



Physiological modulation of plants by salicylic acid under drought stress - a review

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ABSTRACT

Abiotic stresses are well known to harm crop performance worldwide. Drought stress is widely considered to be one of the most dangerous stresses, the intensity of which is likely to increase owing to alarming change in the climate. Change in plant water relations, stomatal conductance, photosynthetic rate, generation of active oxygen species, and imbalance in hormonal concentration are many few of the changes which are inclusively acceptable to be responsible for the reduction in crop performance. To enhance crop productivity under drought conditions several strategies have been proposed and espoused so far, one among them being the priming or spraying with phytohormones. As far as the literature is concerned salicylic acid (SA) seems to be one of the best remedial phytohormones under drought conditions with promising results like up-regulation in the synthesis of osmoprotectants and antioxidants and leading to improvement in the activity/content of most of the physiological, biochemical and molecular aspects. Keeping in view the beneficial role of SA, this review is being outlined to prepare a report which enlightens some of the physiological roles of SA among its diverse activities related to drought tolerance that in turn would be helpful for the researchers to enhance the drought resilience in plants.

Keywords: Abiotic, drought, phytohormones, plants, salicylic acid

Drought is considered the most devastating and a chief restricting factor to agricultural production of all the abiotic stresses and is projected to worsen further because of the persistent climate change (Zaffar *et al.*, 2018). Drought is continued soil moisture deficiency resulting in severe implications on plant growth, development, and reproduction when soil moisture levels fall below the required amount for a prolonged period. The effects of drought turn out to be very chronic in regions with irregular rainfall during the plant's life cycle (Rosegrant and Cline, 2003). Historically, the occurrence of drought has facilitated important famines and posed a threat to the world food supply in the near future (Okorie *et al.*, 2019). The plant undergoes several modifications as a result of drought stress. Reduced leaf and stem growth, root spread, and altered water relations in the plant are just a few of the symptoms Muhammad *et al.* (2009). Furthermore, agricultural output losses by drought have been linked to the closure of stomata, change in cell membrane properties, and declined enzyme functioning particularly those associated with CO₂ fixation and ATP generation. Stomatal closure and increased metabolic flux caused by photorespiration lead to the formation of free radicals in the plant cells, which in turn degrade macromolecules and promote cell death (Agurla and Raghavendra, 2016). The changes responsible for the reduction in crop yield by drought stress have been summarised in the following flow diagram (Fig.1)

