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The role of salicylic acid in the plant defense mechanism

Abstract. *Pollution and climate change negatively affect plant health. The growing demand for global food production in the agricultural sector is a decisive driving force for the development of new disease control methods that are effective against known pathogens. Plants possess specialized structures, chemicals, and complex defense mechanisms against pathogens. Understanding these defense mechanisms and pathways is critical to developing innovative approaches to protecting crops from disease. Plant stress can be reduced by applying salicylic acid, which is involved in plant signaling. Salicylic acid induces pathogenetic gene expression and the synthesis of protective compounds involved in local and systemic acquired resistance. For this reason, salicylic acid can be used against pathogens, heavy metal stress, and salt stress. The applied salicylic acid enhances photosynthesis, growth, and various morphological, physiological, and biochemical mechanisms in stressed plants. In this article, we look at the use of exogenous salicylic acid for the relief of bacterial, fungal, and viral diseases.*

Keywords: *Exogenous salicylic acid, plant diseases, biotic stress, abiotic stress.*

Abbreviations: *SA-salicylic acid, PAL- phenylalanine ammonia-lyase, ICS- isochorismate synthase.*

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Introduction

Both biotic and abiotic stresses continuously affect plants [1]. The various types of pathogenic infections include common biotic stresses that cause serious problems in growth and development, as well as in crop production, which ultimately affect the economy and human health. Plant stress is estimated to cause yield losses of up to 42% for the eight most grown crops worldwide [2]. To protect against these stresses, plants have evolved with a strong and integrated immune system. Their cellular receptors identify stress factors and induce immune responses both in local foci of infection and in distant places. The low molecular weight hormone salicylic acid, due to its participation in both local and systemic immune responses, plays a fundamental role in stimulating immune response [3]. Plant phytohormones such as abscisic acid, jasmonic acid, ethylene, and salicylic acid (SA) are important components of various signaling pathways involved in plant protection [4-7].

Plants are mainly composed of carbohydrates, proteins, lipids, nucleic acids, vitamins, and other cellular components. These biochemicals make up the basic cellulose/plant architecture. They also regulate the metabolism, growth, and development of plants. Collectively, they are called primary metabolites [8]. These organic compounds are structurally and chemically different from each other and do not directly participate in plant metabolism, growth, and development. These various phytochemicals are collectively referred to as secondary metabolites, by-products, or natural products [9]. Although they are not essential for plant growth and development, they are important for human well-being in various economic aspects such as pharmaceuticals, nutraceuticals, nutritional supplements, and agrochemicals [10]. However, in an ecological context, they protect plants from herbivorous and microbial pathogens. Moreover, due to the sweet aroma and attractive coloration caused by these compounds, they attract animals to facilitate successful pollination and seed dispersal [9,11]. Based on their structure and chemical nature, they are classified into three groups: (a) terpenes, (b) phenolics, (c) nitrogen-containing compounds (Figure 1).

Secondary metabolites		
Terpenes/Terpenoids:	Phenolics:	N-containing compounds
1) Monoterpenes (10-C) 2) Sesquiterpenes (15-C) 3) Diterpenes (30-C) 4) Triterpenes (40-C) 5) Polyterpenes	1) Simple phenolics such as caffeic acid, ferulic acid, vanillin, salicylic acid 2) Complex phenolic macromolecules such as lignins and tennins and flavnonoids	1) Alkaloids such as cocaine, nicotine, morphine, and caffeine 2) Poisonous group of cyanogenic glycocides and glucosinolate

Figure 1. Classification of plant secondary metabolites [9]

Terpenes are made up of branched 5-C units called isoprene. The mixture of these terpenes or terpenoids constitutes an essential oil that gives the plants their characteristic odor and acts as an insect repellent [12,13]. These phytochemicals include limonene, menthol, and azirachtin. Plant phenolic compounds or polyphenols are composed of thousands of phytochemicals synthesized by the shikimate/ phenylpropanoid pathway or the "polyketide" acetate/malonate pathway. They are ubiquitous secondary metabolites that are known to counteract various environmental, nutrient, and nutrient deficiencies [14]. N-containing secondary metabolites come from amino acids such as lysine, tyrosine, or tryptophan. They contain hundreds of alkaloids such as cocaine, nicotine, morphine, and caffeine. Moreover, this category also includes some highly toxic groups of cyanogenic glycosides and glucosinolates [9].

