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Heat Stress in Vegetables: Impacts and Management Strategies - A Review

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ABSTRACT

Global climate change has not only caused a significant rise in the average temperature around the world but has also threatened crop productivity and food security. Heat stress disrupts various plant physiological and biochemical processes, such as inhibition of growth and development, reduction of photosynthesis rate and nutrient uptake, consequently causing yield losses. The destructive effects of heat stress are expected to worsen in the coming years. Thus, it has become imperative to understand how vegetables respond and adapt to heat stress in order to improve their heat tolerance ability. Various approaches have been adopted to enhance heat stress tolerance in vegetables, including modifying cultural practices and crop improvements through several breeding methods. This review gives comprehensive and up-to-date information on the effects of heat stress on vegetables; and existing as well as emerging methods adopted to enhance heat tolerance in vegetables. It also provides a brief overview of a new method called speed breeding, which can be leveraged to fast-track the breeding process for developing heat stress-tolerant vegetables.

Keywords: Breeding method; environmental stress; food security; high temperature

ABSTRAK

Perubahan iklim global bukan sahaja menyebabkan kenaikan suhu purata yang signifikan di seluruh dunia tetapi juga telah mengancam produktiviti tanaman dan sekuriti makanan. Tekanan haba mengganggu pelbagai proses fisiologi dan biokimia pokok seperti perencatan pertumbuhan dan perkembangan, pengurangan kadar fotosintesis dan pengambilan nutrien yang akhirnya menyebabkan pengurangan hasil. Kesan kemusnahan disebabkan oleh tekanan haba dijangka akan lebih teruk pada tahun terkehadapan. Oleh itu, adalah penting untuk memahami bagaimana sayur-sayuran bertindak balas dan beradaptasi dengan tekanan haba untuk meningkatkan keupayaan toleransinya terhadap tekanan. Pelbagai pendekatan telah diambil bagi meningkatkan toleransi terhadap tekanan haba dalam sayur-sayuran termasuklah mengubah suai amalan penanaman dan menambah baik tanaman melalui pelbagai kaedah pembiakbakaan. Ulasan ini memberikan maklumat yang komprehensif dan terkini tentang kesan tekanan haba kepada sayur-sayuran dan kaedah sedia ada serta baharu yang diguna pakai untuk meningkatkan toleransi sayur-sayuran terhadap tekanan haba. Ulasan ini juga memberi gambaran ringkas tentang kaedah baharu yang dipanggil pembiakbakaan pantas yang boleh dimanfaatkan untuk mempercepat proses pembiakbakaan bagi menghasilkan sayur-sayuran yang toleran terhadap tekanan haba.

Kata kunci: Jaminan makanan; kaedah pembiakbakaan; suhu tinggi; tekanan persekitaran

Introduction

Vegetables have long been included in the human diet due to a wide range of healthy and beneficial compounds, such as vitamins, dietary fibres, vitamins and antioxidants, provided for the body upon consumption. In recent years, vegetable production has increased from 0.55 billion tonnes in 1997 to 1.09 billion tonnes in 2017 (Dong et al. 2020). However, this output is still considered insufficient for the ever-growing world population. As a result, scientists and farmers emphasize improving environmental conditions to boost vegetable production. However, due to the shortage of fertile farmland for agricultural production globally, vegetable cultivation is regularly done under extreme conditions, including high abiotic stress, biotic stress and contaminated environments (Malhi et al. 2021). Generally, vegetables are susceptible to a wide range of extreme climate conditions, such as heat, drought, and submergence, which are the primary causes of yield loss in vulnerable regions across the globe (Ahmad et al. 2021), accounting for more than half of the yield losses (Malhi et al. 2021). The continuous rise in the ambient temperature of our immediate environment is regarded as one of the most detrimental and significant abiotic stress. Based on the Intergovernmental Panel on Climate Change (IPCC) fourth assessment report, it was documented that a 0.2 °C rise in air temperature would be experienced every ten years. Unfortunately, in 2014, IPCC showed that 4.5 °C rise in the air temperature would occur by the end of the 21st century (Giordano, Petropoulos & Rouphael 2021).

High temperatures significantly impact the morphological, physiological, biochemical, and molecular processes in crops. The emergence of heat stress at the seedling stage negatively affects seed germination, emergence and establishment. At the vegetative stage, heat stress disrupts the photosynthetic pigments, light perception, carbon metabolism and transportation of organic solutes in plants. During the reproductive phase, heat stress often leads to an imbalance in mineral nutrition, deactivation of antioxidant enzymes and generation of reactive oxygen species (ROS), leading to oxidative stress (Ali et al. 2020). At the molecular level, high temperature alters the gene expression directly engaged in scavenging plants against heat stress (Hasanuzzaman et al. 2013). Approximately 10-17% of crop losses have been recorded due to an increase in temperature during different plant developmental stages (Faiz et al. 2020). The recent global warming episodes have brought about great economic losses of approximately US$125 billion (Kompas, Pham & Che 2018). In the coming decades, it is predicted that yield loss due to heat stress is likely to increase by approximately 40% (Ali et al. 2020).

