Review Article

Physiological responses of Vegetables in changing climate

ABSTRACT

The ever- growing human population and substantial decline in productive land make the world's food production at risk.Vegetables are rich source of vitamins, carbohydrates, minerals,proteins and phytochemicals, especially antioxidants.They are the best means of overcoming micronutrient deficiencies and provide higher incomes and more jobs per hectare to small holder farmers than staple crops.Most of the vegetables that humans rely on for nutrition and energy use the C3 pathway and these crops are expected to consume less water and yield more harvestable goods than C4 crops.The positive direct effect of increase in carbon dioxideon agricultural productivity, however, may be countered by other climate change impacts, such as increased temperature and changing precipitation patterns.Major challenges faced by vegetable growers are increased terminal heat stress, rainfall variability leading to flooding, drought, irrigation water availability, salinity, incidence of pests and diseases.A rapid increase in temperature as well as unpredictable precipitation at any stage of the crop growth can alter the normal growth, flowering, pollination, and fruit development, ultimately diminishing crop production in future.In a warmer, high carbon dioxide environment, changes in food quality are to be expected, such as lower protein and mineral nutrient concentrations and changed lipid composition. In order to sustain the vegetable production, breeding programs focusing on identifying genotypes with higher yield and quality under stress conditions should be streamlined for ensuring food security.

Keywords: **Climate change, crop physiology, temperature rise, elevated CO_2, salinity, precipitation**

Abbrevations: - Elevated CO_2(eCO_2), Free-Air CO_2 Enrichment (FACE), Net photosynthetic rate(Pn),stomatal conductance(gs)

INTRODUCTION

Climate change is one of the significant challenges that plant scientists currently facing.It has resulted in erratic rainfall, rising temperatures, change in weeds, pests,microbes,fluctuations in atmospheric carbon dioxideand ozone levels and variation in sea level.The agricultural production system is affected both directly and indirectly by the changing climate and thereby influencing food security. Direct effects include the effect on production systems brought by a change in temperature levels and rainfall distribution. When changes are made to other species, such as pollinators, pests, disease vectors, and invading species, it has an indirect effect on production. Thus crop production and climate change are intrinsically linked affecting the global food production.

According to the Global Monitoring Lab's annual report, the average amount of carbon dioxide in the atmosphere has reached 417.06 ppm in 2022 and the mean rise in atmospheric carbon dioxide between 2021 and 2022 was 2.13 ppm, marking the 11th year in a row where the increase was greater than 2 ppm (NOAA, 2023).The consequences of elevated atmospheric carbon dioxide and associated increase in temperature and precipitation variations were anticipated to have impacts on the distribution, relationships, and ecophysiology of plants (IPCC, 2014). The longer elevated carbon dioxideexposure may result in photosynthetic adaptation because of an increase in soluble sugars, which leads to an imbalanced C: N ratio, faster leaf senescence, and/or limited growth rate, which affect crop yield and quality. It is believed that crop quality is a multifaceted and a complex process that involves growth, assimilation, partitioning, storage, pre- and post-harvest, as well as nutritional, technological and environmental components (Hay & Porter, 2006).

Extreme weather events and variations in seasonal climatic conditions impacted rainfed traditional agriculture and home garden food production systems in rural areas, leaving people more vulnerable to food and nutrition insecurity (IPCC, 2014). The land and ocean combined global surface temperature data (1880–2019) from the NOAA shows a change of 13.9°C compared to the 1901–2000 average.As temperatures continues to warm, global average precipitation will also increase by the end of the century. This increase is not, however, expected to be distributed evenly around the globe or throughout the seasons in a given year. Many parts of the world could experience increase in the frequency and intensity of extreme, heavy rainfall events, and in other parts of the world, dry conditions may become more severe and last longer.It may be noted that many areas, especially in low- and midlatitude regions, are expected to suffer from more frequent and more severe droughts(IPCC Working Group I, 2021).

