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Recent Breakthroughs in the Study of Salicylic Acid Biosynthesis under Changing Environment: A Review

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Abstract: Salicylic acid, a naturally occurring plant hormone of phenolic nature acting as an important signaling molecule adds to tolerance against abiotic stresses (such as heavy metals, ozone, UV-B radiation, high salinity, low/high temperatures, and water stress). These stresses induce various adverse effects in plants, impair biochemical/ physiological and molecular processes, and ultimately cause reductions in plant growth, development and overall bio-productivity. SA is also involved in endogenous signaling to trigger plant defense against biotic stresses including bacteria, virus and fungi. This positive effect of SA could be attributed to an increased CO₂ assimilation and photosynthetic rate, membrane permeability, inhibition of ethylene biosynthesis processes and increased mineral uptake by the stressed plant under the application of SA. This chapter provides a review of the critically appraises the role of SA in plants exposed to major abiotic, biotic and their interaction and also possible mechanisms for abiotic stress responses controlled by SA will be discussed.

Recent results show that not only does exogenous SA application moderate stress effects, but abiotic stress factors may also alter the endogenous SA levels in the plant cells. This review compares the roles of SA during different abiotic stresses.

We also describe recent successes in identifying the roles of phytohormones under stressful conditions. We conclude by describing the recent progress and future prospects including limitations and challenges of phytohormone engineering for inducing abiotic stress tolerance in crop plants.

Keywords: Salicylic acid; Abiotic stress; Biotic stress; Interaction of biotic and abiotic stress; antioxidant system; plants

Salicylic acid, a naturally occurring plant hormone of phenolic nature acting as an important signaling molecule adds to tolerance against abiotic stresses (such as heavy metals toxicity, ozone, UV-B radiation, high salinity, drought and low/high temperature). These stresses induce various adverse effects in plants, impair biochemical/ physiological and molecular processes and ultimately cause reductions in plant growth, development and overall bio-production. SA is also involved in endogenous signaling to trigger plant defense against biotic stresses including bacteria, virus and fungi. This positive effect of SA could be attributed to an increased CO₂ assimilation and photosynthetic rate, membrane permeability, inhibition of ethylene biosynthesis processes and increased mineral uptake by the stressed plant under the application of SA. Recent results strongly suggest that not only does exogenous SA treatment moderate stress effects, but abiotic stress factors may also alter the endogenous SA levels in the plant cells. This review also conclude by describing the recent progress and future prospects including limitations and challenges of phytohormone engineering for inducing abiotic stress tolerance in crop plants also possible mechanisms for abiotic stress responses controlled by SA will be discussed.

Abbreviations: APX, Ascorbate peroxidase; CAT, Catalase; DHAR, Dehydroascorbate reductase; ETC, Electron transport content; GB, Glycinebetaine GR, Glutathione reductase; ICS, isochorismate synthase; MDHAR, Monodehydroascorbate reductase; NPQ, Non-photochemical quenching; OEC, Oxygen evolving complex; POD, Peroxidase; PQ, Plastoquinone; PAL, Phenylalanine ammonia lyase; ROS, Reactive oxygen species; RWC, Relative water content; SA, Salicylic acid; SAR, System acquired resistance; SOD, Superoxide dismutase

I. INTRODUCTION

Plants can activate defense responses to protect themselves against abiotic stresses and herbivorous insects. These defense responses are inflected by the induced production of a hormonal blend in the plant. The plant hormones salicylic acid (SA) is an important regulator of induced defense mechanisms (Pieterse *et al.*, 2012) against environmental stresses. It is an ortho-hydroxyl benzoic acid of phenolic nature which is ubiquitously distributed in whole plant kingdom (Hayat *et al.*, 2010). The word salicylic acid was derived from a Latin word "Salix". It is obtained from the bark of the willow tree and it was first discovered by Rafacle Piria in

1938, by fusing salicylic aldehyde with potassium hydroxide. Generally, it is characterized in 36 plants, belonging to diverse groups (Raskin et al., 1990). The leaves of 27 thermogenic species and floral parts of seven species exhibited substantial variation in the level of SA (Raskin et al., 1990). Studies over the last few decades have shown that SA has most important regulatory functions in the plants. Naturally, it is present in plants in small quantity ($\mu\text{g/g}$) fresh weight or less (Raskin et al., 1990), either in a free state or in the form of glycosylated, methylated, glucose-ester or amino acid conjugates (Lee et al., 1995). However, in Free state, it is found in a crystalline powder form having a 157-159°C melting point and pH of 2.4. SA is considered to be an important signaling mediates molecule response to abiotic stresses such as heavy metal (Zhang et al., 2015), salinity (Singh et al., 2015), drought (Fayez and Bazaid, 2014), combination of drought and salinity (Chauhan et al., 2015), osmotic (Jafari et al., 2015), and heat stress (Khan et al., 2013b). Kumar, (2014) stated that apart from its involvement in the induction of defense-related abiotic stresses and stress tolerance in also biotic stressed plants. Exogenously SA is applied to stressed plants, either through seed priming, adding to the nutrient solution, irrigating or foliar spraying was addressed to induce major abiotic stress tolerance-mechanisms (Khan et al., 2014). SA is a well-known plant growth regulator for plant immunity and SAR (systemic acquired resistance). It is well proved that it has a regulatory effect on activating biochemical pathways associated with tolerance mechanisms in plants. Further, its role is evident in seed germination, vegetative growth, photosynthesis, fruit yield, glycolysis, flowering in thermogenic plants, stomatal conductance and transpiration (Chauhan et al., 2015; Hayat et al., 2010). However, seed production and especially seed quality of the crops are greatly influenced by SA addition, which may also induce senescence and a kind of cell death that is not associated with the hypersensitive response (Hayat et al., 2010; Rivas San Vicente and Plasencia, 2011). It is well known that how plants synthesize SA has been studied for almost half a century. According to Ribnicky et al. (1998) biochemical studies suggest that SA is synthesized from phenylalanine with benzoate as the immediate precursor. On the other hand, Serino et al. (1995) indicated in the genetic analysis that the bulk (>90%) of SA is synthesized from isochorismate. While the role of plant isochorismate syntheses in SA production has been well documented, plant enzymes that convert isochorismate to SA have not been recognized. Thus, how SA is synthesized in plants is still not fully defined. In the current effort, in addition to overviews historical background, biosynthesis and metabolism of SA in plants under both optimal and stressful conditions, the role of SA in plants exposed to major abiotic stress conditions and the effect of SA on various components of photosynthetic machinery in plants under abiotic stress conditions is critically discussed. Here the effect of the interaction of abiotic and biotic stress in plants is also reviewed with an emphasis on elucidating the molecular mechanisms involved.

