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REWIEW PAPER

HORTICULTURAL STUDIES

Current Progress on the Responses of Eggplant to Ultra-Low Temperatures during Production

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Abstract

Cold stress has an adverse effect on eggplant growth and is a yield-limiting factor. Low temperatures are prevalent during early spring cultivation in temperate climates, and they have a negative impact on eggplant growth and development. Temperatures below the eggplant's optimum growth temperature (22-30ºC) are considered low and detrimental to growth and development. In this review, we described how eggplants respond to moderately low and cold temperatures at different scales. We compiled literature on the current understanding of physiological, cellular responses to cold stress in eggplant as well as the transcriptional regulation during cold stress. Subsequently, we also highlight the genetic and molecular evidence, particularly the function of cold-responsive genes in strengthening cold tolerance in eggplant. Lastly, we covered the role of mineral nutrients and useful microorganisms in alleviating the consequences of cold stress in eggplant roots. Agronomic management practices such as the use of AMF species may mitigate the detrimental effects of low temperature and the enhancement of crop varieties with high yield throughout cold stress.

1. Introduction

Every year, there is a significant loss of crop yield and quality due to a range of abiotic stresses such as drought, salinity, high, and low temperature. Plant growth, development and yield are significantly affected by temperature (Prabhavathi and Rajam, 2007; Zhou et al., 2018). In the eggplant (*Solanum melongena*), a thermophilic vegetable and one the most important in the Mediterranean region and Asia, low temperatures affect productivity (eggplant yield and quality) particularly during early spring in those regions. Thus, the top eggplant producing countries (China, India, Egypt and Turkey) are located in Asia and in Mediterranean regions (Alam and Salimullah, 2021). Eggplant is ranked in the top ten vegetables with high anthocyanin content particularly in fruit peels. This particularity is mostly noticed in dark/purple skin eggplant cultivars. Furthermore, anthocyanins as important secondary metabolites play an important role in human health (Jiang et al., 2016). In contrast to other *Solanaceous* crops, eggplant is substantially more sensitive to low temperature (Wan et al., 2014). The growth and development of eggplant is optimum under this following range of temperatures; from 22 to 30ºC. Under low temperatures, the chilling damage devastates mostly freezing-sensitive eggplants. It is often followed by abnormal growth with disordered metabolism. During the winter season, low temperatures limit root growth, reduce plant vigor, and produce deformed fruits (Concellón et al., 2005; Zhou et al., 2018; Alam and Salimullah, 2021). It is also reported that low temperature stress in eggplant throughout the cool season (temperature below 15ºC) engenders gradual loss of pollen fertility and leads to the development of seedless fruit (Nothmann and Koller, 1975; Abak and Guler, 1994; Makrogianni et al., 2017). The combination of insufficient light, low temperature, and/or high humidity under greenhouse cultivation decrease fruit yield and quality in eggplant (Acciarri et al., 2002). For instance, in North-China, it is reported that eggplant lower yield and poor quality subsist due to the cultivation in unheated greenhouses during winter season characterized by low temperatures and reduced light intensity (Gao et al., 2008).

In recent years, more attention has been given low temperature stress due to its adverse effects and its frequent occurrence in early spring (Yang et al., 2020). Thus, growing cold-tolerant varieties is affordable way to avoid huge losses arising from cold stress. Eggplant (*Solanum melongena* L.) originated in the subtropical climatic region. Moreover, it is famously grown in temperate climatic zones, both in the open field and in under covers. In temperate latitudes, eggplant seedlings growing usually starts in greenhouses (Pohl et al., 2019). Eggplant needs a temperature of approximately 15ºC (night) and 23-25ºC (day) for satisfactory development and yield; unless plant growth rate slows and fruit set is hampered. Heating in the Mediterranean Basin's low-cost and low-input greenhouses has not expanded due to the high cost of fuel. During the winter, for instance, temperatures are typically kept to a minimum, with nighttime temperatures sometimes falling below 10-15ºC (Makrogianni et al., 2017). It has been reported that treating flower buds with phytohormones alleviates the negative effects of suboptimal weather conditions on fruit production in the Mediterranean region, particularly during the winter season in unheated greenhouses. Unfortunately, because of the cost of both chemicals and labor, this treatment method is more expensive (Acciarri et al., 2002).