Biosynthesis of salicylic acid in plants

It is widely accepted that plants possess both an isochorismate synthase (ICS) and phenylalanine ammonia-lyase (PAL) pathway to synthesize SA, both starting from chorismate (Fig2). However, not all enzymes catalyzing these pathways have been identified in plants. The importance of these pathways for the biosynthesis of SA varies in different plant species. In *Arabidopsis*, the ICS pathway is the most important, while the PAL pathway seems to be more important for SA accumulation in rice. Both pathways contributing equally is also a possibility, as is the case in soybeans. Furthermore, SA biosynthesis regulation can even be different within the plant. In rice, for example, the basal SA levels in shoots are much higher than in roots [15,16].

Salicylic acid can undergo several modifications in the plant. Most of them cause SA to become inactive. When SA is glucosylated, SA glucoside (SAG) can be produced. This compound can be stored in the vacuole in large quantities [17]. As a result of glucosylation by Salicyloyl glucose ester (SGE) is another SA sugar conjugate that can be formed in plants. Methylation increases the membrane permeability of SA and makes it more volatile. This derivative can be released from the plant and serves as a cue for plant-insect interactions [18]. Another major modification is amino acid (AA) conjugation, possibly involved in SA catabolism [19]. Hydroxylation of SA results in 2,3- and 2,5 dihydroxybenzoic acid (2,3-DHBA and 2,5 DHBA) [20]. Recently, a glycosyltransferase has been identified that can convert **MeSA to MeSA glucoside (MeSAG)[21].**

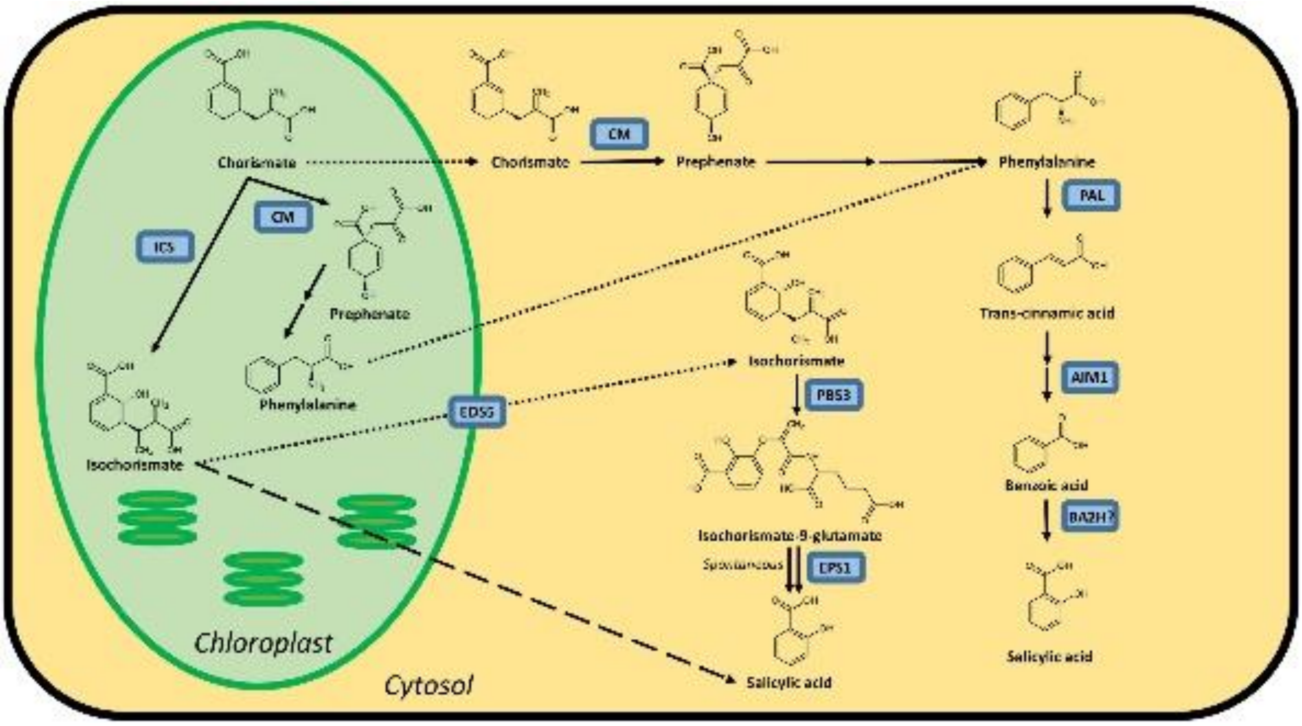

Figure 2. Possible pathways for SA biosynthesis in plants. Solid lines - conversion stages, datted lines - transport from chloroplast to cytosol, dashed line - an alternative, unknown biosynthesis pathway