II. BIOSYNTHETIC PATHWAYS IN PLANTS AND METABOLISM

The importance of SA as a signal for abiotic stress tolerance has stimulated considerable interest in its biosynthesis. In the early 1960s, it was suggested that SA is synthesized in plants from cinnamic acid by two possible pathways. One pathway that involves biochemical studies using isotope feeding have suggested that the plants synthesize SA from cinnamate produced by phenylalanine ammonia lyase (PAL) (Fig. 1). Phenylalanine is converted into cinnamic acid by phenylalanine ammonia lyase. SA can be formed from cinnamate via ortho-coumarate or benzoate depending on whether the hydroxylation of the aromatic ring takes place before or after the chain-shortening reactions that is shown in figure. Alternatively, the side chain of cinnamic acid is initially oxidized to give benzoic acid, which is then hydroxylated in the ortho position (Sticher et al., 1997). It has been well reported by many researchers that in tobacco, SA was first proposed to be synthesized from free benzoic acid, but later results indicated that benzoyl glucose, a conjugated form of benzoic acid, is more likely to be the direct precursor of SA (Yalpani et al., 1993; Chong et al., 2001). Klambt et al. (1962) has also reported that in sunflower, potato and pea, isotope feeding shows that SA was formed from benzoate, which is synthesized by cinnamate chain shortening reactions most likely through a β -oxidation process analogous to fatty acid β -oxidation. Cinnamic acid-derived synthesis of SA also takes place in cucumber, potato and rice (Sticher et al., (1997). Another pathway, SA biosynthesis in plants has been addressed from shikimic acid via chorismic acid and comaric acid (Horváth et al., 2007; An and Mou, 2011)(Fig. 1). This pathway takes part in the biosynthesis of most plant phenolic compounds. Herrmann and Weaver, (1999) reported that the shikimic acid pathway simply converts simple carbohydrate precursors derived from glycolysis and pentose phosphate pathways to the aromatic amino acids including SA precursor, phenylalanine.

Various abiotic stress factors have been proven to modulate major enzymes involved in plant-SA biosynthesis. Overproduction of SA via enhanced activity of SA biosynthetic pathway enzymes (mainly isochorismate synthase, ICS; PAL) in plants help in their defense against abiotic stresses. These enzymes are key regulators of SA functions and are known to be modulated by different abiotic and biotic stress factors. Popova et al. (1997) well documented that SA has got a property of forming conjugates with a variety of molecules either by glycosylation or by esterification. Further Tanaka *et al.* (1990) stated that conjugated form of SA as-glucoside-SA was reported in suspension cultures of *Mellotus japonicas* and also in the roots of *Avena sativa* seedlings (Yalpani et

al., 1993). Further he stated that the enzyme that catalyzes the metabolism of SA to -glucoside-SA was identified and named as SA glucosyltransferase (Gtase). Billek and Schmook, (1967) stated that SA may also be metabolized to 2,3-dihydrobenzoic acid or 2,5-dihydrobenzoic acid as was recognized in the leaves of *Astilbesinensis* and *Lycopersicon esculentum* after administering the radiolabel edcinnamic acid or benzoic acid.

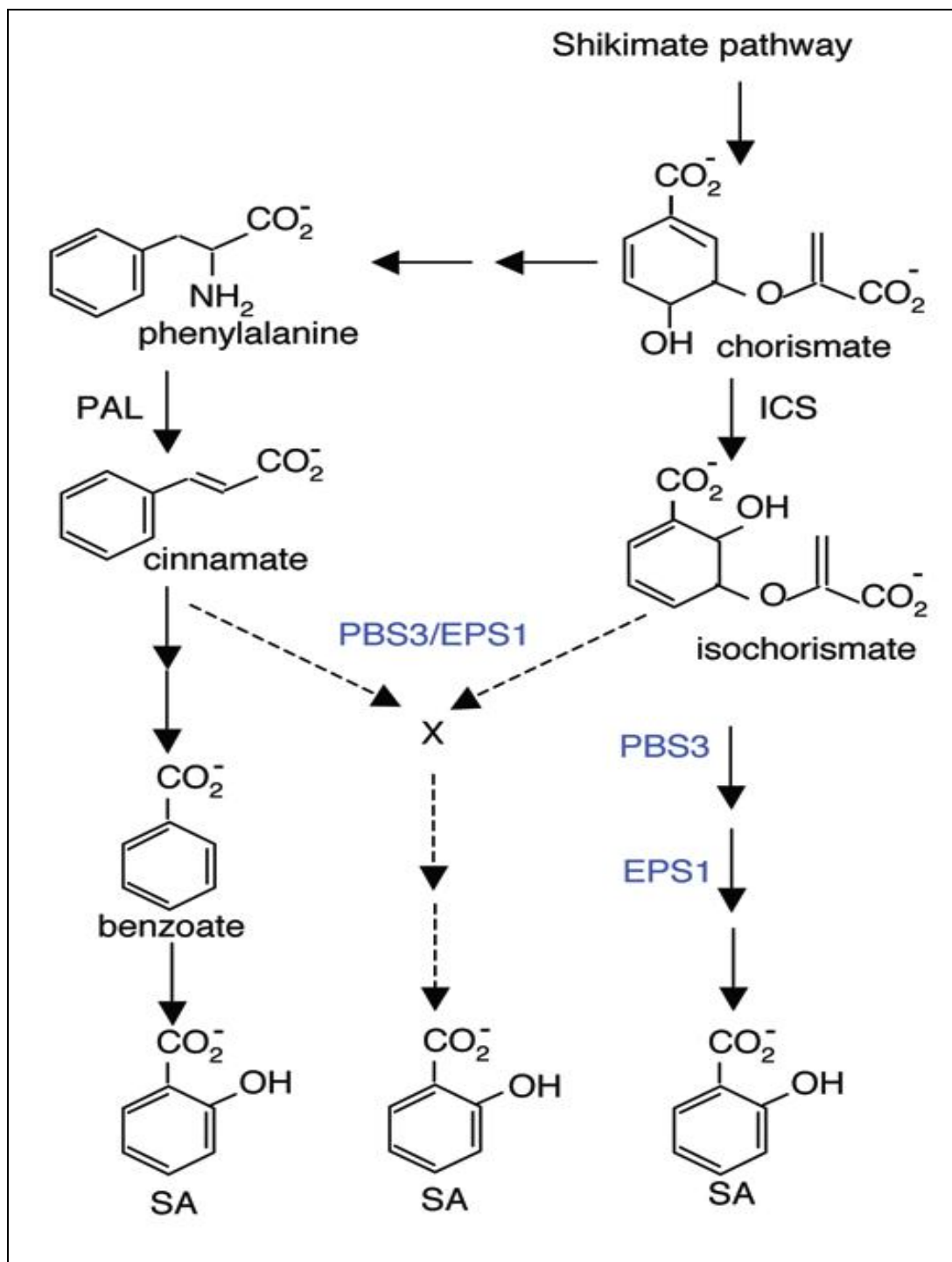


Fig 1. A model of Salicylic acid (SA) biosynthesis pathway in plants. Isotope feeding experiments suggest that simply plants synthesize SA from cinnamate produced by phenylalanine ammonia lyase (PAL). Given the importance of both PAL and ICS(isochorismate synthase) in SA accumulation demonstrated from experiments using genetic mutants, gene silencing and chemical inhibition, it is possible that the PAL and ICS pathways are integrated through a metabolic or regulatory grid in SA biosynthesis.