Climate change significantly influences agriculture either directly or indirectly, especially for small-scale tropical vegetable farmers and food production as a whole. Therefore, having comprehensive knowledge and understanding of the changes that occur in vegetables under elevated temperatures is imperative to facilitate the selection and development of heat-tolerant genotypes. Several approaches, including improvement of cultural practices and crop improvements through breeding approaches, have been explored to mitigate the impact of heat stress on vegetables. Furthermore, several outstanding review papers on heat stress and its management strategies have been published. This review provides updated and in-depth information on the impacts of heat stress specifically on vegetables as well as the approaches adopted to improve yield and productivity under adverse environmental conditions.

IMPACTS OF HEAT STRESS ON THE MORPHO-PHYSIOLOGICAL AND BIOCHEMICAL TRAITS

IMPACTS ON MORPHOLOGICAL TRAITS

Heat stress greatly impacts plant growth and development (Table 1). Germination is the first stage of plant development. Temperature increase during the seedling phase is harmful to plants (Mattos et al. 2014). High temperatures reduce plant emergence, germination percentage, seedling vigour and radicle emergence, and increase abnormal seedlings (Hasanuzzaman et al. 2013). At 30 °C, lettuce seedlings developed malformations while at 45 °C, watermelon seedling germination was completely inhibited (Ayyogari, Sidhya & Pandit 2014). Under heat stress, seed germination is reduced due to impaired protein synthesis and disruption in the activities of enzymes needed for the breakdown of starch and accumulation of abscisic acid (ABA) (Hassan et al. 2020). Heat stress reduces plant height, stem growth, leaf area, leaf size and weight (Hemmati, Gupta & Basu 2015), and root and shoot dry weight (Ali et al. 2020). Plant reproduction is one of the processes most affected by heat stress, resulting in lower yield (Ahmad et al. 2021). Heat stress inhibits pollen germination and viability, impairs pollen tube growth, receptivity and function of the stigma and ovary, disrupts fertilization, impairs embryogenesis and egg viability, and induces ovarian abortion and poor seed set (Ahmad et al. 2021). Rapeseed (*Brassica napus*) ovule development was poor under heat stress, as were its pollen viability, and seed and pod development (Chen et al. 2021). Heat accelerates flowering, triggering reproduction before the plant accumulates sufficient resources for seed development (Zinn, Tunc-Ozdemir & Harper 2010). The pollen viability of tomato was reduced by 20% when exposed to temperatures between 43-45 °C for 3-7 days before anthesis. However, pollen grain count and germination rate remained unchanged (Krishna et al. 2019). At the reproductive stage, high night temperatures have caused a significant reduction in canola yield (Ahmad et al. 2021).

TABLE 1. Response of vegetable crops to high temperature

Crop	Growth condition	Heat treatment	Effects	References
Lettuce (*Lactuca sativa*)	Glasshouse	13 °C and 25 °C	Reduction in biomass accumulation	Al-Said et al. (2018)
	Growth chamber	25 °C and 33 °C	Decrease in leaves water potential, leaf dry matter and biomass	Giordano, Petropoulos & Rouphael (2021)
Tomato (*Solanum lycopersicum*)	Glasshouse	long-term moderate heat	Decrease in pollen viability, pollen number, female fertility, seeded-fruit set	Xu et al. (2017)
	Open field	Long term heat stress	Reduction in the total flavonoids, lycopene and pH	Dasgan et al. (2021)
Chilli (*Capsicum annuum*)	Growth chamber	40/32 ºC	Decrease in chlorophyll contents and photosynthesis	Hussain et al. (2021)
	Plastic house	Long term heat	Decrease fruit weight, the fruit diameter, the fruit length and number of seeds per fruit	Thuy et al. (2015)
Kale (*Brassica rapus*)	Greenhouse	35/25 °C	Reduced number of fertile pods and seeds set per floret	Chen et al. (2021)
	Open field	24-35 °C	Reduction in chlorophyll and osmoprotectants contents	Aleem et al. (2021)
Spinach (*Spinacia oleracea*)	Growth chamber	10-35 °C	Reduction in germination percentage	Chitwood et al. (2016)
	Growth chamber	42 °C	Inhibition of plant growth and decrease in photosynthetic activities	Guo et al. (2020)
Cucumber, watermelon (*Cucumis sativus, Citrullus lanatus*)	Greenhouse	above 32 °C	Reduction of flowers and sugars. Shape and color alteration	Giordano, Petropoulos & Rouphael (2021)
Eggplant (*Solanum melongena* L.)	Growth chamber	45/35 °C	Reduction in leaves number per plant, leaf area, shoot and root lengths and plant dry matter	Faiz et al. (2020)

IMPACTS ON PHYSIOLOGICAL AND BIOCHEMICAL TRAITS

One of the most significant impacts of heat stress is the disruption of the photosynthesis pathway, which subsequently affects plant growth and development. Heat stress closes stomata, reducing photosynthesis and intercellular CO_2. Moreover, heat stress causes lipid peroxidation in membranes and chloroplasts, resulting in chlorophyll pigment loss. In hot weather, the reduced chlorophyll fluorescence (Fv/Fm) ratio can also reduce the photosynthesis rate (Hassan et al. 2020). It also reduces the synthesis of starch and sucrose by inhibiting several enzymes (sucrose phosphate synthase, ADP-glucose pyrophosphorylase and invertase). Furthermore, prolonged heat stress causes carbohydrate depletion in plants, lowering photosynthesis rates (Hasanuzzaman et al. 2013).