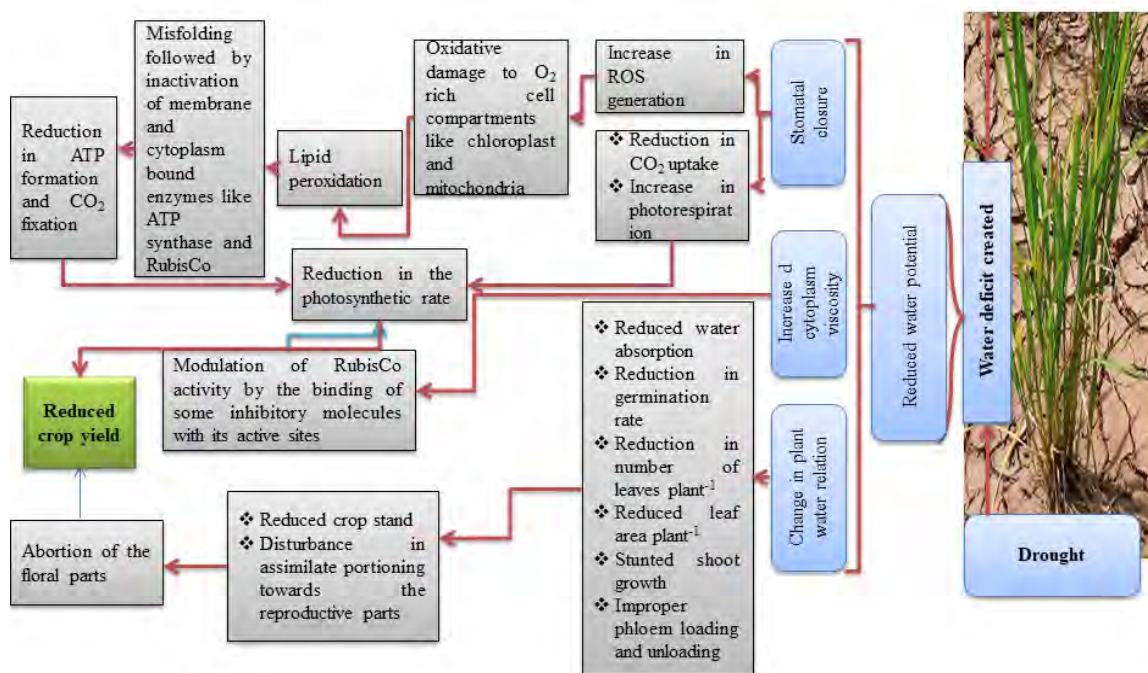


Fig. 1: General response displayed by plants under drought stress

In light of drought-related negative impacts, as well as increased food demand it seems imperative to develop strategies or technologies that can enhance plant drought tolerance with minimum impact on plant productivity. To improve plant stress tolerance, researchers have used a variety of strategies such as seed priming, osmoprotectant treatment, nutrient application, nano-technological instruments, and metabolic engineering (Mahmoud *et al.*, 2021). Growth hormones are now being researched as a long-term solution for reducing the negative impacts of water scarcity on crops. Over the past few years, SA has gained greater prominence as a way to regulate key plant metabolic processes (Khan *et al.*, 2000; Rahat *et al.*, 201; Miura and Tada, 2014). SA is a phenolic molecule that, in addition to drought stress, protects plants from a variety of other abiotic stresses besides regulating plant growth and development (Raskin, 1992; Miura and Tada, 2014; Zhang *et al.*, 2015). The activity of SA has been reported to depend on its concentration, time, and application method (Kováčik *et al.*, 2009; Shi *et al.*, 2009; Miura and Tada, 2014) as shown in table-1. To enhance the overall performance of cultivated plants under changing climatic conditions, it seems sensible to use existing knowledge on SA to alleviate drought resistance in cultivated plants. Therefore, this review was framed with an aim to collect the knowledge and some possible roles of SA concerning drought stress, which in turn could be useful for researchers to develop the ideotypes with the highest resistance to drought.

Plant water relations in response to SA under drought conditions: The absolute need for water is an outstanding element for sustaining plant survival (Onwugbuta-enyi Jane 2004). During plant growth, drought affects the plant moisture level, hence strongly disrupting its entire metabolism contingent on the strength, time, and span of the stress. (Sharma *et al.*, 2020; Osakabe *et al.*, 2014). Cell desiccation developed under deficient soil moisture content is reflected in terms of essential modifications brought about in plant biochemical and physiological processes, cell membrane properties, and structure of different cell organelles (Tuba *et al.*, 1996; Sarafis 1998; Yordanov *et al.*, 2003). At the morphological level the first visible change developing in the plants owing to the lack of soil moisture is the change in the plant canopy architecture because of the reduced total leaf area hence plants are encountered with so many problems including a reduction in the gaseous exchange, growth and development of vegetative and reproductive parts (Rahmati *et al.*, 2018) and hence affecting the crop yield. Besides so many reasons like variation in hormonal balance, plant nutrition and carbon balance the change in plant water status is a significant factor contributing to a reduction in the crop yield under drought stress (Munns *et al.*, 1982). Appraisal of plant water status is extraordinarily vital to measure the resistance of plants to water deficit as it gives a useful sign of the potential of crop species to keep up their physiology under drought (White *et al.*, 2000). Parameters regularly

used as indicators of the degree of water stress include relative water content (RWC) and leaf water potential (LWP) (Omae *et al.*, 2007; Luis and Marco, 2001; Nayyar *et al.*, 2005).

