

Shamsul Hayat · Aqil Ahmad
Mohammed Nasser Alyemeni *Editors*

Salicylic Acid

Plant Growth and Development

 Springer

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Preface

The healthy plant canopy that we recognise is the result of integrated metabolic functions administered by a number of factors, including hormones, of which six (Auxins, Gibberellins, Cytokinins, Abscissic acid, Ethylene and Brassinosteroids) are well recognised for their regulatory functions. However, the others (Salicylic acid, Polyamines and Jasmonates) can not be excluded from the list of hormones because of their well-recognised involvement in plant metabolism and growth.

This book is providing recent information related with Salicylic acid (SA), that was first noticed to be a major component in the extract from *Salix* (willow) bark and was used as an anti-inflammatory drug. It belongs to the phenolic group and is ubiquitous in plants. SA is involved in signal transduction, pondering over the plant resistance to stress and generates significant impact on photosynthesis, transpiration, uptake and transport of ions and plant growth and development. However, the observations related with this presumed plant hormone are very much scattered. It was, therefore, decided to compile all in the form of a book, based on 16 chapters written by various experts, working in this field. A total of 47 experts have explained their results based on the practical work carried over by them and of others on various selected aspects of plants under stress. After going through these chapters it may be concluded that this hormone has a wide range of actions mediated through genes and/or the cell membranes and can be grouped as a stress hormone. It is the second revised edition of the book.

With great pleasure, we extend our sincere thanks to all the contributors for their timely preparation of excellent and up-to-date contributions and also for their consistent support and cooperation. The first two editors (Hayat and Ahmad) are thankful to Aligarh Muslim University, Aligarh, India that gave us the employment and the seat to work. Whereas, Hayat and Alyemeni are also thankful to King Saud University, Riyadh, Saudi Arabia for their present assignment. Thanks are also due to Springer, The Netherlands for expeditious acceptance of our proposal and completion of the review process. Subsequent cooperation and understanding of their staff, especially, Malanie van Overbeek, publishing assistant, is also gratefully acknowledged.

We express our sincere thanks to the members of our family for all the support they provided and the neglect, what so ever, they suffered during the preparation of this book.

Finally we are thankful to the Almighty God.

Shamsul Hayat
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Chapter 1

Salicylic Acid: An Update on Biosynthesis and Action in Plant Response to Water Deficit and Performance Under Drought

Hanna Bandurska

Abstract Salicylic acid (SA) and its derivatives are the most widely known drugs in the world used to reduce pain and fever, helping to treat many inflammatory diseases, in the prevention of coronary heart disease and heart attacks, and in tumor suppression. This substance is also characterized by a high metabolic and physiological activity, which enables it to perform regulatory functions in plant development and reaction to biotic and abiotic stress factors. Under non-stress conditions, SA is present in plant tissues in quantities of several mg to several ng in one g of fresh mass. Its level substantially increases in plants exposed to water deficit. The accumulation of SA may result from its *de novo* synthesis through activation of enzymes involved in the synthesis of SA from phenylalanine, i.e. phenylalanine ammonia lyase (PAL) and benzoic-acid-2-hydroxylase (BA2H). SA accumulated in plants growing under the conditions of water shortage may be involved in the regulation of mechanisms responsible for resistance to drought through the control of water balance and activation of antioxidant system. Large body of evidences revealed that exogenous application of SA was effective in modeling plant responses to water deficit. Plant pre-treatment with SA resulted in higher tissue water content, increased activity of antioxidant enzymes, decreased level of lipid peroxidation and membrane injury and it also protected nitrate reductase activity against inhibition under water deficit conditions. These changes enable plants to survive under drought and play an essential role in countering the adverse effects of stress on growth and yield.

Keywords Drought · Salicylic acid · Water deficit · Stress resistance

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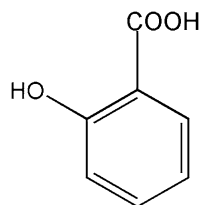
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1 Introduction

Salicylic acid (SA) or *ortho*-hydroxybenzoic acid (Fig. 1), belongs to a varied group of phenolic compounds well known in the plant kingdom.