In this review, we compiled various published research on eggplant's growth and development-related responses to moderate low and cold temperature. It is well known that plants have built effective responses at the biochemical, physiological and morphological levels enabling them to mitigate and/or adapt to abiotic/biotic and disadvantageous environmental conditions. Thus, such responses to stress are complex and involve numerous factors such as signaling, hormones, transcription factors, and secondary metabolites.

2. Physiological changes during eggplant cultivation under low temperatures

It is acknowledged that unfavorable environmental conditions inhibit fruit set and growth in a variety of vegetable crops. High or low temperature and humidity, low light intensity, strong wind and heavy rain all have a negative impact on several stages of the reproductive cycle, including pollen formation, dissemination, and germination, fertilization, and seed maturation. As a result, they reduce fruit production (Donzella et al., 2000). It is reported that temperature lower than 17ºC causes a slowdown in eggplant growth and when it gets lower than 10ºC metabolic and physiological disturbance occurs. Moreover, low temperature is detrimental to the cell membrane system leading to the increase of relative conductivity with a change in Malondialdehyde (MDA) content and electrolyte leakage (Chen et al., 2011; Lv et al., 2017). Cold stress reduces the hydraulic conductance and osmotic potential in the cell, resulting in stomatal control setback (Latef et al., 2016). These physiological changes have a negative impact on pigment composition, chloroplast development and chlorophyll fluorescence which reduces photosynthetic efficiency (Pasbani et al., 2020).

Chilling temperatures generally refers to low temperatures in the range of 0-15ºC and that are somehow non-freezing. These kinds of temperatures are common during early spring in temperate regions. Thus, they are often detrimental to the productivity of chilling-sensitive plants (Pohl et al., 2019). According to reports, chilling stress induces a reduction of cell membranes' activities as well as the root respiratory intensity. Hence, undesirable active oxygen is produced in the eggplant. Accordingly, numerous enzymes of plant defense system, such as catalase (CAT), superoxide dismutase (SOD) and peroxidase (POD) as well as the antioxidants (ascorbic acid and reduced glutathione) are promptly employed to scavenge reactive oxygen species (ROS) (Gao et al., 2008). At the cellular level, accelerated ROS production alters homeostasis due to stress factors (Gao et al., 2008; Pohl et al., 2019). Additionally, adverse effect on the photosynthetic apparatus in tropical and subtropical plants are known to be caused by chilling temperatures as well as the reduction of plant photon energy utilization efficiency and acceleration of the oxygen generation resulting in low photosynthetic rate (Gao et al., 2008). By assessing the acclimation mechanisms of several eggplant (*Solanum melongena* L.) cultivars to chilling stress, Pohl et al. (2019) demonstrated that less chilling-sensitive eggplant cultivars were able to modify antioxidant system during exposure to low temperature stress (6ºC) compared to control plants kept at 18°C. Thus, eggplant's defense systems were quite enough to scavenge the surplus of ROS. Briefly, the antioxidant defense system played a vital role in the tolerance potential of eggplant cultivars and peroxidases (POX) and soluble sugars (SS) contributed to the anti-oxidative mechanisms involved in the stress response. Eggplant cultivars engage in metabolic efforts to raise SS content in leaf tissues. SS are reported in several publications as a major player in stress response and changes in ROS balance. They serve as signaling molecules and osmoprotectants to cellular membranes, not forgetting their role as energy providers and main building units. Sugars are also referred to as protectors of chloroplasts and photosynthesis stabilizers in stress conditions (Peshev et al., 2013; Gangola and Ramadoss, 2018; Pohl et al., 2019).

