Journal of Plant Growth Regulation (2021) 40:464–485
https://doi.org/10.1007/s00344-020-10152-x

Multifaceted Role of Salicylic Acid in Combating Cold Stress in Plants: A Review

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Received: 24 January 2020 / Accepted: 20 May 2020 / Published online: 2 June 2020

Abstract

Plants face different types of stresses, including biotic and abiotic stresses. Among various abiotic stress, low-temperature stress alters various morphological, cytological, physiological, and other biochemical processes in plants. To thrive in such condition's plants must adopt some strategy. Out of various strategies, the approach of using plant growth regulators (PGRs) gained a prominent role in the alleviation of multiple stresses. Salicylic acid, application triggers tolerance to both biotic and abiotic stresses via regulation of various morpho-physiological, cytological, and biochemical attributes. SA is shown to alleviate and regulate the various cold-induced changes. Both endogenous and exogenously applied SA show an imperative role in the alleviation of cold-induced changes by activating multiple signaling pathways like ABA-dependent or independent pathway, Ca^{2+} signaling pathway, mitogen-activated protein kinase (MAPKs) pathway, reactive oxygen species (ROS), and reactive nitrogen species (RNS) pathways. Activation of these pathways leads to the amelioration of the cold-induced changes by increasing production of antioxidants, osmolytes, HSPs and other cold-responsive proteins like LEA, dehydrins, AFPs, PR proteins, and various other proteins. This review describes the tolerance of cold stress by SA in plants through the involvement of different stress signaling pathways.

Keywords Antioxidants · Cold stress · Cold responsive proteins · Salicylic acid · Signaling · Tolerance

Introduction

Temperature extremes of both low and high are one of the severe environmental stresses, which restrict the overall growth and development of plants. Due to changes in climate, it is becoming an exceptional challenge for plant scientists to explore strategies and adopt measures for reducing damage inflicted on the various crops by extreme temperatures. Out of these two extreme temperature regimes, low temperature is one of the greatest suppressing environmental factors for the crop, which leads to consequential crop losses (Yadav 2010). Plants facing low temperatures have been categorized into chilling-sensitive, chilling tolerant, and freezing tolerant. Out of all these categories, freezing tolerant plants actually faces the cold stress. In contrast, chilling-sensitive plants die at the onset of stress conditions and do not actually withstand the stress conditions. Both chilling and freezing stress harmfully affect plant growth and productivity (Guo et al. 2018; Liu et al. 2018). The distribution and growth of every organism are determined by temperature. Two major approaches can be distinguished: stress avoidance and stress tolerance (Levitt 1980). In the case of stress avoidance, the plants escape themselves from stressful conditions; for example, cactus has adapted themselves to hot and arid climates. However, in stress tolerance, plants successfully and steadily deal and cope with harsh environmental conditions. In the plants exposed to low temperature, hardening is induced and the plants get acclimated to survive in cold stress conditions. Tolerance to many stresses increases when plants are exposed gradually to these unfavorable conditions. The changes that develop in the acclimation process are plastic and are reversible as these vanish when adverse conditions discontinue; on the other hand, the changes that occur in the adaptation process are permanent and are inherited. Freezing stress leads to nucleation of ice,

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loss of water and even death of the whole plant. Plants show variability in the capability to develop tolerance to either freezing (0–15 °C) or chilling stress (< 0 °C). It has been revealed that the plants of temperate regions are tolerant to chilling stress and endure acclimation to cold. So cold stress is the critical abiotic stresses, as it causes considerable losses in crops.

Various speedy and efficient measures are adopted to alleviate the harmful effects of cold stress in plants. Out of multiple measures, the use of plant growth regulators (PGR) plays a significant role in the plants facing various abiotic stresses. Among different plant growth regulators, salicylic acid (SA) plays a diverse role in improving several morphological, cytological, physiological, and biochemical attributes in the plants facing both biotic and abiotic stresses. Accumulation of SA in chilling stress has been revealed in numerous plant species (Wan et al. 2009; Kosova et al. 2012). Its application has improved tolerance to cold stress in several plant species as it was first demonstrated in maize (Janda et al. 1999), followed by various other species such as potato, rice, etc. as depicted in Fig. 1 (Parvaiz and Prasad 2012). Also, the accumulation of endogenous free SA and glycosyl SA has been reported in Arabidopsis and wheat plants exposed to low-temperature stress (Scott et al. 2004; Kosova et al. 2012), signifying relationship between SA and cold stress responses.

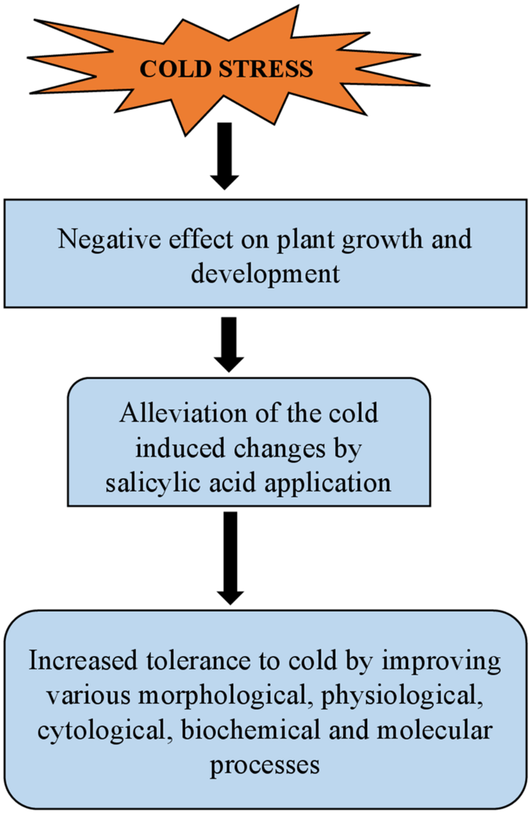

Fig. 1 Role of salicylic acid in overcoming the negative effect of cold-induced damage in plants

The present piece of work has been designed with an aim to study the ameliorative role of SA on the morphological and physio-biochemical parameters altered by the cold stress and also to dissect various strategies adopted by plants to cope up changes caused by low-temperature stress.

Biosynthesis of SA

SA has recently been added in the list of classical plant hormones that belong to one of the diverse groups, i.e., a phenolic compound chemically called 2-hydroxy benzoic acid. It has a cyclic benzoic ring with –OH group in the 2nd position as a functional group. The word salicylic acid is originated from the plant willow tree (*Salix alba*) as it was first isolated from the bark of *Salix alba* in 1826. In contrast, John Buchner successfully isolated it in a large amount in 1928. It was first known as salicin, but later on, Rafacle Piria, in 1938, renamed it as salicylic acid because salicin is a glucoside of alcohol which is converted into SA upon oxidation. SA is a colorless crystalline compound and extensively used in the production of organic compounds like acetylsalicylic acid (aspirin). SA has recently been added as a potential regulatory compound, distributed throughout the plant kingdom (Raskin et al. 1990; Raskin 1992). It is present either in the conjugated form (such as glycosylated in the glucose ester or the methylated form) or in free form (Dempsey et al. 2011). In the plant kingdom, it is biosynthesized via the shikimic acid pathway, as depicted in Fig. 2. It is produced either through the isochorismate pathway (IC), which operates in the chloroplast or through the phenylalanine ammonia-lyase pathway (PAL), which occurs in the cytosol where chorismate acts as a branch point for the synthesis of SA (Mustafa et al. 2009; Maruri-Lopez et al. 2019). PAL is a regulatory enzyme involved in the biosynthetic pathway of SA, playing a vital role in stress tolerance (Carver et al. 1991). In tomato, *Arabidopsis* and *Nicotiana benthamiana,* the primary route of biosynthesis of SA occur through the IC pathway (Uppalapati et al. 2007; Catinot et al. 2008). Different forms of isochorismate synthase enzymes (ICS1 and ICS2) have been described in *A. thaliana* (Nawrath and Metraux, 1999). In the IC pathway, chorismic acid (CA) is transformed into isochorismic acid in the presence of enzyme isochorismate synthase (ICS), which is then converted into salicylic acid in the presence of isochorismate pyruvate lyase (IPL) enzyme (Fragniere et al. 2011). Moreover, in the PAL pathway, chorismic acid is converted into prephenic acid in the presence of chorismate mutase (CM), which is then transformed into phenylalanine via reduction and then into trans-cinnamic acid (t-CA) by phenylalanine ammonium lyase (PAL). From t-CA, synthesis of SA could