High temperature triggers the over-production of reactive oxygen species (ROS) which targets the lipids, proteins, and polysaccharides. Excessive ROS production causes oxidative damage, increasing membrane peroxidation and severe membrane damage. The damage caused by ROS production alters the membrane permeability, causing an increase in electrolyte leakage (Aleem et al. 2021) and a decrease in the cell membrane thermostability (CMT) (Hemmati, Gupta & Basu 2015). Oxidative stress induced by the accumulation of ROS causes increased hydrogen peroxide content, malondialdehyde content and superoxide anions that significantly impact vegetable production. In the future, a 31.5% reduction in vegetable production is expected with a 4 °C rise in temperature (Malhi et al. 2021) as a result of the accumulation of ROS and other factors induced by elevated temperature. ROS accumulation leads to early leaf senescence owing to the degradation of polymeric proteins into soluble forms. Plant exposure to long-term heat stress results in ROS accumulation at the outer surfaces of the plant plasma membranes, resulting in membranes depolarization and activation of Ca-induced respiratory burst oxidase homolog D. Under such conditions, ROS accumulated in cells can induce programmed cell death (Hassan et al. 2020).

Plants respire rapidly at temperatures between 0 °C and 40 °C. At temperatures above 50 °C, the respiratory mechanism is damaged, reducing respiration, which in turn reduces photosynthesis, and negatively affects the ratio of the two (Bisbis, Gruda & Blanke 2018). Even in high temperatures, plants tend to keep respiration rates low. In one study, spinach grown at 15/10 °C had higher respiration than spinach grown at 30/25°C in all treatments (Bisbis, Gruda & Blanke 2018). When moisture is available, plants tend to retain water in their tissues during heat stress, but limited water supplies during high temperature are detrimental to plant survival. In tomatoes, high temperatures reduce leaf water relations and root hydraulic conductivity. A higher transpiration rate causes water deficiency in plants and a decrease in water potential, disrupting several physiological activities. Plants lose more water during the day than at night when stressed (Singh et al. 2017). At 40/35 °C, C4 plants, like sweet corn, transpire more, causing excessive water loss to the environment and reducing water use efficiency (WUE). Conversely, C3 plants control and reduce water loss by closing their stomata, reducing photosynthesis, especially when heat and drought stress coexist (Bisbis, Gruda & Blanke 2018).

High temperatures often reduce the concentration and amount of essential nutrients in plants, reducing their overall nutrient content. The severity of these claims varies on the types of plants and nutrients (Hassan et al. 2020). It also causes a decline in growth parameters, such as root growth and mass, affecting the development of the aboveground tissue by limiting water and mineral nutrients availability, impacting the hormones produced in the root regions and transported to shoots, and altering sink-source relationships between shoots and roots (Giri et al. 2017). It also affects the activities of enzymes in nutrient metabolism (e.g., nitrate and ammonium assimilation). Under elevated temperatures, reduction in the acquisition of nutrients can be attributed to various factors, such as reduction in the root mass, surface area or nutrient uptake per unit root (Giri et al. 2017). Reduced nutrient uptake per unit root may be associated with a decrease in the liable C (total non-structural carbohydrate), and therefore, energy in roots (e.g., as a result of the decrease in the transport of shoot C to roots or an increase in root respiration). The direct damage of the root by high temperature ultimately may cause a reduction in the production and function of nutrient-uptake proteins (Giri et al. 2017). The impact of high temperatures on the nutrient uptake proteins is still not fully understood, and further research needs to be conducted for clarity (Hassan et al. 2020).

IMPACTS ON YIELD AND YIELD QUALITY

Concerns over plant productivity and food security are growing due to the rising global temperatures across the globe. The effect of heat stress is so severe that even a slight spike in temperature detrimentally impacts crop output. Heat stress primarily disrupts the phenological development processes, affecting crop output. Reduction in crop productivity due to heat-associated stress has been reported in vegetables such as mustard and canola (Hasanuzzaman et al. 2013). Formisano et al. (2021) reported a reduction in fresh yields of lettuce cultivars (‘Ballerina’, ‘Opalix’ (‘Oak leaf’) and ‘Integral’ (‘Romaine’)) by 16.0%, 26.9% and 13.2%, respectively under different Greenhouse Irradiance Levels (to non-shading conditions) compared to shaded conditions. At a temperature of more than 30 °C, canola (*Brassica* spp.) experienced an 89% decrease in seed output on the main stem although all branches contributed to a 52% reduction in the total yield. The reduction in yield reported in canola was attributed to heat-induced infertile pods, decreased seed weight and seeds per pod (Hasanuzzaman et al. 2013).