A. Genetic studies of the Salicylic acid biosynthetic pathways in *Arabidopsis thaliana*

SA induces the accumulation of pathogenesis-related (PR) proteins in a variety of plants. SA biosynthesis was initially studied biochemically in tobacco leaves and a benzoic acid-dependent route has been discovered. Recently, work using *Arabidopsis thaliana* mutants suggested that the isochorismate-dependent pathway is likely to be predominant in this species, which has been established for SA biosynthesis in some bacteria genera. *Arabidopsis thaliana* generates SA locally and systemically after pathogen infection and develops SA-dependent SAR Summermatter et al., (1995). It also contains two ICS genes: ICS1 also known as SID2 and ICS2 (Wildermuth et al., 2001). Wildermuth et al., (2001) suggested that the presence of a plastid transit peptide and cleavage site in the ICS1 gene indicates plastid localized synthesis of SA and provides support for the idea that the SA pathway in *Arabidopsis thaliana* might derive evolutionarily from prokaryotic endosymbionts.

The remaining levels of SA in pathogen induced ICS1 mutants might be synthesized by ICS2 or through another pathway. To check out these possibilities, Garcion et al. (2008) have investigated ICS1 and ICS2 double mutant plants and compared them with the *ics1* single mutant plants for UV-induced SA accumulation. The result obtained that Upon UV exposure; the *ics1* mutant accumulated roughly 10% and the *ICS1*, *ICS2* double mutant accumulated about 4% of total SA compared to the wild type.

Table (1). Salicylic acid (SA) – hormone synthetic pathways and genes in *Arabidopsis thaliana*

| Gene name | Locus name | Description |
|-----------|------------|--|
| ICS1/SID2 | At1g74710 | Isochorismate synthase |
| ICS2 | At1g18870 | Isochorismate synthase |
| BSMT1 | At3g11480 | Benzoic acid/salicylic acid carboxyl methyltransferase |
| UGT74F1 | At2g43840 | Salicylic acid glucosyltransferase |
| UGT74F2 | At2g43820 | Salicylic acid glucosyltransferase |
| AtMES1 | At2g23620 | Methyl salicylate esters |
| AtMES2 | At2g23600 | Methyl salicylate esterase |
| AtMES7 | At2g23560 | Methyl salicylate esterase |
| AtMES9 | At4g37150 | Methyl salicylate esterase |

B. Effect Of Exogenous Salicylic Acid On Plant Growth And Bio-Productivity

In nature, plants often face the problem of various environmental conditions, which include various abiotic stresses that exert adverse effects on plant growth and development ultimately causing considerable losses in the crop productivity. According to Hung et al. (2005) the severity of stress depends on numerous intrinsic (e.g. cultivar) and extrinsic (e.g. the fluctuation of temperature, duration of exposure, the water scarcity of soil, drought, salinity or sometimes both and the intensity of light) factors. Meanwhile, Chauhan et al. (2015); Sanadhya et al.(2012) mentioned that the water deficit and salinity are a major factor of environmental stresses and both are a key determinant of crop productivity. Since, the amount and rate of the uptake of water and nutrients are decreased by these stresses consequently photosynthetic, physiological and biochemical activities are impaired (Li et al., 2014). To combat these impaired activities, SA and other salicylates are known to affect various physiological and biochemical responses of plants and may play a key role in regulating their growth and productivity (Orabi et al., 2015) and this actual role in abiotic stresses remains unresolved. SA and its close analogues enhanced the leaf area and dry mass production in *Lycopersicon esculentum* under salt stress (Arbaoui et al., 2015). Enhanced germination and seedling growth were recorded by Anaya et al. (2015) in *Vicia faba* under salinity, when the grains were subjected to pre-sowing seed-soaking treatment in SA. Growth and photosynthetic parameters

were significantly enhanced in *Brassica juncea*, when lower concentrations of SA were applied under cadmium stress; however, higher concentrations of SA had an inhibitory effect (Hayat et al., 2014).

When plants are stressed, they produce stress substances that manage gene expression to get adapt to the stress conditions, the main stress substances include reactive oxygen species, nitric acid, jasmonic acid, SA, ethylene, and abscisic acid (Liu and Zhang, 2004; Hey et al., 2010; Jaspers and Kangasjarvi, 2010). Among these stress substances, SA and ethylene have been addressed to activate flowering sensation in many crops. Flowering is another important parameter that is directly related to productivity of crops. According to Martin-Mex et al. (2005) the different plant species, including ornamental plant *Sinningia speciosa* flowered much earlier as compared to the untreated control, when they treated an exogenous foliar spray of SA. Promising result was obtained when plants of *Carica papaya* were supplemented with SA, which showed significantly higher fruit setting (Herrera-Tuz, 2004). Thus, it may be concluded that the presence of SA acts as an endogenous regulator that probably affects the growth and productivity in plants.