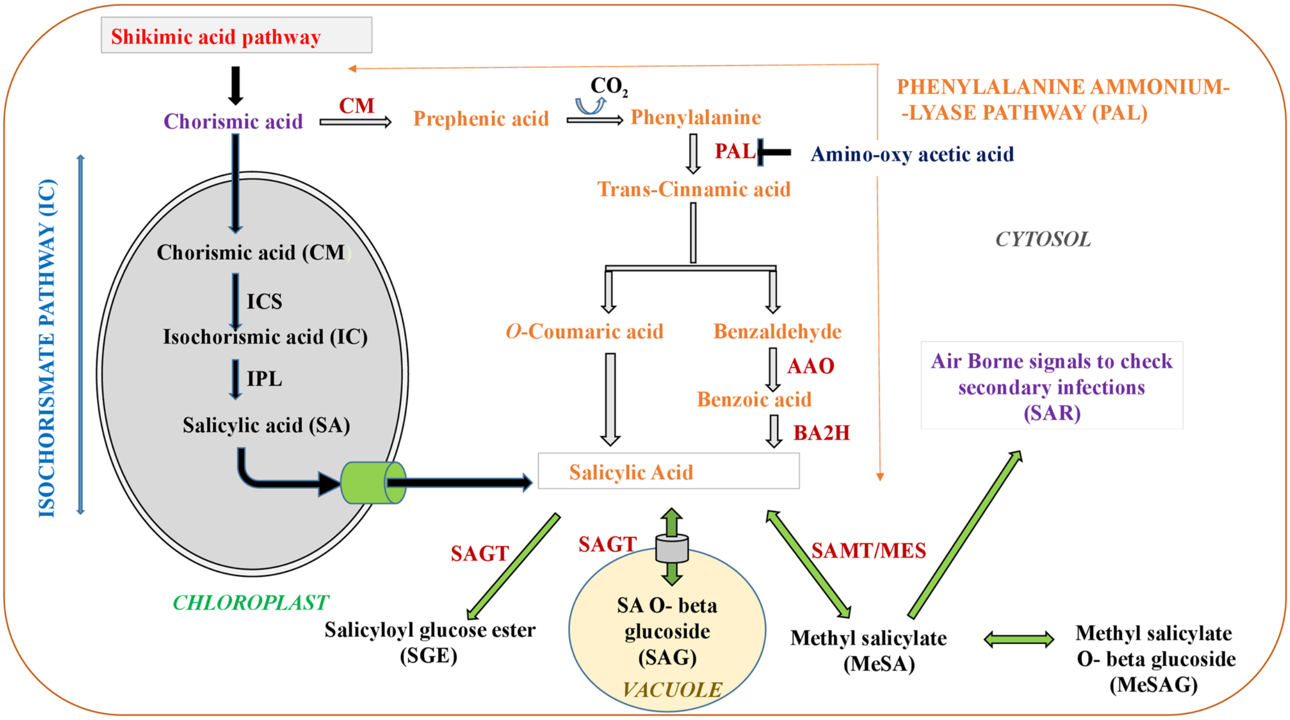

Fig. 2 Biosynthesis of SA by shikimic acid pathway in which chorismic acid acts a branch point for isochorismate and phenylalanine lyase pathway. Site of IC pathway is chloroplast in which chorismic acid is converted into IC in the presence of isochorismate synthase (ICS) which is subsequently converted into SA by enzyme isochorismate pyruvate lyase (IPL). Phenylalanine ammonium lyase pathway occurs in cytosol in which chorismic acid is converted into phenylalanine by chorismite mutase (CM), phenylalanine is then subsequently converted into trans-cinnamic acid in the presence of enzyme phenylalanine ammonium lyase (PAL) which is inhibited by amino-oxy acetic acid. Phenylalanine is subsequently converted into two metabolites, i.e., ortho-coumaric acid and benzaldehyde. O-coumaric acid is converted directly into SA, whereas benzaldehyde is first converted into benzoic acid by aldehyde oxidase (AAO) which is finally converted into SA by enzyme benzoic acid 2-hydroxylase (BA2H). Active SA is modified into other forms of SA by either glucosyltransferases (SAGT) or by methyltransferases (SAMT), by methylesterases (MES). Methylated SA becomes volatile and through this, secondary infections are checked by sending air borne signal as in systemic acquired resistance (SAR). *Source* modified from Dempsey et al. (2011)

be routed either through o-coumaric acid (o-CA) or benzoic acid (BA), which varies in different species of plants (Garcion et al. 2008). SA is directly formed from o-CA, whereas in another case, benzoic acid is synthesized from benzaldehyde by enzyme aldehyde oxidase (AO) and lastly in the presence of benzoic acid 2-hydroxylase (BA2H) SA is formed from benzoic acid as depicted in Fig. 2.

The levels of SA are controlled by various chemical modifications when SA is formed. These chemical modifications produce various inactive forms of SA, such as methyl salicylic acid (MeSA), methyl salicylate O-β glucoside (MeSAG), salicyloyl glucose ester (SGE), and SA ortho-β-glucoside (SAG). These inactive molecules are stored within the cell, till there is pressing need to generate responses that are mediated through SA. Formation of glucosides (glucosylation) of SA is carried out by activity of UDP-glucosyltransferase enzymes UGT74F1 and UGT74F2, the genes of both of these enzymes are localized in cytosol and induced by SA (Dean and Delaney 2008; Park et al. 2017). F1 catalyzes the formation of SAG, whereas F2 glucosyltransferase enzyme mainly forms SGE, but also biosynthesize SAG (Dean and Delaney, 2008; Dempsey et al. 2011). The glycosylated form of SA is stored in the vacuole (Maruri-Lopez et al. 2019). In addition to glucosylation, SA forms MeSA by the activity of carboxy methyltransferase (SAMT) (Zubieta et al. 2003). It is revealed in Arabidopsis that carboxy methyltransferase is encoded by the AtBSMT1 gene, which uses either BA/SA as substrate and forms MeSA, particularly during pathogen infection (Chen et al. 2003; Liu et al. 2010). Methylation of SA makes it more volatile and the plant sends airborne signals (SAR) to check secondary infections (Liu et al. 2010).

Both biotic and abiotic stresses stimulate the biosynthesis of SA in the chloroplast, which is then transported to the cytosol (Fragniere et al. 2011). The mechanism of its intracellular transport from chloroplast to cytosol has recently been reviewed (Maruri-López et al. 2019). Two mutants *sid1* and *sid2* (deficient in SA induction) of Arabidopsis had shown impaired biosynthesis of SA and enhanced disease susceptibility to pathogens and *sid1* is found to be allelic to EDS5 protein, which is a class of MATE (multidrug and toxin extrusion) transporter family protein (Nawarth and Matraux 1999). It is also revealed that EDS5 protein is confined in the membrane of the chloroplast, which indicates that it might play a role in the transport of SA from chloroplast to cytosol (Serrano et al. 2013). The EDS5 homolog (EDS5H) protein is also known to be localized in chloroplast, which transports phenolic compounds across chloroplast but not SA, it specifies that there are unique carrier proteins involved in the transport of particular compound (Parinthawong et al. 2015). As of now, EDS5 (ENHANCED DISEASE SUSCEPTIBILITY-5) protein is a unique SA transporter involved in the transport of SA from chloroplast to the cytosol. SAG, the product of glycosylation of SA, is transported to the vacuole and has been reported in various plants like tobacco, soya bean, *Arabidopsis thaliana* and red beet (Dean and Mills 2004; Dean et al. 2005; Vaca et al. 2017). Dean et al. (2005) revealed that the transport of SAG from the cytosol to the vacuole is carried out by H^+-antiporter, in red beet and tobacco. In contrast, in soybean, it is transported through ATP binding cassette (ABC) transporter (Dean and Mills 2004). Vaca et al. (2017) reported in *A. thaliana* that SAG is accumulated in the vacuole and SGE is kept in the cytosol and from cytosol to vacuole, it is transported through the MgATP-dependent process. SA is hardly permeable to the cuticle of plant cells, so to go through the long-distance transport, it undergoes methylation and formation of volatile compound viz. MeSA that acts as an airborne defense signal and is assembled via the phloem to stimulate SAR (Park et al. 2007). Manosalva et al. (2010) revealed that MeSA is converted into SA by the activity of the MeSA esterase (MES) in tissues of plant-mediated through SA binding protein (SABP2). All these findings indicate that SA acts as one of the key regulators in stimulating SAR in the plants facing any biotic stress.

Effect of SA on Seed Germination Under Cold Stress

Among various germination factors, the temperature is one of the most critical factors affecting seed germination (Fu et al. 2017; Verma et al. 2010). Cold stress commonly causes delayed seed germination and growth; it strongly inhibits the average length of coleoptile and radicle (Sharifi 2010). Cold stress may decrease germination percentage, seed vigor and seedlings growth and may also induce oxidative stress (Airaki et al. 2012). The detrimental effects of low-temperature stress on seeds germination can be ameliorated by the treatment of SA. It was revealed that the application of SA upregulated various essential proteins, which are vital for the germination of seeds like the stimulation of 20S proteasome, initiation, and elongation factors and multiple proteases. Besides this, SA plays an essential role in releasing the plant from the quiescent state by enhancing the activity of enzymes involved in main pathways like pentose phosphate pathway (PPP), gluconeogenesis, glycolysis, and glyoxylate cycle (Rajjou et al. 2006). Under cold stress, exogenous application of SA increased the germination rate in the muskmelon plant and mountain rye (Ansari et al. 2012; Kaur and Gupta 2017). It has been shown that the application of 0.1 mM SA by seed soaking considerably increases the percentage of seed germination in optimal and in low-temperature stressed conditions (Gharib and Hegazi 2010). Interestingly, when the lower concentration of SA is applied exogenously, positive effects were noted in the establishment and germination of seeds under abiotic stress conditions (Rajjou et al. 2006; Alonso-Ramirez et al. 2009). However, there is complete inhibition of seed germination in maize when 3–5 mM SA was used (Guan and Scandalios 1995). Treatment of SA (>1 mM and >0.25 mM) to Arabidopsis and barley plants, respectively, inhibit the germination of seeds (Rajjou et al. 2006; Xie et al. 2007). This negative role of SA in seed germination could be most probably due to SA induced oxidative stress. So, SA causes its negative (high concentration) or positive (low concentration) impacts on the germination of seeds in a dosage-dependent manner.

