Salicylic Acid in Root Growth and Development

In plants, salicylic acid (SA) is a hormone that mediates a plant's defense against pathogens. SA also takes an active role in a plant's response to various abiotic stresses, including chilling, drought, salinity, and heavy metals. In addition, in recent years, numerous studies have confirmed the important role of SA in plant morphogenesis.

1. Introduction

Recognized as the sixth plant hormone in 1992 [1], 2-hydroxybenzoic or salicylic acid (SA) belongs to a family of naturally occurring phenolic compounds which possess an aromatic benzene ring bearing one or more hydroxyl groups. Since then, a huge amount of data has been accumulated on SA's involvement in various biological processes. As reviewed in [2][3], SA has secured a reputation as a vital defense hormone. At the same time, SA's impact on cell, tissue, and organ phenotypes is well established (reviewed in [4]). Despite the growing evidence that SA is an important growth regulator, its morphogenetic role, especially in relation to roots, has rarely been summarized in reviews.

It is worthy of note that, in roots, SA content and its dynamic during development may differ from that in shoots [5][6][7][8], which can potentially cause differences in SA functions. For instance, SA basal level in shoots is 2–100 times higher than in roots, depending on the species [5][6]. The ratio between free and conjugated SA forms, also differs [6]. For example, the shoots of wheat seedlings, three days after germination (DAG), contain about 48 times more free than conjugated SA, whereas in the roots, the contrary is seen, with conjugated SA levels exceeding the level of free SA by about six times. During wheat seedling growth, SA content in both free and conjugated forms gradually decreases in shoots but not in roots. In 14 DAG seedlings, the conjugated SA becomes prevalent in both organs but the ratio of free to conjugated form still differs slightly and amounts to 0.4 and 0.5 for shoots and roots, respectively. These differences provide ample reason to consider the role of SA in root morphology, distinct from its function in shoots.

The phenotypic analysis of SA deficient/accumulating lines and SA-treated plants provides insight into the role of SA in plant growth and development. However, the data on changes in root morphology in SA mutants are scarce and often contradictory. For example, decreased root length is reported in SA-accumulating Arabidopsis mutants [9][10][11] and in SA-depleted rice mutants [12][13]. In rice, the inhibitory effects of an SA deficiency on root length have been reported in relation to both SA biosynthesis mutant *aim1* [12] and plants transgenic for the bacterial *Naphthalene hydroxylase G* (*NahG*) gene, encoding salicylate hydroxylase that inactivates SA by converting it to catechol [13]. In contrast, transgenic *Lotus japonicus* plants expressing *NahG*, demonstrate enhanced root growth [14]. These contradictions may be due to species-specific basal SA levels, which vary greatly between plant species, even those belonging to the same family [4][15].

2. SA Metabolism and Signaling in Plants

SA metabolism has been comprehensively described in numerous reviews, for example, [16][17][18][19][20]; therefore, the researchers touch only briefly on this aspect in this review. SA is synthesized in plants, bacteria, and fungi from chorismate, the final product in the shikimate pathway (reviewed in [16]). Chorismate is also the primary source for the biosynthesis of aromatic amino acids (tryptophan, phenylalanine, and tyrosine) and a wide range of aromatic secondary metabolites, including flavonoids, alkaloids, and lignins. SA biosynthesis (**Figure 1**) starts in plastids, where chorismate is converted into either isochorismate via isochorismate synthase (ICS) or prephenate via chorismate mutase (CM), giving rise to two parallel ICS and phenylalanine ammonia-lyase (PAL) pathways of SA biosynthesis (reviewed in [16][17][19][20]). The relative contributions of the ICS and PAL pathways to SA biosynthesis are species-dependent with an equal contribution being made in soybean and a prevalence of ICS and PAL pathways being seen in Arabidopsis and rice, respectively. In the ICS pathway, ENHANCED DISEASE SUSCEPTIBILITY 5 (EDS5) transports isochorismate to the cytosol, where it is conjugated with glutamate by avrPphB Susceptible 3 (PBS3) to produce isochorismate-9-glutamate, which is either spontaneously decomposed into SA or converted to SA by an acyltransferase Enhanced Pseudomonas