C. Effect Of Salicylic Acid On Various Components Of Photosynthetic Machinery In Plants Under Abiotic Stress

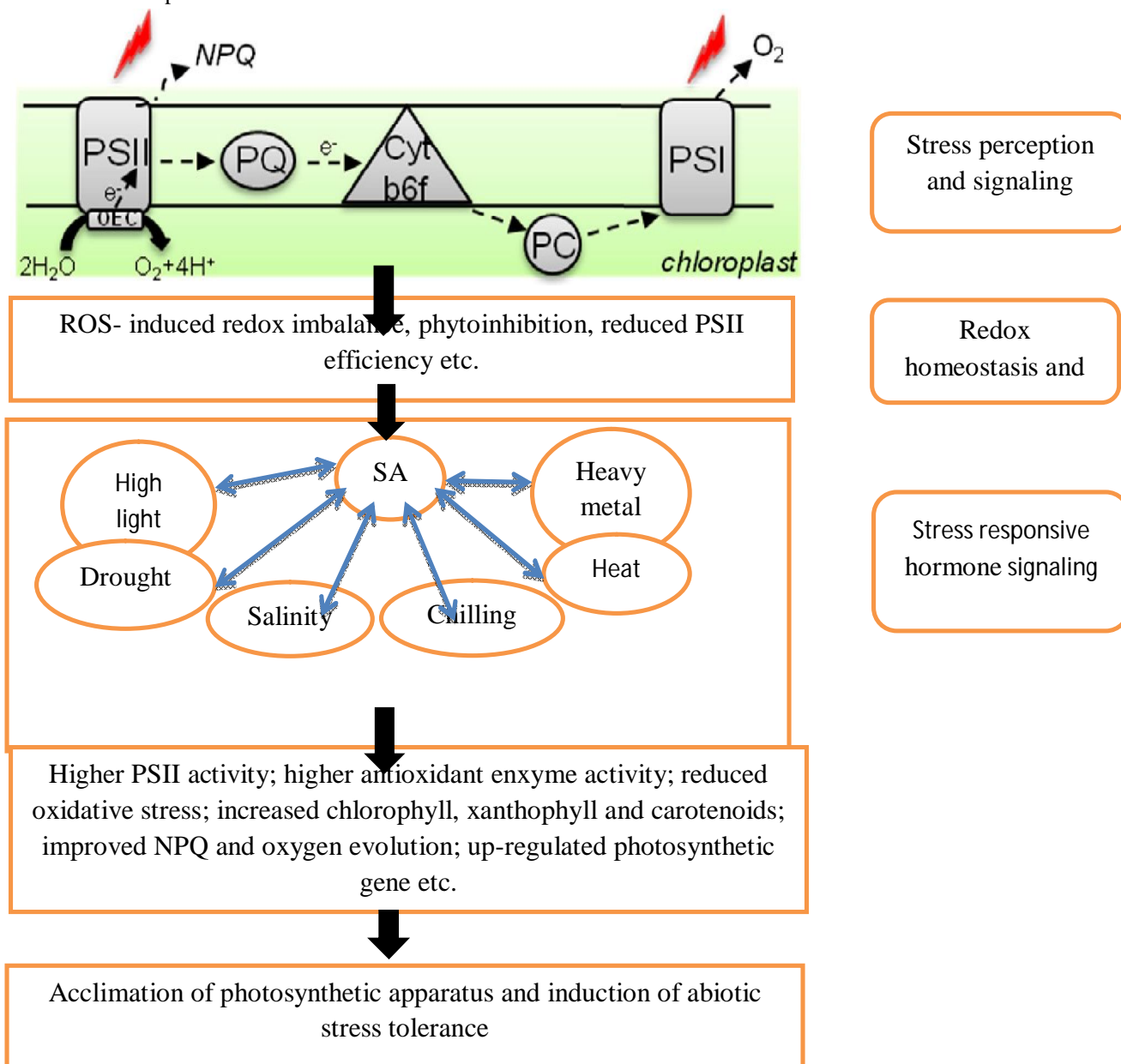
It is a well-documented fact that SA potentially produces a wide array of metabolic responses in plants and also affects the photosynthetic pigments (chlorophyll and carotenoids) and plant water relations (RWC). Ghasemzadeh and Jaafar, (2012) has reported while working with ginger that foliar supplementation of SA enhances biomass production, photosynthetic pigments, and also photosynthetic rate. Photosynthesis is one of the most sensitive processes that gets severely influenced by the onset of abiotic stress. Takahashi and Badger, (2011) reported that abiotic stress results in the over-reduction of the electron transport chain (ETC) which, in turn, leads to photo-oxidation. In order to survive under these stressful conditions, plants go through a mechanism where excessively absorbed light energy is transferred into thermal energy and an optimal rate of electron transport is achieved. Many researchers have suggested that the process of dissipation of excess energy in the form of heat is commonly referred to as non-photochemical quenching (NPQ) that is shown in figure (2) (Nath et al., 2013; Gururani et al., 2015). The photo system II (PSII) protein complex is the most vulnerable component of the photosynthetic machinery to various environmental stresses. In fact photo damage to the PSII complex is a process in all photosynthetic organisms; further Murata et al. (2007) stated that, these organisms have developed a process to prohibit the over-accumulation of damaged PSII complex by recovering the damaged PSII via the PSII repairing system. Thereafter, recently, the PSII damage repair mechanism has gained a lot of attention among researchers. The following given table(2) summarizes and evaluates the understanding of the influence of SA on the photosynthetic machinery under abiotic stress conditions.

Table (2). Recent studies on Salicylic acid (SA) reported to affect various components of photosynthetic machinery in different plants under abiotic stress conditions.

| Plant | Stress | Effect on photosynthetic components | Reference |
|-----------------------------|------------------|--|--------------------------|
| <i>Arabidopsis thaliana</i> | Drought | Higher PN, maximum efficiency of PSII, and maximum quantum yield of PSII | He et al., 2014 |
| Wheat | High salinity | Increased quantum yield of PSII | Arfan et al., 2007 |
| Wheat | Heat, high light | Improved PSII efficiency, slower degradation and accelerated recovery of damaged D1 protein | Zhao et al., 2011 |
| Wheat | Drought | Upregulated expression of luminal, oxygen-evolving enhancer, and PSII assembly factor proteins | Kang et al., 2012 |
| Rice | Drought | Higher PN, stomatal conductance, and transpiration rate | Li et al., 2012 |
| Mustard | High salinity | Improved PN, stomatal conductance, and water use efficiency | Yusuf et al., 2008 |
| Mustard | High salinity | Improved PSII efficiency, PN, Rubisco activity, water-use efficiency, and stomatal conductance | Nazar et al., 2015 |
| Cotton | High salinity | Increased PSII activity, PN and transpiration rate | Liu et al., 2014 |
| Maize | High salinity | Increased PN and Rubisco activity | Moussa and Khodari, 2004 |
| Grapevine | Heat | Improved PN, chlorophyll a fluorescence, higher stomatal conductance | Wang and Li, 2007 |
| Grapevine | Heat | Improved PN, enhanced Rubisco and PSII activities | Wang et al., 2010 |
| Tomato | Drought | Higher PN, stomatal conductance | Hayat et al., 2008 |

| | | | |
|----------------|---------------|--|-----------------------------|
| Common sage | Drought | Maintenance of maximum efficiency of PSII and protection of photosynthetic apparatus | Abreu and Munne-Bosch, 2008 |
| Torreyagrandis | High salinity | Increased PN | Li et al., 2014 |

Figure (2) shows the abiotic stress factors; mainly target the photosynthetic reaction centers, photosystem I (PSI) and photosystem II (PSII). Whereas, PSII is the most susceptible reaction center as it is included in the water-splitting process of photosynthesis where water is converted to oxygen and protons through the oxygen-evolving complex (OEC) and the electrons (e^-) are released and also converted to the PSI complex via plastoquinone (PQ), cytochrome b6f complex (Cytb6f), plastocyanin (PC), and several other intermediary molecules. Under environmental stress conditions, plants dissipate the excess energy in the form of heat through the light-harvesting antenna molecules and this phenomenon is known as non-photochemical quenching (NPQ). Abiotic stress-induced photo inhibition creates a redox imbalance and reactive oxygen species (ROS) molecules are generated that are highly detrimental to the plant cells. In addition, ROS molecules prevent the PSII damage-repair process. With the onset of environmental stress in plants, the phytohormone (SA) signaling also gets altered and the endogenous levels of these hormones change according to the intensity and duration of specific stress.