Effect of SA on Morphological Attributes Under Cold Stress

Overall growth and development of plants are affected by cold stress, which reduces the accumulation of dry matter in plants. Fariduddin et al. (2011) revealed that *Cucumis sativus* plants grown under low-temperature stress (10 or 5 °C for 18 h) had reduced the growth of a plant. Furthermore, exposure of tomato varieties to cold temperatures of 12 °C developed reduced growth and development (Hu et al. 2006). However, SA plays an important role in growth, improved rate of photosynthesis and pigment content in normal and stressed plants (Pancheva et al. 1996; Fariduddin et al. 2003; Hayat et al. 2005). As it has been revealed that exogenous application of 0.5 mM of SA via seed soaking or foliar way significantly enhanced the growth of watermelon plant subjected to chilling stress (Sayyari et al. 2013). Similarly, Cheng et al. (2016) investigated that moderate concentration of SA acts as a potent molecule in improving growth in cold stressed *Citrulla lanatus* plant.

Effect of SA on Cytological, Biochemical, and Physiological Attributes Under Cold Stress

In response to low-temperature stress, various cytological, biochemical, physiological, and molecular processes like photosynthesis, the permeability of plasma membrane, the status of water, osmotic balance, and other processes are altered. At the molecular level, it has been reported that chilling stress affects the synthesis of proteins and gene expressions and favors the development of secondary structures in RNA (Rajkowitsch et al. 2007; Ruelland et al. 2009). Different proteins are upregulated in *Oryza sativa* in response to cold stress such as 20 s proteasome, ascorbate peroxidase, elongation factors (FF 1β, Tu), adenylate kinase, and ATPase, and various others are downregulated like Ef-G, calreticulin, rubisco (large and small chain precursors), ATP synthase (β subunit), and UDP glucose phosphorylase (Cui et al. 2005; Yan et al. 2006; Hashimoto and Komatsu 2007; Renaut et al. 2008). The various processes affected by low-temperature stress in plants are depicted in Fig. 3.

Cytological Attributes

Cytological attributes of plants are also affected by low-temperature stress. Tomato developing at 5 °C temperature for three days has shown failure in turgor pressure, cytoplasmic vacuolization, enlargement, and breakdown of specialized cellular subunits in the cotyledons (Salaj and Hudak 1999). The plasma membrane is influenced by low-temperature stress in such a way that the fluidity of the plasma membrane gets altered (Murata and Los 1997). Generally, the decline in the fluidity of the plasma membrane occurs chiefly due to the unsaturation of fatty acids and also, due to changed composition and proportion of protein to lipid in plasma membranes (Los and Murata 2004; Wang and Li 2006). Membrane changes from an elastic fluid crystalline state to a solid gel state; thus, diverse functions of the cell are altered in various ways making the membrane leaky for ions and other substances (Farooq et al. 2009). Findings have generated sufficient evidence that cell membrane is the hot spot for the perception of cold stress (Steponkus et al. 1998; Thomashow 2001). As the temperature drops below 0 °C, then nucleation of ice commonly initiates in intracellular areas of the cell. Electrolyte seepage is an indicative parameter to determine the injury caused by cold stress. Cytoplasmic and tonoplasmic deposits have been detected in cells of roots, epidermal, mesophyll, tonoplasts of potato cotyledons (Salaj and Hudak 1999), and vascular cells of *Episcia reptans*after chilling stress (Murphy and Wilson 1981), which causes irreversible dysfunction of tonoplast (Salaj and Hudak 1999). Swelling and disorganization of the chloroplast, swollen nuclei with fragmented chromatin, nucleoli and microfilaments in cytoplasm and nucleus of mung bean, *Vigna radiata* and leaves of *Saintpaulia* have also been observed (Ishikawa 1996; Yun et al. 1996; Kratsch and Wise 2000). However, the application of SA to normal and stressed plants plays important role in stimulation of defensive reactions involved in maintaining the pigments and integrity of membranes (El-Tayeb 2005). SA is recognized to regulate organization of leaf and chloroplast (Uzunova and Popova 2000; Wang and Li 2006). It has also been shown that the application of SA to cold stressed grape plants reduced the oxidative degradation of lipids and membrane permeability and thereby inducing

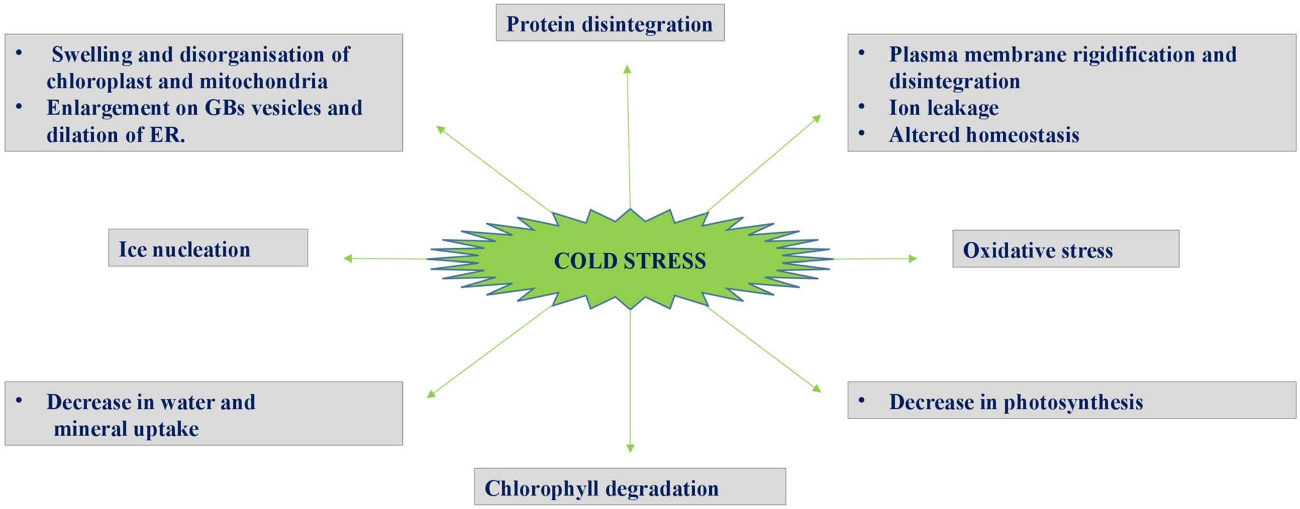

Fig. 3 Effects of cold stress on plants shows modulationin cytological, physiological, and biochemical attributes. *Source* modified from Rasool et al. (2014)

tolerance against cold (Wang and Li 2006). Similarly, it has been found that SA plays key role in alleviating chilling stress by substantially decreasing the chilling-induced membrane permeability and membrane lipid peroxidation, thus maintaining the overall structure of a cell Siboza et al. (2014). This prevention of cell membrane structure might be due to role of SA in maintaining the composition and ratio of fatty acids in membranes (Popova et al. 2012).

Effect on Biochemical and Physiological Attributes

Effect of SA on Photosynthesis

Among various biochemical processes affected by cold stress, photosynthesis is one of them, which is severely hampered, affecting the overall health of a plant. Low temperature leads to inhibition of photosynthetic characters, because of disturbance in source-sink relation, decline in stomatal resistance, damage of chloroplast and water oxidizing complex; uncoupling of ETC and inactivity in main enzymes of C3 and C4 cycles (Venema et al. 1999a, b; Van Heerden et al. 2003; Garstka et al. 2007). The effects of cold stress have also been noted at other levels, such as changes in stomatal frequency (Equiza et al. 2001). *Solanum melongena* grown at 10 °C temperature for nine days had reduced content of chlorophyll, PSII and conductance of stomata; high level of proline and soluble protein (Gao et al. 2016). SA regulates various vital metabolic processes in *Brassica juncea* like photosynthesis, stomatal conductance, transpiration rate, internal CO_2 concentration and water status (Fariduddin et al. 2003). It is recognized to regulate organization of leaf and chloroplast (Uzunova and Popova 2000), movement of stomata (Khokon et al. 2011), pigment contents (Fariduddin et al. 2003), and enzymatic activity of carbonic anhydrase (CA) and ribulose 1,5 bisphosphate carboxylase/oxygenase (Slaymaker et al. 2002; Hayat et al. 2012; Yusuf et al. 2012). Pigment content in wheat seedlings grown from the grains pretreated with a lower concentration of SA (10^{-5} M) was considerably increased, while higher level proved inhibitory (Hayat et al. 2005). Foliar supply of SA to *Brassica juncea* also increased the content of photosynthetic pigments (Baghai et al. 2002). Foliar application of 0.5–2.5 mM SA to *Cucumis sativus* alleviated the cold stress-induced changes such as PN, Fv/Fm, rate of transpiration, leaf area, and Ci (Wei et al. 2009). Exogenous pretreatment of SA to leaves of a grape plant grown under cold stress maintains the organization of chloroplast by regulating the calcium homeostasis (Wang and Li 2006).