Susceptibility 1 (EPS1). In the PAL pathway, there are two ways of prephenate elaboration into phenylalanine (reviewed in [18]). In plastids, prephenate aminotransferases (PPA-ATs) catalyze its transition to arogenate, which is then converted by arogenate dehydratase (ADT) into phenylalanine. In the cytosol, the prephenate–phenylalanine transition is realized through phenylpyruvate by prephenate dehydratase (PDT) and phenylpyruvate aminotransferase (PPY-AT). PAL turns phenylalanine into trans-cinnamic acid, following which the formation of SA occurs either through ortho-coumaric acid or benzoic acid (reviewed in [16][17][19][20]). In the latter case, Abnormal Inflorescence Meristem 1 (AIM1), a 3-hydroxyacyl-CoA dehydrogenase, contributes to this process. Benzoic acid is hydroxylated to SA, possibly by benzoic acid 2-hydroxylase (BA2H).
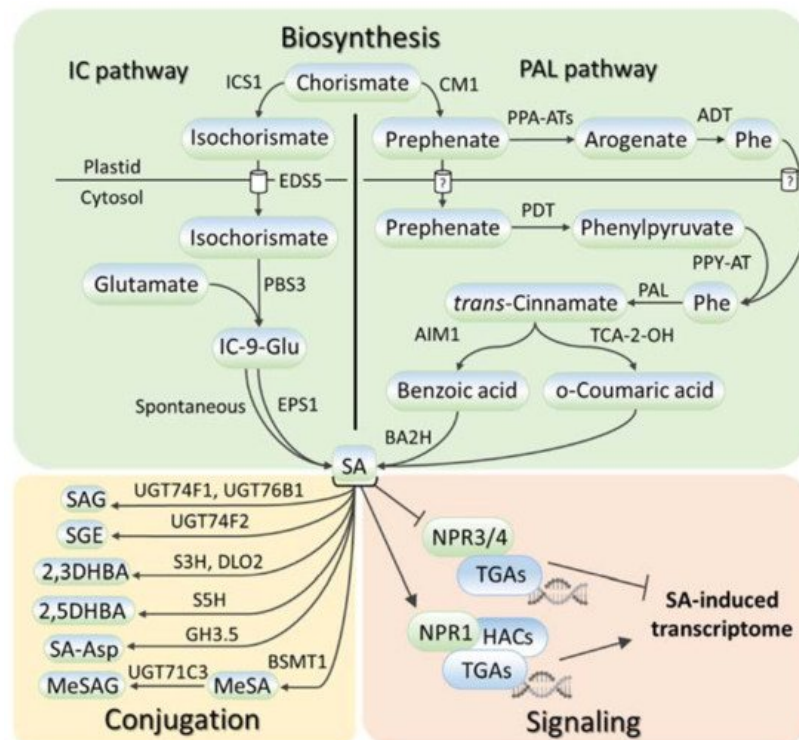

Figure 1. SA metabolism and signaling in plants. SA is synthesized via two routes, the isochorismate pathway or the phenylalanine ammonia-lyase pathway, which both start with chorismate. SA conversions include SA glycosylation, methylation, hydroxylation, and amino-acid conjugation. SA signaling depends on the interaction of SA receptor NPR1 with TGA transcription factors and histone acetyltransferases. SA, salicylic acid; ICS1, isochorismate synthase 1; EDS5, ENHANCED DISEASE SUSCEPTIBILITY 5; PBS3, avrPphB Susceptible 3; EPS1, Enhanced Pseudomonas Susceptibility 1; IC-9-Glu, isochorismate-9-glutamate; CM1, chorismate mutase 1; PPA-ATs, prephenate aminotransferases; PDT, prephenate dehydratase; PPY-AT, phenylpyruvate aminotransferase; ADT, arogenate dehydratase; PAL, phenylalanine ammonia-lyase; AIM1, Abnormal Inflorescence Meristem 1; TCA-2-OH, trans-cinnamic acid 2-hydroxylase; BA2H, benzoic acid 2-hydroxylase; UGT74F1/74F2/76B1/71C3, UDP-glucosyltransferases 74F1, 74F2, 76B1 and 71C3; S5H, SA-5 hydroxylase; S3H, SA-3 hydroxylase; DLO2, DMR6-LIKE OXYGENASE 2; GH3.5, Gretchen Hagen 3.5; BSMT1, benzoic acid/salicylic acid methyltransferase; SAG, salicylic acid 2-O-β-D-glucose; SGE, salicylic acid glucose ester; 2,3/2,5-DHBA, 2,3/2,5-dihydroxybenzoic acid; SA-Asp, salicyloyl-L-aspartate; MeSA, methyl salicylate; MeSAG, methyl salicylate O-β-glucoside; NPR1/3/4, NONEXPRESSOR OF PATHOGENESIS RELATED GENES 1/3/4; HACs, histone acetyltransferases; TGA, TGACG SEQUENCE-SPECIFIC BINDING PROTEIN.

