Review Article

Salicylic Acid Enhanced Low Temperature Stress Tolerance in Vegetables: A Review

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Abstract

Low temperature stress adversely affects growth, productivity and triggers a series of morphological, physiological and biochemical changes in plants. It is a major environmental cue that limits the vegetable productivity of plants, particularly in hilly areas. Development of procedures to enhance low temperature stress tolerance in plants is crucial and attracts considerable attention. The tolerance to low temperature stress is an intricate process that involves morphological, physiological and biochemical modifications. Salicylic acid is a vital signalling molecule for modulating plant response to various abiotic stresses. Salicylic acid induced alleviation of low temperature stress has been reported in vegetables. In this review, the aim is to emphasise the ameliorative effects of SA on growth, physiological, biochemical changes, yield and quality of plants growing under low temperature stress. On the basis of different studies, it has been concluded that SA enhanced the low temperature stress tolerance significantly and increased plant growth, photosynthetic pigments, accumulations of osmoprotectants and activity of antioxidant enzymes. It also increased production and quality of vegetables under low temperature stress.

Keywords: Photosnthetic pigments, osmoprotectants, antioxidant enzyme, growth, yield and quality

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Introduction

Environmental stress such as cold, heat, salinity and drought adversely affect growth and productivity and trigger a series of morphological, physiological, biochemical and molecular changes in plants that eventually interrupt plant life [1, 2]. Most of the arable lands of world, which when exposed to these abiotic stress conditions have an adverse impact on global vegetables production. These abiotic stress conditions decrease crop productivity upto 50-70% [3]. Plants undergo several metabolic cascades for their survival during these stress conditions [4]. Plant's response is a complex phenotypic and physiological phenomena which is highly influenced by low temperature stress. To enhance the food production, crops are often grown under stressful environments which result in lower yield. The key factors to reduce yield and quality of crops are fluctuations in climatic conditions, such as low temperature stress. During winter season, low temperature stress adversely damages vegetable production. In response to low temperature stress, several phenotypic symptoms such as stunted seedling, poor germination, reduced leaf expansion, yellowing of leaf (Chlorosis) and wilting occur, which sometimes results into tissue damage (necrosis) [5].

Vegetables have an imperative role to play in the diversification of agriculture. They ensure food and nutritional security of the ever budding population of India. However, vegetables are sensitive crops and their production is hindered by various abiotic stresses. Temperature, both low and high, is the most serious environmental stresses. Low temperature stress has been reported as one of the most restraining environmental factors for agricultural crops, particularly vegetables, which accounts for significant crop losses [6]. Summer vegetables are sensitive to chilling temperature (0-15°C) throughout plant development *i.e.* seed germination, vegetative growth and reproduction. Under low temperatures, lots of seeds do not germinate or germinate irregularly and plants grow differentially with delayed plant formation leading to variability in crop development. During later stages, plant growth and development are extremely retarded that either limit or lead to no flower and fruit production [7]. Numerous factors affect the degree of injury which may be temperature, time of exposure, organ or tissues of the plant exposed and the physiological stage and temperature at which the plant is being grown [8]. Weak fruit set after a cold period could be due to the poor pollen viability [9]. Chilling sensitivity can occur at two distinct developmental stages i.e., pollen formation (from meiosis to release of mature pollen) and pollen function [10]. Low temperature stress affects the reproductive stages of plant with delayed flowering which makes the pollen sterile that severely affects the crop yield [6, 11]. Low temperature stress also limits the agricultural productivity of plants in hilly areas and has a major impact on the survival and geographical distribution of the plants. The plant growth and crop productivity gets disturbed which results in substantial crop failure [12].

Plant hormones have an essential role to play in regulating the developmental processes and signaling network in plants suffering from abiotic stress. Recent studies have shown that plant hormones have potent role in reducing or eliminating the adverse effects of abiotic stress [13, 14]. Recently, salicylic acid (SA) has been added to the existing list of classical phytohormones and is considered as a possible tool to boost tolerance in plants to environmental stress. Salicylic acid is an endogenous plant growth regulator and reportedly has a wide range of metabolic and physiological responses that affect the growth and development of plants [15]. SA, an active phenolic compound plays an important role in providing resistance to plants against pathogens. It takes part in the defense mechanism of plants in response to abiotic stresses such as low and high temperature stress [16-18]. SA is a plant hormone which plays a crucial role in the regulation of physiological and molecular mechanisms to acclimatise plants in extreme environmental conditions and is believed to have a role in plant's response to abiotic stress [16, 17, 19, 20]. SA and other phenolic compounds (benzoic acid, acetyl SA, SSA) have been found to increase cold tolerance of plants when applied exogenously [16, 21].