Effect of SA on Respiration and ATP Generation

Respiration a cellular process opposite to photosynthesis, which consumes sugars and oxygen to generate energy for growth and development of the plant. It involves various sequential pathways such as glycolysis (occurs in cytosol), oxidative decarboxylation (a linkage step between glycolysis and Krebs cycle), tricarboxylic acid (TCA) cycle, which occurs in mitochondrial matrix and electron transport chain (ETC) located in inner membrane of mitochondria which is coupled with synthesis of ATP by ATP synthase through oxidative phosphorylation (Atkin and Tjoelker 2003). It has been revealed that photosynthesis is strongly dependent on various processes that occur in mitochondria (Noctor et al. 2004), as mitochondrial ETC is vital for photosynthesis because it provides ATP for the synthesis of sucrose in cytosol and dissipation of excess reducing equivalents (NADH and FADH2) synthesized in the chloroplast. In ETC, two pathways operate in mitochondria, cytochrome pathway (CP), which is common in all aerobes, and the other is cyanide insensitive alternative oxidase pathway (AOX), which operates at UQ level of CP as depicted in Fig. 4 (Vanlerberghe and Ordog 2002). Cytochrome pathway is coupled with ATP synthesis, whereas the AOX pathway is uncoupled from proton transport and thereby the synthesis of ATP, i.e., the AOX pathway merely wastes energy. In the AOX pathway, electrons are directly transferred to oxygen, which is facilitated by alternative oxidase enzymes (Cruz-Hernandez and Gomez-Lim 1995). At low temperatures, the rate of respiration is high in mitochondria because of the involvement of two energy releasing systems, i.e., plant uncoupling mitochondrial protein (PUMP) and AOX pathway (Purvis and Shewfelt 1993). So, the activity of *the AOX* gene is triggered by stresses such as cold stress, biotic stress, and other factors that inhibit the flow of electrons through cytochrome pathway *(*Ito et al. 1997). In thermogenic plants, instead of ATP heat is produced by this AOX pathway, this heat volatizes the compounds and helps in the attraction of insects. Moreover, in non-thermogenic plants, it is activated in numerous situations such as by treatment antimycin A as an inhibitor of cytochrome pathway (Vanlerberghe et al. 1994), accumulation of SA (Kapulnik et al. 1992) and by wounding (Hiser and McIntosh 1990). However, in the non-thermogenic plants like tobacco, the expression of AOX enzyme has been increased many folds by treatment of SA (Norman et al. 2004). Out of many analogs of SA, only aspirin and 2,6-dihydroxybenzoic acid stimulate the process of heat production in plants. Rhoads and McIntosh (1993) also revealed that SA enhances heat production by activating the AOX pathway in mitochondria. Unlike the cytochrome respiratory pathway, the flow of electrons via the AOX pathway produces ATP only at one stage, with heat being dissipated as potential energy (Vlot et al. 2009). AOX is said to function as antioxidants to scavenge reactive oxygen species (Noguchi et al. 2001). It is because of this role, AOX has gained attention

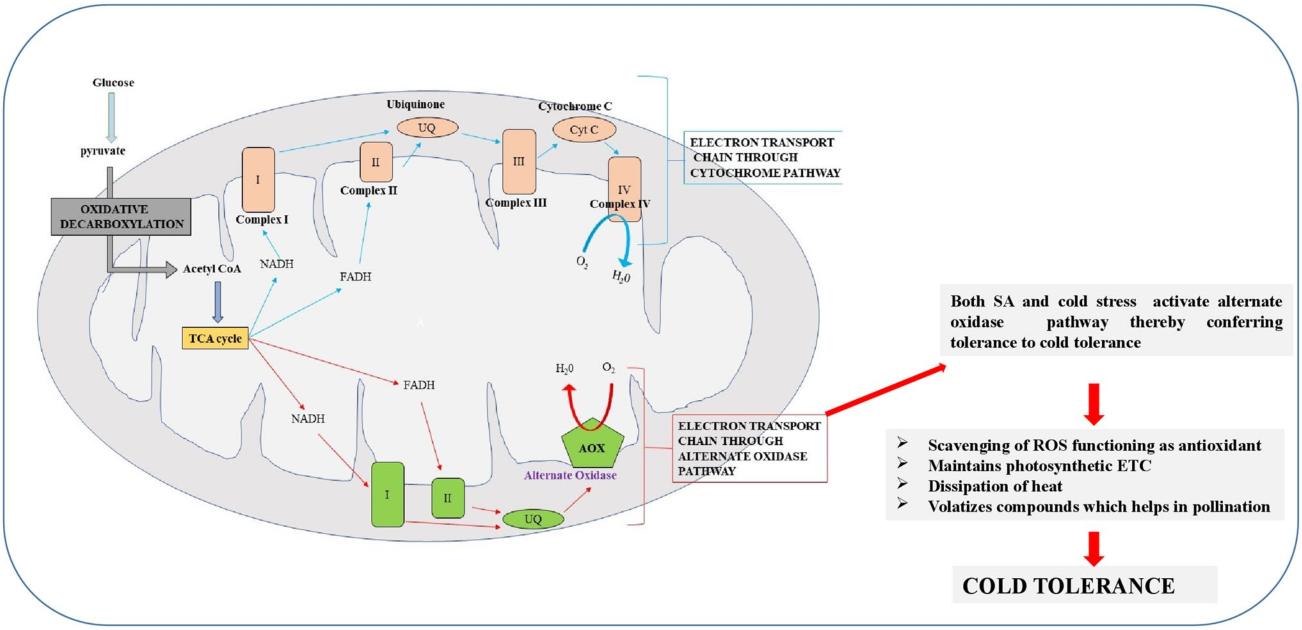

Fig. 4 Alternate oxidase pathway in plant mitochondrial respiratory chain in which SA and cold stress activates alternate oxidase (AOX). AOX catalyses the reduction of oxygen to water without translocation of protons across the inner mitochondrial membrane. Source modified from Vanlerberghe (2013)

in relation to photosynthesis in stressful conditions. It has been revealed in wheat leaves that AOX inhibition in drought conditions leads to a decrease in the activity of PSII. Therefore, AOX is vital for maintaining photosynthetic ETC, particularly in stress full conditions. Methyl SA and methyl jasmonate alleviate chilling injury in *Capsicum annuum*, which was correlated with an increase in expression of the AOX gene by methyl SA and methyl JA (Fung et al. 2004).

Interaction of SA with Mineral Nutrients

Mineral nutrition is essential for the survival of plants in both favorable and unfavorable conditions. Cold stress leads to a decrease in the amount and uptake of water and nutrients, thereby leading to cell desiccation and starvation. Mineral nutrition plays a vital role in the mitigation of various abiotic stresses. SA acts as a critical hormone in improving the uptake and status of mineral nutrients under stress conditions (Sheteiwy et al. 2019; Wang et al. 2011). By modulating the metabolism and assimilation of nutrients, SA considerably improves the growth and development of various plants grown under salt, heavy metal and oxidative stress (Wang et al. 2011; Khokon et al. 2011; Tufail et al. 2013). However, studies are yet to reveal the relationship between signaling of SA and mineral nutrient status under cold stress, but various genes of N, K, or S have been identified, which are altered by either being up or downregulated.

SA and Accumulation of Osmolytes

Osmoregulation, a defensive mechanism that regulates water balance and turgor pressure in plants, is mediated by osmolytes without interfering with other processes (Misra and Saxena 2009). Osmolytes are compounds that are being dissolved in the solution or in other liquids of a cell and play a vital role in regulating the amount and balance of water in a cell. An elevated level of soluble sugars and sugar alcohol have been known to confer tolerance to plant under stress (Murakeözy et al. 2003). Various osmolytes have been identified, which functions as osmoprotectants like proline, GB, TMAO, sarcosine, taurine, glycerophosphocholine, myo-inositol and others. These osmoprotectants provide defense from various stresses mainly by detoxification of reactive oxygen species, enzymatic or protein balance, regulation of osmosis and maintaining the integrity of membrane (Verbruggen and Hermans 2008). In natural conditions, the amount of soluble sugars is enhanced during the onset of wintertime when plants are exposed to cold; on the other hand, soluble sugars decrease in spring (Siminovitch 1981). Current investigation in *Petunia hybrida* indicates that an increase of sugar in leaves is stimulated by cold which has preventive function against the severe cold temperature, that hampers the mobilization and consumption of sugars in sink areas (Bauerfeind et al. 2015). Exogenous application of GB improves the growth of low-temperature stressed tobacco and Arabidopsis plants (Somersalo et al. 1996; Xing and Rajashekar 2001). Proline, a stress amino acid commonly exists in plants and it piles up in a more significant amount in reaction to unfavorable environmental conditions (Ashraf and Foolad 2007). Proline provides tolerance to various stress and regulate osmotic balance, stimulate many stress-related proteins, maintain enzymes and cell membranes as well as involved in quenching of reactive oxygen species (Szabados and Savouré 2010). Proline also shows chaperone-like activity, which maintains the integrity and functioning of various enzymes and proteins. Cold stress tolerance is not achieved in the majority of cold-sensitive plants until a higher concentration of proline is used before stress (Kushad and Yelenosky 1987; Xin and Li 1993). Thus, proline might be prospective to improve cold stress stimulated changes in chilling-sensitive plants. Breakdown of PSII, the activity of Rubisco and detoxification of toxic ions are prevented by an increase in GB concentration in stressed plants (Ashraf and Foolad 2007). Remarkably, SA increases the accumulation of GB against cold, salt and drought stress to enhance the growth and development of plants (Jagendorf and Takabe 2001; Misra and Misra 2012). The exogenous application of SA stimulated the accumulation of proline and total soluble sugars under cold stress in *Phaselous vulgaris* (Soliman et al. 2018). SA induces the metabolism of proline, which might be due to induction in the biosynthetic enzyme of proline (pyrolline-5-carboxylate reductase and γ-glutamyl kinase). This increase in the compatible solutes and total soluble sugars by SA application significantly protect the plants from cold stress, as these osmolytes gives cell membranes more cryostability which is prerequisite for cold tolerance in plants (Gusta and Wisniewski 2013; Luo et al. 2014).

