

Response of Solanaceous Vegetables to Increasing Temperature and Atmospheric CO₂



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1 Introduction

The climate change has made its strong footprint in the world to the scientific consensus. The foremost reason for this havoc is the emission of greenhouse gases mainly through the anthropogenic (human-caused) activities (Cook et al. 2016). The climate system is on the verge of facing a long-term irreversible impact in all of its components. Global warming, certainly, is one of the serious threats to our ecosystems (IPCC 2014). There will be further warming of the globe with the continued greenhouse gas emissions. The last few decades have witnessed a slow but steady escalation in the global temperature (Fig. 1) as well as atmospheric CO₂ concentrations (Fig. 2). In this chapter, the consequences of rising temperature and elevated atmospheric CO₂ (eCO₂) on plants in general and Solanaceous vegetables in particular are elaborately discussed.

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91

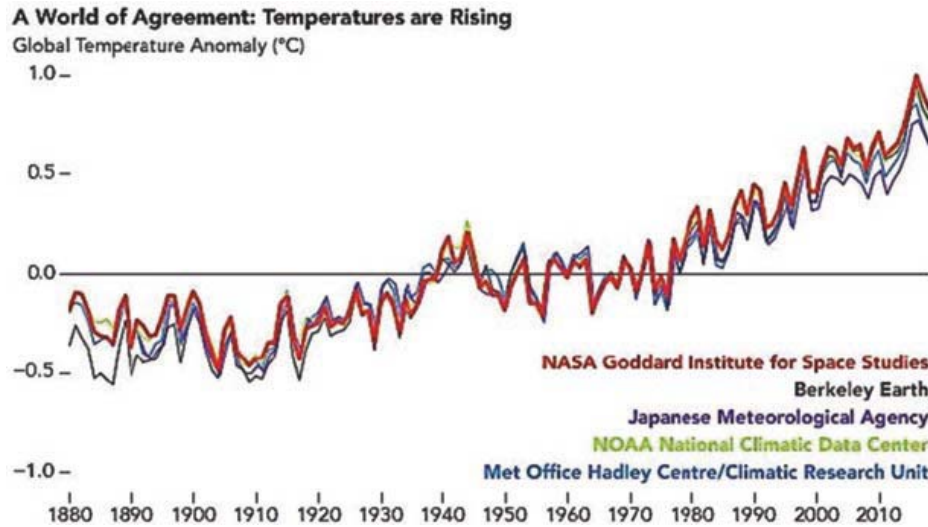


Fig. 1 Temperature data showing rapid warming of the globe. (Source: <https://climate.nasa.gov/scientific-consensus/>)

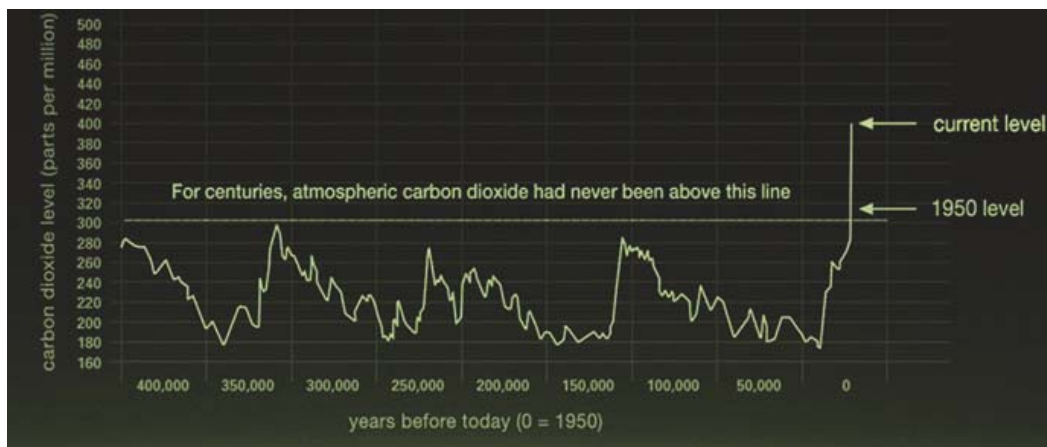


Fig. 2 The relentless rise of atmospheric carbon dioxide. (Source: <https://climate.nasa.gov/evidence/>)

