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# Response of vegetable crops to heat stress

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**Abstract**
High temperature (HT) stress is a major environmental stress that limits plant growth, metabolism, and productivity worldwide. Plant growth and development involve numerous biochemical reactions that are sensitive to temperature. Plant responses to HT vary with the degree and duration of HT and the plant type. The adverse effects of heat stress can be mitigated by developing crop plants with improved thermotolerance using various genetic approaches. For this purpose, however, a thorough understanding of various responses of plants to high temperature, mechanisms is imperative. High temperature may adversely affect photosynthesis, respiration, water relations and membrane stability, and also modulate levels of hormones and primary and secondary metabolites. Furthermore, throughout plant ontogeny, enhanced expression of a variety of heat shock proteins, other stress-related proteins, and production of reactive oxygen species (ROS) constitute major plant responses to heat stress. The crop survival under HT stress depends on the ability to perceive the high temperature stimulus, generate and transmit the signal, and initiate appropriate physiological and biochemical changes. In this chapter response of different vegetable crops to heat stress are reviewed.

**Keywords:** Response of vegetable, heat stress, ROS

## Introduction

Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. In general, a transient elevation in temperature, usually 10–15 $^{0}$C above ambient, is considered heat shock or heat stress. However, heat stress is a complex function of intensity (temperature in degrees), duration, and rate of increase in temperature. The extent to which it occurs in specific climatic zones depends on the probability and period of high temperatures occurring during the day and/or the night. Heat stress due to high ambient temperature is serious threat to crop production worldwide (Hall, 2001) [29]. The temperature is the most important climatic factor influencing sink strength consequently photo assimilates partioning between the plant organs. Most tissues of higher plants are unable to survive extended exposures to high temperatures. Non-growing cells or dehydrated tissues (seed, pollen) can survive higher temperatures than hydrated tissue. Heat stress is major limiting factor for adaption and productivity of vegetable crops, especially when high temperature coincides with critical stages of plant development and drastically reduces yield. Global warming will have a profound effect on production and productivity of heat sensitive potato crop in near future in India. Heat stress during seed germination may slow down or completely inhibit the germination and in later stages of development heat stress adversely affect photosynthesis, water relation, carbon dioxide exchange rate and the level of hormones and metabolites.

All vegetable needs an optimum temperature for their proper growth and development, but optimum temperature required varies from crop to crop in addition to this, temperature limits the range and production of many crops. With changing climate the crop will be exposed to increased temperature stress. The high temperature can affect different vegetable crops in different ways.

Among the vegetable crops potato will be adversely affected by climate change. Potato required exact temperature and day length for tuber formation and flowering, so it will be adversely affected by climate change. The effect of climate change on potato production in India has previously been studied by Singh *et al*., (2009) [70]. Luck *et al*., (2010) [47] expected 16% decline in tuber yield of potato by 2050 for West Bengal if any special strategies are not adapted. Germination and seedling emergence from seeds and planting materials are highly sensitive to thermal stress (Grass and Burris 1995; Egli *et al*. 2005; Farooq *et al.* 2009) [24, 15]. Heat stress seriously reduces the germination and early seedling growth in a number of plant species including sugarcane (Wahid *et al*. 2008, 2010) [78].

However, plant age and the duration of exposure to heat stress are important (Wahid *et al.* 2007) [73-75, 77]. Germination of cucumber and melon seeds is greatly suppressed at 42 and 45 °C, respectively besides germination will not occur at 42 °C in watermelon, summer squash, winter squash and pumpkin seeds (Kurtar, 2010) [42]. In okra, high temperatures cause poor germination of seed during spring summer season Flower drop in okra is recorded at high temperatures above 420 ˚C (Dhankhar and Mishra, 2001) [56], whereas flower abscission and ovule abortion in French bean occurs at temperature above 35 ˚C (Prabhakara *et al.*, 2001) [60]. Temperature has a considerable influence on lettuce seed germination. Experimental trials have shown 90% germination temperatures between 15 °C and 20 °C (Kretschmer, 1978) [41]. Soil temperatures above 24 °C result in reduced germination, while little germination occurs at or above 30 °C (Lovatt *et al*., 1997) [46].