Vegetable crop quality is greatly affected by heat stress, potentially causing a reduction in the marketability of produce. For instance, under elevated temperatures, peas’ sugar content was reduced, which might be associated with higher respiration during warm nights or the shorter period over which the crop develops. In crops such as leafy vegetables, the product quality was reduced when the flowering stage was induced due to heat stress (Abouhussein 2012). In lettuce, the accumulation of latex was observed under high temperatures, making the leaves bitter and rigid (Mattos et al. 2014). Exposure of tomatoes to high temperatures decreased the fruit set and fruit quality (Malhotra 2017), and affected the fruit appearance or color, flavor and taste (Krishna et al. 2019). Heat stress also reduced melon sweetness (Ayyogari, Sidhya & Pandit 2014).

MANAGEMENT STRATEGIES OF HEAT STRESS IN VEGETABLES

CULTURAL PRACTICES

Conventional and routine agricultural practices have also been shown to reduce plant heat stress. Adding legumes to vegetable crop rotations and adjusting nitrogen application rates have been shown to reduce the impact of global warming on plant production (Min et al. 2016). In hot climates, adjusting sowing time is also considered an important factor. Because plants transpire to maintain leaf temperature, a better water management can help plants cope with heat stress. Adjusting irrigation time may help plants get access to water during a period of high heat (Driedonks, Rieu & Vriezen 2016). Overhead watering, misting and sprinkling can reduce tissue temperature and water vapour pressure deficit. Another farm practice, mulching, is thought to help reduce the impact of heat stress on plants by maintaining transpiration and thus, keeping the canopy cool. Using low-density, organic and reflective mulches like straw can help reduce surface radiation by reflecting and dissipating heat, and save water. Partial shading may also help reduce the effects of heat stress on plants, especially leafy greens like lettuce (Sharma & Manjeet 2020). The application of 10% kaoline to the leaves reduced plant evapotranspiration (Sharma & Manjeet 2020).

APPLICATION OF NUTRIENTS

Mineral nutrient deficiencies and impaired soil fertility are major problems that affect crop production. Proper and adequate nutrient supply is important for plant structure stability and essential physiological processes. For instance, nitrogen and magnesium are crucial components of chlorophyll for photosynthesis processes (Hassan et al. 2020). Exogenous application of nutrients, such as selenium (Se), boron (B), manganese (Mn), nitrogen (N), potassium (K), sulfur (S) and calcium (Ca) has been reported to play a crucial role in enhancing heat tolerance in plants by regulating the stomatal and upregulation of physiological and metabolic processes (Ahmad et al. 2021), subsequently enhancing crop growth and development, and ultimately economic yield. The application of Se improved osmolyte production and antioxidant activities, all of which was important in enhancing cucumber growth, photosynthesis rate and cucumber production. When applied during flower initiation, Se reduced the impact of heat stress on cucumber (Balal et al. 2016). Exogenous selenate has also been shown to reduce heat-induced stress disorders in lamb’s lettuce growth and metabolism (Hawrylak-Nowak et al. 2018). The application of Si improved photosynthetic traits and yield, and reduced water loss in cucumber grown under high temperatures (Shalaby et al. 2021). Foliar application of S alleviated heat stress in canola by improving the rate of photosynthesis and stomatal conductance, subsequently increasing yield (Ahmad et al. 2021). Adding sodium nitroprusside and calcium together reduced oxidative stress by increasing antioxidant enzyme production in tomatoes at high temperatures (Siddiqui et al. 2017). Adequate zinc supply reduces plant heat stress while an insufficient supply significantly reduces plant growth parameters. The stability of antioxidant properties has also been observed with zinc addition (Ali et al. 2020).

USE OF ORGANIC SUBSTANCES

Organic materials, like biochar, plant residues, manures and composts have been used to reduce crop stress. There have been several studies on the use of organic compounds to reduce abiotic stress in plants. Biochar is used as a fertilizer to improve crop yield and soil quality (Ali et al. 2020). Using biochar and phosphorus together increases photosynthesis, water use efficiency and grain size, resulting in higher yields and better grain quality (Fahad et al. 2016). Furthermore, biochar amendments enhanced the number of leaves, root biomass, plant height and final biomass of lettuce and cabbage compared to treatment without biochar (Carter et al. 2013). Compost and biochar have shown great promise in reducing greenhouse gas emissions. Adding 10% biochar to poultry litter reduced methanogens while increasing methanotrophs and lowering greenhouse gas emissions during the thermophilic stage (Arif et al. 2020). In hot weather, applying manure with other materials increased tomato crop growth and biomass (Ali et al. 2020).