2 Impact of Rising Temperature on Plants

According to IPCC (2007), about 2–3 °C change in temperature is predicted over the coming 30–50 years. Temperature plays a pivotal role in plant growth and development. Each plant species requires a defined range of temperature for completion of its life cycle. With the rise in temperature to the optimum level, the vegetative development is higher as compared to reproductive development. During the reproductive phase of the plant, the extremely high temperature influences the fertilization, pollen viability, and fruit/grain production (Hatfield et al. 2011). Yield potential can be significantly hampered if there are extreme temperatures during the pollination, fruit set, or initial fruit growth stage as well as the reproductive stage. Plant's

cardinal temperature requirements decide its yield response towards the extreme temperatures. The rise in temperature changes the vapour pressure deficit at the leaf surface resulting in increased transpiration. Hastening of foliage aging and shortening of plant growing season (e.g., shorter grain-filling period) are the major detrimental effects of higher canopy temperature (Van de Geijn and Goudriaan 1996). Enzymes are highly influenced by temperature and play a significant role in carrying out different biochemical reactions inside the plant cells. The plant may not function properly or even dies if any one of the essential enzymes fails. For this reason, most of the plant species can survive the high temperature up to a relatively narrow range, i.e., 40–45 °C (Senioniti et al. 1986). The temperature, causing the inhibition of various cellular functions in C₃ species in the cool season, may not apparently influence the warm-season C₃ species like rice, etc. and C₄ species, viz., sugarcane, maize, sorghum, etc. (Abrol and Ingram 1996). Abrupt exposure to high temperature may lead to membrane injury, loss of cellular contents, disruption of cellular functioning, or even death of plant (Ahrens and Ingram 1988). In higher plant species, heat stress results in the reduced synthesis of normal proteins while increased production of a new set of proteins, viz., heat shock proteins (HSPs) is accompanied (Wang et al. 2014). Phenological development of photosensitive crops like soybean is also likely to be prominently disturbed due to the high temperature. Throughout the twenty-first century, about 2.5–10% of yield loss may occur across numerous crop species (Hatfield et al. 2011). As compared to annual crops, perennial crops possess a more complicated relationship with temperature. Exposing the apple plants to the high temperature stress (>22 °C) improved the fruit size and soluble solids but the firmness, a desirable quality, reduced (Warrington et al. 1999).

3 Elevated Atmospheric CO₂ Levels and Plant Responses

The concentration of atmospheric CO₂ is increasing at an alarming rate. The average atmospheric level of CO₂ persistently rose from 315 parts per million (ppm) in 1959 to about 409.78 ppm in 2019 (<https://www.esrl.noaa.gov/gmd/ccgg/trends/global.html>). Such a higher level of CO₂ is not only likely to have a profound effect on the global climate system but also imparts a substantial direct effect on growth, development, and various physio-chemical processes of plants (Ziska 2008).

CO₂ is the base of all life forms on the earth. Plants utilize CO₂ as the basic raw material for building up their tissues, which consequently become the ultimate source of food for all animals, including humans. A number of research outcomes have established the fact that elevated CO₂ level in the atmosphere leads to better plant growth (Singer and Idso 2009). Long back in 1804, de Saussure, for the first time demonstrated better growth in pea plants that are exposed to the increased CO₂ concentrations as compared to the control plants in ambient air. An upsurge of about 33% in agricultural yield with CO₂ enrichment has been reported (Kimball 1983). There is an upsurge in the photosynthetic carbon fixation rate by leaves in response to the elevated CO₂ concentrations in the atmosphere. Towards the rising CO₂

concentrations, plants experience and response differently in an open-field condition as compared to the closed chamber system. Keeping this in mind, free-air carbon dioxide enrichment (FACE) technique was developed in the late 1980s. This method allows the researchers to raise the CO₂ concentrations in an isolated area and measure the resultant response of the plants.

Ainsworth and Rogers (2007) reported about 40% increase in the leaf photosynthetic rates in a range of plant species at an increased CO₂ level of 475–600 ppm. Over the last 35 years, a substantial amount of greenery has been noticed in a quarter to half of the global vegetated lands due to the escalation in the level of atmospheric CO₂ that ultimately led to the increase in leaves on the plants causing greening (Zhu et al. 2016).

3.1 CO₂ Fertilization Effect

It is a well-believed perception that the C₄ plant species (maize, sugar cane, sorghum, millets, etc.) are likely to be less responsive towards elevated CO₂ than the plant species following the C₃ photosynthetic pathway (potatoes, rice, cotton, wheat, barley, etc.). But, in a twenty-year field experiment, this C₃-C₄ elevated CO₂ paradigm is surprisingly reversed as during the last 8 years of the experiment, a significant enhance in the biomass was observed in C₄ instead of the C₃ plants (Reich et al. 2018). This contradictory finding may be because of the availability of nitrogen to the C₃ plants in a lesser amount than that of the C₄ plants with passing time. So, not only the plants but also the soil chemistry and microbes play an important role in getting this astonishing outcome.

3.2 CO₂ Anti-Transpirant Effect

The atmospheric CO₂ also influences the crop plant in another imperative manner. Higher levels of atmospheric CO₂ lead to the decrease of water lost through transpiration in the plants, thus increasing the water-use efficiency. This is due to the contraction and/or decrease in the number of tiny pores, i.e., stomata present in the leaves through which plants transpire (Wolfe and Erickson 1993; Kimball 2011; Deryng et al. 2016).