**Response of vegetable crops to heat stress**

Transitory or constantly high temperatures cause an array of morphological, anatomical, physiological, and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield.

**Morphological responses**

High temperatures can cause considerable pre and post-harvest damages, including scorching of leaves and twigs, sun burns on leaves, branches and stems, leaf Senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage, and reduced yield. Various symptom of heat stress on different vegetable crops are presented in Table.1). Tomatoes are strongly modified by temperature alone or in conjunction with other environmental factors (Abdalla and Verkerk, 1968) [1]. In tomato, reproductive processes were adversely affected by high temperature, which included meiosis in both male and female organs, pollen germination and pollen tube growth, ovule viability, stigmatic and style positions, number of pollen grains retained by the stigma and fertilization (Foolad, 2005) [21] and also cause the production of exerted style (i.e. the stigma is elongated beyond the anther cone) which prevent self pollination in tomato. According to (levy *et al*., 1978) [44] splitting of the antheridial cone is an important factors adversely affecting the fruit set at high temperature. High temperature induce poor pollen development, poor pollination, disintegration of embryonic pistil cell and hormonal imbalance (Aung, 1979) [8].

An increase in temperature of above 21 $^0$C cause sharp reduction in the potato tuber yield, at 30 $^0$C complete inhibition of tuber formation occurs (Sekhawat, 2001). Abdelmageed and Gruda (2009) [2] perceived that morphological traits including number of fruits and flower per crop, percentage of fruit fresh weight and fruit set were diverse in heat resistant and heat susceptible tomato lines. Haibushi, a heat tolerant cultivar of common bean has a higher pod weight per plant, number of pods per plant, average pod weight, pod set ratio, number of branches, and rate of biomass allocation to pods, but lower rates of biomass allocation to leaves, stems, and roots, than Kentucky Wonder, a heat-sensitive cultivar, across all temperature regimes, higher biomass allocation to pods and higher pod set in branches, which vary with the cultivar and temperature, play an important role in achieving a higher harvest index in the heat-tolerant compared to the heat-sensitive cultivars. Reduction in pod and seed set due to enhanced abscission of flower buds, flowers, and pods as reported by (Omae *et al*., 2006) [57]. The duration of onion gets shortened due to high temperature leading to reduced yields (Daymond *et al*., 1997). In onion temperature increase above 40 ºC reduced the bulb size and increase of about 3.5 ºC above 38 ºC reduced yield (Lawande *et al*., 2010). In broccoli, the main dysfunction induced by high temperatures occurs later in development. Once inflorescence or head development is initiated, relatively high temperatures (30 °C) arrest head development, also induce incomplete head development, uneven bead size, bracting in heads, and rough head surface (Farnham and Bjorkman, 2012). The various symptoms of heat stress in different vegetables are presented in Table 1.

**Anatomical response**

Under high temperatures, alterations anatomy was not explored in detail in most of the vegetable crops and a little information was accessible. In general, it is obvious that high temperature influences markedly plants anatomy at the tissue, cellular, and sub-cellular levels. The additional impacts of all these alterations in high temperature stress can lead to crop low growth and yield (Wahid *et al*., 2007) [73-75, 77]. In all plant organs, there is a common trend of closure of stomata and loss of curtailed water, diminished size of cell, enhanced densities of stomata, and higher root and shoot's xylem vessels (Anon *et al*., 2004) [7].