Development of methods to enhance stress tolerance in plants is crucial and attracts considerable attention. The tolerance to cold stress is an intricate process that involves morphological, physiological and biochemical modifications. Salicylic acid is a vital signal molecule for modulating plant response to various abiotic stresses [15]. Salicylic acid induced alleviation of cold stress has been reported in tomato [21-23], cucumber [24], squash [25] and watermelon [26]. In this review, the ameliorative effects of SA on growth, physiological, biochemical changes, yield and quality of plants growing under low temperature conditions have been discussed.

Amelioration of Low Temperature Stress

Use of plant growth regulators (PGRs) to induce low temperature stress tolerance in pants is one of the possible approach. In recent studies, several PGRs have been tested to alleviate the low temperature stress in plants [22, 23, 27, 28]. Salicylic acid (SA) is a plant produced phenolic compound that can function as a PGR. It's an endogenous plant growth regulator and has been found to generate a wide range of metabolic and physiological responses in plants affecting their growth and development [15]. SA has received much attention due to its major functions in plant's responses to biotic and abiotic stresses. Several studies have been reported about various beneficial effects of SA on plants under abiotic stresses [18, 29]. Sayyari [26] reported that foliar application of SA increased cold tolerance of cucumber. In tomato and bean plants, the lower concentration of SA and ASA (acetyl salicylic acid) @ 0.1 mM and 0.5 mM have been found more effective against low temperature stress [22, 30]. ASA is a close analogue of SA and when applied exogenously is converted to SA spontaneously, having similar effects to SA in plant defense processes [31-33]. Orabi [22] reported that SA led to enhancement of endogenous growth regulators under low temperature. SA enhanced plant growth and cell division via regulation of other hormones [34] and mitigating abiotic stresses by increasing the growth regulating hormones like auxins and cytokinins [35]. Moreover, the application of SA increases the content of auxin and ABA and prevents the reduction of cytokinin under drought and salinity stress conditions thereby producing a higher total biomass and seed vigor index[35, 36].

Plant Growth and Development

Salicylic acid is a natural phenolic compound that plays the role of a key signaling molecule in induction of plant defense mechanism and reduces symptoms of abiotic stress as well as regulates growth and development of plants [16, 18]. Low concentration of SA enhances and influences the differentiation of cells, tissues of plants and increases the plant growth and development [37]. The enhanced fresh and dry matter of plants under stress conditions in response to SA might be related to the increase of antioxidant response that enhances the tolerance of plants to damage by environmental stress [38-40]. Exogenous application of SA enhanced the activity of cell division by stimulating the mitosis of the apical meristem of seedling roots which caused an improvement in plant growth and deve lopment [41]. Application of SA under low temperature stress significantly increased the growth attributes viz., plant height, number of leaves per plant, fresh and dry weights of leaves and root length in tomato [21, 22]. Similar results obtained by Sayyari [26] in watermelon and Imami [42] in chickpea showed that the growth parameters increased significantly with the application of SA under cold stress. The ability of SA to enhance growth parameters, ameliorating the adverse effects of low temperature stress, may have significant implications in increasing the plant growth and development, and overcoming the growth barrier. Gharib [43] reported that enhanced photosynthetic activity in basil with the application SA at low concentration enhanced plant growth attributes *viz.*, plant height, number of branches and leaves per plant as well as leaf area, fresh and dry weights. Similar there are reports that application of SA significantly enhanced growth parameters such as; length and dry weight of root and shoot, leaf area, specific leaf area, specific leaf weight and leaf weight ratio under stress conditions [44-47]. Application of SA increased photosynthetic rate due to increased leaf area as has been reported by Gharib [43]. Hussein [48] and Hayat [10] also reported increased productivity due to an improvement in all growth attributes including plant height, number of leaves, leaf area, dry and fresh weight of shoot, leaves and plant with the application of SA under stress condition. Fariduddin [49] observed that the dry biomass per plant increased significantly with the application of low concentration of SA. However, application of higher concentrations of SA had an inhibitory effect on dry biomass under stress [15].