It was determined by Xia et al. (2013) that under salt stress physiological changes of sensitive and tolerant eggplant seedlings are slightly different. Particularly in the leaves of sensitive eggplant materials, they observed a high increase of malondialdehyde (MDA) and O_2 contents, enzyme activities such as SOD and POD also rise as well as an increase in soluble protein and proline contents. All above mentioned increases changes are less significant in tolerant eggplant materials. The authors concluded that under cold stress, tolerant materials can mitigate cold damage by regulating enzyme activities to maintain plant metabolism and growth at normal rate. Likewise, Xia et al. (2018) advanced that under cold stress, the chlorophyll content in eggplant leaves diminish. However, an increase of proline, MDA, soluble sugar and soluble protein contents in the seedlings is noticed. Authors also reported the existence of high correlations between the electric conductivity (EC) and the MDA/soluble sugar content. Similarly, Lv et al. (2017) have confirmed that under cold stress, cold tolerant eggplant materials display high activity increase of POD, SOD, CAT as well as and a moderate increase of electrolyte leakage (EL) and MDA content compared to cold sensitive eggplant materials (Figure 1). Furthermore, soluble sugar, electric conductivity and MDA have been reported as suitable for assessing eggplant seedling cold tolerance (Xia et al., 2018).

It was also reported by Wang et al. (2009) that cold stress alters photosystem II, the second type of photosynthesis known for capturing the energy from sunlight and employing it to extract electrons from water molecules. Moreover, it is recognized that during rapid changes in temperatures (low/high) an immediate cellular acclimation reaction is initiated in chloroplasts. It consists of changes in thylakoid-located mechanisms as well as the stroma and transport activities alteration throughout the chloroplast envelope. Thus, these reactions reinstate homeostatic level and assist in plant stress tolerance (Schwenkert et al., 2022). Eggplants are good for the human diet due to their high antioxidant and low carbohydrate content (Makrogianni et al., 2017). However, some studies have demonstrated that low-temperature stress has an effect on antioxidant content. Pohl et al., (2019) demonstrated, for instance, that during chilling acclimation at extremely low temperatures (6°C), eggplant seedlings, particularly chilling-sensitive cultivars, exhibit an increase in antioxidant activity, followed by an increase in malondialdehyde (MDA) and H_2O_2 content.

3. Molecular mechanisms of low temperature response in eggplant

A comprehensive understanding of the molecular mechanisms governing low temperature tolerance is necessary to ensure high yield and quality productivity of eggplant and can facilitate the creation of crop varieties that can mitigate the severity of cold stress on productivity (Yang et al., 2020; Zhou et al., 2020). The sensing and signalling of low temperature stress is a complex process remodeling biochemical, morphological and physiological processes in plants. Numerous transcriptional factors, core genes and pathways associated with the regulation of plant growth, development and response to low temperature have been reported in literature (Mehrotra et al., 2020; Yang et al., 2020). Table 1 shows a number of cold-responsive genes in eggplant. However, more studies are needed before developing stress-tolerant eggplant varieties.

Previously, quantitative genetics was also tried in stress-related studies in eggplants. For instance Yang et al. (2017) utilized high throughput sequencing to investigate the role of MicroRNAs (miRNAs) in plant development and stress responses in wild eggplant (*Solanum*

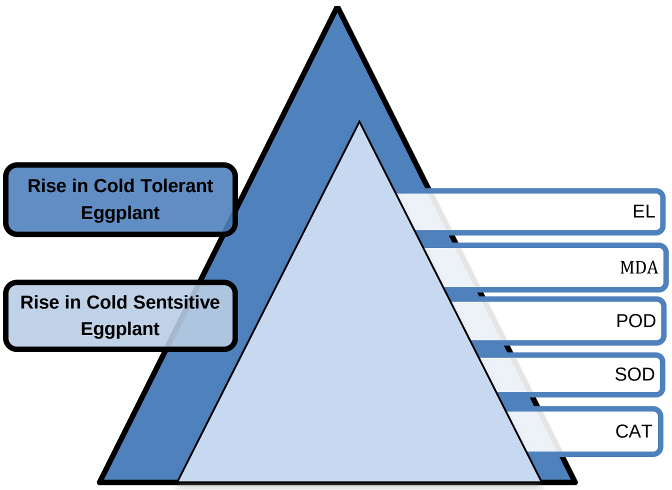

Figure 1. Major physiological changes of cold sensitive and tolerant eggplants under cold stress.

