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Role of Salicylic Acid in Plants to Trade-Off Growth-Immunity

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Introduction

Salicylic acid (SA) belongs to salicylates, which are phenolic compounds synthesized by plants, possess an aromatic ring and a hydroxyl group. The metabolite SA is a beta hydroxy benzoic acid, described as a phytohormone. SA plays a crucial role in resistance of plants against pathogens with a biotrophic lifestyle (Ding and Ding, 2020). SA plays a crucial role during plant growth development and during the plant innate immunity including resistance in both local and systemic tissue upon biotic attacks, hypersensitive responses, and cell death (Klessig et al., 2018). The main hormones involved during the innate immunity are SA, jasmonic acid, and ethylene.

Plants accumulate SA and activate immune responses upon detection of pathogens such as viruses, fungi, and bacteria. While plants are fully engaged in fighting pathogens, the accumulated SA actively suppresses growth and developmental processes, leading to an interruption of biomass increase. When the pathogen threat has subsided, SA levels and SA-mediated immune responses drop, while growth suppression is relieved, allowing the plant to regain biomass.

Biosynthesis

Salicylic acid biosynthetic pathway in plants has evidence for two distinct pathways, the isochorismate (IC) pathway found in plastids and the phenylalanine ammonia-lyase (PAL) pathway in cytosol. Both pathways require the primary metabolite chorismate, the end-product of the shikimate pathway, to produce SA. Once SA is synthesized, its levels are regulated by a number of chemical modifications, to produce inactive forms, including salicyloyl glucose ester (SGE), SA O-β-glucoside (SAG), methyl salicylate (MeSA), and methyl salicylate O-β-glucoside (MeSAG). These inactive molecules can be stored until required to activate the SA-triggered responses.

Transport of Salicylic acid

The synthesis of SA, is localized in the chloroplast and afterward transported to the cytosol (Fragnière et al., 2011).ENHANCED DISEASE SUSCEPTIBILITY 5 (EDS5), is the unique transporter involved in SA transport from chloroplast to cytosol. Once extruded, SA is conjugated with glucose to form SAG or SGE and then SAG is transported into the vacuole by ABC transporter/H+ -antiporter systems. The next step of journey is its distribution to neighboring cells (Kawano et al., 2004). Often SA is spread via the apoplast . Because of its chemical features (weak acid and poor water solubility), SA crosses through plant cell plasma membranes by pH-dependent diffusion and carrier-mediated mechanisms (Bonnemain et al., 2013). SA phloem loading may be based on a symplastic outer cell transport, phloem apoplast intake, through an ion trap mechanism and an apoplast intake mediated by a carrier system. After a pathogen attack, SA levels rise in the primary infected tissue. SA is converted to MeSA by carboxyl methyltransferase enzyme (SAMT). The accumulating MeSA is translocated to the uninoculated systemic tissue. MeSA is demethylated to form SA and induces de-novo synthesis of SA at the distal tissue.

Regulation of Salicylic acid

Arabidopsis carries five paralogs of NPR1, which act as receptor of SA. NPR1 and NPR2 play positive roles in regulating downstream genes in response to SA, while NPR3 and NPR4 seem to serve as negative regulators (Ding, et al., 2018).

Two working models have been proposed to explain how NPR proteins respond to increased SA levels:

- Upon binding with SA, NPR3/4 work with the proteasome to degrade NPR1 so as to negatively regulate defense
- NPR1 and NPR3/4 work in antiparallel in response to SA, in which SA activates NPR1 positive regulation and deactivates NPR3/4 negative regulation by direct binding to the respective NPR proteins

Salicylic acid and the Growth–Immunity Trade off

Plants have evolved a sophisticated immune system to combat pathogens and other attackers. Activation of the immune system often comes at the expense of growth. The

balance between growth and immunity is strongly influenced by phytohormones, which can work antagonistically or synergistically.

Accumulation of SA triggers a plethora of immune responses like -massive transcriptional reprogramming, cell wall strengthening by increased lignin and callose production, synthesis of antimicrobial secondary metabolites like phytoalexins, and synthesis of antimicrobial proteins like glucanases and chitinases, which degrade pathogen cell walls (Pieterseet et al. 2009).

Pasternak et al. (2019) showed that exogenous SA treatment at low (below 50 µM) and high (greater than 50 µM) concentrations affect root meristem development in two different PR1-independent ways. Kumaraswamy et al. 2019 reported that salicylic acid-chitosan nanoparticles (SA-CS NPs) act as a biostimulant for promoting plant defense and growth in maize. Napoleão et al. 2017 found that in response to salicylic acid, plant growth was reduced coupled with significant changes in cell wall composition. Ullah et al. (2019) concluded that SA activates flavan-3-ol (catechin and proanthocyanidins) biosynthesis in poplar against rust infection. Tang et al. (2019) showed that, simultaneously silenced three GhWATs (GhWAT123-silenced cotton plants), inhibited plant growth and increased plant resistance to *V. dahliae*, indicating that these genes were functionally redundant. In the GhWAT123-silenced plants, the expression of SA related genes was significantly upregulated compared with the control, resulting in an increase of SA level.

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