Effect of SA on the Antioxidant System

The antioxidant system is one of the most important systems which prevents the other molecules from oxidation. As oxidation reactions generate reactive oxygen species, which initiates a series of reactions, thereby leading to injury or cell death. So, to prevent plants from these ROS, there is a system in plants known as the antioxidant system, which inhibits the generation and progression of these molecules and reactions. The antioxidants are generally classified as (1) non-enzymatic antioxidants include; (a) water-soluble antioxidants such as glutathione and ascorbate, (b) lipid-soluble membrane-associated antioxidants which involves α-tocopherol, β-carotene and ubiquinone and (2) enzymatic antioxidants include peroxidase (POX), catalase (CAT) and superoxide dismutase (SOD). CAT converts H_2O_2 into H_2O and O_2, whereas SOD carries the dismutation of two superoxide radicals into H_2O_2 and O_2. POX carries oxidation of H_2O_2 and yield water and another oxidizing molecule. Ascorbate–glutathione cycle (water cycle or Asada-Halliwell pathway) involves the action of various enzymes such as glutathione reductase (GR), dehydroascorbate reductase(DHAR), ascorbate peroxidase (APX), and monodehydroascorbate reductase (MDHAR), which are also concerned with the removal of hydrogen peroxide and superoxide radicals (Asada 1999). There occurs balance between ROS generation and scavenging processes when plants grow in favorable environmental conditions, but this equilibrium gets disturbed on the onset of unfavorable environmental conditions like extreme temperature, other biotic and abiotic stresses, this imbalance between the scavenging and ROS production leads to a physiological condition known as oxidative stress. Cold stress also generates oxidative stress through the generation of a surplus amount of ROS like, $O_2^{\cdot -}$, OH^-, and H_2O_2 (Prasad 1996; Miller et al. 2010). This surplus amount of ROS proves fatal for the overall health of plant growth and development, thereby declining the yield of the crop (Wahid et al. 2007). In response to low-temperature stress, the rate of oxidation reactions is increased, which poses a threat to plant from oxidative damage. The numerous effects caused by uncontrolled oxidative stress include alteration in vital biomolecules, increased cell death and inhibition of overall growth and development (Gill and Tuteja 2010; Anjum et al. 2012; Nafees et al. 2019). Activities of various enzymatic antioxidants like APC, CAT, SOD, and POX are altered in plants by treatment of SA to cold stressed plants (Mutlu et al. 2013). SA plays key role in alleviating cold-induced damage in barley, wheat, and bean plants by regulating antioxidative defense system (Mutlu et al. 2016; Soliman et al. 2018; Ignatenko et al. 2019). SA controls the expression of various key enzymes of Asada and Halliwell pathway like GR, GSH synthetase, GPX (GPX1 and GPX2), MDHAR and DHAR, which reflects that SA plays a vital role in abiotic stress tolerance in plants via Ascorbate–Glutathione cycle (Mustafa et al. 2018; Yan et al. 2018).The role of SA in scavenging of surplus ROS through the ascorbate glutathione cycle is depicted in Fig. 5. SA induced the activity of SOD that is associated with the rise in calcium level and H_2O_2, which stimulate the activity of antioxidants and finally leading to quenching of free radicals (Arfan 2009).

Relationship of SA and Cold Signaling

It is proposed that the sequential application of SA to plants could improve tolerance to cold stress; however, its persistent use may also reduce tolerance. Chilling stress in different species of plants leads to an increase in the content of endogenous SA (Wan et al. 2009; Kosová et al. 2012). Besides this, the use of SA enhanced cold tolerance in numerous species of plants like maize, potato, rice, etc. (Ahmad and Prasad 2012). This suggests that signaling of cold and SA could be interconnected and its effect may be tissue-specific and dose-dependent. Based on available information, a signal transduction cascade involving SA during

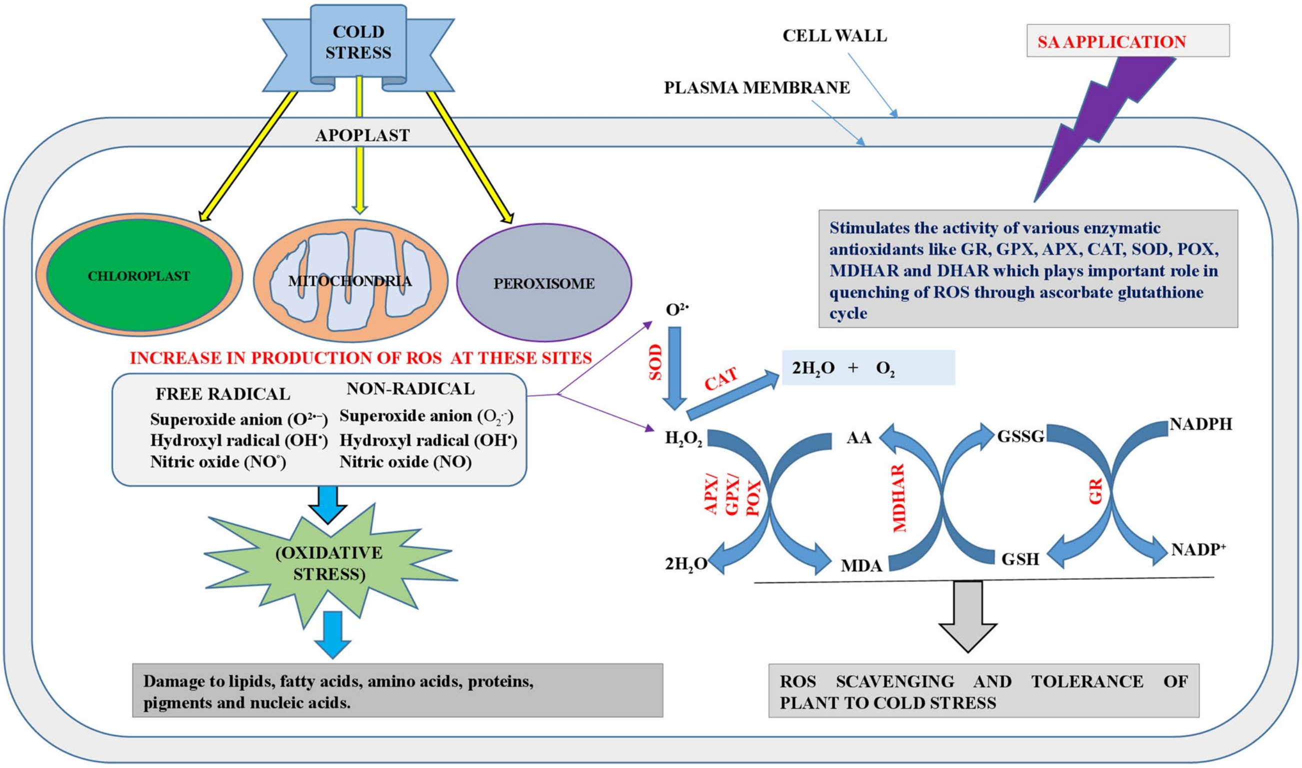

Fig. 5 Cold stress induced production of ROS in chloroplast, mitochondria, peroxisome, and apoplast of a cell which leads to oxidative stress by damaging lipids, proteins, and nucleic acids. SA stimulates the activity of various enzymatic antioxidants which play pivotal role in quenching of ROS as depicted in ascorbate glutathione cycle. Enzymes and substrate involved are glutathione reductase (GR), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), and monodehydroascorbate reductase (MDHAR), glutathione peroxidase (GPX), superoxide dismutase (SOD), catalase (CAT), reduced glutathione (GSH), oxidized glutathione (GSSG), monodehydroascorbate (MDA), and ascorbate (AA). *Source* modified from Foyer and Noctor (2011)

cold stress has been depicted in Fig. 6, which is explained in the following headings.