PLANT GROWTH REGULATORS

Plant growth regulators (PGRs) are chemical substances that significantly impact the growth, development and differentiation of plant cells, tissues and organs. They also serve as chemical messengers for intercellular communication (Upreti & Sharma 2016). Naturally, PGRs are divided into five classes: auxins, gibberellins, cytokinins, ethylene and abscisic acid (ABA). Many of these PGRs have been used to enhance plant development and yield (Upreti & Sharma 2016). Plant growth regulators (PGRs) strengthen plant tolerance against environmental stress by scavenging ROS, adjusting osmotic pressure, maintaining the structural and functional integrity of membranes and enzymes, increasing the production of antioxidant-related genes and uptake of nutrients, and enhancing the biosynthesis of secondary metabolites and osmolytes (Waqas et al. 2021). Many PGRs, such as salicylic acid, abscisic acid, γ-aminobutyric acid, ascorbic acid and thiourea confer heat tolerance in plant when applied exogenously. Exogenous salicylic acid increased all growth-related parameters and biomass production in pea under heat stress according to Ali et al. (2020). Exogenous ascorbic acid at 0.5 mM also conferred heat tolerance in tomato seedlings by scavenging ROS and increasing ascorbic acid content, proline and photosynthetic pigment (Alayafi et al. 2020). According to Ahmad et al. (2021), γ-aminobutyric acid effectively reduces heat and drought stress in sunflowers by increasing the production of proline, total protein, osmolyte metabolism, gene expression and antioxidant enzyme. Exogenous application of 24-epibrassinolide was found to increase mustard tolerance to heat stress by enhancing the activities of the antioxidant system (Hassan et al. 2020). Thiourea (TU) has recently been used to improve heat tolerance in plants by upregulating gas exchange and water relations (Ahmad et al. 2021). Melatonin has been shown to reduce heat stress by promoting antioxidant activity, reducing malonaldehyde and electrolyte leakage, and regulating membrane stability and cell structure. It also protected tomato cellular protein structure and stability by increasing heat shock protein expression (Zhao et al. 2022).

CHITOSAN: A NEW ALTERNATIVE APPROACH TO ALLEVIATE HEAT STRESS IN VEGETABLES

Chitosan is a linear polysaccharide found in crab shells, shrimp, insect exoskeletons, fungi and algae as chitin. Chitosan is thought to improve food production by reducing plant stress (Ali et al. 2020). The use of exogenous chitosan at 200 ppm has recently been reported to improve heat tolerance in cucumbers by regulating osmotic balance and cell turgor pressure, and increasing yield potential (Ali et al. 2021). The amendment of soil with chitosan improved leaf dry weight, leaf photosynthesis rate, chlorophyll fluorescence and gas exchange of lettuce (Xu and Mou, 2018). Using chitosan, zinc and humic acid mixture could help reduce heat stress in late-sown dry beans (Bibi et al. 2021; Hidangmayum et al. 2019). Studies on plants, especially vegetables, responses to heat stress using chitosan alone or in combination with other compounds are limited. However, some evidences suggested that abscisic acid (ABA) could activate heat shock-related genes, such as *ABF3*, which could help enhance and confer heat tolerance (Hidangmayum et al. 2019). Thus, it is believed that chitosan can help alleviate stress by inducing the expression of defense-related genes and ABA-biosynthesis genes, resulting in the activation of defense-related proteins and ABA level (Kuyyogsuy et al. 2018).

USE OF SUPERABSORBENT: A POTENTIAL MANAGEMENT STRATEGY

Superabsorbent polymers (SAP) like hydrogel absorb large amounts of water while maintaining their shape. Several studies have shown improved water retention, crop growth, and productivity when soil is amended with hydrogel, especially in arid and semi-arid regions (Ostrand et al. 2020). The application of SAP at 225 kg/ha helped improve the dry weight, leaf surface area, growth and yield of soybean under drought stress (Mnyika 2020). Recently, the hydrogel has been combined with organic compounds to improve plant growth and productivity under drought conditions. For instance, with 35% irrigation rate, rabbit manure and SAP improved eggplant growth and yield (Mnyika 2020). Study conducted by Ekka et al. (2022) found that hydrogel amendment enhanced traits, such as plant height, number of leaves per plant, plant spread, survival percentage, average leaf area, average leaf weight and yield/hectare in lettuce. Using a mixture of biochar, vermicompost and polymer was shown to reduce plant stress (Aboelsoud & Ahmed 2020). To date, there have been no reports on plant, especially vegetable responses to heat stress using SAP only or in combination with another compound. Based on previous reports, organic compounds (biochar, manure) and cultural practices have been used to mitigate heat stress (Aboelsoud & Ahmed 2020). Heat stress has a direct relationship with drought. Therefore, water management is important to increase productivity under heat-stress conditions. Moreover, many field crops can easily survive high temperatures (up to 40 °C) with an adequate supply of water whereas a limited supply of water dehydrates plant leaves and significantly lowers the overall output. The decline in production at high temperatures is associated with the fact that drought-stressed plant attempts to conserve water by closing their stomata. As a result, evaporative cooling is significantly reduced and without cooling, leaf temperature reaches up to 50 °C. At such high temperatures, the physiological processes of the plants are impaired, consequently leading to a decline in the final yield (Hassan et al. 2020). This indicates that adequate irrigation of plants can be considered a good practice that can help alleviate heat stress. However, the availability of freshwater for agricultural purposes has greatly been reduced, sometimes making it impossible for full irrigation to be implemented during critical heat stress regimes. Therefore, we suggest that the amendment of soil or other soilless media with SAP alone or in combination with other organic compounds will help mitigate or alleviate the impact of heat stress in the plant by having accessibility to water during critical temperature regimes. However, a greenhouse or field experiment is required to verify this suggestion.