A question mark indicates an unidentified protein. It is unclear whether the steps leading to phenylalanine are performed in the chloroplast or the cytosol, or both, since chloroplast and cytosolic CMs exist. Enzymes are marked in blue and have the following abbreviations: ICS, isochorism synthase; CM, chorizmatmutase; PAL, phenylalanine ammonia-lyase; AIM1 - abnormal meristem of inflorescence1; BA2H, benzoic acid 2-hydroxylase; |5, increased disease resistance 5; PBS3, avrPphB susceptible3; EPS1, increased stability of pseudomone 1 [22].

SA and Plant Immunity

Plants being sessile are constantly exposed to a number of pathogenic microbes, which based on their infectious lifestyles can be broadly divided into biotrophs and necrotrophs[23-25]. Biotrophic pathogens rely on nutrients from living host cells, whereas necrotrophic pathogens feed on dead cells. Plants employ distinct immune responses to counter these pathogens and this aspect has been covered in detail in several recent reviews [26,27].

The two major types of systemic resistance intensely studied in plant microbial interactions are SAR [26] and ISR [28]. SAR and ISR are based on distinct phytohormonal signals. SAR describes defenses against (hemi-)biotrophic pathogens activated after a local challenge by a pathogen in systemic, uninfected tissues. The SAR signaling cascade is triggered by microbe-associated molecular patterns (MAMPs) leading to MAMP-triggered immunity or triggered by pathogen effectors leading to effector-triggered immunity [29]. Subsequently, the defense in systemic uninfected tissues is induced in an SA-dependent manner and acts against a broad range of pathogens [30,26]. Various compounds have been proposed as potential signals for SAR activation. For instance, methyl salicylate is a phloem-mobile compound that can be transported to systemic plant parts, where it is hydrolyzed to the bioactive SA to induce resistance [31]. For defense induction and in addition for attracting predators of herbivores, methyl SA might also act as a volatile signal [32-35].

Induction of local responses is associated with the transport of defense signals throughout the plant resulting in broad-spectrum disease resistance against secondary infections. This phenomenon, known as systemic acquired resistance (SAR), is conserved among diverse plants and confers long-lasting resistance to unrelated pathogens [36-42]. Among the signals contributing to SAR are salicylic acid (SA) and several components of the SA pathway including the methylated derivative of SA (methyl SA, MeSA)[43].

Induction of systemic resistance in agricultural crops by the exogenous application of chemical inducers, for example, methyl jasmonate [44], functional analogs of salicylic acid, benzothiadiazole, and 2,6-dichlororizonicotinic acid [46] and oxalic acid [45] is a potentially valuable component in complex pathogen control strategies that complement traditional control methods.

SA is best known as a hormone associated with defense [47-52]. The first observations that SA are involved in plant immunity were presented by Raymond F. White in 1979, who described that the use of aspirin (acetyl-SA) in virus-susceptible tobacco (*Nicotiana tabacum cv.Xanthi-nc*) confers tobacco resistance to a mosaic virus (TMV) [53]. This indicates the protective role of SA in plant resistance. In the tobacco cultivar (*N. tabacum*) carrying the viral resistance gene, endogenous SA increased during viral infection and the proteins associated with pathogenesis (PR) accumulated [54]. Likewise, SA was shown to increase in cucumber phloem juice before induced resistance was found in systemic tissue [55]. Both studies show that endogenous SA can play the role of an internal protective signal for plant immunity.

Early characteristics of plant immune responses included a pathogen-induced hypersensitive response (HR), which can reduce the penetration and spread of pathogens through the local death of plant cells at the site of infection [56]. In arabidopsis (*Arabidopsis thaliana)*, the HR-like lesion (hrl) mutant hrl1, which accumulates a higher level of endogenous SA, demonstrates a reduced leakage of HR-associated ions [57]. Moreover, SA-deficient Arabidopsis mutants exhibit enhanced immune associated ion leakage [58]. Overall, these observations indicate that SA and/or related metabolites play a critical role in HR regulation and cell death.