Vegetables are rich source of vitamins, carbohydrates, mineralsand proteins. They are the best means of overcoming micronutrient deficiencies and vegetable farming provides much higher incomes and more jobs per hectare to small holder farmers than staple crops.After China, India is the second-largest producer of vegetables worldwide **(**www.fao.org**).** According to the National Horticulture Database's (3rd Advance Estimates) report, India produced 204.84 million metric tonnes of vegetables from an area of 11.35 million hectares (www.apeda.gov.in). Vegetables can be classified as fruit-vegetables such as tomato, cucumber, watermelon, peas; roots and tuber vegetables such as carrot, potato, sweet potato, radish, elephant foot yam; green leafy vegetables like amaranth, celery, cabbage, curry leaves and bulb vegetables like onion and garlic (Abewoy, D, 2018).Unfortunately these crops are highly susceptible to unpredictable weather conditions and are highly perishable. Vegetable cultivation becomes unprofitable due to crop failures, low yields, poor quality, and an increase in pests and diseases caused by changing climatic conditions (Lal *et al.*, 2014).They are sensitive to environmental extremes*viz.*, high temperatures and limited soil moisture. These extremes affect many physiological and biochemical processes like reduced photosynthetic activity, altered metabolism and enzyme activity, tissue heat damage, reduced pollination, and fruit production, etc., which will be exacerbated by climate change (Abewoy, D.2018).In the context of climate change major challenges faced by vegetable farmers are crop failures, low yield, decreased quality, and an increase in pest and disease incidence. Besides these, other primary limiting factors hindering the vegetable production are decreased irrigation water supply, floods, salts etc.Hence crop physiologists need to better consider the needs of breeders and processors in this situation by evaluating, characterizing, and simulating variations in food quality among crop varieties and species under scenarios of climate change (Hay & Porter, 2006).

CO$_2$fertilisation effect on C3 and C4 vegetables

Carbon dioxide is one of the greenhouse gases whichhassignificant direct effects on plant development, physiology, and chemistry (Ziska, 2008). The elevated carbon dioxide condition will affect growth and yield of both C3 and C4 plants by enhancing the net photosynthetic rate (Kimball *et al*. 2002; Reddy *et al*. 2010) and improving water use efficiency (Long *et al*., 2004).Around 96% of a normal plant's dry matter is made up of carbon, hydrogen and oxygen absorbed into organic molecules during photosynthesis(Marschner, 1995). Hence, photosynthesis is at the core of plant’s nutritional metabolism and increasing the amount of carbon dioxideavailable for photosynthesis can have a significant impact on plant growth.According to Ainsworth & Rogers (2007) the development of plants under increased carbon dioxideconcentrations of 475–600 ppm results in an average 40% increase in leaf photosynthetic rates. The opening of stomata through which plants exchange gases with the environment are regulated by carbon dioxide concentrations. The stomatal pores in plants close whencarbon dioxideconcentrations are higher than ambient and they open when carbondioxideconcentrations are lower. Water may flow out of leaves through open stomata which also allow carbon dioxideto permeate into leaves for photosynthesis. So plants can maintain a highphotosyntheticrates with low stomatal conductance at higher carbon dioxideconcentrations.Sincephotosynthesisandstomatalbehaviourarecentraltoplant metabolism,growingplantsunderelevatedcarbon dioxide hasavarietyofsecondaryeffectsonplantphysiology.Theavailabilityofadditionalphotosynthesisallowsmostplantstogrowfasterandproducedrymatterunderincreasedlevels.Here elevated carbon dioxide (eCO2) has been widely employed as a gas fertiliserin the growing of greenhouse vegetables, especially in recent years(Bisbis*et al*., 2018).But the positive direct impact of elevated carbon dioxide may be countered by other climatic change effects like increased temperature, higher tropospheric ozone concentrations, and altered precipitation patterns.

Greenhouse vegetables have a very positive effect on carbon dioxide enrichment by increasing dry mass, plant height, production of leaves and lateral branches (Mortensen, 1987). Long, 2004has found that duetoincreasedphotosyntheticactivity,leafnonstructuralcarbohydrates(sugarsandstarches)perunitleafareaincreasedbyanaverageof30–40%underFree-air carbon dioxideenrichment (FACE)elevatedcarbon dioxide condition. Plant quality, growth habit and number of flowers are often improved by carbon dioxide enrichment. Which decreasesoxygen inhibition ofphotosynthesis and increases net photosynthesis in plants. This is the basis for increased growth caused by elevated carbon dioxide concentration (Mortensen, 1987). So the excess assimilate can be used directly to promote leaf development in leafy vegetables such as lettuce (Hicklenton, 1988) or stored as a reserve to divert fruit to areas with high sink potential, such as fruit development in tomatoes (Slack, 1986). According to Hamim (2005) a rise in photosynthesis brought on by higher carbon dioxide particularly at the onset of a drought, may enhance the solute accumulation of organic acids and sugars necessary for osmotic adjustments. Peet and Willits (1987) reported that increasing the time of carbon dioxide enrichment significantly increased cucumber yield. According to Mortensen (1994), increasing carbon dioxidelevels resulted in yield increases of 18%, 19%, and 17% for lettuce, carrots, and parsley respectively. The yield of tomato and pepper increased by 15% and 11% respectively with elevated carbon dioxide and morelight (Fierro *et al.*, 1994). Since higher carbon dioxide causes the plants to transpire less and assimilate more carbon dioxide, it has been hypothesised that this will improve the water use efficiency (WUE) of C3 species.Drake *et al.* (1997) found that the photosynthetic rate of C3 species increases by around 58% as a result of an increase of carbon dioxide, implying that their reaction to increasing carbon dioxide may be advantageous than that of C4 species.