THE USE OF ARBUSCULAR MYCORRHIZAL INOCULATION

Arbuscular Mycorrhizal (AM) fungi enhance and help facilitate growth and development as well as plant establishment. They help boost immobile nutrient absorption and uptake. They also help enhance soil structure and alleviate environmental stresses in the plant (Malhi et al. 2021). It was reported that positive changes were observed when plants were inoculated with AM under heat conditions due to the cordial correlation between AM, and plant growth and development (Begum et al. 2019). The use of AM inoculation in vegetables has brought about improved biomass production, stomatal conductance, leaf water potential and water and mineral nutrition absorption under stress conditions (Malhi et al. 2021). However, limited studies have been conducted regarding heat tolerance by using AM inoculation in vegetables. Under heat stress, inoculation of AM was reported to improve soybean tolerance by enhancing the plant growth parameters, chlorophyll content, photosynthesis as well as seed yield compared to the control (without AM) (Jumrani et al. 2022).

CONVENTIONAL BREEDING

Traditional breeding methods are critical for generating unique genetic variants and conserving natural resources and germplasms. Traditionally, breeding programs are conducted in climatic conditions similar to the final harvest. As a result, heat tolerance breeding genotypes are screened in arid environments with high temperatures. This strategy appears to work as genotypes from warmer climates are more heat tolerant than genotypes from cooler climates (Driedonks, Rieu & Vriezen 2016). For example, after screening thousands of tomato accessions under heat stress conditions, the Asian Vegetable Research and Development Center (AVRDC) discovered less than 1% were tolerant. In these conditions, a heat-tolerant Chinese cabbage cultivar with a compact head was identified (Hall 1992). However, due to uncontrolled conditions, screening for heat-tolerant genotypes in the open field is difficult to select heat tolerance genotypes (Ahmad et al. 2021). To solve these issues, a controlled environment (greenhouse) was used to screen tolerant genotypes. From seedling to the reproductive stage, these conditions can be used to screen for heat tolerance (Wahid et al. 2007). Selection criteria used to determine susceptible and tolerable varieties under hot conditions include fruit set, pollen germination and viability, and seed set (Wahid et al. 2007; Xu et al. 2017).

Pedigree, backcrossing and recurrent selection methods have all been used to develop heat-tolerant genotypes (Hall 1992). Pedigree selection is a very suitable technique for developing tolerance cultivars, particularly traits controlled by major genes. This approach has the potential to combine multiple genes controlling biotic and abiotic stresses. However, the main drawbacks associated with pedigree selection include periodically screening many lines throughout the planting seasons, making it time consuming (Oladosu et al. 2019). Backcrossing avoids unwanted genes from the donor parent to the recipient line. Tomatoes with improved heat tolerance have been developed using pedigree breeding backcross (Hall 1992). During the reproductive stage of tomatoes, recurrent selection was used to combine diverse heat tolerance traits into one genotype (Hall 1992). Short breeding cycles, control of genetic gain and increased genetic variation and diversity among breeding lines are all advantages of recurrent selection breeding (Annegowda et al. 2021).

In addition to the above methods, hybridization is a useful breeding strategy to improve plant tolerance under heat stress conditions. This can be achieved by crossing two genetically different parents to produce a new variety called a hybrid with improved and desirable traits compared to the parent, subsequently enhancing growth and productivity. For instance, heat-tolerant lines have been developed by crossing tolerant and susceptible genotypes to produce a hybrid. As an example, tomato variety L72 was created by crossing heat-tolerant cultivar, Summertime, with heat susceptible genotype, Campbell 28 (Hazra et al. 2007).

Long-term use of traditional breeding can reduce genetic diversity. Enlarging desired traits requires introducing new genes via mutational breeding (Ahmar et al. 2020a). Mutagenesis is a process whereby sudden heritable alterations occur in the genetic makeup of living cells as a result of chemical, physical or biological agents rather than genetic segregation or recombination (Oladosu et al. 2019). Mutational breeding is used to develop new alleles that are not present or exhausted in the germplasm pool. HT7 (mutant tomato) was recently identified as heat tolerant due to its ability to produce fruit with seed, and increased number of fruit, total pollen number and viability compared to the control. Enhanced agronomical traits recorded in HT7 were attributed to increased expression of heat-related genes including heat shock transcription factor (*SlHsfA1b*) and heat shock protein (Pham et al. 2020). The use of conventional breeding techniques has helped develop heat-tolerant lines. However, one of the main disadvantages of conventional breeding is that the programs depend on relatively advance starting material that has previously been used in the particular breeding areas specifically related to the targeted market segment. This signifies that low genetic diversity constrains the possible increase in heat tolerance level (Driedonks, Rieu & Vriezen 2016).