Table 1. Gene related to low temperature stress in eggplant.

No	Gene	Family/Subfamily and/or Superfamily	Function	Mechanism of action	Reference
1	*SmAP2/ERF* genes	*AP2/ERF*[b] superfamily	Transcription factor	Response to plant hormones and stress conditions such as response to low temperature.	(Li et al., 2021)
2	*SmNAC* genes (*SmNAC19, SmNAC75* and *SmNAC31*)	*NAC* family/ATAF subfamily	Transcription factor	The control of a broad range of responses to different abiotic stresses.	(Wan et al., 2021)
3	A total of 20 Hsf (*SmeHsf*) genes were identified	*SmeHsf* family	Transcription factors	Under stress conditions, Hsfs are implicated in a variety of protein homeostasis. They improve tolerance to a variety of abiotic stresses, including low temperature stress.	(Wang et al., 2020)
4	*CTR1* and *EBF1/2*	N/A	Transcription factor	Response to low temperature and ethylene signal transduction during cold stress.	(Yang et al., 2020)
5	*SmWRKY* genes (*SmWRKY26* and *SmWRKY32*)	*WRKY* gene family	Transcription factors	They favorably regulate the response to cold stress.	(Yang et al., 2020)
6	*SmICE1a*	*CBF*[a] family	Transcription factor	It trigger expression of SmCBF2, SmCBF1 and SmCBF3 and it plays a crucial role in cold response.	(Zhou et al., 2020)
7	*SmMYB113*	*CBF*[a] family/	Transcription factors	It is involved in cold-controlled anthocyanin biosynthesis.	(Zhou et al., 2019)
8	*SmCBFs* (*SmCBF1, SmCBF2* and *SmCBF3*)	*CBF*[a] family/ CBF-*DREB* subfamily	Transcription factors	They are engaged in abiotic stress response in eggplant including in response to low temperature.	(Zhou et al., 2018)
9	P_{SAG12}-*IPT*	*IPT* gene	N/A	The overexpression of the PSAG12-IPT gene defers leaf senescence and also triggers abiotic stress tolerance.	(Xiao et al., 2017)
10	*SmCHS*[d], *SmCHI*[c], *SmF3H*[e], and *SmDFR*[f]	N/A	Anthocyanin biosynthesis genes	Up-regulation under cold stress.	(Jiang et al., 2016)

[a]*CBFs*: The C-repeat binding factors, [b]*AP2/ERF*: APETALA2/Ethylene Response Factor, [c]*SmCHI*: chalcone isomerase, [d]*SmCHS*: chalcone synthase, [e]*SmF3H*: flavanone 3-hydroxylase, [f]*SmDFR*: dihydroflavonol 4-reductase.

aculeatissimum) subjected to low temperature stress. They discovered nine significant miRNAs that are expressed in response to low temperature stress. Furthermore, many target genes of miRNAs involved in the chilling response were identified. Thus, target genes were engaged in a variety of roles, such as the expression of anti-stress proteins and antioxidant enzymes. Such studies contribute to the broad knowledge on cold-tolerance regulation mechanisms as well as a theoretical background for future research on low temperature stress in eggplant.