In C4 species, photosynthesis seems to be saturated at current atmosphericcarbon dioxideconcentration (Von Caemmerer*et al.*, 1997). This is attributed to the fact that in C4 species carbon dioxide concentrating mechanisms (CCM) help plants to maintain their rate of carbon dioxide absorption even when water supply is limited and stomatal conductance is decreased (Knapp AK, Medina E. 1999). According to Amthor and Loomis (1996) the ability of C4 species to respond to carbon dioxide enrichment is limited by the carbon dioxide concentrating mechanism they adopt. The effect of elevated carbon dioxidefertilization on C4 species is not well understood, although evidence suggests that carbon dioxide enrichment increased leaf net carbon dioxide assimilation rate (Pn) (Ziska *et al.*, 1999) and reducedtranspiration rate may cause an increase in *Pn*of C4 species by increasing leaf temperature (Ghannoum *et al.* 2000). Therefore C4 species may exhibit a more apparent benefit from elevated carbon dioxideon photosynthesis at drought condition (Seneweera*et al.* 1998).

High temperature stress on vegetable production

Long-term global mean temperature estimates indicate a rise of 1.1-4.8 °C over the previous 50 years, depending on the scale of future greenhouse gas emissions (Walsh *et al.* 2014).These changes in global temperature would cause an increased frequency of heat waves, fewer days of freezing temperatures, less rainfall but more intense precipitation and a higher incidence of droughts and other weather extremes experienced around the world, all of which would have a negative impact on agricultural production (Dempewolf *et al.,* 2014). Extremeeventslike heavy precipitation leads to flooding which has detrimental effect on vegetable production due to disturbed physiological functioning(Gibbs and Greenway, 2003).Flood affected tomato plants accumulate endogenous ethylene that causes damage to the plants which hasten rapid wilting and death of tomato plants which is generally observed following a short period of flooding at high temperatures (Mohorović et al., 2023). Onion is also sensitive to flooding during bulb development resulting in yield loss up to 30-40% (Kumar SN, 2017).

Vegetable crops are extremely vulnerable to climate change such as rapid temperature at any stage of crop growth (Afroza *et al.*, 2010).The environmental fluctuations have a substantial impact on the various developmental phases including vegetative growth, flowering, and fruiting. Thephysiologicaldamagescausedby hightemperaturessuch as leaf abscission,leaf burning,senescenceand restrictedroot andshoot developmenthave a significantimpact on crops and ultimatelyreduce production. Alsoit canlead to lower seed germination rates,plantemergence, weak seedlingvigor,aberrant seedlings, and reduced radical and plumule development (Bita *et al.*, 2013). High temperatures may disrupt a number of metabolic processes that occur in guard cells; thestomatal response is typically regulated by transpiration rate, photosynthetic rate, plant water status and vapour pressure deficit (Urban *et al.*, 2017). High temperatures increase the rate of evapotranspiration throughout the vegetative and reproductive stages, which restricts the amount of water that plants can take in. Thiseffects dehydration which inhibitgrowth of both the individual organs and the entire plant (Fahad *et al*., 2017).

The reproductive stage is the most sensitive time in a crop's life cycle and this sensitivity causes a considerable reduction in seed set and crop output (Hein *et al.*, 2021). It isfound to have a negative impact on various aspects of reproductive development in a variety of species including meiosis in both male and female gametes, pollen germination and pollen tube growth, pollen/pistil interactions, ovule viability, pollen grain number, formation of endosperm and embryo development, fertilization and post-fertilization processes. Pollen viability is lost as a result of high-temperature stress due to changes in membrane integrity, protein, carbohydrate and lipid mechanisms and phospholipid profiles (Djanaguiramana*et al.*, 2018).

