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THE EFFECT OF SALICYLIC ACID ON DIFFERENT PLANT PROCESSES – A REVIEW

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ABSTRACT. Salicylic acid (SA) is a well-known signaling molecule that plays an important role in resistance against pathogens, as well as adaptation to some abiotic stress factors, such as drought, heavy metal toxicity, chilling, heat and osmotic stress and can be a factor effective treatment for plants. The impact of SA on different plant processes under optimal environmental conditions is controversial. Also, SA as a plant growth regulator may have a positive effect on the regulation of physiological and biochemical processes of different plant species, such as seed germination, seed production, respiration, vegetative growth, flower formation and photosynthesis. In addition, SA as a regulator of cell growth, could contribute to maintaining cellular redox homeostasis by induction of the alternative respiratory pathway and the regulation of antioxidant enzymes activity and to regulating gene expression by inducing a RNA-dependent RNA polymerase. However, SA may act as a stressor, and may have a negative impact on different plant processes. Recent results indicate that the exogenous application of SA to plants have affect several on many physiological processes, such as control of ion absorption, stomatal closure and transport, reducing of stress and stimulation of growth and differentiation of plants, and also the controlled levels of SA in plants are important for improving performance and adaptation to environmental stimuli and emphasize its important role in plant health and protection. The present study investigated the effect of SA on different plant processes.

Keywords: signaling molecule; plant processes; stress.

INTRODUCTION

Salicylic acid (SA) or orthohydroxybenzoic acid is a phenolic compound known as plant growth regulator and affects various processes, such as inhibition of ethylene synthesis and glycolysis (Martín-Mex *et al.*, 2015).

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Salicylic acid is also one of the water-soluble antioxidants that can control plant growth (Muthulakshmi and Lingakumar, 2017). On the other hand, it is a signaling molecule that plays an important role in abiotic stress tolerance, such as drought tolerance (Popova *et al.*, 1997). In addition, some of the effects of SA may be due to chemical properties. Some evidence suggests that SA has a unique and specific regulatory role (Muthulakshmi and Lingakumar, 2017). Studies show that many phenolic compounds are involved in regulating physiological processes, including plant growth, stomatal closure, photosynthesis, and ion uptake (Kabiri *et al.*, 2014; Mohajeri *et al.*, 2018). Phenolic molecules produced by plant roots are essential for germination and plant growth (Popova *et al.*, 1997). Studies show that SA acts as an endogenous regulator on flowering and in combination with plant regulators; *e.g.* gibberellin induces flowering (Cleland and Ajami, 1974). In addition to flowering, SA affects anthocyanin and chlorophyll levels in some plants. Reports indicate that high SA concentrations had no effect on plant growth and physiological properties, but low concentrations can have a significant effect on plant growth and yield (Khatiby *et al.*, 2017). The uptake of SA was pH dependent. So, that at the appropriate concentration and pH conditions, SA can dramatically increase the mineral uptake of plants (Harper and Balke, 1981). The aim of this study was to evaluate the effect of SA on different plant processes.

Functional of SA in plants

SA as a hormone

SA is one of the phenolic compounds with a hydroxyl or derivative group made by plants (Cetinkaya and Kulak, 2019). In general, plant phenols are classified as secondary metabolites involved in important functions, such as lignin biosynthesis, as well as allelopathic compounds that control plant responses to living stimuli (Kulbat, 2016) or play an important role in heat regulation (Vlot *et al.*, 2009) and in resistance to plant diseases or defense signaling activity (Kulbat, 2016). SA is effective on seed germination, cell growth, respiration, stomatal closure, response to stresses, heat tolerance and fruit yield (Morris *et al.*, 2000; Metwally *et al.*, 2003). Its effect may be indirect on some of these processes because SA is affected by certain plant hormones including jasmonic acid (JA), ethylene (ET) and auxin, causing changes in the synthesis and/or signaling of SA (Vlot *et al.*, 2009).