Another important aspect of plant innate immunity is related to the concept of systemic acquired resistance (SAR). The acquired resistance caused by pathogens or symbiotic microbes was well generalized and investigated by Chester in 1933 [59]. In 1961, the term SAR was first used by A. Frank Ross to describe induced systemic resistance in TMV-infected tobacco. The initial infection of the plant in the "primary" site of infection was sufficient to limit the growth of a wide range of pathogens, which were subsequently inoculated into the distal secondary site of infection [60].

SA in Plant Resistance to Biotic Stresses

SA is a plant defense-related hormone that plays a key role in resistance to various microbial pathogens such as viruses, bacteria, fungi, and oomycetes [61,62]). In plants, there is a well-established positive correlation between endogenous SA levels and resistance responses against biotrophic and hemibiotrophic pathogens [63]. SA at low concentrations also promotes faster and stronger activation of callose deposition and gene expression in response to pathogenic or microbial elicitors, a process called "priming" that promotes induced defense mechanisms [64].

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Table 1

Increase in disease resistance when applying exogenous SA in different plants [65]

Host plant	Pathogen (infection style)	SA conc.and treatment method	effect	References
Tomato *(Lycopersicon esculentum)*	*Fusarium oxysporum* (hemibiotrophic) *Botrytis cinerea* (necrotrophic) *Alternaria alternata* (necrotrophic) *Potato purple top* (PPT) *phytoplasma* (biotrophic)	0.2mM 2mM 0.4mM 100ml of 0.1mM SA is sprayed and 100 ml of 0.1 mM siol-drenched	~55% reduction in disease incidence ~62% reduction in disease severity ~57% reduction in disease serverity ~47% reduction in disease incidence	Jendoubi et al. (2017) Li and Zou (2017) Esmailzadeh et al. (2008) Wu et al. (2012)
Pepper *(Capsicum annuum)*	*Ralstonia solanacearum* (hemibiotrophic) *Fusarium oxysporum* (hemibiotrophic)	0.5mM 0.5 mg/l	*R.solanacearum* - induced seedling growth inhibition is recovered. Notably, 0.5 mM SA itself enhanced seedling growth by ~ 150% ~50% reduction in disease incidence	Chandrasekhar et al. (2017) Yousif (2018)
Rice *(Oryza sativa)*	*Magnaporthe grisea* *Xanthomonas oryzae* (hemibiotrophic) *Oebalus pugnax* (piercing and sucking insect)	8 mM 1 mM 1 mM 16 mM	~70% reduction in disease serverity Leaf blight lesion length is reduced ~30% reduction in disease serverity ~35% reduction in number of bugs found in plots; tetarded nymph development to adult insect	Daw et al. (2008) Mohan Bahu et al. (2003) Le Thanh et al. (2017) Stella de Freitas et al. (2019)
Orange *(Citrus sinensis)*	*Xanthomonas axonopodis* (biotrophic)	0.25 mM	~45% reduction in disease incidence	Wang and liu (2012)

Banana *(Musa acuminata)*	*Fusarium oxysporum* (hemibiotrophic)	Roots were dipped in 0.1 mM SA for 2 days	Disease symptom (corn browning) is not observed 3 weeks after inoculation with the pathogen Note, 0.2 mM SA-induced necrosis on roots	Wang rt al. (2015b)
Chickpea *(Cicer arietinum)*	*Fusarium oxysporum* (hemibiotrophic)	10µl of ~ 14.5 mM SA is injected at the base of stem 10 ml of ~ 0.58 mM SA is soil - drenched	~20% reduction in disease serverity (also increased ~ 6% in both shoot and root growth length) ~ ~ 20% reduction in disease serverity (also increased ~ 10 and 4.5%% in both shoot and root growth length, respectively)	Saikia et al. (2003)
Black gram or urdbean *(Vigna mungo)*	*Mungbean yellow mosaic Indian virus* (MYMIV) (biotrophic)	0.1 mM	~71% reduction in disease serverity	Kundu et al. (2011)
Pumpkin (*Cucurbita pepo*)	*Zucchini yellow mosaic virus* (ZYMV)(biotrophic)	0.1 mM	~66% reduction in disease serverity	Radwan et al.(2007)
Peanut *(Arachis hypogaea)*	*Peanut mottle virus* (PeMoV) (biotrophic)	0.2 mM	~42% reduction indisease serverity	Kobeasy et al. (2011)
Tea flower *(Camelia oleifera)*	*Colletotrichum gloeosporioides* (hemibiotrophic)	~ 1 mM	~40% reduction in disease serverity	Wang et al. (2006)
Rubber tree *(Hevea brasiliensis)*	*Phytophthora palmivora* (hemibiotrophic)	5 mM	~41% reduction in disease serverity (>10 mM SA – induced leaf shrinkage)	Deenamo et al. (2018)
Arabidopsis *(Arabidopsis thaliana)*	*Botrytis cinerea* (necrotrophic)	5 mM	~62% reduction in lesion size	Ferrari et al. (2003)