The heat-tolerant cultivars possess better stomatal control over $CO_2$ and $H_2O$ exchange in leaves in response to high temperature. This is evidenced by the fact that the sensitive cultivar of common bean Kentucky Wonder and strain 92783 show greater water loss at high temperature compared to resistant cultivar, Haibushi (Omae *et al*., 2006) [58]. Heat-tolerant cultivar Haibushi and strain Ishigaki- 2 display an association between photosynthesis and leaf conductance and leaf water potential, while this is absent in the heat-sensitive cultivars (Kumar *et al*., 2005). This indicates that the heat-tolerant cultivars possess better stomatal control over $CO_2$ and $H_2O$ exchange in leaves in response to high temperature. Grafting experiments with ABA deficient mutants of tomato showed that stomata can close independently of the leaf water status suggesting that there is a chemical signal produced by the roots that controls stomatal conductance (Holbrook *et al*., 2002) [35].

**Phenological responses**

The susceptibility of species to high temperature varies with the stage of plant development, but all vegetative and reproductive stage are affected by heat stress to some extent**.** During vegetative stage, for example, high day temperature can damage leaf gas exchange properties. During reproduction, a short period of heat stress can cause significant increases in floral buds and opened flowers abortion, Impairment of pollen and anther development is another important factor contributing to decreased fruit set in many crops at moderate - high temperatures. Massive accumulation of proline has also been reported in anthers and was associated with the protection of cellular structures, particularly during pollen dehydration (Schwacke *et al*.1999, Smirnoff *et al*., 1989) [69, 71], In addition, proline abundance in pollen grains was thought to function as energy storage, for fueling the rapid demand of energy during pollen tube elongation (Hong-qu and Croes, 1983) [36].

In common bean Pollen-stigma interaction, pollen germination, pollen tube growth, and fertilization are all negatively affected by high temperature, with the lowest pod set observed in plants exposed to high temperature 1-6 days prior to anthesis (Graham and Ranalli, 1997) [23]. Exposure to 35/20 ˚C or 35˚C reduced pollen viability (evaluated by pollen staining) (Halterlein *et al*., 1990). Lower pod and seed set caused by high temperature at anthesis (32/21℃) (Weaver and Timm, 1988) [79]. Photoperiod sensitive crops, e.g., cow pea, would also interact with temperature causing a disruption in phenological development. In a study the premature degeneration of the tapetal layer and lack of endothecial development may be responsible for the low pollen viability, low anther dehiscence, and low pod set under high day/night temperature i.e 33/30 ˚C (Ahmed *et al*. 1992) [3]. Reproductive tissue abnormalities may reduce translocation of proline from anthers to pollen (Ahmed *et al*. 1992) [3], which has been associated with male sterility in cowpea (Mutters *et al*. 1989) [52].

**Physiological Response**.

**Accumulation of compatible Osmolytes**

Water status of tissues is most crucial factor for survival of plants. Plants tend to maintain stable water status of tissues but high temperature impairs this particularly if water is limiting **(**Machado and Paulsen, 2001) [48]. To enhance stress tolerance, plants accumulate different osmolytes such as sugars and sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds and tertiary sulphonium compounds (Sairam and Tyagi, 2004) [64]. These compounds help to maintain stable water status of tissues by absorbing and retaining water. As accumulation of low-molecular-weight chaperones, compatible solutes are often regarded as a basic strategy for the protection and survival of plants under abiotic stress (Chen *et al*., 2007). These osmolites stabilize and protect the structure of enzymes and proteins, maintain membrane integrity and scavenge reactive oxygen species ROS. Glycinebetaine (GB) and proline are such known osmolytes known to occure widely in plants and normally accumulates in large quantities in response to environmental stresses (Kavi Kishore *et al*., 2005) [38]. These osmolytes buffer cellular redox potential under heat and other environmental stresses (Wahid and Close, 2007) [73-75, 77]. Increasing day temperature from 25 to 36 $^0$C resulted in marked increase in starch levels in leaves (Dinar, 1983), similarly under high temperatures, fruit set failed due to the disruption of sugar metabolism and proline transport during the narrow window of male reproductive development (Sato *et al*., 2006) [66] in tomato. Changes in carbohydrate profiles was reported under short and prolonged heat shock treatment of 32–36 ˚C, and was associated with the failure of tomato fruit set (pressmen *et al*., 2002; Sato *et al*.2006 and Firon *et al*., 2006) [63, 66, 20]. Major alterations in anthers were mainly observed for soluble sugars such as sucrose, fructose and glucose. Indeed, sucrose content increased in stressed anthers as compared to control tissues. Proline content of the sensitive genotypes of pepper decreased under high temperature conditions compared to low temperature and the heat tolerant variety produced higher quantity of proline in leaf under high temperature conditions (Saha, 2010). It has been postulated that GB increases resistance to high-temperature stress. More recent experiments showed that transformed Arabidopsis that accumulated GB exhibited enhanced tolerance to high temperatures during the imbibitions and germination of seeds, as well as during the growth of young seedlings (Alia *et al.*, 1998). It also seems likely that GB might alleviate the effects of heat shock because the extent of the induction of heat-shock proteins was significantly reduced in these transgenic plants.