ABA Signaling

ABA is known as a universal stress hormone as any stress may generate variation in ABA status. The various stresses like cold, drought and salt, stimulate the production of ABA, which plays a positive role in stress tolerance of plants. In *S. lycopersicum* both normal as well as in stressed conditions, SA increases the amount of ABA, which plays an important role like improvement in photosynthetic pigments, growth characteristics, and osmotic adjustments (Szepesi et al. 2009). It has been revealed that the biosynthesis of ABA is a vital factor for developing tolerance in tomato plants to sub-optimal root zone temperature (Ntatsi et al. 2013). In *Phaseolus vulgaris*, it has been revealed that acetylsalicylic acid alleviates chilling-induced changes by improving growth, photosynthesis, and antioxidants and by up-regulating the expression of cold-responsive proteins like CBF3 and COR 47 (Soliman et al. 2018). Moreover, cold stress triggers biosynthesis of polyamines, which also activate the synthesis of the signal molecule ABA (Cook et al. 2004; Kaplan et al. 2004; Pál et al. 2018). Low-temperature stress leads to loss of water, primarily a decrease in the uptake of water through roots accompanied by stomatal closure and these processes are mediated by ABA maintaining the status of water in plant body (Mahajan and Tuteja 2005).

ABA plays an essential role in stress by stimulating various downstream signaling responses that operate by either dependent or independent pathways (Chinnusamy et al. 2004). Both these pathways transfer signal through different transcription factors like MyB, MyC, ABREB/A and DREB1/2, thereby activating various regulatory sequences like DRE/CRT, MYBRS, MYCRS, ABRE, or NACRS (Shinozaki et al. 2003; Agarwal and Jha 2010). It also controls many functions of plants like development of seeds, flowering, accumulation of the lipids and proteins, morphogenesis in embryo, the opening of stomata and stimulation of remobilization and biological aging also stimulate synthesis of drought-tolerant proteins (Xiong and Zhu 2001; Nambara and Marion-Poll 2005; Cutler et al. 2010). ABA also helps in the removal of excess ROS generated by low temperatures, mainly by stimulation of antioxidant defense system,

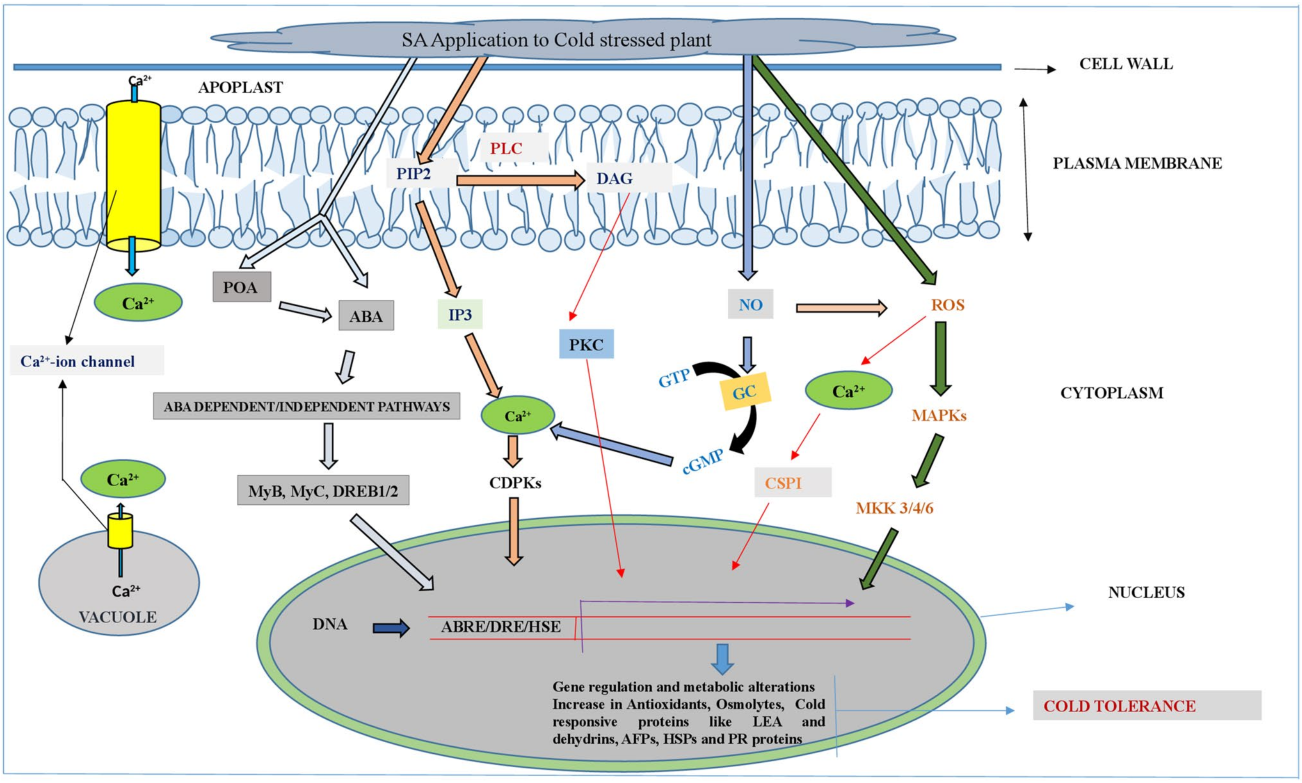

Fig. 6 Signalling of SA in cold stressed plants which activates: ABA-dependent and independent signalling (which helps in formation of LEA, dehydrins, AFPS, HSPs, and PR proteins), Ca signalling, mitogen-activated protein kinase pathway (MAPK), and ROS/RNS (reactive oxygen/nitrogen species) signalling pathways (which trigger formation of more antioxidants, osmoprotectants, and HSPs). Various components involved are *Ca* calcium, *POA* polyamines, *ABA* abscisic acid, *PIP2* phosphotidyl inositol-2-phosphate, *IP3* inositol triphosphate, *CDPKs* Ca-dependent protein kinases, *PLC* phospholipase C, *DAG* diacylglycerol, *PKC* protein kinase C, *NO* nitric oxide, *GC* guanalate cyclase, *GTP* guanosine triphosphate, *cGMP* cyclic guanosine monophosphate, *CSPI* CDPKs interacting protein, *ROS* reactive oxygen species, *MAPKs* mitogen-activated protein kinases, MKK3,4,6 mitogen-activated protein kinase kinase 3,4,6, *ABRE* ABA response element, *DRE* dehydration response element and *HSE* heat shock element

thereby preventing plants from oxidative stress (Guo et al. 2012). RD29A and RD29B (responsive to desiccation) gene induced under low temperature, high salt, and dehydration conditions are activated from both ABA independent and dependent pathways utilizing ABRE (ABA response element) and DRE:C-repeat (dehydration response element) as cis-acting elements (Jia et el. 2012).

Ca Signaling

The plasma membrane acts as a boundary between external and internal cellular environmental conditions and plays a vital role in perceiving exogenous information. It is hypothesized that a sensor protein, two-component histidine kinase system senses the cold stress in cell membranes. In yeast and other animals, the MAPK (mitogen-activated protein kinase) pathway, which leads to the synthesis of antioxidants and osmoprotectants, is stimulated by G-protein coupled receptor (GPCR), two-component histidine kinase and protein tyrosine kinase receptors. Among all these receptors, protein histidine kinase has been recognized in plants (Urao et al. 1998).

Calcium signaling plays a fundamental role in conferring cold tolerance in plants as reviewed by (Yuan et al. 2018). It is also revealed that SA increases tolerance to cold stress by maintaining the homeostasis of Ca^{2+} (Wang and Li 2006). The increase in the level of calcium in cytosol activates many calcium-binding proteins such as CDPKs (calcium-dependent protein kinases), which are the vital signaling proteins activated by abiotic stress. In the genome of Arabidopsis, almost 34 reputed CDPKs are encoded (Harmon et al. 2001), which are activated by abiotic stress and involved in signaling cascade (Tahtiharju et al. 1997; Hwang and Sheen 2001). Martin and Busconi (2001) revealed that cold stress stimulates CDPK associated with membranes in rice plants. Also, osmotic and cold stress enhanced the activation of OsCDPK7, which enhanced tolerance in rice plants (Saijo et al. 2000). In plants, a remarkable result was revealed with the help of yeast two-hybrid screen, a CSPI (CDPK interacting protein) was found which functions as an activator of transcription, signifying the possible role of CDPK in transmitting information from the cytosol to nucleus (Patharkar and Cushman 2000).

Osmotic stress, which often accompanies with chilling injury, may also lead to alterations in the composition of phospholipids (Munnik et al. 1998). Phospholipids present in membranes act as the backbone and its exposure to stress may result in the formation of secondary messenger molecules, by important enzymes which are A1, A2, C, and D phospholipases, and out of these phosphoinositide-specific phospholipase C (PI-PLC) is a most important cleaving enzyme. Ion homeostasis is affected by phospholipid phosphatidyl inositol-2-phosphate (PIP2) present in the plasma membrane by increasing the activity of PI5K (phosphatidylinositol 4-kinase) enzyme the synthesis of PIP2 is increased in osmotic stress (Mikami et al. 1998). Similarly, in Arabidopsis, levels of PIP2 were found to be elevated in salt and hyperosmotic stress (Pical et al. 1999; DeWald et al. 2001). PIP2 itself acts as a secondary messenger and is related to numerous processes like targeting/transport of various complexes of signaling molecules to particular sites of membranes (Martin 1998). Stress leads to overexpression of PI-PLC, which cleaves PIP2 into two vital secondary messengers, one is confined to membrane diacylglycerol (DAG), and another inositol 1,4,5-triphosphate (IP3) inside the cell is as depicted in Fig. 6. Protein kinase C (PKC) is activated by DAG, whereas IP3 triggers the release of calcium from vacuoles and intracellular sites by stimulating calcium ion channels (Sanders et al. 1999; Schroeder et al. 2001). The concentration of IP3 is also elevated by ABA in protoplasts of guard cells in *Vicia faba* (Lee et al. 1996) and in the seedlings of *Arabidopsis* (Sanchez and Chua, 2001; Xiong and Zhu 2001). Biosynthesis of ABA is induced under stress, possibly through calcium-dependent phospho-relay cascade (Xiong and Zhu 2001; Xiong et al. 2002).