Table-1 Response of plants to different concentrations of SA used through different methods at different growth stages and soil moisture level

Name of Crop	Stage of drought imposition	Moisture level	Concentration of SA used	Method of SA application	Modification brought about by SA	References
Winter Wheat	Before tillering to flowering	30% of field capacity (FC)	0.5 mM	Foliar spray a week after germination	➤ Induction of stress proteins ➤ Enhancement in the activity of antioxidants followed by increase in membrane stability. ➤ Improvement in the photosynthetic rate.	Masoumeh <i>et al.</i> (2021)
Wheat	At three leaf stage for the next 15 days	10% of FC	1mM	Foliar spray after two weeks of germination	➤ Increased leaf water status, Chl a, Chl b and carotenoid content ➤ Enhancement in the activity of antioxidants	Ammar <i>et al.</i> (2020)
Rice	At four leaf stage	50% of FC	100 ppm	Foliar spray at five leaf stage	➤ Maintenance of tissue water potential by accumulation of compatible solutes ➤ Enhanced potency of antioxidant system	Muhammad <i>et al.</i> (2009)
Maize	From the 14 th leaf stage until blister growth stages	50% of FC	140 ppm	Foliar spray at 16 th leaf and 18 th leaf stages	➤ Increase in antioxidant enzymes activity ➤ Accumulation of compatible solutes like proline and soluble sugars	Ramadan <i>et al.</i> (2021)
Mustard	10 days after germination	10% and 20% PEG	50 μ M	Foliar spray 10 days after germination	➤ Enhancement in antioxidant defence mechanism ➤ Increase in the activity of glyoxalase systems	Md. Mahabub <i>et al.</i> (2013)
Sunflower	At three leaf stage	10% of FC	25ml/pot	Foliar spray at three leaf stage	➤ Increase in sugar, chlorophyll, protein, carotenoid and phenolic contents	Naeem <i>et al.</i> (2018)
Barley	After germination	One irrigation at the time of sowing	0.5mM	Foliar spray 21 days after sowing	➤ Increase in chlorophyll concentration and relative water content ➤ Increase in the activity of antioxidant enzymes	Khaled <i>et al.</i> (2020)
Tomato	After 30 days of seedling emergence	Withholding water for 10 days	10 ⁻⁵ M	Foliar spray after 45 days of seedling emergence	➤ Increase in leaf water potential, nitrate reductase and carbonic anhydrase activity, chlorophyll content and photosynthetic parameters. ➤ Increase in the antioxidant content and membrane stability index ➤ Accumulation of proline	Shamsul <i>et al.</i> (2008)
Chickpea	From vegetative to reproductive stages	Vegetative to reproductive stages	200 ppm	Foliar spray	➤ Accumulation of proline	Siamak <i>et al.</i> (2014)

Drought in the long run outcomes in the development of a water deficit in the leaf cells with perceptible abatements in LWP and RWC with a simultaneous increase in leaf temperature (Siddique *et al.*, 2000). Drought altered the plant water relations in soybean (Chowdhury *et al.*, 2017), snap bean (Omae *et al.*, 2007), rice (Cruz *et al.*, 1986) wheat (Siddique *et al.*, 2000), etc. The decrease in RWC in stressed plants might be due to a decrease in plant vigor (Techawongstien *et al.*, 1993) and lower stomatal index in the adaxial surface or to a higher capability for soil extraction under drought stress (Rosales-Serna *et al.* 2004). Halder and Burrage (2003) reported that drought stress is accompanied by the accumulation of solutes in the

root zone that drastically reduce the root permeability hence resulting in restricted moisture uptake from the soil in turn facilitating the reduced LWP. Under reduced soil moisture levels following response is displayed by the roots.