4 Solanaceous Vegetables

Solanaceae or the nightshade family consists of about 98 genera and 2700 species (Olmstead and Bohs 2006). The economically important edible members of this family are tomato (*Solanum lycopersicum* L.), potato (*Solanum tuberosum* L.),

eggplant (*Solanum melongena* L.), and pepper (*Capsicum annuum* L.). This family also includes a wide array of plant species like tobacco, cape gooseberry, henbane, climbing nightshade, belladonna, mandrake, Jimson weed, petunia, etc. belonging to the diverse groups based on their nature (Rubatzky and Yamaguchi 1997).

5 Response of Solanaceous Vegetables Towards Rising Temperature and Elevated Atmospheric CO₂

Climate change, caused mainly by the anthropogenic greenhouse gas emissions, has disrupted the ecosystem and these greenhouse gases (CFCs, N₂O, CH₄, CO₂, etc.) are the major culprits in the depletion of ozone layer. Vegetable crops under the family Solanaceae have occupied a prime position in the world of vegetables. With the changing scenario vis-à-vis climate systems, along with other agricultural crops, these crops are also significantly influenced. Solanaceous vegetables are basically warm season crops requiring an optimum temperature of 20–27 °C for better growth and development except for potato which requires a cooler climate. The consequences of high temperature (Table 1) and elevated CO₂ are briefly discussed with special reference to important members of the Solanaceous vegetable group.

5.1 Tomato

At the optimum temperature range, viz., 21–24 °C, the tomato plant growth achieves the peak of the sigmoid curve. Deviation from this range will impart a detrimental influence on the growth and development of plant. The exposure of tomato plants to short periods of high temperature affect more severely if coincide with the critical plant growth phase (Geisenberg and Stewart 1986; Haque et al. 1999; Araki et al. 2000). Both day and night temperature play significant role in fruit yield and quality

Table 1 High-temperature injury symptoms in solanaceous vegetables

Vegetable	Injury symptoms
Tomato	Flower drop and underdevelopment of ovaries, no fruit setting beyond 35 °C day temperature, interruption of lycopene synthesis in fruits; sunscald and blotchy ripening in the affected tissues
Potato	Reduction or complete inhibition of tuberization, reducing sugar contents, physiological weight loss of tuber, bacterial wilt, black scurf/canker and black heart disorder
Hot and sweet pepper	Decrease in pollen production, reduced fruit set, reduced seed set, smaller fruit size, premature loss of fruits with sunburn necrosis, blossom end rot on the fruits, poor ripening, and color development of fruits.
Brinjal	Poor fruit and seed set, distorted floral buds and fruits, decrease in pollen production, yellow, bronze, or brown spot on the fruit due to sunburn.

(Iwahori and Takahashi 1964; Abdalla and Verkerk 1968; Kuo et al. 1979; Hann and Hernandez 1982). However, within a certain range, tomato plants have the potential to integrate temperature. Tomato plants exposed to a constant temperature regime may suffer a yield loss whereas a fluctuating temperature regime often does not impart any significant effect on yield (Adams et al. 2001; de Koning 1988, 1990). Both the vegetative and reproductive phases are considerably influenced by high temperature which ultimately affects the fruit yield and quality (Figs. 3, 4 and 5). The number of days for seed germination in tomato is decreased in response to the elevated temperature. Temperature does not have any pivotal impact on dry matter partitioning (Heuvelink 1995) while the fruit ripening can be hindered due to the extreme temperatures (Lurie et al. 1996). In the experiments conducted by Hurd and Graves (1984, 1985), it is demonstrated that there is a decrease in the time taken for fruit maturity in the initial part of the season. The reason may be due to the higher mean temperature in the early phase of the season. There is a positive correlation between fruit temperature of 10–30 °C and fruit growth rate, with an increase of $5 \mu\text{m h}^{-1} \text{ } ^\circ\text{C}^{-1}$ in the fruit diameter (Pearce et al. 1993). A shorter crop production time is the outcome of higher temperature during the plant growth, but with lower yield and small-sized fruits (Rylski 1979a, b; Sawhney and Polowick 1985).

The plant developmental rate and timing of first flowering are affected by the temperature differences during vegetative phase. The fruit firmness, development time, and yield are also significantly influenced by the timing, duration, and magnitude of short-term temperature pulses (Adams and Valdés 2002; Mulholland et al. 2003). For successful tomato production, an average daily temperature of 29 °C during the two-week period up to the opening of flowers has been considered as the critical temperature (Deuter et al. 2012). The constant air temperatures of ≥ 30 °C can hinder the normal ripening and softening of detached mature green tomato fruits (Mitcham and McDonald 1992). If the temperature surpasses 32.2 °C during



Fig. 3 Effect of high temperature on tomato plants (a) susceptible (pot 1) vs. heat-tolerant (pot 2) tomato plant, and (b) Field view of susceptible (yellow encircled) and heat-tolerant (white encircled) tomato plants. (Source: NICRA project, ICAR-Indian Institute of Vegetable Research, Varanasi)