ROS Signaling

Reactive oxygen species (ROS) such as superoxide, hydrogen peroxide, and hydroxyl radicals accumulate against various abiotic stresses like cold, drought, heavy metals, and salt (Choudhury et al. 2013). These accumulated ROS trigger the signaling cascade via calcium or directly through the main proteins of signaling (Price et al. 1994; Kolupaev et al. 2015). ROS signaling in HR response is believed to be affected by SA (Klessig et al. 2000). It is also revealed that SA and osmotic signaling utilize some common MAPK in signaling transduction pathways (Hoyos and Zhang 2000; Mikolajczyk et al. 2000). Cold stress has been shown to upregulate many genes as revealed from studies utilizing the microarray technique (Bohnert et al. 2001; Kawasaki et al. 2001; Seki et al. 2001; Majláth et al. 2012). Cascade of MAPK is involved in distributing the ROS/SA signaling to control the expression of various genes (Rodriguez et al. 2010; Ahmad et al. 2019). In Arabidopsis, different kinases like MPK3, MPK4 and MPK6 are stimulated by various abiotic stresses (Gudesblat et al. 2007) and also by SA (Neupane et al. 2019). Mockaitis and Howell, (2000) revealed that in Arabidopsis, SA is associated with the phosphorylation of MPK6. Also, osmotic and cold stress in Arabidopsis is reported to activate MAPK AtMPK6 (Yuasa et al. 2001). So, it could be established from these studies that MAPK cascade arbitrate both ROS and osmotic stress signal transduction pathways. MAPK pathway is preserved pathway of signaling in higher organisms depicted in Fig. 6, as MEKKs are stimulated by MKKs, which in turn stimulates MPKs. In Arabidopsis, MPK6 and MPK3 are activated by MKK4 and MKK5 respectively, MPK3 is induced by wound and MPK6 is regarded as homologs of SA induced protein kinase (Zhang and Klessig 1997; Yap et al. 2005).

NO Signaling

In plants, NO is regarded as a ubiquitous signaling molecule. It is generated in plants subjected to low-temperature stresses and plays a vital role in physiological, biochemical processes and involved in the regulation of redox homeostasis (Puyaubert and Baudouin 2014; Kolbert et al. 2017, 2019). NO also plays a crucial role in the germination of seeds and improved photo-morphogenesis, leaf growth, root development, phytoalexin production, and suppresses the development of floral meristem (He et al. 2004; Bethke et al. 2007; Mishina et al. 2007). NO has been shown to mitigate the harmful effects of ROS and reactive nitrogen species (RNS), thereby helping to develop tolerance against various stresses (Kopyra 2004; Corpas et al. 2008). It has been revealed that NO is instantly formed as plants are subjected to cold stress and participate in inducing cold-responsive genes (Zhao et al. 2009; Guillas et al. 2011). Moreover, exogenous application of NO has been shown to modulate the activity of antioxidant systems and synthesis of osmolytes in *Cicer arietinum* and *Pistia stratiotes* plants (Ahmad et al. 2016; Farnese et al. 2017).

NO mediates signal through cGMP (cyclic guanosine monophosphate), which is formed by activating enzyme guanylate cyclase (GC) by converting guanosine triphosphate (GTP) to cGMP and could interact with other mediators such as Ca, H_2O_2 and SA directly or indirectly as depicted in Fig. 6 (Lamotte et al. 2004; Wendehenne et al. 2006; Dubovskaya et al. 2019). Moreover, it has been shown that NO arbitrate signaling through lipids as phytosphingosine phosphate (PHS-P) and it has been affirmed that ceramide phosphate (Cer-P) are rapidly produced in response to cold stress (Cantrel et al. 2011; Guillas et al. 2011) thereby stimulating the activity of cold-responsive genes such as C-repeat/dehydration-responsive element binding factors (CBFs), cold regulated (COR), low-temperature-induced (LTI), and heat shock proteins (HSPs) (Cantrel et al. 2011). NO plays an important role in PTMs (post-translational targeting modifications) by nitration and the S-nitrosylation (Abat and Deswal 2009). Various enzymes that play an important role in regulating the overall growth and development of plants in stressful conditions such as SOD, CAT, APX, DHAR, MDHAR, and GR are easily targeted by PTMs (Antoniou et al. 2016; Begara-Morales et al. 2016). Beside cold stress, SA has also been shown to induce the activity of NO synthesizing enzymes and it has been revealed that among the phytohormones, SA is the vital hormone that interacts with NO and regulates various biochemical, physiological, and molecular processes (Hao et al. 2010). Furthermore, NO acts in close proximity with SA during its signaling in osmotically stressed seedlings of *Triticum aestivum* (Naser Alavi et al. 2014).

Cold Responsive Proteins

The proteomic studies have revealed that low-temperature stress triggers the expression of different proteins in plants. A variety of proteins expressed under low-temperature stress and SA application have been explained in the following sections.

Anti-freezing Proteins (AFPs)

SA has also been shown to be able to reduce ice nucleation and to induce AFPs in plants (Taşgín et al. 2003; Bredow and Walker 2017). These proteins are also known as ice structuring proteins produced by certain plants, animals, fungi, and bacteria to survive the harsh low-temperature conditions. These AFPs possess the capability of thermal hysteresis, which inhibit the growth of ice recrystallization in the intercellular space of a cell under cold stress (Griffith and Yaish 2004; Griffith et al. 2005). These proteins inhibit fusion of minute ice crystals into large ice crystals inside the cell, thereby preventing the cells from mechanical injury. Nearly six AFPs ranging from 16 to 36KD build up in the intracellular spaces (apoplast) of winter rye during cold acclimation and through sequencing of N-terminal amino acid and immunoblot analysis, it has been revealed that AFP's are homologous to pathogenesis-related (PR) proteins as two of the AFPs were found as endochitinase, two were β-1,3-glucanase and two were thaumatin-like proteins (Antikainen and Griffith 1997; Griffith and Yaish 2004). Plants AFPs differ from another organism as they have weaker thermal hysteresis and their physiological role seems to inhibit the recrystallization of ice rather than in preventing the ice formation and the majority of them are evolved PR proteins. So ice crystals formed in cold stress binds with AFPs and stop the crystallization process in plants, thereby conferring tolerance to plants from freezing.

LEA and Dehydrin Proteins

Late Embryogenesis Abundant (LEA) proteins were first discovered in cotton, but later on, its presence was also reported in many other plant species (Manfre et al. 2006; Delahaie et al. 2013). Initially these proteins were revealed to accumulate in plant embryos to help in desiccation tolerance or anhydrobiosis, but later on these proteins were also found to accumulate in vegetative tissues in response to various stresses like freezing, heat, drought, salt and also in plants having resurrection ability (Hoekstra et al. 2001; Cuming et al. 2007; Amara et al. 2014; Stevenson et al. 2016). These proteins also show some unique characteristics like the occurrence of IDRs (intrinsically disordered regions), highly hydrophilic with a higher number of polar amino acids (Goyal et al. 2005; Battaglia et al. 2008). LEA proteins are intrinsically disordered proteins (IDPs), which show moonlighting activity, i.e., to stabilize other proteins and perform the chaperone-like activity (Chakrabortee et al. 2012; Covarrubias et al. 2017). Dehydrins (DHNs), a type of LEA proteins, show the ability to behave chaperone-like activity and generally expressed during late embryogenesis (Kovacs et al. 2008; Liu et al. 2017). Dehydrins are the most frequently described LEA proteins and like LEA protein, it is highly hydrophilic and thermostable. Dehydrins have commonly been found in angiosperms (Lv et al. 2017), gymnosperms (Perdiguero et al. 2014), and bryophytes (Li et al. 2017). About 23 DHNs have been revealed in *Brassica napa* (Liang et al. 2016), 13 in barley (Tommasini et al. 2008), 11 in poplar (Liu et al. 2012), 10 in Arabidopsis (Hundertmark and Hincha 2008), 9 in *Malus* (Liang et al. 2012), 8 in rice (Verma et al. 2017), and 4 in *Vitis* (Yang et al. 2012). Several dehydrins such as ERD10 (early response to dehydration10), ERD14, citrus CuCOR19, wheat WCOR410, peach PCA60 and barley DHN5 helps the plants to withstand stress caused by low temperature, by functioning as chaperones and by interaction with the vesicles of phospholipids through electrostatic interactions (Kovacs et al. 2008). Abiotic factors and phytohormones stimulate the expression of dehydrins (Liu et al. 2017) like ABA is known to stimulaterab16D (response to abscisic acid) proteins (Tiwari et al. 2019). ABA signaling pathway is involved in the upregulation of the LEA gene in drought stress (Stevenson et al. 2016). Dehydrins contribute appreciably in stabilizing membranes, enzymes, and nucleotides in cells under abiotic stress. The majority of dehydrins are low molecular weight proteins ranging from 9 to 200 kD (Graether and Boddington 2014). DHNs show conserved specific motifs (Y, S or K segments) and these DHNs are divided into five subclasses; Kn, KnS, SKn, YnKn, and YnSkn (Banerjee and Roychoudhury 2016; Malik et al. 2017).