Photosynthesis

Photosynthesis is one of the most vital physiological processes that contribute to plant growth. Photosynthetic ability in crops is a major component of dry matter production. As environmental factors change, the rate of photosynthesis changes, which in turn affects plant growth and function (Hayat *et al.*, 2010). SA is an important regulator of photosynthesis and affects leaf structure, chloroplast, stomach closure, chlorophyll and carotenoid content, and activity of enzymes, such as rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase, resulting in changes in leaf area (Afshari *et al.*, 2013). It, eventually, decreases the width of the adaxial epidermis and mesophilic tissue. These changes are associated with increased chloroplast volume, granular thylakoid swelling, and stromal coagulation. Also, the increase in photosynthesis induced by SA is associated with stomatal or non-stomatal factors (Hayat *et al.*, 2005). Reports indicate that high concentrations of SA affect the thylakoid membrane and light-inducing reactions and decrease photosynthesis. While low concentrations of SA have good effects on photosynthesis, which may lead to inhibition of SA oxidation by SA, also auxin levels and nitrate reductase activity are elevated (Rivas-San Vicente and Plasencia, 2011).

Stomatal closure

Many pathogens use stomata pores as a site for penetration into tissues of the leaf. The stomatal aperture in the epidermis of the leaves of the plant is composed of a pair of guard cells. These guard cells can respond to a variety of stimuli, including drought, light, external calcium, salicylic acid, abscisic acid, and water loss. The plant develops mechanisms to optimize growth that integrate stress inputs and then produce stomata openings in guard cells (Melotto *et al.*, 2017). SA plays an important role in the stomatal clousing. Stomatal closure is another important factor for photosynthesis and plays an important role in the control of phytohormones (Prodhan *et al.*, 2018). On the other hand, the stomatal closure by SA is also one of the strategies to prevent the entry of bacteria (Okuma *et al.*, 2014). SA signaling with other signaling (*e,g.* ABA signaling) plays a role in stomatal immunity. Ca^{2+}-dependent protein kinases (CPKs), such as CPK3 and CPK6 and the Ca^{2+}-independent protein kinase Open Stomata1 (OST1), are active in the ABA signaling cascades. The mechanism of action of SA and ABA signaling is that SA activates the ROS signal and activates phosphorylation of both Ca^{2+}-dependent protein kinase and other protein kinases. The Ca^{2+}-dependent protein kinase signaling domain is important for the interaction of SA signaling with ABA signaling in guard cells (Prodhan *et al.*, 2018). ABA activates anion channels and leads to stomatal closure *via* this way (Khokon *et al.*, 2011) and increases calcium and sphingosine-1-phosphate, which is related to the signaling pathway Ca^{2+}-dependent and Ca^{2+}-independent signaling (Prodhan *et al.*, 2018). However, there may be a close relationship between SA signaling and sphingolipid metabolism that affects plant growth (Khokon *et al.*, 2017). Thus, the functions of SA and ABA have been reported as key mediators for the closure of stomatals caused by biotic stress (Montillet *et al.*, 2013).

Germination

Environmental factors and interactions between plant hormones, such as abscisic acid (ABA), jasmonic acid, gibberellins, ethylene, brassicosteroids, auxin, and cytokinins, can regulate seed germination (Rivas-San Vicente and Plasencia, 2011; Cetinkaya and Kulak, 2019). The role of SA in seed germination has been studied and conflicting reports indicate that salicylic acid can both enhance seed potency and inhibit germination, which may be related to SA concentration (Rajjou *et al.*, 2006). Some studies show that low-concentrations SA treatment regulates translation initiation and elongation factors, proteases, and two proteasome 20S subunits; SA improves seed germination and seedling establishment under different stress conditions by protein synthesis. This is essential for seed germination. Also, SA can activate the biosynthesis of several enzymes involved in metabolic pathways, such as the glycosylate cycle, the pentose phosphate pathway, gluconeogenesis and glycolysis, and enhance the formation of a strong seedling by releasing dormancy (Rao *et al.*, 1997). The effect of SA as a negative regulator of seed germination is probably due to SA-induced oxidative stress (Rajjou *et al.*, 2006). High concentrations of SA lead to H_2O_2 accumulation due to increased superoxide dismutase (SOD) and a decrease in catalase (CAT) activities and simultaneously decrease germination rate. Consequently, the use of the appropriate SA dose is a possible method for the control of growth and response to environmental stress due to enzymatic and non-enzymatic antioxidant activity (Yanik *et al.*, 2018; Khatiby and Shadmehri, 2019).