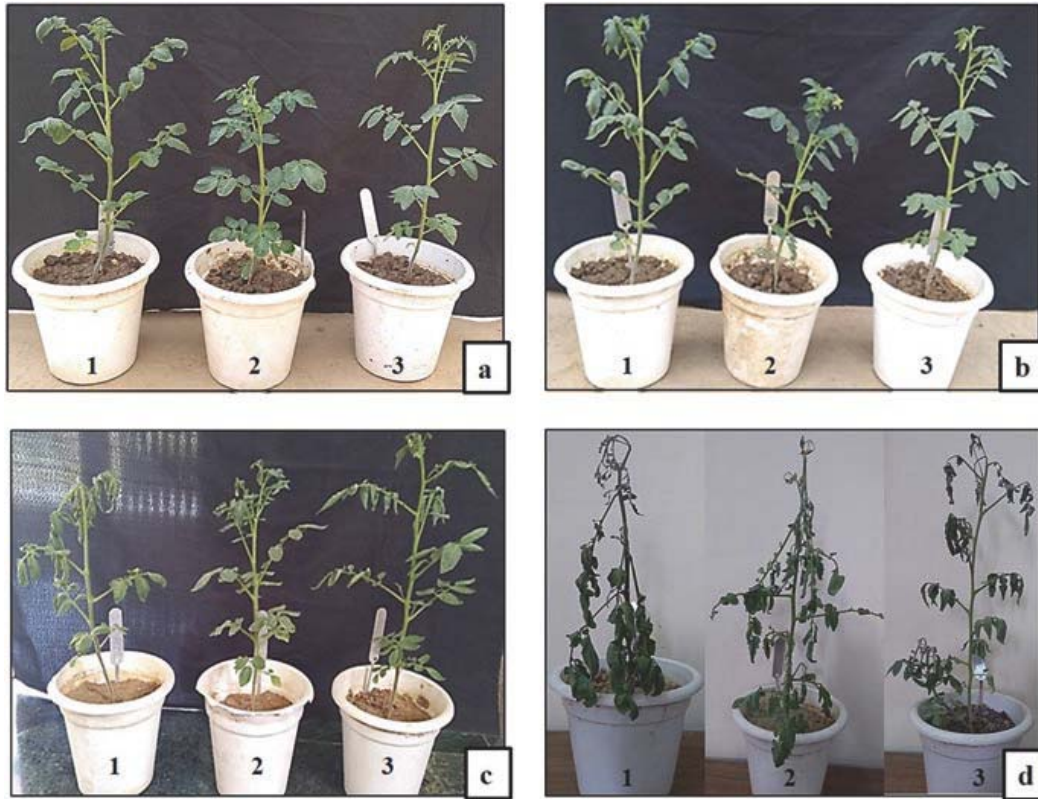


Fig. 4 Response of tomato varieties (pot 1: Punjab Chuhara, pot 2: CLN-1621, and pot 3: H-88-78-1) to high temperature; exposure period (a) 0 h (b) 16 h (c) 32 h, and (d) 48 h. (Source: ICAR-Indian Institute of Vegetable Research, Varanasi)

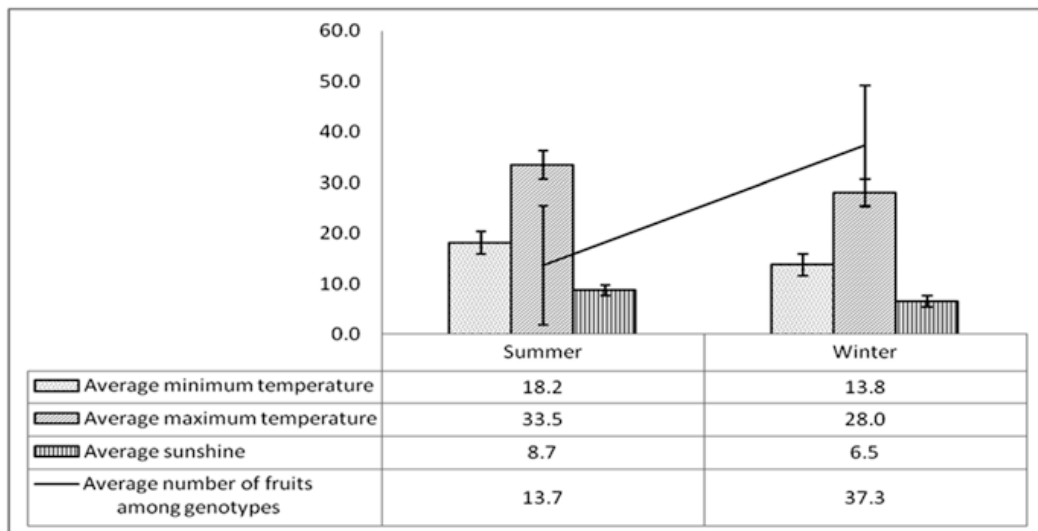


Fig. 5 Effect of temperature on fruit set in tomato during winter and summer seasons. (Source: Kumar et al. 2017)

the critical stages of flowering and pollination, the yield is severely affected as the fruit set is reduced and the fruits become smaller in size and of poor quality (Sato et al. 2001). At elevated temperatures, the flower clusters emerge faster (Adams et al. 2001), and consequently, more number of fruits per plant appear initially (Fig. 3). Vegetative growth is penalised due to the growth of these fruits, however a delay in growth and development of newly set fruits, or flower or fruit abortion may occur (De Koning 1989; Kumar et al. 2017). A single factor cannot be the sole reason for poor fruit set in tomato at elevated temperature as it is considered as a complex trait (Rudich et al. 1977; Prendergast 1983).

