoic Acids. *Molecular Plant*, **8**, 83-97. https://doi.org/10.1016/j.molp.2014.12.001

[86] Hamberger, B. and Hahlbrock, K. (2004) The *4-Coumarate*: *CoA Ligase* Gene Family in *Arabidopsis thaliana* Comprises One Rare, Sinapate-Activating and Three Commonly Occurring Isoenzymes. *Proceedings of the National Academy of Sciences*, **101**, 2209-2214. https://doi.org/10.1073/pnas.0307307101

[87] Jarvis, A.P., Schaaf, O. and Oldham, N.J. (2000) 3-Hydroxy-3-Phenylpropanoic Acid Is an Intermediate in the Biosynthesis of Benzoic Acid and Salicylic Acid but Benzaldehyde Is Not. *Planta*, **212**, 119-126. https://doi.org/10.1007/s004250000377

[88] Hertweck, C., Jarvis, A.P., Xiang, L., Moore, B.S. and Oldham, N.J. (2001) A Mechanism of Benzoic Acid Biosynthesis

in Plants and Bacteria That Mirrors Fatty Acid *β*-Oxidation. *ChemBioChem*, **2**, 784-786. https://doi.org/10.1002/1439-7633(20011001)2:10<784::aid-cbic784>3.0.co;2-k

[89] Long, M.C., Nagegowda, D.A., Kaminaga, Y., Ho, K.K., Kish, C.M., Schnepp, J., *et al*. (2009) Involvement of Snapdragon Benzaldehyde Dehydrogenase in Benzoic Acid Biosynthesis. *The Plant Journal*, **59**, 256-265. https://doi.org/10.1111/j.1365-313x.2009.03864.x

[90] Moerkercke, A.V., Schauvinhold, I., Pichersky, E., Haring, M.A. and Schuurink, R.C. (2009) A Plant Thiolase Involved in Benzoic Acid Biosynthesis and Volatile Benzenoid Production. *The Plant Journal*, **60**, 292-302. https://doi.org/10.1111/j.1365-313x.2009.03953.x

[91] 谷晓勇, 刘扬, 刘利静. 植物激素水杨酸生物合成和信号转导研究进展[J]. 遗传, 2020, 42(9): 858-869.

[92] Ogawa, D., Nakajima, N., Sano, T., Tamaoki, M., Aono, M., Kubo, A., *et al*. (2005) Salicylic Acid Accumulation under O_3 Exposure Is Regulated by Ethylene in Tobacco Plants. *Plant and Cell Physiology*, **46**, 1062-1072. https://doi.org/10.1093/pcp/pci118

[93] Takagi, K., Tasaki, K., Komori, H. and Katou, S. (2022) Hypersensitivity-Related Genes *HSR201* and *HSR203J* Are Regulated by Calmodulin-Binding Protein 60-Type Transcription Factors and Required for Pathogen Signal-Induced Salicylic Acid Synthesis. *Plant And Cell Physiology*, **63**, 1008-1022. https://doi.org/10.1093/pcp/pcac074