SA is present in plants as a free phenolic acid and as a conjugate form, which may be generated by glucosylation, methylation or hydroxylation of the aromatic ring (Raskin 1992; Lee et al. 1995). The best known natural SA derivative is salicin (β -glucoside salicylic alcohol), occurring in white willow (*Salix alba*) and other willow species including *S. purpurea*, *S. daphnoides* and *S. fragilis*. The highest salicin content in that plant is observed during spring or summer and the lowest in winter (Foster and Tyler 1999). The highest content of free SA was monitored in bark of *S. laponum* ($3 \text{ mg}\cdot\text{g}^{-1}\text{fr. mass}$) and in the branches of *S. purpurea* and *S. plantifolia* (about $2.1 \text{ mg}\cdot\text{g}^{-1}\text{fr. mass}$) (Peterek et al. 2007). The name salicylic acid is derived from the Latin word for willow tree (*Salix*), from whose bark Johan B uchner isolated in 1828 a small amount of salicin (Raskin 1992). Later, in 1838 the Italian scientist Rafaele Piria obtained SA from flower buds of Meadowsweet (*Spiraea ulmaria* known as *Filipendula ulmaria*). At the end of the nineteenth century, in 1899 the Bayer Company formulated a new drug, acetylsalicylic acid, and called it at first acetyl-spiric-acid (from *Spiraea*) and then aspirin (Ansari and Misra 2007). Recently, Blazics et al. (2010) showed that *Filipendula ulmaria* is a rich source of salicylic acid, which is present in its herb and flowers at an amount of about $1.4 \text{ mg}\cdot\text{g}^{-1}$ dry mass. A large amount of salicylates also occurs in tissues of wintergreen (*Gaultheria procumbens*), known as checkerberry or teaberry. The salicylate predominantly present in that plant is a derivatized form of methyl salicylate called gaultherin (Rybnický et al. 2003). SA acid and its derivatives are the most widely known drugs in the world used to reduce pain, fever, helping to treat many inflammatory diseases and in the prevention of coronary heart disease and heart attacks. Lately, large body of evidences suggests that salicylates also affect tumor suppression (Brummelkamp et al. 2003; Ansari and Misra 2007; Elwood et al. 2009). These therapeutic substances for humans also play an important role in the plant kingdom. SA is characterized by a high metabolic and physiological activity, which performs regulatory functions in plant cells. For over twenty years, this compound has been under investigation for its role in the response of plants to various stress factors (Horv ath et al. 2007; San-Vincente and Plasencia 2011). Under optimal conditions SA content in leaves of *Arabidopsis*, tobacco, corn, and rape is lower than $0.1 \text{ }\mu\text{g}\cdot\text{g}^{-1}$ fresh mass.

Fig. 1 Structure of salicylic acid



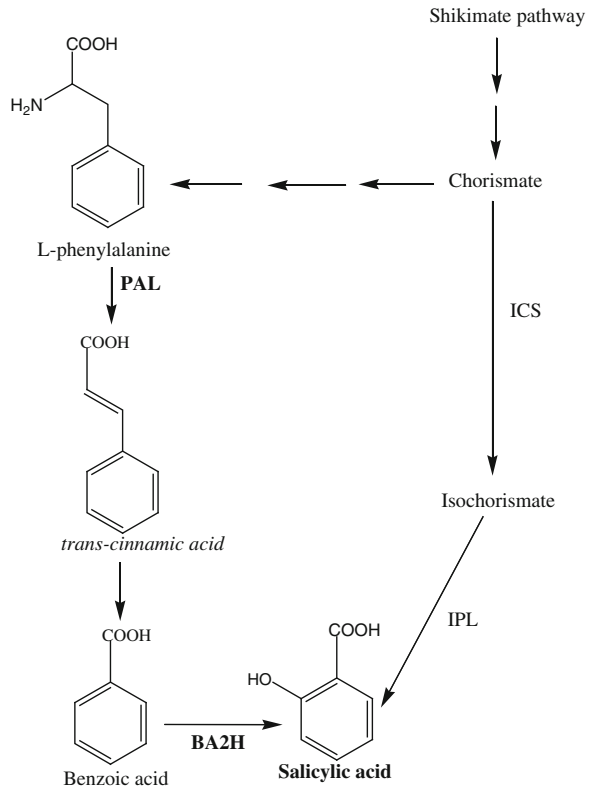
Higher SA levels were detected in leaves of tomato ($0.27 \mu\text{g}\cdot\text{g}^{-1}$ fr. mass), bean ($0.86 \mu\text{g}\cdot\text{g}^{-1}$ fr. mass), barley ($2.13 \mu\text{g}\cdot\text{g}^{-1}$ fr. mass) and the highest in rice, which varied from 5 to $30 \mu\text{g}\cdot\text{g}^{-1}$ fr. mass, depending on the cultivar (Raskin et al. 1990; Yang et al. 2004). The increased level of endogenous SA after pathogen infection, and its participation in plant responses to biotic stresses, has been confirmed in numerous studies and presented in several papers (Durner et al. 1997; Pieterse and Loon 1999; Metraux 2001; Shah 2003; Vlot et al. 2009). SA has also been recognized as a regulatory molecule, mediating plant responses to abiotic stress factors. The present work focuses on the results of studies examined the role of SA in the regulation of plant responses to water deficit.