Temperature alone or with other environmental parameters influences both the vegetative and reproductive phases of tomato. Several consequences of high temperatures on tomato plants include unnatural flower development, bud drop, persistent flower and calyx, anther splitting, poor anther dehiscence, degeneration of embryo sac and endosperm, scanty pollen production, reduced stigma receptivity and fertilization, low pollen viability, ovule abortion, decreased carbohydrate availability and protein content, reduction in number of seeds per fruit and fruit size, and other developmental abnormalities (Hazra et al. 2007). Sato et al. (2002) discussed the developmental modifications in anthers, especially anomalies in the endothecium and epidermis, poor pollen formation, and the problem of stromium opening are the resultant of elevated temperature during the pre-anthesis stage. There are also reports of splitting of stigma, antheridial cone, and stylar exertion (Rudich et al. 1977; Levy et al. 1978; El Ahmadi and Stevens 1979). Peet et al. (1998) observed the harmful effect of heat stress on development of ovule and embryo, and ovule viability. The pollination is restricted as the stigma dehydrated due to high temperature. A 2–4 °C increase from the optimal temperature imparted detrimental effect on gamete development and suppressed the capability of pollinated flowers to become seeded fruits (Peet et al. 1997; Sato et al. 2001; Firon et al. 2006). Seven to fifteen days prior to anthesis is the critical phase of sensitivity to moderately elevated temperatures (Sato et al. 2002). Under moderately high temperature, the decrease in the fruit set is not primarily due to scanty pollen production rather because of poor pollen release and viability (Sato et al. 2006). The high temperature-tolerant genotypes produced higher number of pollen grains than the sensitive genotypes (Abdelmageed et al. 2003). So, this criterion can be useful in picking heat-tolerant genotypes. In cherry tomato, reduction in lycopene and starch content is observed as the fruit temperature increased by about 1 °C (Gautier et al. 2005). Most of the research works that have targeted the thermo-effect on fruit quality attributes were primarily on postharvest ripening (Dalal et al. 1968; Lurie et al. 1996).

Tomato, being a C₃ plant, is expected to be influenced by the eCO₂ levels under the changing climate system. Nilsen et al. (1983) have reported about the upsurge in the photosynthetic rate in tomato cv. Viroso, grown at the elevated CO₂ concentrations of 500–2000 ppm. There is an increase of early yield in tomato by 15% in response to the elevated CO₂ of 900 μmol mol⁻¹ with additional light (Fierro et al. 1994). In tomato (cv. Arka Ashish), a significantly higher plant height, leaf area per plant, and stem dry mass were recorded when the plants are exposed to 550 ppm of CO₂ whereas for the parameters like number of branches, leaves per plant, leaf dry

mass, and total dry mass, 700 ppm CO₂ was found to be superior. Moreover, CO₂ at 700 ppm concentrations have demonstrated highest photosynthetic rate, number of flowers, fruits per plant, fruit set (%), and fruit yield per plant as compared to CO₂ at 500 ppm and the control (Mamatha et al. 2014). Nutritional quality of tomato is also significantly influenced by increased CO₂ levels. According to Wei et al. (2018), eCO₂ has resulted in a substantial increase in nitrate content in tomato fruits. The total antioxidant capacity, phenols, and flavonoids have decreased to a greater degree at 550 $\mu\text{mol mol}^{-1}$ CO₂. However, ascorbic acid concentration increased notably at 700 $\mu\text{mol mol}^{-1}$ (Mamatha et al. 2014). At early fruiting phase, the sucrose content of fruits has increased greatly due to the elevated CO₂ as compared to the later stage of fruiting (Islam et al. 1996). There has been a mismatch between fruit colour and maturity as eCO₂ exposure of plants leads to the increase in the synthesis of colour pigments in fruits but up to a lower degree than the total solids and soluble sugar synthesis (Zhang et al. 2014). As the sugar concentration in tomato fruits gradually increases from green to red stage, the elevated CO₂ thus resulted in higher accumulation of soluble sugar (Winsor et al. 1962). Khan et al. (2013) demonstrated the acceleration of maturity along with the promotion of fiber and soluble sugar accumulation in *cv.* Eureka. In normal nitrogen availability condition, eCO₂ had negatively affected the lycopene, soluble sugar, and soluble solids content in the fruits whereas in higher nitrogen availability, their concentrations are promoted (Helyes et al. 2012). Under salt-stress conditions (7 dS m⁻¹), there was an upsurge in the fruit yield due to the elevated CO₂ levels while the other quality attributes like acidity, total soluble solids, and total soluble sugar remain constant (Li et al. 1999). The effect of eCO₂ on lycopene content is inconsistent, possibly due to the thermo-sensitivity of lycopene (Krumbein et al. 2012), so no significant impact has been established (Dong et al. 2018).