Physiological and Biochemical Mechanisms

Plant species have developed various physiological and biochemical mechanisms to cope with abiotic stresses. For instance, to mitigate low temperatures stress induced damage, plants may up regulate different scavenging mechanisms, such as enzymatic antioxidants catalase (CAT), ascorbate peroxidase (APX) and peroxidase (POD) and osmoprotectants (stress signaling substance) [50, 51]. These compounds protect membranes and photosynthetic apparatus from the injurious effects caused by abiotic stresses [52, 53]. Phenolic compounds are common plant produced signaling molecules responsible for enhanced tolerance to environment stresses [54]. SA acts as a cofactor for various enzymes and regulates the phytohormone mediating signaling processes and many physiological and biochemical processes in plants. SA is a vital signaling molecule in plants which defends the plant from various abiotic stresses like cold stress [50, 51, 55].

Several studies reported that SA is a crucial regulator of photosynthesis because it affects chloroplast and leaf structure, stomatal closure, chlorophyll and carotenoid contents [49]. Application of SA enhanced the photosynthetic net CO_2 assimilation in mustard seedlings. The role of SA at a certain stage with moderate and grievous environment stress may be a part and can be attributed to redox regulations in plant cells and protection of the cell structure under low temperature stress [56, 57]. SA plays crucial roles in response to external stimulation and by activating defense system in plants. Activation of phospholipase D is an early response to low temperature, involved in the accumulation of free SA and the development of thermotolerance induced by low temperature acclimation in grape berries [58]. SA acts as an endogenousphytohormone from phenolic compound family, having the capacity of antioxidant protection system and regulates different physiological and biochemical processes in plant such as: activity of photosynthesis pigments, maintenance of tissue water contents and reduced membrane permeability, adjustment of the activity of antioxidant enzymes, stomatal conductivity and tolerance to various abiotic stresses [15, 36, 50, 59]. Furthermore, SA treatment maintains IAA and cytokinin levels in the plant tissues, which enhance the cell division and dry weight as reported by Sakhabutdinova [41]. Miura and Tada [18] observed that the effects of SA on the physiological and biochemical processes of plants depend on the concentration and period of application, type of plant, the stage of growth and environmental conditions [22]. Several workers have reported that low concentration of SA may increase the activation of antioxidants [50] and tolerance to various abiotic stresses, similar reports have been made by Senaratna [30] that treatment at low concentrations of (0.1 and 0.5 mM) promoted tolerance to chilling stress in bean and tomato. But high concentrations of SA may cause negative results or susceptibility to abiotic stresses [60]. The exogenous application of SA (0.5 mM) enhanced the low temperature stress tolerance of cucumber [61] and potato [62]. Similarly, Kang [63] reported that the foliar application of SA @0.5mM on the leaves of banana enhanced the chilling tolerance.

Regarding SA effect, Khodary [38] and Szepesi [64] reported that application of SA enhanced the photosynthetic pigments (chlorophyll, carotenoid contents), increased the photosynthetic efficiency, photosynthetic rate, dry weights and reduced the membrane leakage, leading to increased plant growth in tomato plants under stress conditions. Similarly, Shi [65] noticed that exogenous application of SA significantly increased net photosynthetic rate which could be due to the improvement in the functioning of photosynthetic machinery in plants either by the mobilization of internal tissue nitrate or by chlorophyll biosynthesis. Suitable concentrations of SA and ASA inhibit chlorophyll degradation and enhanced photosynthesis by prohibition of chlorophyll oxidase enzyme activity in tomato [15, 22, 23, 66]. Environmental stresses enhance injures of cellular membrane including the increased electrolyte leakage MDA and H_2O_2 content due to oxidative damage and they are considered to be sensitive stress markers [22, 23, 67, 68]. However, several workers have reported that the decrease of electrolyte leakage, MDA and H_2O_2 content in tomato with the application of SA and also mentioned that foliar application of SA regulates and maintains the membrane functions of tomato plants[22, 40, 69]. Further, SA and ASA can curtail the injuries in cell membranes through increased antioxidant enzyme activity of plants under several abiotic stress conditions and partly maintain membrane permeability as well as reduce the amount of electrolyte leakage [22, 61, 70]. Similarly, Kabiri [71] and Orabi [22] reported that application of SA increased the reduction in the level of lipid peroxidation and electrolyte leakage from leaves as well as with more profound growth processes as compared to non stress plants of tomato.