4. Reaction of transgenic eggplant to low temperature stress

Several studies have found that eggplant transgenic lines have some level of tolerance to a set of abiotic stresses, including low temperature stress. Wan et al. (2014) discovered that the expression of Arabidopsis cold-regulated 15A (*AtCOR15A*) and C-repeat binding factor 3 (*AtCBF3*) genes in transgenic eggplants (*Solanum melongena*) increases significantly under extreme low temperature (2 ± 1ºC) stress. Consequently, it improved eggplant chilling tolerance. Likewise, Prabhavathi and Rajam (2007) tested transgenic eggplant seeds with increased polyamines (PA) particularly due to exogenous adc (arginine decarboxylase) gene (introduced through primary transformants self-pollination) in low temperature tolerance assays performed *in vivo* and *in vitro* growth conditions. They discovered that after being exposed to extra low temperatures (6–8ºC), transgenic seeds germinated 4 days and one week earlier *in vivo* and *in vitro*, respectively, when compared to control seeds. Thus, transgenic lines showed increased tolerance to low temperatures and other abiotic stresses, as well as rapid growth. Furthermore, Acciarri et al. (2002) studied the growth and fruit development of *DefH9-iaaM* transgenic hybrid eggplants (parthenocarpic hybrids) grown during early spring production in two regions of Italy with average temperatures ranging from 7 to 17ºC. They discovered a significant yield increase (up to six-fold higher) when compared to controls (commercial hybrids and open-pollinated parthenocarpic cultivars).

Donzella et al. (2000) conducted a similar study in which they assessed the productivity of transgenic eggplant hybrids (containing the parthenocarpic gene *DefH9-iaaM*) under cold stress (unheated greenhouse). Transgenic eggplant was compared to controls (untransformed eggplant hybrids) and commercial parthenocarpic cultivars treated or untreated with phytohormones, which trigger fruit set and growth (the transformation of an ovary into a fruit) in greenhouse-grown eggplant. In both cases, they discovered that the productivity of transgenic eggplant was still higher. It was proved that transgenic parthenocarpic eggplants rise winter production and can be beneficial to all Mediterranean region where unheated greenhouses still prevail (Donzella et al., 2000; Acciarri et al., 2002). Furthermore, it was reported by Ying et al. (2009) that at low temperatures (~12.8ºC), the eggplant parthenocarpic gene is expressed normally, resulting in the formation and development of parthenocarpic fruits at 100%. Thus, under cold stress, eggplant resources with parthenocarpic ability demonstrated a greater ability to bear multitude fruits without pollination than non-parthenocarpic resources that require pollination. Parthenocarpy can overcome flower and fruit loss as well as increase eggplant yield, and lower the production costs (Lv et al., 2017).

6. Low temperature stress mitigation approaches in eggplant

Grafting is one the approaches used to mitigate the impact of abiotic stresses such as low temperature during preharvest. Handful studies conducted in eggplant have identified rootstock-scion combinations able to improve the low temperature tolerance. For instance, Darré et al. (2021) in their experiment, a cold-tolerant rootstock (Java) were combined with (cv. Monarca) scion and they found that the grafting enhanced plant vigor and fruit growth rate by reducing time to harvest by 10 to 15%. Thus, grafted eggplant showed reduced contents of dry matter content and phenolic compounds (~15–20% each), as well as lower respiration (~60%) than controls. Obviously, it results in higher tolerance to chilling injury of grafted eggplants. Remarkably, eggplant growth performance under cold stress was improved significatively. Gao et al. (2008) have reported a successful improvement of cold tolerance in eggplant seedling scions and rootstocks. The authors found that after a chilling treatment at 10/4ºC (day/night), chilling-tolerant rootstocks (Hiranasu) in which they grafted a cold tolerant scion "Jinong 2000" resulted in stronger cold tolerant eggplant with a more improved scion tolerance. In the same manner, it was reported by Gao et al. (2006) that a rootstock with stronger cold tolerance improves eggplant root activity as well as the cold resistance. This conclusion was obtained after evaluating physiological and biochemical property changes of grafted eggplant seedling roots under low temperature stress. Yan et al. (2009) also contributed to evaluate grafted eggplant seedlings tolerance to winter cold stress. They employed a rootstock/scion interchangeability between two eggplant cultivars; one tolerant (Hiranasu) and other susceptible (Daidaro) to cold stress. After measuring several physiology criterions (such as MDA content, electrolyte leakage, and essential osmotic adjustment substances) before and after low temperature treatment in grafted seedling leaves, it was concluded that only the tolerant cultivar was able to enhance cold tolerance through both its root and shoot.