5.2 Potato

The potato has occupied the third most important food crop position after rice and wheat, and is considered as the most important non-grain crop in the world. Potato performs well under cool climatic conditions and is highly affected by elevated temperatures at different stages of its life cycle (Levy and Veilleux 2007). For net photosynthesis, the lowest, optimum, and highest temperatures reported are 0–7 °C, 16–25 °C, and 40 °C, respectively (Kooman and Haverkort 1995). The establishment stage is affected by the temperature, particularly soil temperature. There are alterations in the morphological attributes of the plant like smaller size of compound leaves and leaflets leading to the reduction in leaf area index (Ewing 1997; Fleisher et al. 2006). A linear correlation is observed between the leaf appearance rate and temperature range (9–25 °C), and beyond 25 °C, no subsequent increase is detected (Kirk and Marshall 1992). Moreover, Benoit et al. (1983) also reported 25 °C to be the optimum temperature for leaf expansion. Light interception reduces as the leaves cannot undergo full expansion in response to the increasing

temperature. A reduced specific leaf area is reported in the varieties grown in hot climatic conditions (Midmore and Prange 1991). Therefore, there is a linear rise in the leaf expansion up to 24 °C, but at 35 °C, a linear decline is observed (Kooman and Haverkort 1995). Similarly, a linear relationship between temperature and stem elongation is noted up to 35 °C (Manrique 1990) and is accelerated by low night and high day temperatures (Moreno 1985). As yield is a resultant of light use efficiency and intercepted radiation, yield is penalized at elevated temperatures owing to the declined ground-cover duration that is positively interlinked with yield (Vander Zaag and Demagante 1987). High temperatures strongly suppress the tuber formation, reduce the fitness of seed tubers, lessen the shelf life of potato tubers, lower the amount of assimilated carbon partitioned to tuber starch, and hastens the leaf senescence (Menzel 1985; Ewing 1981; Fahem and Haverkort 1988; Wolf et al. 1991; Hancock et al. 2014; Sonnewald et al. 2015). Warmer temperature below 21 °C was found to accelerate the tuber initiation (Kooman et al. 1996). Moderately elevated temperature can also lead to severe tuber yield reduction without any considerable effect on total biomass and photosynthesis (Peet and Wolfe 2000). Moreover, at higher temperature, the translocation of biomass production is also restricted. Above two-thirds of the total photosynthates were translocated to the tubers at 18 °C, however hardly 50% translocated at 28 °C (Randeni and Caesar 1986) which suggests that the shoot portion of the plant is more favored for assimilates over the tubers resulting higher growth of haulm and restricted tuber production. High temperature also significantly restricts the tuber bulking rate in potato (Struik 2007) which may be due to the relationship with the hindered sugar to starch conversion (Krauss and Marschner 1984). The sprout growth is also inhibited by temperatures above the optimum (Midmore 1984) as a result of subapical necrosis (McGee et al. 1986). Kim et al. (2017) revealed a contrasting result of substantial decrease of 11% of tuber yield per degree of temperature rise in the range of 19.1–27.7 °C than the reported value of about 3–4.6% reduction per 1 °C temperature increase in the range of 13.81–25.45 °C (Peltonen-Sainio et al. 2010; Fleisher et al. 2017). At elevated temperatures, the marketable tubers become smaller in size due to the decreased sink strengths of tubers (Geigenberger 2003; Baroja-Fernández et al. 2009). At elevated temperature, there is a higher utilization of assimilated carbohydrate for respiration, thus resulting in reduced tuber formation (Hijmans 2003). During a study on potato cvs. Kufri Surya (heat tolerant) and Kufri Chandramukhi (heat susceptible), a significantly higher rate of transpiration, stomatal conductance, and photosynthesis was observed in Kufri Surya at the higher temperature. Moreover, the rise in temperature led to an upsurge in chlorophyll content in both the cultivars whereas biosynthesis of gibberellic acid was restricted in cv. Kufri Surya (Singh et al. 2015). The CO₂ compensation point and dark respiration rates increased at high temperatures. The net photosynthesis rate has revealed a decline at the high temperature of 40–42 °C or after shifting the plants from the temperature regimes (daytime) of 22–32 °C (Wolf et al. 1990). The combined effect of heat and drought stress that sustained for 14 days has reduced the yield of the tolerant cultivars by about 25% and by over 50% in susceptible cultivars of potato (Rykaczewska 2013). A rise in temperature during the later stages of plant development had a detrimental effect on

the sprouting of tubers in the soil prior to harvest. The growth stage of the plant largely influences the thermo-response of the potato cultivars. The earlier the growth stage, higher will be the damage severity with respect to the plant growth and total tuber yield. The physiological defects of tubers and secondary tuberization should also be taken into consideration along with total tuber yield regarding the thermo-tolerance in potato (Rykaczewska 2015). High temperature also affected the infection rate of various diseases of potato. Chung et al. (2006) have reported the highest number of plants infected with potato virus Y-O and potato virus A at 20 °C; and potato leafroll virus at 25 °C. The infestation of *Myzus persicae* (potato peach aphid) is advanced by 2 weeks for each 1 °C increase in the mean temperature. Furthermore, there is a positive correlation between aphid population upsurge; and minimum relative humidity and maximum temperature (Dias et al. 1980; Biswas et al. 2004). Most of the Indian potato varieties are furnished with single specific trait of interest, viz., high yielding, early maturing, high biotic/abiotic stress tolerance/resistance, etc. (Table 2).