**Photosynthesis**

It has been previously reported that high temperatures are responsible for changes in the thylakoid membrane, altering not only its physicochemical properties, but also its functional organization (Berry and Bjorkman, 1980) [9]. PSII, particularly, is the most sensitive component of the photosynthetic system (Berry and Bjorkman, 1980; Mamedov *et al*., 1993) [9, 50]. Stress is proper indexes of thermo resistance of the crop as they are correlated with growth. When photosynthesis is limited, crop development can be prohibited at high temperatures. Alterations in various photosynthetic attributes under heat stress are good indicators of thermotolerance of the plant as they show correlations with growth. Any constraint in photosynthesis can limit plant growth at high temperatures. Photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplast have been suggested as the primary sites of injury at high temperatures (Wise *et al.*, 2004) [80]. It alters the energy distribution and changes the activities of carbon metabolism enzymes, particularly the rubisco, thereby altering the rate of RuBP regeneration by the disruption of electron transport and inactivation of the oxygen evolving enzymes of PSII (Salvucc and Crafts-Brandner, 2004) [65]. PSII is intensely thermo labile and its function is highly diminished at high temperatures (Bukhov *et al.*, 1999; Camejo *et al.*, 2005). Havaux, 1992 reported the complete and irreversible inhibition of PSII in well watered tomato leaves at 42˚C heat treatment, similarly HS (42˚C for 2h) resulted in reduction of net photosynthesis rate of young plant of the heat sensitive genotype Campbell-28, because of effectd on calvin cycle and also in the PS-II functioning, but not in Nagcarlang, a wild heat tolerant genotypes (Camejo *et al*., 2005). A correlation between photosynthetic thermotolerance and production of specific heat shock protein was demonstrated in tomato (Preczewski *et al*., 2000) [61]

**Assimilate partitioning**

Heat stress, a reduction in source and sink activities may occur leading to severe reductions in growth, economic yield and harvest index affect apoplastic and symplastic pathways. Reduction in source and sink activities. The partitioning of dry matter (the ratio of dry weight of individual parts to that of total dry matter) was analyzed in the common bean at four temperature regimes (24/20, 27/23, 30/26 and 33/29˚C) (Oman *et al*., 2006 and Oman *et al*., 2007) [58, 57]. Haibushi, a heat tolerant cultivar, has a higher pod weight per plant, number of pods per plant, average pod weight, pod set ratio, number of branches, and rate of biomass allocation to pods, but lower rates of biomass allocation to leaves, stems, and roots, than Kentucky Wonder, a heat-sensitive cultivar, across all temperature regimes (Oman *et al*., 2006) [58]

Konsens *et al.* (1991) [40] recognize that high night temperature promotes branching in the common bean. Drought stresses induce genotypic variation of shoot biomass accumulation, pod and seed number, and biomass partitioning index. Porfirio and James (1998) report that a high partitioning index (chiefly harvest index) shows high heritability, contributing to drought stress in the common bean. Higher biomass allocation to pods was observed in

Haibushi a heat tolerant cultivar at high temperature as compared to Kentucky wonder a heat sensitive cultivar of common bean.