1. Approaching the zone of suberization towards the root tip diminishes the root growth and length of root absorption zone.
2. Reduction in the gradient in root water potential and the medium water potential which in turn critically reduces the root permeability as well as the water supply towards the root (Raper and Kramer, 1983; Turner and Kramer, 1980).

Chopard (2004) proposed that other than the fluctuations achieved in the root qualities, its density and distribution could be considered as a critical component for water take-up by a plant in the soil the two of which altogether decline under dry spell consequently influencing the plant water relations. Transpiration can be regarded as the dominant process in plant-water relations. Many plants limit transpiration by stomatal closure at low negative LWP originated during the drought period (Fisher *et al.*, 2008) as indicated by reduced RWC (Heshmat *et al.*, 2012).

SA showed promising results to help plants with drought stress. It is also involved in the regulation of so many plant processes including plant water relations hence protecting the plants against environmental stresses (Miura and Tada 2014; Hayat *et al.*, 2010) by reducing the negative effects of drought (Hussain *et al.*, 2009). An increase in RWC by SA application has been reported in drought-stressed chrysanthemum (Vahdati *et al.*, 2012), strawberry (Ali *et al.*, 2017), maize (Kiran *et al.*, 2015), wheat (Bhupinder and Usha, 2003), and shara (Jalal Ud-Din *et al.*, 2012). Proline (2-oxopropanoic acid), glycine betaine (3-hydroxy-N,N-dimethylglycine) and soluble carbohydrate might act as compatible osmolytes in plants, by acting largely at the early stages of drought-induced senescence of root tissue leading to an increase in RWC by SA as reported by Demiralay *et al.* (2013). Scientific data have found that drought-stressed plants show an increase in sugar levels when they are treated with SA. Another study described SA treatment helping to resist drought because of its function in enzyme protection along with the maintenance of osmoregulation, membrane stabilization, and protection against hydroxyl radicals (Shao *et al.*, 2006.) Sugars, which are often associated with this increase in plant root length by SA, help to minimize the effect of drought stress by exploiting the soil moisture in the deeper layers (Tas and Tas, 2007) as has been reported in maize (Kiran *et al.*, 2015) and wheat (Heshmat *et al.*, 2018). Increased root length, which is found in some strains that have been treated with SA, has been shown to be linked to increased cell division under one form of drought stress (Zafar *et al.*, 2021; Brito *et al.*, 2018 and Sakhabutdinova 2003).

Chlorophyll retention by SA under drought stress: In terms of physiological and biochemical disturbances caused by drought, diminution in leaf chlorophyll (Chl) content is considered as the most severe issue affecting plant growth and yield (Rahdari *et al.*, 2012; Ommen *et al.*, 1999). The Chl concentration is commonly used as a measure of the activity of the source tissues (Zobayed *et al.*, 2005), therefore it is reasonable to look at its decrease as one of the non-stomatal limiting factors under water deficit conditions. Decrease in Chl content under drought stress stands confirmed in maize (Majid and Roza, 2011; Majid, 2012), rice (Shamima *et al.*, 2020), tomato (Sivakumar *et al.*, 2017), paddy (Syamsia *et al.*, 2018), peanuts (Xing *et al.*, 2018) and so many other agricultural and horticultural crops of economic importance contingent upon the span and magnitude of dry spell (Kpyoarissis *et al.*, 1995). Other than harming the chloroplast structure extreme dry spell represses the photosynthetic capacity of plants by lessening the biosynthesis of Chl as well as its components which include glutamate-1-semialdehyde, 5-aminolevulinic acid, Mg-protoporphyrin IX monomethyl ester, and protochlorophyllide (Iturbe-Ormaetxe *et al.*, 1998; Vijay and Baishnab, 2012). Drought slows down the chlorophyll formation in plants, leading to a reduction in their Chl content. This has been connected to the reduction in the levels of various porphyrin components that contribute to chlorophyll biosynthesis, such as protoporphyrin IX, protochlorophyllide, magnesium-protoporphyrin IX, and its methyl ester on account of the down-regulation of most enzymes involved in their biosynthesis, particularly in the Chl branch (Thu-ha *et al.*, 2011). Jain *et al.* (2013) reported that a major drop in aminolevulinic acid content (ALA) and aminolevulinic acid dehydratase (ALAD) activity is linked with a substantial reduction in Chl synthesis. During drought stress, down-regulation of the key enzymes of Chl biosynthesis which include Glutamyl-tRNA reductase 1 (HemA) and magnesium-chelatase subunit (ChlH) contribute to inhibition of Chl biosynthesis (Hortensteiner and Krautler 2011). Xing *et al.* (2018) proposed that inhibition of Chl biosynthesis is brought about by a sharp reduction in the expression of an enzyme encoded by AhPORA gene. PORA, PORB, and PORC, three structurally related NADPH: protochlorophyllide oxidoreductases (PORs), have been discovered to play a key role in catalysing the light-dependent reduction of protochlorophyllide a to chlorophyllide a, which is then converted to Chl during