2 Biosynthesis of Salicylic Acid and Accumulation Under Water Deficit Conditions

SA is synthesized in plants through two (Fig. 2) distinct enzymatic routes, which require chorismate as a primary metabolite (Wildermuth 2006; Chen et al. 2009). One is chloroplast-localized SA synthesis from chorismate via isochorismate in a two-step reaction catalyzed by isochorismate synthase (ICS) and isochorismate pyruvate lyase (IPL) (Wildermuth et al. 2001). It was shown that SA synthesized through the isochorismate route has an important role in plant defense against pathogen infection as well UV- or ozone-treated *Arabidopsis thaliana* L., *Nicotiana benthamiana* and tomato (Ogawa et al. 2005; An and Mou 2011). An alternative SA biosynthetic pathway is the phenylalanine route localized in the cytoplasm. Chorismate-derived phenylalanine (Phe) is converted to trans-cinnamic acid (t-CA) by phenylalanine ammonia lyase (PAL) and later t-CA is oxidized to benzoic acid (BA). The hydroxylation of the aromatic ring of BA catalyzed by benzoic-acid-2-hydroxylase (BA2H) leads to SA formation (Leon et al. 1993; Lee et al. 1995). This pathway was confirmed to operate in ozone-exposed tobacco leaves, heat-treated pea plants, and salt-stressed rice seedlings (Ogawa et al. 2005; Sawada et al. 2006; Pan et al. 2006). According to Chong et al. (2001) conversion of benzoic acid to SA requires the presence of hydrogen peroxide (H_2O_2), which stimulates the activity of BA2H. A number of studies have shown that water deficit induces an increase in the activity of PAL in leaves of wheat and white clover seedlings, and in fruits of pepper (Sung 2005; Tian and Lei 2007; Lee et al. 2007). Recently we examined the effect of water deficit on SA accumulation and the activity of two enzymes involved in the synthesis of SA from phenylalanine, i.e. PAL and BA2H. Moderate water deficit increased the activity of both enzymes and triggered an increase of SA level in leaves and roots of barley seedlings (Bandurska and Cieřlak 2012). So, these studies indicate that the cinnamic acid \rightarrow benzoic acid \rightarrow SA route is activated in plants exposed to water deficit.

Taking into account the presence in plant tissue of conjugated forms of SA and its precursors another possibility is that the release of free SA from conjugates

Fig. 2 Schematic diagram of SA biosynthetic pathways. Abbreviations: *PAL* phenylalanine ammonia lyase, *ICS* isochorismate synthase, *IPL* isochorismate pyruvate lyase, *BA2H* benzoic-acid-2-hydroxylase



takes place under water deficit conditions. This route may proceed via decarboxylation of conjugated forms of t-CA to conjugated forms of BA followed by its hydroxylation to salicyl-glucose ester and salicyl-CoA and then release of free SA, as was found in tobacco plants infected with mosaic virus (Lee et al. 1995; Chong et al. 2001).