Respiration

SA is an endogenous signal that increases the capacity of the alternative respiratory tract, leading to the induction of thermogenesis (Rhoads and McIntosh, 1992; Dempsey and Klessig, 2017). Energy for thermogenesis is provided by enhancing mitochondrial electron transport by alternative oxidase (AOX); AOX deflects electron transport from the cytochrome c pathway and inhibits ATP production (Meeuse, 1975). SA regulates oxidase pathway (AOX). Thus, SA treatment induces AOX expression and/or respiratory pathway in non-thermogenic plant species. AOX binds to the ubiquinol oxidation, which is associated with reduction of O_2 to H_2O (Norman *et al.*, 2004). AOX is thought to play an important role in reducing mitochondrial respiratory chain production of ROS. AOX is a non-proton carrier, driving ATP synthesis to maintain homeostasis for growth, which is one of the SA targets for regulating plant growth (Rivas-San Vicente and Plasencia, 2011); Rhoads and McIntosh, 1992). Concentrations of millimolar SA can be accumulated inside the cell. In isolated mitochondria, SA acts as an electron transport fragment at concentrations less than 1 mm. At higher concentrations, it acts as a potent inhibitor of electron transport, and appears to inhibit electron transfer from substrate dehydrogenases to ubiquitin (Norman *et al.*, 2004).

Flowering

Flowering is directly related to plant yield and productivity (Hayat *et al.*, 2010). SA induces flowering in some plants (Vlot *et al.*, 2009). Researchers have shown that stress-induced flowering in poor diet is inhibited by amino-oxyacetic acid, a phenylalanine ammonia lyase inhibitor, and reversed by salicylic acid. However, application of SA does not induce flowering under non-stress conditions, suggesting that SA may be necessary but not sufficient to induce flowering (Wada and Takeno, 2010). In addition, in cucumbers and tomatoes, when fruits were sprinkled with lower concentrations of SA, fruit yield increased significantly (Javaheri *et al.*, 2012). Application of SA on soybean foliage also increased flowering and pod formation (Kumar *et al.*, 1999). In some studies, the flower inducing factor is known as SA, which is consistent with reports of the use of SA in the induction of organic tobacco flowering (Muthulakshmi and Lingakumar, 2017). However, the precise mechanism of the SA inducer property has not yet been investigated. Therefore, it can be concluded that SA can act as a regulator that affects plant growth and productivity (Hayat *et al.*, 2010; Khatiby and Shadmehri, 2019).

Aging

SA is involved in the regulation of aging as a phytohormone. Aging is characterized by an increase in reactive oxygen species (ROS) levels and a decrease in photosynthetic activity due to the loss of antioxidant ability. These events may partly be due to the accumulation of SA (Rivas-San Vicente and Plasencia, 2011; Rhoads and McIntosh, 1992). The rate and percentage of germination in old seeds is much lower than in healthy seeds. Using low concentrations of salicylic acid significantly increases seed germination and early seedling growth and has the greatest effect on preventing aging (Parmoon *et al.*, 2017). In addition, SA delayed fruit ripening processes during post-harvest storage (Islam *et al.*, 2018). Therefore, the use of specific concentrations of salicylic acid also increased the post-harvest life of tomato and Guava fruits (Baninaiem *et al.*, 2016; Madhav *et al.*, 2018).