photomorphogenesis (Masuda and Takamiya 2004; Michal *et al.*, 2015). There is a piece of strong evidence that drought can cause Chl levels to decrease by inducing chloroplast destruction, instability of the Chl proteins (Khan *et al.*, 2015), photo-oxidation and dissolution of pigment molecules (Shakeel *et al.*, 2011) and excessive production of active oxygen species (AOS) (Smirnov, 1995; Majid and Roza, 2011).

SA (SA) has been discovered to play a crucial role in plant growth, development, and protection responses by functioning as a buffer against biotic and abiotic stresses. During drought stress, increased growth and yield enhancement with SA preconditioning is seen as an outward signal of a shift in metabolism within plant cells. Various mechanisms have been suggested to assist the plant in achieving tolerance by SA amongst which Chl retention is a key parameter (Mutlu *et al.*, 2009). Among the several physiological characteristics induced by exogenous SA infusions, increases in Chl a, Chl b, and total Chl have been reported to promote plant drought resistance (Mutlu *et al.*, 2009; Rao *et al.*, 2012). Application of SA improved the pigment content in mustard (Alam *et al.*, 2013), wheat (Heshmat *et al.*, 2012), soyabean (Nasrin *et al.*, 2017; Leslie and Romani, 1988), chickpea (Taibi *et al.*, 2016), and peppermint plants (Abeer, 2019) under stress conditions. Researchers have verified that the effect of SA reduces Chl degradation in plants under water stress via inflicting a build-up of photosynthetic pigments (Ma *et al.*, 2017). SA counterparts the immortality of leaves of water-stressed plants through the preservation in their pigment content by retarding ethylene synthesis, inhibiting membrane depolarization, and reduced membrane permeability thus preventing the leaves from senescence (Leslie and Romani, 1988). The activation of protein kinase synthesis, which is vital for cell division and development at various stages, is another high-quality action of SA (El-Tayeb, 2005). SA reduces the consumption of oxygen through enhancement rate in epoxidase and de-epoxidase reactions, thus protecting the thylakoid membranes from oxidative damage (David, 2002). Damage to the cell membrane, photosynthetic machinery, and Chl molecules caused by excess electrons and AOS has also been reported to decrease via an increase in the xanthophylls and carotene cycle (Jagtap and Bhargava, 1995; Costa *et al.*, 2005) by SA pre-conditioning. It has been discovered that it regulates Chl, protein synthesis, transpiration, photosynthesis, and protective enzymes including superoxide dismutase (SOD) and peroxidase (POD), all of which promote plant tolerance to environmental challenges (Mutlu *et al.*, 2009).