3 Effect of Salicylic Acid on Plant Resistance to Water Deficit

Three experimental approaches are commonly used in studies focus on the role of SA in plant response to stress factors. One is to examine the stress resistance of plants treated with various concentrations of SA. Another approach is to study the effect of certain stress factors on the level of SA in plant tissues and its relationship with other biochemical and physiological parameters responsible for resistance. The third approach consists in testing the resistance of transgenic plants, which

have increased or decreased levels of SA, to a particular stress factors. Yang et al. (2004) revealed that SA-deficient transgenic rice exhibited increased susceptibility to oxidative stress and suggested that SA may play an important role in plant resistance to oxidative stress caused by biotic and abiotic stress agents. In the available literature there are no data with regard to transgenic plants having modified capacity for SA synthesis in terms of the role of this regulator in resistance to water deficit. However, we have shown that SA may play a role in the mechanism of *cross-resistance* in plants subjected to the combined action of UV-B and water deficit. UV-B applied before water deficit induced an increase of endogenous SA level in the leaves of barley seedlings and alleviated the damaging effect of water deficit on cell membranes and leaf hydration. This was evidenced by the lack of membrane damage as well as the lack of a decrease in leaf water content of plants pre-treated with UV-B before water deficit imposition, in spite of occurrence of such damage after the sole action of water deficit (Bandurska and Cieślak 2012).

In the studies related to the involvement of SA in plant responses to water deficit most of the investigations are concentrated on the impact of exogenous application of SA on plant resistance to stress. However, some research also focuses on the interplay between changes in the level of SA in water deficit treated plant and its resistance to water deficit.

3.1 Effect of Water Deficit on SA Level in Plant Tissues and Stress Resistance

The endogenous SA content increased in the leaves of drought-stressed Mediterranean plant, *Phillyrea angustifolia*. However, it was revealed that SA level showed a strong negative correlation with the level of leaf hydration (relative water content, RWC) and a positive correlation with α -tocopherol level during drought, which may indicate the possible involvement of SA in the regulation of water balance as well as activation of antioxidative mechanisms (Munné-Bosch and Peñuelas 2003). Water deficit induces leaf senescence, which is sometimes regarded as a negative consequence of stress. However, senescence of mature leaves permit nutrient remobilization to the youngest leaves, allowing plant survival during prolonged periods of drought (Munné-Bosch and Alegre 2004). It has been reported that drought stress induced SA accumulation in leaves of field-grown common sage plant (*Salvia officinalis*) that may regulate leaf senescence and plant survival under water deficit conditions (Abreu and Munné-Bosch 2008). Our results provide the first confirmation that water deficit effects a significant increase of SA content in barley seedlings. We have shown that polyethylene glycol-induced (PEG 6000) water deficit causes a significant increase of SA content in barley roots after 6 and 24 h of stress, where as in leaves SA level did

not change at this time (Bandurska and Stroński 2005). The results of our recent study revealed that water deficit of the same level but acting longer affected the increase of SA level both in leaves and roots of barley seedlings. However, an increase of SA content was first observed in roots (after 3 days) than in leaves (after 6 days), which indicates the involvement of SA in signal transduction between roots and leaves (Bandurska and Cieślak 2012). A significant increase of SA under the conditions of PEG-induced water deficit was also shown in leaves of soybean. The examined soybean plants had a higher SA level and were more resistant to water deficit at the reproductive than the vegetative stage (Hamayun et al. 2010).

3.2 Effects of Exogenous Application of SA on Plant Resistance to Water Deficit

Exogenous application of SA was found to be effective in modeling of plant metabolic and physiological processes that may enhance resistance to water deficit. SA application at various concentrations through roots, seed soaking and foliar spraying in a concentration-dependent manner alleviated the negative effect of water deficit on tissue water status, stomatal conductance, chlorophyll content, membrane properties and plants physiological activities (Horváth et al. 2007; Hayat et al. 2010). The application of SA in muskmelon, either through seed soaking or foliar application, provided protection against drought. Lower concentrations within the range of 0.1–0.5 mM were more effective in reducing the negative effect of drought than higher concentration (1 mM). The mode of application did not make any significant difference (Korkmaz et al. 2007). In cucumber, the application of SA by seed soaking or foliar spray ameliorated injury caused by water deficit. SA was more effective when applied by soaking the seeds and the best results were obtained using 0.5 mM SA solution (Baninasab 2010). However, application of SA (0.7 mM) in rice was more effective in ensuring better resistance to water deficit when applied by foliar spray than seed treatment (Farooq et al. 2009). Much higher SA concentrations used to the foliage were effective in protecting amaranth, tomato (3 mM) and *Satureja hortensis* (1.0–3.0 mM) plants against water stress (Umebese et al. 2009; Yazdanpanah et al. 2011). In wheat, a beneficial effect on improving resistance to water deficit was shown after leaf spraying with relatively high SA concentrations, i.e. 3.0 and 50 mM (Singh and Usha 2003; Aldesuquy et al. 2012). Foliar spraying with much lower SA concentration (1 μ M) alleviated the damaging effect of long term drought stress in *Ctenathe setosa* and maize providing increased resistance to stress (Kadioglu et al. 2011; Saruhan et al. 2012). Increased resistance to drought in bean was obtained similarly as in cucumber by soaking seeds in 0.5 mM SA concentration before sowing (Sadeghipour and Aghaei 2012). Seedlings of four chickpea genotypes