The arbuscular mycorrhizal fungi (AMF) have been employed as a mitigation approach to cold stress in eggplant, particularly in *Solanum melongena*. Pasbani et al. (2020) inoculated and evaluated several AMF species on three ranges of temperature including low temperatures (15ºC and 5ºC). They found that three from four inoculated AMF species (*Claroideoglomus etunicatum*, *Funneliformis mosseae*, and *Rhizophagus irregularis*) alleviated cold stress in *S. melongena* despite their low level of root colonization. Thus, they activated antioxidant defense systems, improved photochemical reactions as well as the accumulation of protecting molecules (free phenolics and prolines), and also reduced membrane damages. Cytokines are known to play a role in the regulation of plant abiotic stress tolerance and adaptation. Chen et al. (2015) tested the effect of an exogenous and synthetic cytokinin, 6-benzylaminopurine (6-BA), on eggplant (*Solanum melongena*) seedling growth, osmoregulation responses, and antioxidant defense system under low temperature stress. Moreover, exogenous 6-BA pretreatment (through spray application) has also been shown to significantly reduce the low-temperature-induced decrease in eggplant growth. As shown in Figure 2, it also improves the activities of several enzymes and helps to reduce the activities of superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT). Finally, the overall results show that 6-BA pretreatment improves eggplant seedlings' low temperature tolerance.

7. Research perspective and conclusion

High-throughput mRNA sequencing techniques and genome-wide sequencing in broad sense provide clues on the roles and regulatory mechanisms of genes involved in stress responses and can be used for rapid and efficient transcriptome characterization. In the future, the use of these techniques will contribute to a greater understanding of stress regulation in eggplants. A

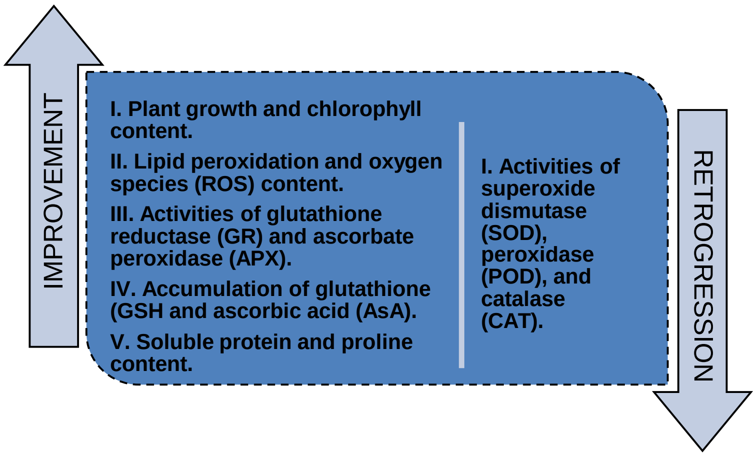

Figure 2. Exogenous application of 6-BA and related improvement under low temperature stress.

mentioned above, the discovery of stress-regulated miRNAs is critical for understanding how eggplant responds to various stresses. So far, only a few studies using these techniques in eggplant have been published and future research in eggplant will be oriented toward the use of high throughput sequencing to understand cold stress regulation mechanisms. Low temperature is among the stresses that endanger eggplant throughout its entire growth phase, resulting in the suppression of growth and development and a drop in productivity (Yang et al., 2020). This review summarizes current knowledge in key areas concerning eggplant low temperature stress tolerance. In addition, a description and repercussions of genetic, biochemical and physiological changes with regard to low temperature are presented. The development of transgenic parthenocarpic eggplants, which ameliorate low-temperature induced deficiencies in fruit set, as well as the use of grafting and arbuscular mycorrhizal fungi, were addressed as potential techniques to boost eggplant productivity in suboptimal conditions often seen during winter particularly in the Mediterranean region and some part of Asia. Furthermore, ectopic expression of genes such as AtCOR15A and AtCBF3 can help eggplants resist low temperature stress.

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