D. *The Relationship Of Salicylic Acid With Antioxidant System And Its Impact On The Plants Exposed To Abiotic Stress*

Abiotic stress conditions such as drought, salinity, heat and chilling favor the accumulation of reactive oxygen species (ROS) such as superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH^{\bullet}) and cause oxidative stress (Panda et al., 2003a). These reactive molecules increased ROS level in plants causing oxidative damage to biomolecules such as lipids, proteins and nucleic acids, thus alters the redox homeostasis (Gille and Singler, 1995). The SA was found to enhance the activities of antioxidant enzymes, Catalase (CAT), Peroxidase (POX) and Superoxide dismutase (SOD), when sprayed exogenously to the drought stressed plants of *B. juncea* (Alam et al., 2013) or to the salinity stressed plants of *B. juncea* (Yusuf et al., 2008). Alam et al. (2013) observed in *Brassica juncea* plants that The priming of seeds with lower concentrations of SA, before sowing, lowered the elevated levels of ROS due to drought exposure and also enhanced the activities of various antioxidant enzymes (CAT, MDHAR, DHAR, GR, GPX and SOD). Generally, abiotic stress caused a marked increase in lipid peroxidation (MDA content), while exogenous SA treatment prevented lipid peroxidation at any level of stress. It was due to the prevention of membrane damage and induction of antioxidant responses by SA, thereby protects the plants from oxidative burst.

E. *Effect Of Salicylic Acid On Various Abiotic Stresses*

Beside plant protection, SA is involved in the response to environmental stresses. However, the actual role of SA in abiotic stresses remains unresolved. Generally, deficiency of SA or a very high level of SA increases plant susceptibility to abiotic stresses. The optimal concentration (0.1 mM to 0.5 mM for most plants) improves abiotic stress tolerance. Because SA is also involved in redox regulation, a high concentration of SA may decrease stress tolerance. The relationship between SA and each abiotic stress is discussed.

F. *Heavy Metal Stress*

Heavy metals-accrued stress has become a subject of great concern to sustainable farming and environmental system. These are released from multiple pathways, including industrial effluents, burning liquid and solid fuel, urban runoff, sewage waste disposal, agricultural toxic chemicals run-off, volcanic activities and domestic garbage dump etc. These sources of heavy metals constitute major problems in cultivation, agriculture, husbandry, and forestry because of their toxicity. Heavy metals (Cd, Zn, Cr, Pb, Al, Hg, Ni, etc.) lead to the enrichment of the farming soil in terms of toxic metals. However, accumulation of cadmium and lead in the agricultural soil and the environment poses a gradually increasing danger for almost all kinds of organisms, including plants and human beings. Heavy metal induced serious visible and metabolic perturbations e.g. leaf roll, chlorosis, browning of leaf tips, decrease in nutrient uptake, morphology of flower, growth, and physiology of plants, and it causes enzyme inhibition, water imbalance, and alterations in membrane permeability (Bohra et al., 2015; Sandalio et al., 2001). The more recent evidences also shows that SA is an important regulator of photosynthesis, photosystemII (PSII), photosynthetic pigments, and the activity of enzymes such as rubisco and carbonic anhydrase under heavy metal stress (Al- Whaibi et al., 2012; Zhang et al., 2015). Exogenous application of SA was also found to alleviate the ill effects generated by other heavy metals like cadmium toxicity in barley (Metwally et al., 2003) lead and mercury in rice (Mishra and Choudhuri, 1999). These researchers also addressed that deterioration of the membranes in the leaves of rice was due to an increased lipoxigenase activity, induced by lead and mercury toxicity which was mitigated by exogenous application of SA. Recently, an increased tolerance of *Linum usitatissimum* to Cd was attributed to SA-mediated control of H_2O_2 accumulation (Belkadhietal.,2014). In a recent study carried out by Khan et al. (2015a) the exogenous SA (3.0 mM) enhanced OsWRKY45 gene expression and increased endogenous content of SA in plants. It has been proved that increased endogenous SA level prevented membrane damage by lowering the H_2O_2 content on Cd-exposed in rice(Chao et al.,2010). Further, Szalai et al. (2013) reported that Involvement of SA(0.5mM)in the phytochelators(PCs)- mediated protection of *Zea mays* plants was evidenced against Cd- toxicity. SA can also significantly prevent Fe-deficiency-caused chlorosis in *Arachis hypogaea* plants(Kong et al.,2014).

G. *Drought*

Water stress has been considered as one of the most acute abiotic stresses presently affecting agricultural production. Janda et al. (2007) reviewed that Exposure of plants to drought stress leads to serious physiological and biochemical dysfunctions including reduction in turgor, growth, photosynthetic rate, stomatal conductance and damages of cellular components. A survey of literature indicates that low concentrations of SA plays a key role in providing tolerance to the plants, exposed to water scarcity (drought or flooding). Habibi, (2012) proved it and reported that low concentration of SA (500 μ M) supplementation to drought stressed *H. vulgare* resulted in increased net CO_2 assimilation rate due to increased stomatal conductance and eventually in increased plant dry

mass. A similar response was observed by Hayat et al. (2008) in drought stressed *L. esculentum* (tomato) plants in response to exogenously applied SA. Further Saruhan et al. (2012) stated that Foliar treatment of SA (1.0 μ M) strengthened antioxidant defense system in drought-tolerant *Z. mays* cultivar to a great extent (vs. drought-sensitive cultivar). Singh and Usha. (2003) observed that the wheat seedlings subjected to drought stress when applied with SA, generally exhibited higher moisture content and also higher dry mass accumulation, carboxylase activity of Rubisco, SOD and total chlorophyll content compared to the unstressed control. Further, the supplementation also provided a considerable protection to the enzyme nitrate reductase thus maintained the normal level of various proteins in the plant leaves (Singh and Usha, 2003). Exogenous treatment of SA also alleviated the dangerous effects of water scarcity on cell membranes of barley plants and concomitantly enhanced the ABA content in leaves, which might have contributed to the improved tolerance of plants to drought stress (Bandurska and Stroinski, 2005). Even, under drought stress conditions low membrane lipid peroxidation but increased plant height and dry mass and less wilting of leaves were reported by Kang et al. (2012), in *T. aestivum* with same treatment of SA (0.5mM). Besides providing tolerance to plants against drought stress, Ghasempour et al. (2001), reported that exogenous supplementation of SA was also remarked to be effective in providing resistance to the plants against the excessive water stress as was noticed in cell suspensions prepared from the fully turgid leaves of *Sporobolus stapfianus*.