QTL FOR HEAT TOLERANCE AND MARKER-ASSISTED BREEDING

Both molecular and transgenic approaches must be used in conjunction with traditional breeding techniques to improve plant heat tolerance, and reduce excessive use of organic or inorganic amendments. Heat tolerance is a quantitative trait, and quantitative trait loci (QTLs) mapping is a quick way to find genes that control it. Heat tolerance QTL analysis requires precise phenotyping. However, some studies have successfully mapped heat tolerance QTLs in lettuce, tomato, and kale. Nevertheless, more research is needed to identify and map more QTLs to improve vegetable production. A recent research found five major QTLs for heat tolerance in tomato seedlings from a cross between LA1698 and LA2093 using simple sequence repeat markers. With the aid of molecular markers, QTLs associated with heat tolerance in tomatoes were identified at various stages (Wen et al. 2019). Aside from tomatoes, heat tolerance QTLs have been found in lettuce and kale. Thirty-six QTLs responsible for tipburn, maturity traits and physiological disorders in lettuce were identified (Macias-González et al. 2019). Several QTLs associated with heat tolerance in cucumbers were also identified (Dong et al. 2020). Although several QTLs for heat tolerance have been identified, this area is still underexplored in vegetables, especially leafy vegetables. QTLs can be introgressed into popular varieties using marker-assisted breeding to improve heat tolerance. Some heat tolerance QTLs have been successfully mapped, but they must be thoroughly validated to determine their functions before being selected for breeding programs.

Marker-assisted selection (MAS) uses DNA markers to select plants with genomic regions involved in the desired trait expression. The success of this process depends on the strength of the association between the DNA marker and the phenotypic genes (Seman et al.

2019). Marker-assisted selection (MAS) is a valuable tool for incorporating desired traits into selected cultivars. The MAS method is less expensive, easier and more precise. Due to the complexity of heat stress, selection via phenotypic traits is not preferred because it is affected by many environmental variables. Thus, the DNA markers and MAS technique are critical for developing long-term resistant vegetable cultivars. The MAS technique has been widely used to improve plant cultivars for several abiotic stresses, such as drought, salinity and submergence. Studies on the use of MAS to improve heat tolerance in plants are very limited and scarce, especially in vegetables. Usman et al. (2018) successfully introgressed heat shock protein (*HSP70*) gene into the Malaysian elite chilli (*Capsicum annuum* L.) variety Kulai via MAS backcrossing. Yield performances of the improved lines were on par with that of the recurrent parent, and heat shock protein (*HSPs*) was upregulated when subjected to heat stress. Recently, marker-assisted breeding has also been used to develop improved rice lines that harbored early morning flowering and heat tolerance QTLs (*qEMF3* and *qHTSF4.1*). The improved lines recorded higher spikelet fertility when exposed to heat stress at the flowering stage (Ye et al. 2022). Based on the limited published studies, the introgression QTLs associated with heat tolerance into elite varieties can be considered as a suitable alternative to enhance plant resilience to heat stress.

GENETIC ENGINEERING FOR HEAT TOLERANCE

Transgenic techniques allow the simultaneous insertion of multiple genes into the plant genome to create broad-spectrum climate-resilient lines. Genetic transformation of plants is mostly achieved by using both *Agrobacterium* and biolistic approaches. The use of *Agrobacterium*-mediated transformation ensures complete, stable and reliable integration of the desired gene into the plant genome (Ashkani et al. 2015). Genetic engineering in the context of heat stress has so far concentrated on engineering genes that encode transcription factors (TFs), chaperones, organic osmolytes, heat shock proteins (*HSPs*), antioxidants and plant growth regulators (Jha, Bohra & Singh 2014). Heat shock proteins (*HSPs*) are produced in plants when they are exposed to high temperatures in order to protect the native proteins from denaturation and to increase protein stability, thereby conferring heat tolerance (Ali et al. 2020). More than 18 different small *HSPs* have been identified in plants, and they can be found in different parts of cell organelles, such as the endoplasmic reticulum, mitochondria, chloroplast, cytosol and cell membranes (Krishna et al. 2019). The role of HSPs in plants has been well understood via the genetic engineering method. Tomatoes have cytosolic *HSP17.4* and chloroplastic *Hsp21*, which confer heat tolerance (Krishna et al. 2019). *HSP21* overexpressed in transgenic tomatoes conferred heat tolerance by preventing photosystem II from oxidative stress (Krishna et al. 2019). EF-Tu and eEF1A (Protein synthesis elongation factor) expression conferred thermotolerance in crops according to Fu et al. (2012) and Momčilović et al. (2016). *Agrobacterium*-mediated transformation of broccoli which involved *HSP101* (*AtHSP101*) from *Arabidopsis thaliana* resulted in a thermotolerant transgenic variant (Kumar & Srivastava 2016). Leaking electrolytes, reduced proline content and leaf discoloration were all observed in peppers with *CaChiVI2* silencing. *CaChiVI2* overexpression increased proline and antioxidant enzyme activity while decreasing malondialdehyde. A study concluded that *CaChiVI2* gene was important in reducing heat stress (Ali et al. 2020).

GENOME EDITING

Genome editing is considered as an effective strategy for enhancing plant traits through gain or loss of gene function, or a multiplex genome-editing strategy. The emergence of engineered or designer nucleases has led to the development of several strategies for genome editing in plants. These nucleases can introduce double-stranded breaks (DSBs) at certain locations in the genome (Lohani et al. 2020). Then, the introduced DSBs are repaired either by non-homologous end joining (NHEJ) or homology-directed repair (HDR). Homology-directed repair (HDR) brings about precise insertion, deletion, or substitution events while NHEJ is error-prone (Lohani et al. 2020). Several genome-editing techniques have been developed to introduce site-specific DSBs in the plant genome. These gene-editing approach include zinc finger nuclease (ZFN), transcription activator-like effector nuclease (TALEN) and CRISPR-Cas9 (Salava et al. 2021). The use of these approaches plays a significant role in enhancing plant tolerance to a wide range of stress. For instance, ZFN system was used to enhance herbicide resistance in maize while TALEN was used to improve transgenic rice tolerance to plant pathogens (Salava et al. 2021). CRISPR-Cas9 has widely been used to improve plant tolerance to heat stress compared to ZFN and TALEN. Yu et al. (2019) recently reported that