became more resistant to drought when their seeds were soaked in 1.0–1.5 mM SA solution (Patel et al. 2011). Seed soaking in much lower SA concentrations was effective in amelioration the negative impact of drought on soybean (0.6 mM) and wheat (0.01–0.05 mM) (Sakhabutdinova et al. 2003; Khan et al. 2012). Bean and tomato seedlings grown from seeds imbibed in 0.1–0.5 mM solutions of SA or the plants which were soil drenched with 0.5 mM solution of SA did not exhibit signs of wilting (Senaratana et al. 2000). There is some evidence that application of SA through roots by mixing with the nutrient solution improved drought resistance. Increased resistance to water deficit was achieved in tomato at 0.01 mM SA concentration and lower, in wheat 0.3–0.7 mM, barley 0.3–0.12 μ M, potato 0.1 mM and in banana 1.0–3.0 mM (Bandurska and Stroinski 2005; Szepesi et al. 2005; Waseem et al. 2006; Deneshmand et al. 2009; Bidabadi et al. 2012).

3.3 Mode of Action of SA in Increasing Resistance to Water Deficit

SA applied exogenously with various methods and concentrations (0.1–10 mM) activates protective mechanisms enhancing resistance to water deficit. It was found that SA improves leaf water status under water deficit conditions (Raskin 1992; Senaratana et al. 2000; Szepesi et al. 2005; Hussain et al. 2009; Bidabadi 2012; Sadeghipour and Aghaei 2012). Some authors reported that foliar application of SA plays a positive regulatory role in stomatal closure and proposed that SA might support the ABA dependent mechanism of stomatal closure. SA application induces production of reactive oxygen species (ROS) via peroxidase-catalyzed reaction, which may lead to the elevation of cytosolic Ca^{2+} and NO production causing stomatal closure (Manthe et al. 1992; Mori et al. 2001; Acharya and Assman 2009). On the other hand, it was shown that exogenous application of SA by seed soaking diminished the reduction of stomatal conductance induced by water deficit (Sadeghipour and Aghaei 2012). Other researchers have revealed that the decrease of stomatal conductance under drought was lower in SA-treated (applied to roots/leaves) than untreated plants (Waseem et al. 2006; Saruhan et al. 2012). The above results are consistent with the findings of Rai et al. (1986), who found that SA application reversed the stomatal closure induced by ABA. However, it appears that the influence of SA on stomatal conductivity may depend among other things on its concentration, the mode of application, duration of treatment, species and physiological state of the plant.

The results of available studies indicate that better leaf hydration under water deficit conditions as a result of SA pre-treatment is not necessarily the effect of stomatal closure. Indeed, in many cases, application of SA did not lead to reduction of stomatal conductance, under water deficit despite a marked influence on improving leaf water status (Singh and Usha 2003; Sadeghipour and Aghaei