H. Salinity

It has been estimated that about 45 million hectares of cultivated land have been damaged by salt stress worldwide and it is one of the serious environmental factors that hamper the productivity of agricultural crops, with adverse effects on germination, plant vigor and crop yield (Chauhan et al., 2015; Munns and Tester, 2008). In fact, the loss of crop productivity due to saline water is increasing day by day worldwide, the consequence of an imbalance in cellular ionic and osmotic balances (Khan et al., 2012b). Salt stress induces serious metabolic perturbations in plants, as it generates ROS, which disturb the cellular redox system in favor of oxidized forms, thereby creating ion toxicity, osmotic stress, nutrient- acquisition and homeostasis/deficiency, impaired stomatal conductance, increased cell-turgor loss, decreased reduction in leaf water potential, altered physiological/biochemical processes, may damage DNA, thereby, caused oxidative stress (Munns and Tester, 2008; Khan et al., 2014; Nazar et al., 2015). In current, literature of Qados, (2015) indicates that exogenous supplementation of SA to the stressed plants of *Capsicum annum* can potentially alleviate the toxic effects, generated by salinity. With the exogenous application of SA, an enhanced tolerance against salinity stress was observed in *B. juncea* (Nazaretal, 2015), *V. radiata* (Khan et al., 2014), *M. sativa* (Palma et al., 2013), and *V. faba* (Azooz, 2009). A similar observation was also seen in tomato plants raised from the seed priming with SA and was presumed to be due to the enhanced activation of some enzymes viz. aldose reductase and ascorbate peroxidase (APX) and to the accumulation of certain osmolytes such as proline (Tari et al., 2004; Szepesi et al., 2005). Furthermore, Li et al. (2014) addressed that SA induce salinity tolerance and increased biomass of *Torreya grandis* as a result of the enhanced chlorophyll content and the activity of antioxidant enzymes that eventually activated the photosynthetic process and also inhibit oxidative stress. Arbaoui et al., (2015) observed that salt stressed plants of *Lycopersicon esculentum* treated with exogenous application of SA produced large amounts of fresh and dry weight and had a higher leaf area in comparison with control plants. Further the activities of various antioxidant enzymes (CAT, POD, APX and SOD) were enhanced with a concomitant increase in proline content as a result of salinity exposure and / or SA treatment, thus providing enhanced tolerance against salt stress (Yusuf et al., 2008; Hayat et al., 2010).

I. Temperature Stress

Recently, changing environmental scenario, both low temperature including cold and chilling stress and high temperatures (heat) has become a potential abiotic stress-threat to crop plants.

J. Chilling/cold Stress

Between low and high temperature, low temperature is one of the serious environmental factors limiting the productivity and quality of economically important crops. Cold stress tolerance can be defined as the ability of the chilling sensitive plant to withstand the strain of the minimum temperature stress. Naturally, cold sensitivity is manifested by susceptible plants whose seed germination, growth, development of reproductive organs and post-harvest longevity are restricted within a range of low temperatures. However, it slows down all the metabolic reactions, but in terms of photosynthesis, those involved in CO₂ fixation, and regulation of stomatal aperture are particularly sensitive. Furthermore, Farooq et al. (2009) reported that CO₂ assimilation by leaves is decreased mainly due to membrane damage, photoinhibition, and disturbed activity of various enzymes. However, Cold stress affects both the maximal catalytic activities and the activation states of photosynthetic enzymes. Besides providing tolerance to the plants against

heavy metal, drought and salinity, the exogenous addition of SA also generates tolerance towards chilling or cold stress (Hayat et al., 2010). Many researchers have reported that SA-supplementation to differentially benefit several plant species exposed to low/chilling temperatures (Wang and Li, 2006; Wang et al., 2012; Khan et al., 2013a,b). Low concentration of SA (2.0 mM)-mediated enhanced synthesis of total phenolics and the activity of PAL was reported to improve low temperature stress tolerance in cold-stored lemon fruit Siboz et al., 2014). SA-supplementation not only provided protection against low and high temperatures, but was equally beneficial in providing tolerance against freezing (Frost) damage to winter wheat (Tasgin et al., 2003). Further Mutlu et al. (2013) stated that exogenously sourced SA results in chilling tolerance by enhancing antioxidant enzymes, ice nucleation activity, and the patterns of apoplastic proteins in *H. vulgare* genotypes. In another report, Kang et al. (2012) reported that SA significantly protected ultra-structures in *Musa acuminata* seedlings under cold stress.

K. Thermo tolerance

Heat stress due to increased temperature is also a serious problem for crop production in many areas all over the world. When it is constant for a long time it causes an array of morpho-anatomical, physiological and biochemical changes in plants, and induces molecular mechanisms and gene expression to modulate plant responses (Siboz et al., 2014; Kazemi-Shahandashti et al., 2014). Similar as chilling stress, extreme temperature may adversely affect photosynthesis, respiration, water relations, membrane stability and also modulate the level of hormones and metabolites (Wahid et al., 2007). Several reports demonstrated that SA may improve tolerance in a concentration dependent manner (Vazirimehr and Rigi, 2014). A foliar spray of lower concentration of SA conferred heat tolerance to mustard. Further Dat et al., (1998) reported that, this application, accompanied with hardening at 45°C for 1 hour increased the H₂O₂ level and also reduced the CAT activity, thereby increasing the potential of plants to withstand the heat stress. In a study carried out by Wang and Li, (2006), it was reported that with the application of SA increased antioxidant system in *Vitis vinifera* and induced activity of APX, GR, and monodehydroascorbate (MDHA), Increased redox ratios of AsA and GSH, and maintained Ca²⁺ homeostasis were addressed in SA-supplemented and heat treated *V. vinifera*. Recently, Khan et al. (2013b) have mentioned that the addition of 0.5 mM SA can alleviate high temperature in *T. aestivum* by increasing Pro-production and restriction of the stress ethylene formation under heat stress.