CRISPR-Cas9-mediated *SlMAPK3* mutants of tomato showed greater resistance to elevated temperature than controls, implying that *SlMAPK3* was a negative regulator of thermo-tolerance. The transgenic tomato showed less membrane damage, less severe wilting, lower ROS levels, and higher levels of antioxidant enzyme activity and transcript abundance (Kim et al. 2021). In tomato, CRISPR-Cas9-mediated genome editing was used to enhance heat tolerance by knocking out the *SlAGL6* gene which brought about enhanced fruit setting under high temperatures (Ahmar et al. 2020b). Another study found that silencing *SlMPK1* with RNAi in transgenic tomato plants improved heat response significantly. When overexpressed, however, a decrease in heat tolerance was observed (Salava et al. 2021).

SPEED BREEDING: A POWERFUL TOOL TO FAST-TRACK THE DEVELOPMENT OF RESILIENT CROPS AGAINST ABIOTIC STRESSES

Breeding cycles need to be shortened to keep up with the rapidly growing population, changing environmental conditions, and consumer satisfaction and preferences. Speed breeding is the process of growing plants in controlled environmental conditions with optimal temperatures, continuous supply of light and high-density planting while using a single seed descent approach to select for key traits (Ayenan et al. 2019). Several selection approaches can be incorporated into speed breeding techniques, including single plant selection, single seed descent, marker-assisted selection and clonal selection, to reduce the breeding process and maximize resource utilization. Using these techniques (speed breeding), up to nine growing cycles can be completed within a year compared to one or two growing cycles using traditional methods. Thus, speed breeding allows for the fast generation of stable and homozygous cultivars, and fast-track development of advanced breeding lines, subsequently bringing about the hastened development and release of new varieties (Wanga et al. 2021). This approach has been utilized in some crops for rapid production. For instance, six growing cycles were completed within a year for crops, such as durum wheat, chickpea, spring wheat, pea, barley and amaranth, while four generations were for canola and groundnut (Samantara et al. 2022; Watson et al. 2018). Furthermore, *in vitro* germination of immature pepper and tomato embryos helped obtain one more cycle than the conventional breeding practice (Samantara et al. 2022). Speed breeding coupled with other breeding techniques (such as MAS) has been effectively utilized to improve salt tolerance in rice (Rana et al. 2019) and multiple disease resistance in barley (Hickey et al. 2017). Despite the advantages of this approach, problems such as the availability of suitable equipment, lack of trained personnel in the procedure, and lack of long-term funding may hinder the acceptability of these techniques, especially in developing countries where power supply is scarce (Wanga et al. 2021). However, speed breeding will help enhance our understanding of plant response to different stresses in the near future and help fast-track the development of heat tolerance vegetable crops. The incorporation of biotechnological approaches, such as genome editing and omics, into speed breeding will help enhance plant traits, confer tolerance against heat stress (Raza et al. 2021) and serve as long-term solution, improving sustainable and precision agriculture and increasing farmer income.

CONCLUSION

Heat stress has a significant negative impact on the morpho-physiological traits of vegetables, such as plant growth and development, biomass, photosynthesis-related traits, and yield and post-harvest quality of produce. To counteract these problems, several techniques have been employed. Some successes have already been achieved in developing crop tolerance by screening for tolerant genotypes in the open field under hot conditions and greenhouses. The application of organic compounds, nutrients, plant growth regulators and various cultural practices have been adopted to alleviate the impact of heat stress on vegetable farmland. The use of genetic engineering methods and recently, genome editing technology are promising in developing tolerant genotypes to heat stress. Although a wide range of methods have been employed in mitigating the impact of high temperatures in vegetable production, further research will be useful to improve heat tolerance in vegetables including the followings: 1) Open field screening should be conducted extensively and intensified using multiple environments due to varying temperatures across the globe. This will help identify the best-performing genotypes suitable for each location. 2) In arid regions where lettuce is cultivated in hot environments, the application of organic, inorganic, and farming management practices in combination should be highly encouraged to mitigate the impact of heat stress on vegetables. Further studies are required to determine the optimum application of organic compounds to prevent the accumulation of heavy metals in produce. 3) Incorporating biotechnological approaches, such as genome editing and omics into speed breeding will help enhance plant traits and confer tolerance against heat stress. Furthermore, due to the complexity of field conditions, the lab-developed heat-tolerant genotypes should be further screened in the open field before being approved for public use. 4) Additionally, most of the studies regarding the use of molecular markers, genetic engineering, genome editing and other new techniques involved the model plant, i.e., tomato. Hence, focus should be placed towards leafy vegetables, such as lettuce and kale to ensure food security, especially in the urban regions where urban farming is prevalent and high temperature is experienced due to the emission of various greenhouse gases.

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