A wide number of regulators control SA biosynthesis (Table S1). Among them, the reactive oxygen species (ROS), particularly hydrogen peroxide, form a self-amplifying feedback loop with SA, in which hydrogen peroxide promotes SA biosynthesis, and SA induces hydrogen peroxide accumulation by inactivating its scavengers [21][22] (reviewed in [23]).

SA levels are regulated not only by SA biosynthesis but also by SA chemical modifications and intercellular transport (reviewed in [18][24]). These processes have been studied mainly in Arabidopsis. SA glycosylation occurs via the conjugation of glycosyl onto the hydroxyl and carboxyl groups of SA, producing two inactive SA storage forms, salicylic acid 2-O-β-d-glucose (SAG) and salicylic acid glucose ester (SGE). Uridine diphosphate (UDP)-glycosyltransferases UGT74F1 and UGT74F2 perform the conversion to the former, while only UGT74F2 is involved in the catalysis to the latter. The carboxyl group can be also methylated by the S-adenosyl-L-methionine (SAM)-dependent methyltransferase, BA/SA carboxyl methyltransferase 1 (BSMT1), producing methyl salicylate (MeSA), the form of SA that has increased membrane permeability. SA hydroxylation by SA-5 and SA-3 hydroxylases generates 2,3-DHBA and 2,5-DHBA dihydroxybenzoic acids. Gretchen Hagen 3.5/WESO 1 (GH3.5/WES1) and another unknown GH3 family enzyme convert

SA into salicyloyl-L-aspartate (SA-Asp). Some of these conjugated forms of SA may also be glycosylated. Inactive SA forms can be stored until they are required to increase the active pool of free SA; alternatively, some of them may be subjected to SA catabolism. SA is often spread via apoplast (reviewed in [24]). Since SA is a weak acid with poor water solubility, the existence of influx and efflux carriers along with pH-dependent diffusion is proposed for its movement through the plasma membrane.

The NONEXPRESSOR OF PATHOGENESIS-RELATED GENES (NPR) are the SA receptors (reviewed in [3][18][24]). At a low SA level, NPR1 oligomerizes in the cytosol. Meanwhile, NPR1 paralogs, NPR3 and NPR4, directly interact with the basic leucine zipper (bZIP) family's TGA transcription factors on the promoters of NPR1 targets, to suppress their expression. SA facilitates the reduction of cytosolic NPR1 oligomers into monomers, which are translocated to the nucleus and activate transcription in complex with TGAs. At the same time, SA inhibits the activity of NPR3 and NPR4 to allow for the transcription of SA-responsive genes. The NPR1 pathway is functional in both shoots and roots [25][26]. SA also binds to A subunits of protein phosphatase 2A (PP2A) and inhibits the activity of this enzyme, thereby altering auxin transport and distribution [26]. There are other SA binding proteins as well but their functions in SA signaling are largely unknown [27] [28][29][30] (reviewed in [31][32]).

3. Modulation of Endogenous SA Levels in Roots

In Arabidopsis shoots, the basal level of SA amounts to 0.25–1 µg per gram of the fresh weight, rising up to 20 µg.g^{-1} at the place of pathogen attack [33] (reviewed in [4]). In many plant species roots also accumulate SA upon invasion of soil-borne pathogens (**Table 1**). Rapid SA accumulation is a part of plant immune signaling, which has been extensively studied in shoots. In this process, SA promotes pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI), effector-triggered immunity (ETI), and systemic acquired resistance (SAR), via an NPR-dependent activation of plant defense genes, to resist biotrophic and semi-biotrophic pathogens (reviewed in [2][3][34]). The mechanisms of plant defense in roots are less studied, yet pathogen-induced SA accumulation is considered an essential factor in root protection from biotic stress [35] (reviewed in [36]). The attacks of soil-borne pathogens are capable of inducing systemic SA accumulation in above-ground tissue [37], and mutants and transgenic plants with a reduced ability to accumulate SA are more susceptible to root infections than wild types [38][39][40][41].

Table 1. The influence of biotic and abiotic stress factors on SA content in roots.