L. Uv Radiation / Ozone Stress

The effects of increased UV- radiation (280–320 nm) on plant growth and development raised concerns on the need of protection mechanisms (Gill et al., 2015). The level of UV radiations in the environment is increasing day by day and the plants, which use direct sunlight for photosynthesis, are unable to avoid UV radiations which impart adverse effects on photosynthesis, physiological and other biochemical processes (Rajendiran and Ramanujam, 2003). Similarly, tropospheric ozone (O₃) is a major damaging air pollutant, generated through photochemical reactions between nitrogen oxides, carbon monoxide and hydrocarbons, released during the burning of fossil fuels in urban areas (Mauzerall and Wang, 2001) and is responsible for causing significant change in both natural and cultivated plants. Ashmore, (2005) stated that Ozone (O₃) enters stomesophyll cells via stomata where it immediately interacts with water and other cellular components to generate phytotoxicity mainly by elevating the generation of ROS (such as O₂^{•-}, H₂O₂, OH[•], and ¹O₂), and triggering a series of signaling cascades and plant defense responses. Literature is full on the role of SA in plants under ozone stress tolerances (Khan et al., 2012a; Pal et al., 2014). It has been addressed earlier that plants accumulate large amounts of SA when exposed to ozone (O₃) or UV radiations. The role of SA in counteracting the damaging effects of ozone (O₃) was best demonstrated in *A. thaliana*, where NahG mutants, deficient in SA biosynthesis were more sensitive to the deteriorating effects of ozone (Sharma et al., 1996). Since, SA improved the activity of the antioxidant enzyme system, therefore, lead to improved tolerance against ozone stress in NahG mutants of *A. thaliana* (Rao and Davis, 1999). It has also been evidenced by Ogawa et al. (2005), that ozone-accrued SA-accumulation can be enhanced by ethylene-mediated regulation of the expression of the PAL and chorismatase (CM) genes in ozone-exposed *Nicotiana tabacum*.

Table (3). Summary of current studies on salicylic acid (SA)-mediated control of various abiotic stress-impacts on plants.

| Plants under abiotic stress | Treatment of SA concentration | Parameters studied | Response | Reference |
|-----------------------------|-------------------------------|--|----------|----------------------|
| High salinity | | | | |
| Vigna radiate | 0.5 mM | Glycinebetaine (GB) production, net photosynthesis, plant dry mass | Increase | Khan et al., (2014) |
| Brassica juncea | 8 µM | Tolerance capacity, Seedling fresh | Increase | Chauhan et al., 2015 |

| | | | | |
|----------------------|---------------------|---|----------|------------------------------|
| | | and dry mass | | |
| Solanum lycopersicum | 10 ⁻⁴ mM | Antioxidants activity (SOD and CAT), Ascorbate peroxidase (APX), Glutathione reductase (GR) | Increase | TARI et al., 2015 |
| Torreyia grandis | 0.5 mM | Chlorophyllcontent,netCO ₂ assimilationrates,prolinecontent | Increase | Li et al., (2014) |
| Glycine max | 0.5 mM | Na+/K+ ratio | Decrease | Ardebili et al., (2014) |
| Hordeum vulgare | 10 ⁻⁴ mM | Content and activity of Rubisco, Rubisco activase | Increase | Lee et al., (2014) |
| Cadmium stress | | | | |
| Cucumis melo | 0.1 mM | Photosynthetic capacity, PSII photochemistry efficiency, water use efficiency | Increase | Zhang et al., (2015) |
| Brassica juncea | 1.0 mM | Mineral nutrients content | Increase | Ahmad et al., (2011) |
| Poa pratensis | 0.5 mM | Nutrient elements content (K, Ca, Mg, and Fe) | Increase | Guo et al., (2013) |
| Chilling stress | | | | |
| Punica granatum | 1 and 2 mM | Total phenolics | Increase | Mirdehghan and Ghotbi (2014) |
| Citrus limon | 2 mM | Total phenolics, activity of phenylalanine ammonialyase (PAL) | Increase | Siboza et al., (2014) |
| Cold stress | | | | |
| H. vulgare | 0.1 mM | Apoplastic antioxidative enzymes, ice nucleation activity, pattern of apoplastic proteins | Increase | Mutlu et al., (2013) |
| Jasminum sambac | 100 μM | Photosynthesis-related parameters and Antioxidant enzyme activities (POD and CAT) | Increase | Cai et al., 2015 |
| | | Reactive oxygen species (ROS) | Decrease | |
| Heat stress | | | | |
| Triticum aestivum | 0.5 mM | Proline content, glutamyl kinase activity, gas exchange, water potential | Increase | Khan et al., (2013b) |
| Drought stress | | | | |
| Simarouba glauca | 0.05 mM | Polyphenol, alkaloids, flavonoid content | Increase | Awate and Gaikwad (2014) |
| Zea mays | 0.001 mM | Leaf rolling degree, water potential, dry weight | | Saruhan et al., (2012) |
| Lolium perenne | 0.75 and 1.5 mM | the content of chlorophyll a, b | Increase | Hosseini et al., 2015 |
| | | Electrolyte leakage, Proline accumulation and Antioxidant enzyme activity | Decrease | |
| UV-B stress | | | | |
| G. max | 0.5 mM | Flavonoid content | Decrease | Li et al., (2014) |
| Oryza sativa | 12.9 gha−1 | PS II activity, crop grain characteristics, total phenolics | Increase | Mohammed and Tarpley (2013) |

M. Biotic stress

Abiotic stress responses are largely disciplined by the hormone SA, while defense against various biotic assailants is specified by antagonism between the salicylic acid (SA) and jasmonic acid (JA)/ethylene signalling pathways. However, in order to defend themselves against the pathogen attacks, plants have evolved various constitutive and inducible mechanisms, one such mechanism being the accumulation of large quantities of SA. Generally, biotic stress is an additional challenge inducing a strong pressure on plants and adding to the damage through pathogen or herbivore attack. However, current findings suggest that SA acts both synergistically and antagonistically with biotic stress signalling, creating a complex network of interacting pathways and protect plants from different pathogen or herbivore attack.

This concept is supported by the observations of Malamy et al. (1990), where large amount of SA is collected on the leaves of TMV resistant tobacco variety *Nicotiana tabaccum* cv. Xanthi, upon inoculation with TMV. This achievement opens a new window for the role in exogenous addition of SA in providing tolerance to the plants against different types of pathogens. However, the exogenous SA in defense signaling has been characterized and well addressed in many dicotyledonous plants.

To complicate matters further, Luna et al. (2011) observed that SA can have either a positive or a negative effect on bacteria-induced callose deposition, depending on other growth and developmental conditions such as a slight and glucose levels, thus switching its effect on the defense response according to the situation of environmental stresses.

N. The Interaction Of Abiotic And Biotic Stresses

The presence of simultaneous abiotic and biotic stresses presents an added degree of complexity, as the responses to these are largely managed by different hormone signaling pathways that may interact and inhibit one another (Anderson *et al.*, 2004; Asselbergh *et al.*, 2008b). Naturally, abiotic and biotic stress signal transduction results from a complex arrangement of interacting more than one factor (Fujita *et al.*, 2006) (Fig. 3). According to Mauch-Mani and Mauch, (2005) certain gene products are crucial to both abiotic and biotic stress signalling, and may therefore control the specificity of the response to multiple stresses. TFs are transcription factors of key importance in generating specificity in stress responses. TFs that may be crucial in controlling the response to biotic and abiotic stresses is given in fig 3. More on the recent analysis, Pardo, (2010), stated that their manipulation provides one of the greatest opportunities for conferring multiple stress tolerance transgenic ally, as they control a wide range of downstream events. Often, the exposure of plants to a pest or pathogen increases the effects of an abiotic stress, such as water scarcity (Audebert *et al.*, 2000), whereas Mittler and Blumwald, (2010) stated that long-term abiotic stress can weaken plants defenses and cause increased pathogen susceptibility. However, when examining the effects of an abiotic stress with the simultaneous impact of a pathogen or herbivore, both positive and negative interactions have been observed depending on the timing, nature, and severity of each stress. Recently, Mittler and Blumwald, 2010 have also reviewed that the deleterious interactive effect on crops of two different biotic stresses has been well studied. Plants have made progressed to live in environments where they are often exposed to various stress factors in combination. Being sessile, they have improved specific mechanisms that allow them to detect precise environmental changes and respond to complex stress conditions, reducing damage while conserving valuable resources for growth and reproduction.