2012; Saruhan et al. 2012). Plant resistance to water deficit may be the result of two strategies responsible for surviving the stress: strategy of avoiding dehydration and strategy of tolerance dehydration (Levitt 1980). In the strategy of avoiding dehydration an important role is played by osmotic adjustment involving the accumulation of osmolytes, which lower cell water potential to prevent dehydration (Farooq et al. 2010). The protective action of SA during water deficit in many plants was demonstrated by the accumulation of different osmolytes such as sugars, sugar alcohol and proline, responsible for osmotic adjustment (Szepesi et al. 2005; Umebese et al. 2009; Farooq et al. 2010, Bidabadi et al. 2012). The improvement of leaf water status under water deficit through preventing dehydration of leaves as a result of osmotic adjustment as well the restriction of reduction stomatal conductance by the application of SA plays a positive role in maintaining photosynthetic activity and reducing damage. Closure of the stomatal aperture prevents water loss, but it also limits the uptake of carbon dioxide and influences on the decrease of photosynthetic rate, which exerts a harmful effect on the growth and productivity of plants (Pinheiro and Chaves 2011). Moreover, the limitation of CO₂ assimilation may affect the accumulation of ROS and H₂O₂ because the reductive power (NADPH) developed in the light phase of photosynthesis is not utilized in the phase, independent of light (Jaspers and Kangasjärvi 2010; Miller et al. 2010; Gill and Tuteja 2010). Plant pre-treatment with 0.5 mM SA, one day before water deficit imposition increased sensitivity to drought because it caused a decrease of stomatal conductance and net rate of photosynthesis and increased damage of cell membranes (Németh et al. 2002). Moreover, Borsani et al. (2001) found that SA application enhanced the generation of ROS in leaves of *Arabidopsis thaliana* and increased development of stress symptoms under water deficit conditions. However, SA reduced the damage of cell membranes in cucumber, rice, wheat, barley, *Satureja hortensis*, banana and maize, exposed to water deficit (Bandurska and Stroński 2005; Baninasab 2010; Farooq et al. 2010; Bidabadi et al. 2012; Saruhan et al. 2012; Yazdanpanah et al. 2011). SA ameliorates the water deficit induced injuries by increasing proline content which protects cell membranes against the harmful effects of ROS (Bandurska and Stroński 2005; Baninasab 2010). The alleviating effect of SA on cell membrane functioning under water deficit conditions can also be associated with the activation of the synthesis of soluble phenolics and anthocyanins, which protect leaf tissue from oxidative damage (Farooq et al. 2010). The application of exogenous SA may also alleviate the damaging effect of water deficit by up-regulation the activity of antioxidant system. The increased activity of antioxidant enzymes with simultaneous reduction in H₂O₂ production and lipid peroxidation level was noted under water deficit conditions in plants pre-treated with SA, at various concentrations through root, seed soaking or foliar spray (Horváth et al. 2007; Korkmaz et al. 2007; Daneshmand et al. 2009, Farooq et al. 2010; Kadioglu et al. 2011; Bidabadi et al. 2012; Saruhan et al. 2012).

3.4 Role of SA in Improving Plant (Crop) Performance and Yields Under Drought Conditions

SA-induced activation of the mechanisms responsible for reducing the damage caused by water deficit and maintenance of normal metabolism plays an essential role in countering the damaging effects of stress on growth and yield (Fig. 3). In muskmelon, the moderating influence of SA on cell membrane permeability under water deficit conditions resulted in the reduction of adverse effect of water stress on leaf chlorophyll level, stomatal conductivity and photosynthetic productivity (Korkmaz et al. 2007). The ability of SA to negate adverse effects of water deficit on cell metabolism had a significant implication in improving growth of wheat under drought conditions. High chlorophyll content and photosynthetic rate coupled with higher activity of Rubisco were responsible for SA-induced improvement of dry matter accumulation and yield under drought (Singh and Usha 2003). Azooz and Youssel (2010) revealed that SA-induced resistance to drought in ‘Hassawi’ wheat resulted from its stimulatory effect on the synthesis of soluble carbohydrates and proteins, which are involved in osmotic adjustment, which causes the reduction of adverse effect of water deficit on plants. As a result, there was observed a marked improvement of water status, enhancement of the biosynthesis of photosynthetically active pigments as well as photosynthetic rate and finally stimulation of growth. In other studies conducted on wheat the protective and growth promoting effects of SA treatment were due to its influence on preventing the decrease in IAA and cytokinin content induced by water deficit (Sakhabutdinova et al. 2003). SA treatment elicited drought resistance in wheat through a mechanism of osmotic adjustment and reduction of membrane injury,