Treatment of SA and cold leads to more expression of YnSKn-type and KS-type of DHNs, respectively, in the wheat plant (Wang et al. 2014; Jing et al. 2016). Among all of these conserved motifs, the K segment is common in all DHN. It is evident from these studies that DHNs are ubiquitously present in cell organelles like vacuole, ER, nucleus, chloroplast, mitochondria, cell membranes, and cytoplasm. Yang et al. (2015) have revealed that under cold stress conditions, dehydrin WZY2 fused with GFP could be seen in both the cytoplasm as well as in the nucleus. Expression levels of dehydrins WZY2 and shDHN increase about 40 and 80 folds, respectively, against cold stress and promoters of these dehydrins contain low-temperature-responsive elements (LTREs). In transgenic tobacco, it has been disclosed that dehydrin PpDHNB improves the tolerance to cold (Agarwal et al. 2017). Like PpDHNB, DHN5, ShDHN also considerably enhance the tolerance against cold and drought stress in transgenic tomatoes, by increasing relative water content (RWC) and by reducing the accumulation of ROS in leaves. Many possible models have been put forwarded on the functioning of dehydrin LEA/DHNs that could attach to liposomes or confiscate with metal ions, thereby forming a complex of metal ion-dehydrin which interact with various molecules (Thalhammer et al. 2014; Hara et al. 2016). Current investigations have revealed that numerous dehydrins form polymers like homo, hetero, or multimers to unite and prevent biomolecules and helping the adjustment and organization of cellular compartments in a stressful environment. So DHNs help in the alleviation of the plants from cold stress by acting as molecular chaperones and by scavenging the ROS.

Heat Shock Proteins (HSPs)

Heat shock proteins are another category of stress protein which were initially seen to be formed in response to stress caused by heat, but these are found to be also stimulated by abiotic stresses like cold, drought, and salt stress (Sabehat et al. 1998). HSPs were discovered in the fruit fly and have now been identified in other animals, plants as well as in microorganisms, which are also known as stress linked molecular chaperones. Timperio et al. (2008) have revealed that cold, osmotic, and salt stresses are the potent inducers of HSP in plants. Based on molecular weight, HSPs have been divided into five main groups as follows: small HSPs (sHSPs), HSP60, HSP70, HSP90, and HSP100 as shown in Table 1. Out of these classes, HSP90, HSP70, and sHSPs have been revealed to mount up in response to low temperature (Lopez-Matas et al. 2004) and apart from functioning as molecular chaperones, these show strong cryoprotective effects (Renaut et al. 2006; Timperio et al. 2008). These proteins play a crucial function in maintaining the configuration of proteins, folding, homeostasis, and equilibrium in abiotic stress conditions (Timperio et al. 2008; Jaya et al. 2009; Hu et al. 2010; Grigorova et al. 2011). HSPs in a plant cell could be localized in the nucleus, chloroplast, mitochondria, and endoplasmic reticulum (dos Reis et al. 2012) each having different functions as sHSPs present in chloroplast and mitochondria are chiefly concerned in oxidative tolerance analogous to usual antioxidants (Hamilton

Table 1 Different classes of HSPs in plants their location and function *Source* modified from Boston et al. (1996)

CLASS OF HSP	SIZE (10a)	Examples in Arabidopsis	Location in a cell	Functions
HSP100	100–114	AtHSP101/AtHSP104	Cytosol, mitochondria, and chloroplast	Protect protein denaturation and aggregation of proteins. ATP controlled dissociation of assembled proteins
H5P90	80–94	AtHSP90	Endoplasmic reticulum and cytosol	Play main role in transducing signals, trafficking of proteins degradation of proteins and control of cell cycle requiring ATP for functioning
HSP70	69–71	AtH5P70	Cytosol, nucleus, mitochondria and chloroplast	Molecular chaperone, protein folding cytoprotection. Stabilize newly synthesized proteins and need ATP for functioning
H5P60	57–60	AtTCP-1	Mitochondria and chloroplast	Functions as chaperone so helping protein folding and subunit assembly in specialized manner also requires ATP
sHSPs	17–30	AtHSP21/AtHSP20/AtHSP18.2	Cytosol, mitochondria, chloroplast and endoplasmic reticulum	Molecular chaperone, translational control and microfilament stabilization

and Heckathorn 2001; Sun et al. 2002). Genes of HSPs are activated by the transcription factors known as Hsfs (heat shock factors), which remains in an inactive state in the cytoplasm (Hu et al. 2009). Each of these factors is said to be having one C-terminal and three N-terminal (Schuetz et al. 1991). Plants show several Hsfs, which are divided into three different classes; HsfA (A1 and A2 in tomato), plant HsfB (HsfB1 in *L. esculentum*) and HsfC (Tripp et al. 2009). These heat shock factors are present in cytoplasm in an inactive state (monomeric form), whenever plants are exposed to stress conditions then these Hsfs are activated (trimeric form) and are able to import into nucleus where they bind with the specific sequence element in DNA known as heat shock elements (HSEs) once these Hsfs bound to DNA, then transcription occurs leading to formation of HSPs (Sorger and Nelson 1989; Larkindale et al. 2005).

In tomato seedlings, SA has been shown to help in the binding of Hsfs to DNA, which points out that SA functions in modulating the binding of Hsfs to DNA (Snyman and Cronje 2008). So, HSPs are increased in cold stressed plants by SA treatment, which functions as molecular chaperones and helps in the proper folding of proteins that get denatured or misfolded under cold stress.

Other Proteins

Pathogenesis-related (PR) proteins are expressed usually in response to the pathogenic attack but are also said to be formed in response to cold and other abiotic stresses. Among PR proteins PR-14 (lipid transfer protein), PR-11 (chitinases), PR-10 (bet v-1 homologs), PR-8, PR-5 (thaumatin-like protein), PR3 and PR-2 (b-1,3-glucanase) proteins are expressed in response to low-temperature stress (Liu et al. 2003). PR-2, PR-5, and PR-11 proteins present in apoplastic space have antifreeze activity, which means that they have the ability to prevent recrystallization of both inter and intracellular nucleation (Griffith and Yaish 2004; Renaut et al. 2006). SAR (systemic acquired resistance) is activated by SA, which leads to the expression of PR proteins. NPR1 (NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1) have been shown to play the role of SA receptor (Wu et al. 2012) which interact with the basic leucine zipper transcription factors such as TGACG-BINDING FACTOR5 (TGA5), TGA6 and TGA2 for SA induced PR expression and resistance against pathogens (Zhang et al. 2006). Depending upon duration and severity of cold stress and application of SA, the expression and activity of several other proteins and enzymes are upregulated which includes enzymatic and non-enzymatic antioxidants, enzymes related to photosynthesis such as ribulose 1,5 bisphosphate (RUBISCO), phosphoenolpyruvate carboxylase (PEPC), photo-respiratory enzymes glycolate oxidase (GO) and catalase CAT) (Yordanova and Popova 2007).

Conclusion and Future Prospects

Low-temperature stress affects various morphological, cytological, physiological, and biochemical attributes in plants. Modulation caused by low-temperature stress at these levels of attributes negatively affects the growth and development of plants. SA, a multidimensional and a potent PGR, plays an essential role in the growth and development of plants during abiotic stress. SA regulates growth and productivity in a dose-dependent manner, where low concentration proved to be beneficial in enhancing photosynthesis and other characteristics of a plant, whereas higher concentration causes an increment in the stress level of plants. SA acts as a remedy in mitigation and regulation of growth and productivity in cold stress by transducing signals through several components of signal transduction pathways. Major components include Ca, ROS, ABA, NO, MAPKs, cGMP, and phospholipid cascades. This SA mediated signal in cold stressed plant leads to the activation of various transcription factors that causes the expression of genes essential for plant survival in low-temperature stress. The genes induced to express in cold stressed plant by SA mediated signaling involves enhancement in activity of antioxidants, more accumulation of compatible solutes and various other cold-responsive proteins like AFPs, HSPs, LEA, and dehydrins, PR proteins and various other proteins that regulate growth and development. There are many questions unanswered about the molecular and cellular mechanisms of SA transport system, SA signaling pathways under cold stress involving SA receptors, mediators, and targets. In addition to this, cross-talk of SA with other phytohormones needs to be investigated so as to obtain a clear picture of the response of a plant to various abiotic stresses.

Acknowledgements M. Saleem gratefully acknowledges the financial support in the form of Junior Research Fellowship rendered by CSIR-UGC, New Delhi Ref. NO. 677/(CSIR-UGC NET JUNE 2018).

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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