Hence, plants activate a specific and unique stress response when subjected to a combination of multiple biotic and abiotic stresses (Rizhsky *et al.*, 2004b). Heat and water deficit in particular can cause disproportionate damage to various crops compared with either stress individuality (Barnabaset al., 2008). Similarly, Chauhan et al. (2015) well reviewed that at any given point of time, crops may encounter two or more stresses e.g. Drought and salinity simultaneously. She also reported that early responses to combined drought and salinity stress are also similar to each other, except the ionic components under salinity. While An increase in high temperature can create a negative interactive effect by lowering resistance to bacterial, viral, fungal, and nematode pathogens: Sharma et al., (2007) maintained that in wheat, higher mean temperatures observed over a 6 year experimental period correlated with heightened susceptibility to the fungus *Cochliobolus sativus*. Anderson et al. (2004); Asselbergh et al. (2008b) reported that it is particularly true for combinations of biotic and abiotic stresses, the signalling pathways of which can act antagonistically.

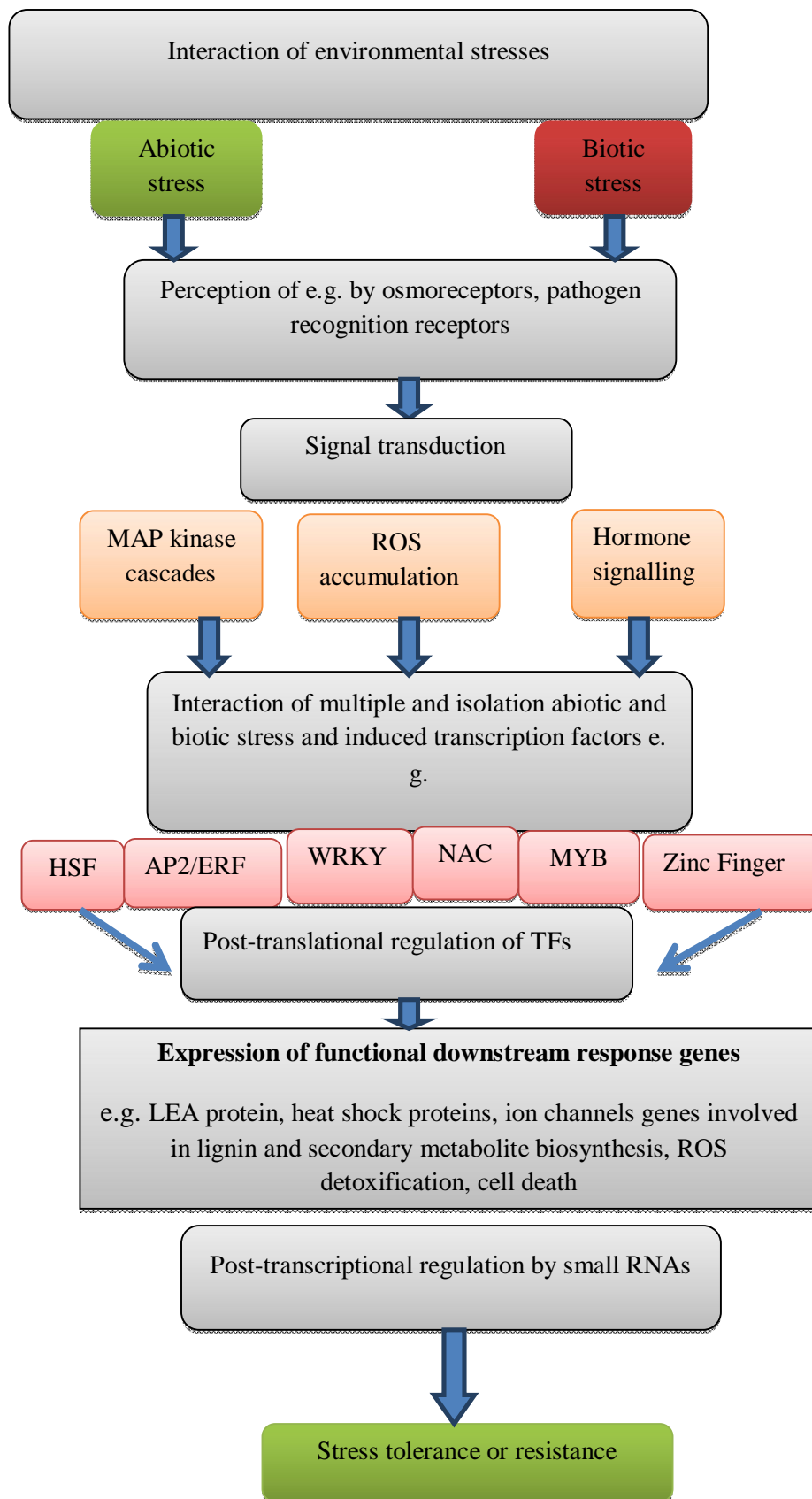


Fig. 3 Key events in the signal transduction pathway activated in response to the interaction of abiotic and biotic stresses.

III. CONCLUSIONS

It may be concluded from the above discussion that SA is a strong and potential tool in reducing or alleviating the adverse effects of abiotic and biotic stress in plants. Addition of SA has been shown to be beneficial for plants either in optimal or stress environments.

- A. Exogenous treatment of SA enhances the growth and bio-productivity of crops.
- B. SA can regulate different plant metabolic processes and modulate the production of varied osmolytes and secondary metabolites, and also maintains plant-nutrient status hence, to protect plants under multiple abiotic stresses simultaneously.
- C. With the addition of SA induces the SAR in plants, thereby provides a considerable protection against various biotic stresses.
- D. The flower inducing domain of SA makes it an important phytohormone that can improve flowering in a variety of ornamental plants.
- E. When lower concentration of SA was used it proved beneficial for enhancing the photosynthesis, growth and various other morphological, physiological and biochemical characteristics of plants.
- F. Exogenous application of SA improves the activities of the antioxidant enzyme system under stressful conditions.
- G. It also can protect and enhance the enzymes of nitrate metabolism under stressful environments.

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