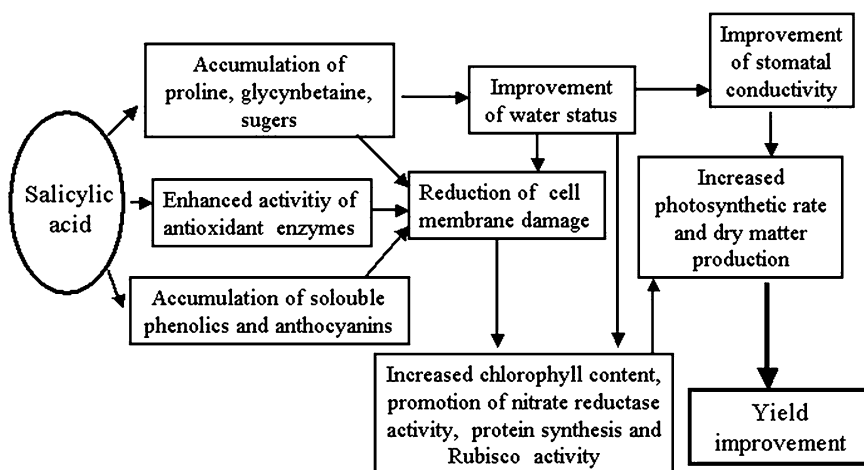


Fig. 3 Schematic model presents the role of SA in the enhancement of plant resistance to water deficit

which improved the yield under stress conditions (Khan et al. 2012). Application of SA enhanced the productivity and yield components of sensitive and tolerant wheat cultivars, grown under water deficit conditions. The effect resulted from the influence of SA on the accumulation of proline, which could act as an osmolyte as well as ROS scavenger (Aldesuquy et al. 2012). SA pre-treatment showed a significant increase on yield and yield components in common bean under water deficit conditions. This impact was associated with the improvement of leaf water status by the activation of osmotic adjustment mechanism, increase of stomatal conductance, and a stimulatory effect on photosynthetic pigment biosynthesis as well as net photosynthetic rate (Sadeghipour et al. 2012). In *Amaranthus* and tomato SA-induced resistance to drought that was caused by increased proline production, which increases the capacity to absorb water from soil and reduces tissue dehydration, enhances nitrate reductase activity and promotes growth of plants under water deficit conditions (Umebese et al. 2009). Exogenous application of SA improved growth and biological yield of sunflower grown under water deficit conditions because of the maintenance of assimilatory surface due to high RWC, which sustained leaf photosynthetic activity (Hussain et al. 2009).

4 Conclusions

From the results presented here it is clear that SA may play a beneficial role in plant response to water deficit stress. Some authors link SA accumulation under water deficit conditions and after pre-treatment with UV-B radiation with amelioration of the damaging effect of water deficit on tissue water status and cell metabolism. Moreover, a body of evidences have revealed that exogenously applied SA effectively protects plants against water deficit induced oxidative stress, membrane injuries, tissue dehydration and metabolic disturbances, which improves plant growth and yield under drought. It seems that SA could be used as a potential growth regulator for improving crop yield under limited soil water availability. The best results were obtained by using a concentration range from 0.5 to 1.0 mM SA and the most convenient method of treatment seems to be pre-sowing seed soaking in the solution of SA. However, further studies are required to fix the most effective SA concentration, the site of application and time of treatment for each crop. In addition, to better understand the specific role of SA in the regulation of plant metabolism under water deficit conditions there are necessary research with mutants producing high levels of SA or mutants with repression of the SA biosynthetic pathway.

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Chapter 2

Salicylic Acid: Physiological Roles in Plants

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Abstract Since ancient times, salicylic acid has been in use by humans because of its therapeutic properties. Salicylic acid, chemically known as 2-hydroxy benzoic acid is one of a diverse group of phenolic compounds, consisting of an aromatic ring bearing a hydroxyl group or its functional derivative, which is synthesized by plants. Salicylic acid biosynthetic pathway in plants has two distinct pathways, the isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway. Moreover, salicylic acid plays exclusive role in plant growth, thermogenesis, flower induction and uptake of ions. It affects ethylene biosynthesis, stomatal movement and also reverses the effects of ABA on leaf abscission. In addition to this, it also enhances the level of photosynthetic pigments, photosynthetic rate and modifies the activity of some of the important enzymes as well. This chapter provides the reader with a comprehensive coverage to above aspects more exclusively with future prospects.

Keywords Growth · Photosynthesis · Salicylic acid · Senescence · Yield

1 Introduction

Since ancient times, plants and their extracts have been used for their therapeutic properties. World Health Organization estimated that approximately 75–80 % of the world's population uses plant medicines either in part or entirely. Ancient

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