Photosynthetic rate as effected by SA under drought: Water availability is a vital element affecting plant growth and yield in arid and semi-arid areas, where plants are often subjected to intervals of drought (Manuela *et al.*, 2003) which turns to be persistent in locations with low water availability or abnormal precipitation in the course of the plant's cycle and therefore reducing its growth and yield through its effect on plant photosynthetic rate (Pr) (Zaffar *et al.*, 2021) on account of the decrease in leaf growth, impaired photosynthetic equipment, untimely leaf senescence and associated reduction in food production (Wahid and Rasul, 2005). The reduction in Pr under drought has been reported in apple (Zhibo *et al.*, 2018), soyabean (Wensen *et al.*, 2018), bean (Zlatko and Ivan, 2004), rice (Halder and Burrage, 2003), wheat (Parisa and Nayer, 2016), potatoes (Moorby *et al.*, 1975) and so many agricultural and horticultural crops of economic importance. Whilst evaluating the stomatal and non-stomatal reasons for the reduction in photosynthesis, the impact of the previous appears to be very least suggesting that besides reduction in the CO₂ uptake by the plant, there is mutilation inside the other plant physiological strategies additionally. Stomatal closure is taken into consideration as the first line of defense towards the drought (Cornic and Massacci, 1996) which alternatively acts as the principal determinant for reduced photosynthesis below mild to mild drought (Cornic and Massacci, 1996; Yokota *et al.* 2002). Dearth in the CO₂ level and its assimilation inside the leaf mesophyll cells brings about a disparity between the excited electrons and their usage in the carbon reaction ensuing inside the production of AOS, commonly superoxide (O₂•⁻) and hydrogen peroxide (H₂O₂) (Reddy *et al.* 2004) which bog down the synthesis of the core D₁ protein of PSII system (Shunichi and Norio, 2008). Reviews regarding the impact of oxidative stress on plant growth and development directly propose harm to lipids, nucleic acids, and proteins (Hasan *et al.*, 2018), resulting in inhibition of biosynthetic pathways for PSII, PSI, light-harvesting Chl-proteins, chaperones, and Chla-b binding proteins (Vijay and Baishnab, 2018; Hasan *et al.*, 2018) which in turn are enormously important for shielding of integrity and inner structure of photosynthetic organs such as chloroplasts and its components (Fengxia *et al.*, 2013). Tezara *et al.* (1999) pronounced that, even under slight drought situations photosynthetic electron transport chain down-regulates ensuing in a decreased rate of photophosphorylation and formation of assimilatory powers required for CO₂ fixation due to reduction in D₁ synthesis. Related to this disorganization and damage to chloroplast structure and retarded activity of the enzymes involved in carbon assimilation and ATP synthesis also contribute to reduced Pr (Ali and Ashraf, 2011; Golldack *et al.*, 2011). Reports on the activity of RubisCO suggest that under severe drought the decreased Pr is not only because of the intense reduction of RuBISCO activity (Bota *et al.*, 2004) but also by its reduced biosynthesis (Joseph *et al.*, 1999) and its tight binding with some inhibitor molecules, as seen in cotton (Parry *et al.*, 2002). Furthermore, elevations in solute concentration in

the cell cytoplasm are hazardous to the contents of the cell, particularly to enzymes engaged in the photosynthetic apparatus (Hoekstra *et al.*, 2001). Under drought conditions, the activity of enzymes such as RubisCo, phosphoenolpyruvate carboxylase, nicotinamide adenine dinucleotide phosphatemic enzyme, and fructose-1, 6-bisphosphatase has been reported to be reduced by 2-4 times, with a 9.1-fold reduction in the activity of pyruvate orthophosphate dikinase compared to unstressed plants (Hoekstra *et al.*, 2001).