Stressful environments induce the generation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), hydroxyl radicals (OH^-) *etc*. in plants thereby indicate a state of oxidative stress [72]. This enhanced ROS level in plants suggests oxidative damage to biomolecules such as lipids, proteins and nucleic acids, thus altering the redox homeostasis [73]. However, Kang [63] reported that SA increased the efficiency of antioxidant system in plants under stress conditions. SA treatments caused marked decrease in CAT activity accompanied by significant enhancement in the activities of POD and APX relative to control plants in fresh leaf and root tissues of tomato under low temperature conditions. The reduction in CAT activity and enhancement in POD and APX activities were more pronounced in response to applications of SA in tomato [22]. Foliar application of SA could regulate the synthesis and activities of antioxidant enzymes and enhance plant tolerance to abiotic stress [74]. Hayat [15] reported significantly enhanced activities of antioxidant enzymes such as POD, CAT and APX with the application of SA to stressed plants [75] which might be due to its regulatory function at transcriptional or translational level. Similarly, Yusuf [76] and Boukraa [77] found that application of SA enhanced the level of antioxidant enzymes such as (CAT, POD, APX and SOD) under stress conditions. Gharib and Hegazi [78] reported that the CAT, POD, APX and SOD may be coordinately regulated during plant growth and development, but differentially expressed in response to various abiotic stresses for controlling ROS homeostasis [79]. SA enhanced low temperature stress tolerance to watermelon by increasing the activities of POD, CAT, APX and SOD. The activities of antioxidative enzymes enhanced significantly in the low temperature stress tolerant watermelon germplasm than that of the cold stress sensitive germplasm [80, 81].

Yield and Quality

Low temperature stress significantly decreases the yield and quality of vegetables. Application of SA enhanced yield and quality of tomato under low temperature stress conditions [21, 22]. Similar reports have been made in cucumber [82]. Number of fruits significantly enhanced in pepper [15] and cucumber [83] in response to foliar application of SA. Several studies revealed that application of phenolic compounds were able to reduce chilling symptoms in tomato fruits [84]. Javaheri [85] reported that the application of SA significantly enhanced the amount of vitamin C, lycopene and also increased rate of pressure tolerance of fruits, improved quantity and quality of tomato fruits. Recent studies suggest the predominant role of the phenolic compounds in the modulation of the response of plants towards environmental stresses by induction of the antioxidant ability [22, 77]. Exogenous application of SA alleviated the toxic action induced by low temperature and decreased lipid peroxidation rates with increasing antioxidant activity. Chandra [86] reported that exogenous application of SA enhanced total soluble sugar and soluble protein of cowpea plants. Khandaker [46] reported that the foliar application of SA in red amaranth significantly enhanced the yield, antioxidant activity, amount of beta-cyanins, chlorophyll and total polyphenols. The application of SA treatments (0.5 mM and 1.0 mM) caused significant increase in Total Soluble Solids (TSS) in fruits of tomato [22]. TSS values are associated with taste and have significant indication for improvement in yield and quality. Moreover, Abdullahi [87] showed that plant growth and TSS levels increased after application of salicylic acid.

Conclusion

Vegetables have an imperative role to play in the diversification of agriculture. They ensure food and nutritional security of the ever budding population of India. However, vegetables are sensitive crops and their production is hindered by various abiotic stresses. Temperature, both low and high, is the most serious environmental stresses. Low temperature stress has been reported as one of the most restraining environmental factors for agricultural crops, particularly vegetables, which accounts for significant crop losses. Low temperature stress adversely affects growth, productivity and triggers a series of morphological, physiological and biochemical changes in plants. It is a major environmental cue that limits the vegetable productivity. The demand for food and vegetables will continue to rise with the increase in global population; therefore improving productivity to ensure sustainable yields under changing environmental conditions is imperative. Development of methods to enhance stress tolerance in plants is crucial and need based. The tolerance to cold stress is an intricate process that involves morphological, physiological and biochemical modifications. SA, an active phenolic compound plays an important role in providing resistance to plants against pathogens and in response to abiotic stresses such as low and high temperature stress. SA plays a significant role in the regulation of physiological and molecular mechanisms to acclimatise plants in extreme environmental conditions and is believed to have a role in plant's response to abiotic stress

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