Plant Species	Stress Factor Type	Stress Factor [1]	SA Level	Reference
Biotic stress				
Cucumus sativus L.	Necrotrophic fungus	*Rhizoctonia solani*	↑	[37]
Zea mays L.	Root herbivore	*Diabrotica virgifera* larvae	↑	[42]
Arabidopsis thaliana L. (Bur-0)	Biotrophic protist	*Plasmodiophora brassicae*	↑	[43]
Arabidopsis thaliana L. (Col-0)	Biotrophic protist	*Plasmodiophora brassicae*	-	[43]
Abiotic stress				
Cassia tora L.	Aluminium	Al (10–50 µM)	↑ (RT)	[44]
Glycine max L.	Aluminium	AlCl$_3$ (30 µM)	↑ (RT)	[45]
Hordeum vulgare L.	Heavy metal	CdCl$_2$ (25 µM)	↑ (F)	[46]
Triticum aestivum L.	Heavy metal	Cd(NO$_3$)$_2$ (250 µM)	↑ (F)	[47]
Arabidopsis thaliana L. (Col)	Heavy metal	CdCl$_2$ (50 µM)	↑	[48]
Oryza sativa L.	Chilling	5 °C	↑ (F + C)	[49]
Cucumis sativus L.	Chilling	8 °C	↑ (F + C)	[50]
Hordeum spontaneum L.	Drought	PEG 6000 (−0.75 to −1.5 MPa)	↑	[51]
Hordeum vulgare L.	Drought	PEG 6000 (−0.5 MPa)	↑	[52]
Scutellaria baicalensis Georgi	Drought	PEG 6000 (15%)	↓ (F + T)	[53]
Scutellaria baicalensis Georgi	Salt	NaCl (150 mM)	↑ (F + T)	[53]
Hordeum vulgare L.	UV-B radiation	UV-B (0.84 W m^{-2})	↑	[52]

Plant Species	Stress Factor Type	Stress Factor [1]	SA Level	Reference
Arabidopsis thaliana L. (Col-0)	Iron deficiency	–Fe (0 µM)	↑ (F)	[54]
Gossypium hirsutum L.	Nitrogen deficiency	–N (0 µM)	↑	[55]
Solanum lycopersicum L.	Alkalinity	pH 9.0 buffer	↑	[56]

SA can also accumulate in roots in response to abiotic stresses such as aluminum, cadmium, chilling, salt, drought, UV-B radiation exposure, alkalinity, and iron- and nitrogen deficiency (**Table 1**), echoing the reported role of SA in abiotic stress resistance (reviewed in [57][58]). In some cases, stress-induced SA accumulates locally in the root, which comes into direct contact with the stress factor, but it can also be transported to the aboveground tissue. For example, in barley, SA accumulates in response to drought in the roots but not in shoots [51]. In grapes exposed to heat stress, SA is progressively transported from the roots to shoots via xylem [59]. Stress-induced changes in endogenous SA levels are species-specific. For example, drought increases SA content in barley [51] but reduces it in *Scutellaria baicalensis* roots [53].

SA (50 µM) treatment promotes adventitious root development at the base of cucumber hypocotyls and strongly increases endogenous SA levels in the rooting zone [60]. It is worthy of note that an SA treatment does not necessarily elevate endogenous SA levels in the root due to exogenous SA uptake. For example, priming wheat seed with SA (50 µM, 3 h) or treating 10 DAG seedlings with 500 µM SA for 1–24 h reduces the endogenous levels of both free and conjugated SA in roots [6][47]. The endogenous levels of total and free SA in *Scutellaria baicalensis* roots also decrease when seedlings are treated with 300 µM SA [53]. Therefore, the type and intensity of exogenous SA effects on plant growth are probably related to changes in the plant's endogenic SA content and/or redistribution of free and conjugated forms. Accordingly, a feasible role of SA biosynthesis in endogenous SA content after an exogenous SA treatment was demonstrated in several studies [61][62]. Priming maize seeds with [3,4,5,6-2 H4]-salicylic acid (D4SA; the SA deuterated isotopomer) during germination allowed researchers to estimate both SA uptake and SA's regulation of its own biosynthesis in developing roots [63]. A low SA concentration (50 µM) increased both SA uptake and biosynthesis, whereas a high SA level (500 µM) more strongly enhanced SA uptake but inhibited SA biosynthesis.

Growing evidence indicates that normal plant growth requires that optimal levels of endogenous SA are maintained. Accordingly, a number of negative regulators that alleviate SA accumulation (such as *CPR5*, *DND1*, *PI4KIIIβ1*, *PI4KIIIβ2* etc.) were described in relation to Arabidopsis [7][8][64][65]. Moreover, hybrids between Arabidopsis accessions with suboptimal and supraoptimal SA content (Columbia and C24, respectively) show root growth heterosis [66]. The chromatin remodeler DECREASED DNA METHYLATION 1 (DDM1) links heterosis with endogenous SA levels. Columbia/C24 hybrid heterosis in the root length is impaired in the *ddm1* mutant background.

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