Resistance to diseases

When a plant is infected with the pathogen, the pathogen multiplies and spreads throughout the plant, causing significant damage and even death of the host plant (Klessig *et al.*, 2000). Lack of plant's resistance may be due to the host plant's inability to detect or effectively respond to infection. The pathogen may also have strategies for overcoming plant defense. Studies have shown that many of these responses can protect the plant by limiting the pathogen and resisting disease (Klessig and Malamy, 1994). In fact, the interaction between the plant and the pathogen can lead to a compatible or incompatible response. In the incompatible response, bacteria and fungi which infect plants induce local responses in the host cells, resulting in an oxidative burst where the level of ROS increases rapidly and cell death happens. Plants have a wide range of defense mechanisms that respond to biological stresses and diseases. In compatible responses, pathogens may be trapped in dead cells and lead to prevent early infection (Prasannath, 2017), by altering cell wall composition, the activation of protein kinases, and the increased expression of plant protective genes, including, peroxidase, glutathione S-transferase, proteinase inhibitors and various biosynthetic enzymes, such as phenylalanine ammonia lyase (PAL). PAL is the first enzyme in the phenylpropanoid pathway, which is involved in the synthesis of antimicrobial compounds known as phytoaloxins (Klessig *et al.*, 2000) and by the synthesis of these antimicrobial compounds prevents the pathogen from penetrating (Su *et al.*, 2018). Adding stimulants to the plant increases plant resistance to disease (Prasannath, 2017; Sabir *et al.*, 2018). SA acts as an intrinsic stimulus and regulator (Vlot *et al.*, 2009), which alerts other plant processes to the plant's resistance to disease and to prevent pathogen proliferation (Klessig *et al.*, 2000; Pirasteh-Anosheh *et al.*, 2012). Due to the establishment of defense mechanisms in plants by a stimulus, plant diseases are reduced before plant infection (Prasannath, 2017; Pieterse and van Loon, 1999). SA is safe for the plant at low concentrations. Thus, low concentrations of SA cause high activity of antioxidant enzymes, which induces plant resistance. However, high concentrations of SA due to toxicity in the plant lead to low activity of antioxidant enzymes (War *et al.*, 2011).

The protection of antioxidant stresses

Stress factors increase ROS and causes oxidative damage to plant macromolecules, such as proteins, lipids, nucleic acids (Seedlings *et al.*, 2003), and also enzymes inactivation, gene expression alterations, and interfere in various pathways of metabolic processes (Chaparzadeh and Hosseinzad-Behboud, 2015). ROS cause free radicals, such as H_2O_2, which cause damage to metabolic events. Salicylic acid can be used to reduce H_2O_2. SA is involved in stimulating specific responses against various biotic and abiotic stresses (Kareem *et al.*, 2017) and many physiological processes of plants, flowering, control of root ions absorption and stomatal closure (Shahmoradi and Naderi, 2018). This molecule is a plant regulator that has a protective effect against oxidative damage. Certain concentrations of SA can inhibit antioxidant enzymes catabolizing H_2O_2 and reduce H_2O_2 accumulation; in fact, H_2O_2 can play a key role in generation of defense responses in the plant. However, this mechanism cannot be generalized (Koç *et al.*, 2013). SA is a pro-oxidant and phytotoxin and the high level of H_2O_2 caused by the high concentration of SA results in the destruction of the lipid structure and the like. Thus, low concentrations of salicylic acid can have positive effects on the protection of antioxidant stresses (Anjum *et al.*, 2008; Krantev *et al.*, 2008).

CONCLUSION

SA is a signaling compound that under normal conditions and stress may affect different plant processes. How it works depends on several factors, such as environmental conditions, plant species and SA concentration. It acts as a mediator at low concentrations, affecting the oxidative state of the plant and increasing the ROS by increasing antioxidant capacity and protecting the plant from severe stress damage. Therefore, with respect to the antioxidant property of SA, it is suggested that this compound can be used to make plants resistant against stress and enhance plant yield, and that controlled levels of SA in plants are important for improving yield and adaptation to environmental stimuli, and it is essential for the health of the plant.

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