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Conclusion

Exogenous salicylic acid increases the internal glutathione cycle, thus improving the antioxidants and metal detoxification systems. Furthermore, exogenous salicylic acid reduces the stress depending on dose, depending on the type of stress as well as the plant species. Salicylic acid is a scavenger of hydroxyl radicals and an iron-chelating compound that inhibits the direct impact of hydroxyl radicals and their effect on plant growth. Hence, further studies on the practical use of SA in different crop plants will contribute to developing a cost-effective and environmentally friendly crop management system.

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Салицил қышқылының өсімдік қорғаныс механизміндегі рөлі

Аңдатпа. Қоршаған ортаның ластануы және климаттың өзгеруі өсімдіктерге кері әсер етеді. Ауылшаруашылық секторындағы әлемдік азық-түлік өндірісіне сұраныстың артуы белгілі қоздырғыштарға қарсы ауруларды бақылаудың жаңа әдістерін жасау үшін шешуші қозғаушы күш болып табылады. Өсімдіктер патогендерге қарсы тұра алатын арнайы құрылымдарға, химиялық заттарға және күрделі қорғаныс механизмдеріне ие. Осы қорғаныс тетіктері мен жолдарын түсіну дақылдарды аурудан қорғаудың инновациялық тәсілдерін жасау үшін өте маңызды. Өсімдіктердің күйзелісін өсімдікке сигнал беруіне қатысатын салицил қышқылын қолдану арқылы азайтуға болады.Салицил қышқылы патогенетикалық гендердің экспрессиясын және жергілікті және жүйелі жүре пайда болған қарсылыққа қатысатын қорғаныс қосылыстарының синтезін индукциялайды. Осы себепті салицил қышқылын қоздырғыштарға, ауыр металдарға қарсы, тұз стрессіне қарсы қолдануға болады. Қолданылатын салицил қышқылы стресске ұшыраған өсімдіктерде фотосинтезді, өсуді және әртүрлі морфологиялық, физиологиялық және биохимиялық механизмдерді күшейтеді. Бұл мақалада біз экзогендік салицил қышқылын бактериялық, саңырауқұлақ және вирустық ауруларды жеңілдету үшін қолдануды қарастырамыз.

Түйін сөздер: экзогенді салицил қышқылы, өсімдік аурулары, биотикалық стресс, абиотикалық стресс.

Қысқартулар: СҚ-салицил қышқылы, ФАЛ-фенилаланин аммиак-лиаза, ИХС-изохоризмат синтаза.

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Роль салициловой кислоты в механизме защиты растений

Аннотация. Загрязнение окружающей среды и изменение климата негативно влияют на здоровье растений. Растущий спрос на мировое производство продуктов питания в сельскохозяйственном секторе является решающей движущей силой для разработки новых методов борьбы с болезнями, эффективных против известных патогенов. Растения обладают специализированными структурами, химическими веществами и сложными механизмами защиты от патогенов. Понимание этих защитных механизмов и путей имеет решающее значение для разработки инновационных подходов к защите сельскохозяйственных культур от болезней. Стресс растений можно уменьшить, применяя салициловую кислоту, которая участвует в передаче сигналов растениями. Салициловая кислота индуцирует экспрессию патогенетических генов и синтез защитных соединений, участвующих в местной и системной приобретенной резистентности. По этой причине салициловую кислоту можно использовать против патогенов, стресса от тяжелых металлов, солевого стресса. Применяемая салициловая кислота усиливает фотосинтез, рост и различные морфологические, физиологические и биохимические механизмы в стрессовых растениях. В данной статье мы рассмотрим использование экзогенной салициловой кислоты для облегчения бактериальных, грибковых и вирусных заболеваний.

Ключевые слова*:* экзогенная салициловая кислота, болезни растений, биотический стресс, абиотический стресс.

Сокращения: СК-салициловая кислота, ФАЛ - фенилаланиновая аммиачная лиаза, ИХС - изохорисматсинтаза.

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