Potato plants with short-term exposure to increased CO₂ have demonstrated an increase in the photosynthetic rates (Donnelly et al. 2001a; Vandermeiren et al. 2002). Sicher and Bunce (1999) proposed that the acclamatory reaction to enhanced CO₂ is the resultant of the reduced RuBisCO (Ribulose biphosphate carboxylase/oxygenase) activity rather than any decline in the leaf content of this protein. Contrarily, Schapendonk et al. (2000) reported that the acclimation is a complicated mechanism caused due to the negative response of sink-source balance induced by high temperature and irradiance. A positive correlation is found between the CO₂ assimilation and concentration. An increase in total biomass by 27–66% is observed by doubling the ambient CO₂ level (Collins 1976; Wheeler et al. 1991; Van De Geijn and Dijkstra 1995; Donnelly et al. 2001a; Olivo et al. 2002; Heagle et al. 2003). At elevated (up to 700 µmol mol⁻¹) and super-elevated (1000–10,000 µmol mol⁻¹) CO₂

Table 2 Trait-specific performance of Indian potato varieties

Variety name	Yield potential (t/ha)	Crop maturity period ^a	Heat tolerance	Drought tolerance	Late blight resistance
Kufri Sindhuri	30–35	Late	High	Medium	Sensitive
Kufri Arun	30–35	Medium	Sensitive	High	High
Kufri Chandramukhi	20–25	Early	Sensitive	High	Sensitive
Kufri Chipsona	30–35	Medium	Sensitive	Medium	High
Kufri Bahar	30–35	Medium	Sensitive	Medium	Sensitive
Kufri Kanchan	25–30	Medium	Sensitive	Medium	Medium
Kufri Surya	25–30	Early	High	Medium	Sensitive
Kufri Megha	25–30	Medium	Sensitive	Medium	High
Kufri Jyoti	25–30	Medium	Sensitive	Medium	Medium
Kufri Khyati	25–30	Early	Sensitive	High	High
Kufri Pukhraj	35–40	Early	Sensitive	High	Medium

Source: Gatto et al. (2016, 2018)

^aEarly: 70–90 days, Medium: 90–100 days, and Late: >110 days

levels, a decrease in the stomatal conductance of potato leaves has been reported (Sicher and Bunce 1999; Lawson et al. 2001; Finnan et al. 2002). It is expected that the reduction in the stomatal conductance enhances the water use efficiency of potato. Olivo et al. (2002) have reported a reduction of 16% in the transpiration rate and increase in the instantaneous transpiration efficiency by 80%. In potato, the leaf chlorophyll content pattern fluctuates in correspondence with the developmental stages of the plants (Finnan et al. 2005). During the later stage of plant growth (after tuber initiation), increased CO₂ level negatively affected the leaf chlorophyll content (Lawson et al. 2001; Bindi et al. 2002). In an open top chamber experiment, an increased CO₂ concentration of 680 ppm resulted in a 40% rise in the light-saturated photosynthetic rate of completely expanded leaves in the upper canopy of cv. Bintje during tuber initiation phase due to the cumulative influence of decrease in the photosynthetic ability and a 12% decline in the stomatal conductance (Vandermeiren et al. 2002). With the exposure to elevated CO₂, the tuber yield is stimulated and the extent of tuber yield is highly dependent on numerous additional factors like growing conditions, agronomy, and cultivar. The starch and dry matter content in potato tubers enhances while the glycoalkaloid and nitrogen content in tubers reduces in response to enriched CO₂ (Finnan et al. 2005). Miglietta et al. (1998) reported about 10% increase rate in the tuber yield for each 100 ppm rise in CO₂ level. The response of potato plant towards the elevated CO₂ varies on the basis of variety and nutrition (Olivo et al. 2002). With optimum supply of nutrients, dry matter yield is significantly influenced by doubling the ambient CO₂ level, whereas, in nitrogen deficit condition, a minor negative response to CO₂ enrichment is noticed (Goudriaan and De Ruiter 1983). Under increased CO₂ concentrations, there are no alterations in the number of tubers; however, improvement was seen in the tuber weight primarily due to the rise in the cell number in tubers without affecting the cell volume (Collins 1976; Donnelly et al. 2001b; Chen and Setter 2003). Contrarily, Miglietta et al. (1998) and Craigon et al. (2002) have reported an increase in the number of tubers. The intensification of starch and soluble sugars in the tubers in response to the elevated CO₂ has resulted in enhanced browning and acrylamide synthesis upon frying (Donnelly et al. 2001b; Kumari and Agrawal 2014). Högy and Fangmeier (2009) revealed a varying effect of eCO₂ on the processing and nutritional quality of potato. Fangmeier et al. (2002) emphasized the need for necessary alterations in fertilizer practices in the upcoming CO₂-rich global climate system with special significance on the quality of potato tubers as the concentration of crude protein was influenced by CO₂ along with O₃. At different water-stress levels, consistency was observed in potato yield enhancement under elevated CO₂ concentrations (Fleisher et al. 2008).