**Hormonal changes**

Hormonal balance, stability, content and biosynthesis are altered under heat stress. Abscisic acid (ABA) and ethylene as stress hormones are involved in the regulation of many physiological properties by acting as signal molecules. ABA induction is an important component of thermo tolerance, suggesting its involvement in biochemical pathways essential for survival under heat-induced desiccation stress (Maestri *et al*., 2002) [49]. Induction of HSPS by ABA enhances the theromotolerance. Increase in the level of ACC was positively correlated with high temperatures, among other hormones, salicylic acid (SA) has been suggested to be involved in heat-stress responses elicited by plants. SA is an important component of signaling pathways in response to systemic acquired resistance (SAR) and the hypersensitive response (HR) (Kawano *et al*., 1998) [39].

Many workers have studied the role of plant growth regulators in alleviating the effect of heat stress in many crop species such as ethylene in Brussels sprouts (Biddington and Robinson, 1993), Salicylic acid in mustard (James *et al*., 1998) and beans (Zhang *et al*., 2000). Firon *et al*.,2012 [19] elucidated ethylene's involvement in pollen heat-stress response and thermotolerance by assessing the effects of interfering with the ethylene signalling pathway and altering ethylene levels on tomato pollen functioning under heat stress. Dhaubhadel *et al.* (1999) [13] demonstrated that mustard and tomato seedlings grown in the presence of EBR (Epibrassinosteriods) are significantly resistant to a heat treatment that is lethal to untreated seedlings. Since a mild heat treatment of seedlings prior to their exposure to the usual lethal heat stress was not required to observe this effect, it is concluded that EBR treatment increases the basic thermotolerance of seedlings. The protective effects of Brassinosteriods (BRs) were also observed in bean plants subjected to heat stress. In an experiment El-Bassiony *et al.* 2012 [16] sprayed bean plants with different concentrations of Brassinosteriods (25, 50 and 100 mg L−1). They observed that spraying bean plants with BRs at a concentration of 25 and 50 mg L−1 increased vegetative growth, total yield and quality of pods under HT. However, there was no difference between the treatments. Spraying of 25 mg $L^{-1}$ BR increased the total free amino acids in leaves and total phenolic acids in the pod compared to control.

**Molecular responses**

**Oxidative stress and antioxidants**

High temperature induce oxidative stress in various plant have been reported by many workers (Upadhyaya *et al*., 1990, Jagtap and Bhargava 1995) [72, 37]. For example, generation and reactions of activated oxygen species (AOS) including singlet oxygen ($^1O_2$), superoxide radical ($O_2^-$), hydrogen peroxide ($H_2O_2$) and hydroxyl radical ($OH^-$) are symptoms of cellular injury due to high temperature. Protection against oxidative stress is an important component in determining the survival of a plant under heat stress. Plant protect cell and sub cellular systems from the cytotoxic effects of these active oxygen radicals using anti oxidant enzymes such as superoxide dismutase, ascorbate peroxidase, glutathionic reductase and metabolite such as ascorbic acid, σ tocopherol and carotenoids (Larson *et al*.1998). Tolerance to high temperature in plant have been associated with the increases in antioxidant enzymatic activity (Gupta *et al*., 1993 and Zhau *et al.*, 1995) [28, 82]. Neta Sharir *et al.*, (2005) reported that chloroplast heat shock protein, Hsp21 protected PS-II from temperature dependant oxidative stress. Rain water *et al.*,1996 demonstrated that following exposure to heat shock condition (34 C compared to 26 ˚C) five tested heat tolerant cultivar exhibited greater antioxidant activity that heat sensitive cultivar and the superoxide dismutase activity found to increased by nine folds in heat tolerant cultivar and decreased in heat sensitive cultivar.