According to Rahat *et al.* (2015), SA is a phytohormone and a potential molecule that might lower plant sensitivity to environmental challenges by regulating a variety of physiological functions, including Pr. According to Adisa and Erna (2018), an increase in photosynthetic rate caused by SA treatment during drought stress is due to a rise in plant pigment content, including Chl a, b, total Chl, and carotenoids, as well

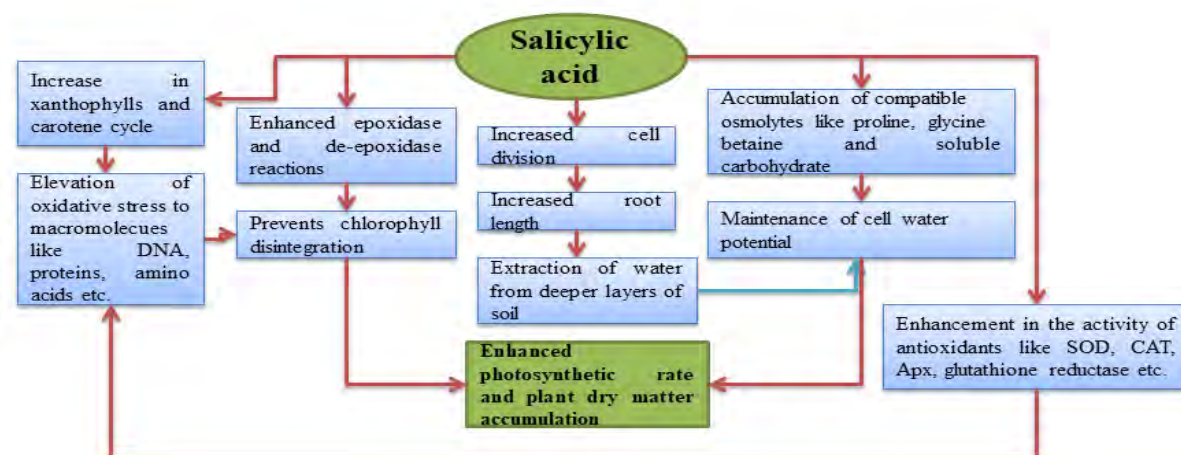


Fig. 2: Role of salicylic acid in enhancing drought stress tolerance

as the prevention of Chl degradation (Ma *et al.*, 2017). Apart from that, SA helps to maintain the integrity of the light-harvesting apparatus (Rahat *et al.*, 2015), a process that may be responsible for increased photosynthesis during drought stress. SA pre-treatment has been shown to increase photosynthetic pigment concentration in *Zea mays* (Khodary, 2004), barley (El Tayeb, 2005), wheat (Sarika *et al.*, 2005), and *Brassica napus* (Navita *et al.*, 2002). Changes in protein kinase and Rubis Co activity, as well as an increase in Chl content, have been reported in response to drought stress (Sun *et al.*, 2009); Kang *et al.*, 2014; Rahat *et al.*, 2015), as evidenced by an increase in protein spots such as ribulose-1, 5-bisphosphate carboxylase activase, two Rubisco large subunit-binding proteins and carbonic anhydrase (Azooz *et al.*, 2011). The production of abiotic stress response genes (Li *et al.*, 2013), biosynthetic enzymes, and proteins in plants by SA have been shown to protect chloroplast against oxidative damage during drought (Rahat *et al.*, 2015; Wang *et al.*, 2019). Signal transduction, photosynthesis, glucose metabolism, energy production, protein metabolism, stress defense proteins including dehydrins, chaperones, and heat shock proteins are all involved in metabolic processes according to findings from SA's protein expression pattern analysis (Kang *et al.*, 2012).

CONCLUSION

The results gained in recent years clearly suggest that SA is a highly promising molecule for reducing crop abiotic stress sensitivity since it has been proven to attenuate the detrimental effects of numerous stress elements in plants. SA is a promising compound to increase plant tolerance to drought stress, and is involved in the regulation of important plant physiological processes including plant water relations by promoting the accumulation of compatible osmolytes like proline, glycine betaine, and soluble carbohydrate in plants subjected to drought stress. An increase in photosynthetic rate caused by SA treatment during drought stress is due to a rise in plant pigment content, including chlorophyll a, b, total chlorophylls, and carotenoids, as well as the prevention of chlorophyll degradation.

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