A significant effect on potato production in India is projected in response to the cumulative effect of eCO₂ and high temperature (Table 3).

Table 3 Per cent change in potato production in India as influenced by increased temperature and elevated CO₂ (without adaptations)

Atmospheric CO ₂ conc. (ppm)	Increase in temperature (°C)					
	Nil (2009)	1 (2020)	2	3 (2050)	4	5 (2090)
369 (2009)	0.0	-6.27	-17.09	-28.10	-42.55	-60.55
400 (2020)	3.40	-3.16	-14.57	-25.54	-58.63	-58.63
550 (2050)	18.65	11.12	-1.25	-13.72	-30.25	-49.94

Values in parentheses are likely years for associated temperature increase and CO₂ concentrations (Source: Singh et al. 2009)

5.3 Pepper

Temperature possesses a pivotal role in proper growth, flowering, and fruit set in sweet pepper (Rylski and Spigelman 1982; Polowick and Sawhney 1985). Even a short-term exposure (20 min) of pepper plants to high temperature, viz., >40 °C can be detrimental to net photosynthesis rate (Hanying et al. 2001).

The pre-anthesis period in sweet pepper is not sensitive to elevated temperature and there is no effect on stamen or pistil viability. However, at later stages of the plant's life cycle, fertilization is affected by high temperature and a reduction in fruit setting is observed (Erickson and Markhart 2002). Fierro et al. (1994) reported a yield increment of 11% in pepper under the influence of enhanced CO₂ (900 µmol mol⁻¹) with supplementary light (ambient +100 µmol m⁻² PAR). Elevated temperatures at the time of flowering are responsible for improper pollen tube growth, faulty germination and fertilization leading to flower abscission and decrease in fruit setting (Usman et al. 1999; Aloni et al. 2001).

The productivity of greenhouse pepper and other C₃ plants increases up to 50% or higher with CO₂ enrichment (Nederhoff 1994; Akilli et al. 2000). With the increase in application duration, the efficiency of CO₂ enrichment has improved. Vafiadis et al. (2012) suggested that the application of CO₂ enrichment is feasible under elevated temperatures with a positive response in terms of yield in pepper. The increased CO₂ level has a significant effect on components of free amino acid in sweet pepper (Piñero et al. 2017). A reduction in nitrogen level in leaves by 10% was observed in comparison with the reference leaves after 58 days under variable CO₂ enrichment conditions (Porrás et al. 2017). Under Mediterranean conditions, variable CO₂ enrichment has demonstrated an enhanced production of sweet pepper (Alonso et al. 2010).

5.4 Eggplant

Flowering and fruit setting in eggplant is highly thermo-responsive (Nothmann et al. 1979). Among the Solanaceous vegetables, eggplant is the most thermophilic one (Abak et al. 1996). An increase in stem diameter and plant height in response to

enhanced temperatures was observed in eggplant (Pearson 1992; Uzun 1996; Cemek 2002). Cemek et al. (2005) observed a higher plant height in eggplants raised in double polyethylene-cladded greenhouses (having a higher temperature) than that of the single polythene-cladded greenhouses. Fruit set in eggplant reduced as low as 10% in warm Mediterranean regions in response to the cumulative effect of low humidity and high temperatures (Passam and Bolmatis 1997). When the maximum temperature enhanced by 1 °C over the range of 28–34 °C during the first five days of flowering, the rate of fruit setting reduced by 0.83% (Sun et al. 1990).

Fruit yield in the eggplant cv. Cava increased by 13%, 28%, and 18% with concentrations of 0.1, 0.2, and 0.3 g l⁻¹ CO₂ in irrigation water, respectively as compared to the control (Aguilera et al. 2000). They also reported the highest fruit weight and fruit yield in 0.3 and 0.2 g l⁻¹ dose.

6 Conclusion

Vegetable crops are highly vulnerable towards the climatic vagaries and respond in terms of reduction in production, productivity, and quality. Environmental constraints like increasing temperature and elevated CO₂ have significantly affected the Solanaceous vegetable crops influencing their yield and quality. Thus, the need of the hour is to undertake more research works to identify and/or develop climate-resilient genotypes and advanced technologies to maintain a sustainable production system and safeguard the food as well as nutritional security under the inconsistent global climate system.

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