**Stress proteins (Heat shock proteins)**

Synthesis and accumulation of specific proteins are ascertained during a rapid heat stress, and these proteins are designated as HSPs. When faced with heat stress, the expression of heat-shock genes increases rapidly, leading to the rapid accumulation of heat-shock proteins (HSPs) as reported by (Yang *et al*. 2016). Induction of HSPs seems to be a universal response to temperature stress. Most of the stress proteins are soluble in water and therefore contribute to stress tolerance via hydration of cellular structures (Wahid and Close, 2007) [73-75, 77]. 5-10 ºC rises in temperature leads to induction of HSPs which help cells to withstand heat stress by acting as molecular chaperones to prevent misfolding of proteins. Expression of HSPs is mainly regulated by heat shock transcription factors (HSFs) on a transcriptional level, and they play a critical role in high-temperature stress responses (Lin *et al.*, 2011) [45]. The HSF gene family has been thoroughly characterized in many species, including Arabidopsis, Chinese cabbage, rice, maize, wheat, pepper and grasses (Guo *et al*., 2008; Lin *et al.*, 2011; Nover *et al*., 2001; Song *et al*., 2014; Xue *et al*., 2014; Yang *et al.*, 2014) [27, 45, 56]. Although tomato HSFs have been identified and classified (Heerklotz *et al.*, 2001; Scharf *et al.*, 1990; Scharf *et al.*, 2012) [34, 68, 67], but only the identification was done in that paper. HSP68, which is localized in mitochondria and normally constitutively expressed, was determined to have increased expression under heat stress in cells of potato, maize, tomato, soybean and barley (Neumann *et al*., 1993) [55]. At high temperature (40 $^0$C), Norchip, the most heat-tolerant cultivar of potato, synthesized small heat shock proteins for a longer time period than the other cultivars and the levels of an 18 kDa small heat shock protein increased up to 24 h in Norchip and Desiree, which are heat-tolerant cultivars, whereas the levels started to decrease after 4 h in Russet Burbank and after 12 h in Atlantic, which are heat-sensitive cultivars (Ahn *et al.*, 2004) [4].

**Table 1:** Effect of heat stress on morphological/ physiological characters of vegetables

| Crop | Symptoms | References |
|---|---|---|
| Brinjal | Reduced extension of main stem, reduced no of branches per plant | Yadav *et al*., 2012 [81] |
| Amaranthus, Palak and Spinach | Reduce their water content thereby reduces their quality | Anonynymous, 1990 [72] |
| Potato | Sharp reduction in the potato tuber yield, at 30 ˚C complete inhibition of tuber formation occurs and decreased starch content | Sekhawat, 2001 |

| | | |
|---|---|---|
| Cauliflower | Ricey, leafy, loose, yellow, small and hard curds | Yadav *et al*., 2012 [81] |
| Tomato | Fruit set failure at high temperatures involves bud drop, abnormal flower growth, poor pollen creation, poor inflorescence and viability, abortion of ovule and reduced carbohydrate existence. | Hazra *et al.* (2007) [33] |
| Cassava | Reduction of leaf area | Yadav *et al*., 2012 [81] |
| Lettuce | Bitter taste, accelerated development of tip burn | Yadav *et al*., 2012 [81] |
| Spinach beet | Bolting rendering the plant unmarketable | Goreta and Leskovar, 2006 [22] |
| Cow pea | Inhibition of floral bud development | Dow El-Medina and Hall 1986 [14] |
| Chili pepper (*Capsicum annuum*) | Reduced fruit width and fruit weight increased the proportion of abnormal seeds per fruit. Abortion of flower prior to anthesis and reduce fruit set | Pagamas and Nawata, 2008 [59]; Aloni *et al.* 2000 |
| Okra | Reduced yield, damages in pod quality parameters such as fibre content and break down of the Ca-pectate. | Gunawardhana *et al*.2011 [25, 26]. |
| Phaseolus vulgaris | Increased vegetative growth, decreased total yield and quality of pods. Increased the total phenolic acids in the pod. | El-Bassiony *et al*., 2012 [16] |

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