High temperature stress has a negative impact on agricultural productivity and also on the quality of agricultural produce**.** It alters the enzyme function in aleafandcauseschangesinthedevelopmental stagesthatare directlyrelatedtocrop yield(Zhu*et al.*, 2018).Theoptimumtemperatureforgrowingcrops is about 15-30°C. However temperatureelevationspredominantlyaffect plant's physiological processesparticularlyphotosynthesis, respiration,transpiration, and yield.Extreme temperatures have a significant impact on photosynthesis in leaves and the mechanisms involved in photosynthetic metabolism (Asthir, 2015) such as lower *Rubisco* activation and drop in stomatal conductance(gs) will decrease the net photosynthetic rate.High temperature influence photosynthetic membranes, ion leakage, the activities of carbon metabolic enzymes, starch accumulation, sucrose synthesis through down-regulating certain genes involved in carbohydrate metabolism. High temperature also has a significant impact on chloroplast throughout the photosynthesis process, including grana stack enlargement and aberrant stacking (Wahid *et al.*, 2005). The chlorophyll production in plastids plays a significant role in light harvesting. Under temperature stress condition, chlorophyll pigments in plastids are harmed and degraded and 5-aminolevulinate dehydratase (ALAD), the initial enzyme of pyrrole biosynthesis, showed reduced enzymatic activity (Ashraf *et al.*,2013). It was also observed that the key phytohormones such as abscisic acid, ethylene, and salicylic acid are increased by high temperatures, whereas gibberellic acid, cytokinin and auxins were reduced. High temperature affects red colour development in ripen chilli fruits and also causes flower drop, ovule abortion, poor fruitset and fruit drop in chilli (Kurtar ES,2010).Reactive oxygen species (ROS) are also produced as a result of high temperatures (Bita and Gerats, 2013) and this increased generation of ROS, including lipid peroxidation, superoxide free radicals and hydrogen peroxide (H_2O_2) induce cell membrane damage (Narayanan *et al.*, 2016) results in oxidative stress (Potters, 2007). High temperature reduces the net assimilation rate induce denaturation of proteins and programmed cell death in some cells or tissues. It causes decreased ion flux, leakage of electrolytes, changes in relative water content, the production of toxic compound and disruption of homeostasis, ultimately reduce cell viability.

Planttissueproteinconcentrationiscloselyrelatedtoplantnitrogenstatus. InFACEexperiments,proteinconcentrationsinwheat,rice,barleygrains,andpotatotubers are decreasedby5–14%withincreasing carbon dioxide(Taub*etal.*, 2008). The nitrogen content of leaves in plant tissue often declines as carbon dioxide levels rise and it is reported an average of 13% less nitrogen per unit leaf mass(Ainsworth&Long2005).Thisdecreaseintissuenitrogenmaybeduetoseveralfactors such asnitrogendilutionduetoincreasedcarbohydrateconcentration,reducedmineraluptakefromthesoilbecauseof reducedstomatalconductivityandplantsabsorblesswater(Taub&Wang2008) and reducedrateofassimilationofnitrateintoorganiccompounds(Bloom*etal*.,2010).A meta-analysis done by Dong *et al*., 2018showed that eCO_2 decreased the protein concentration in vegetables (9.5%). That is about 10.5% reduction in fruit vegetables like cucumber, hot pepper, strawberry, sweet pepper, and tomato and 12.6% reduction in stem vegetables like ginger, onion, potato and 20.5% reduction in root vegetables like carrot, radish, sugar beet and turnip. Also reported that elevated carbon dioxide decreased the nitrate concentration in fruit and leafy vegetables by 26.2% and 18.8% respectively. It indicates that elevated carbon dioxide promotes the nitrate assimilation to a greater extent than nitrate uptake.

Increased carbon dioxide levels may also result in lower plant concentrations of nutrients including calcium, magnesium and phosphorus (Loladze, 2002). Iron content decreased the most in leafy vegetables (31.0%), next in fruit vegetables (19.2%), and finally in root vegetables (8.2%), whereas zinc concentration reduced by 18.1% in both fruit and root vegetables and by 10.7% in stem vegetables (Dong *et al*.,2018). According to Myers *et al*., 2014, a5.2% drop in iron was found in rice and Loladze (2014) reported 10% loss in C3 plants. Increased levels of carbon dioxidein future climates reduced the availability of nutrients in vegetables which led to deteriorating human health especially in growing children (Myers *et al*., 2014).Also various studies reported that the eCO_2 reduced mineral concentrations either via dilution effect (Fangmeier *et al*., 2002; Högy and Fangmeier, 2009; Loladze, 2014) or by restricted transpiration (Mc Donald *et al*., 2002)

Increased carbon dioxide stimulates the accumulation of soluble sugar in plants edible portions. The production of triose phosphate in leaves is stimulated by the increased carbon dioxide fixation under eCO_2 (Long *et al*., 2004) which can be converted into more carbs, such as glucose, fructose, and sucrose. Based on the meta analysis, eCO_2 raised the concentrations of glucose by 13.2%, fructose by 14.2%, sucrose by 3.7% and total soluble sugar by 17.5% in terms of all vegetables. Compared to leafy vegetables, total soluble sugar increased less in fruits and roots, respectively 8.5% and 16.3%. This indicates that carbohydrates synthesized in leaves cannot be fully transferred to fruits or roots, although species differences were noted. Elevated carbon dioxide decreased the concentration of total antioxidant capacity in fruit vegetables, ascorbic acid in root vegetables, chlorophyll a, and carotenoids by 14.4%, 14.8%, 14.1%, and 8.1%, respectively, while having no noticeable effect on the accumulation of pigments like total chlorophyll, carotenoids, lycopene, and anthocyanins (Dong *et al.*, 2018). So the rising carbon dioxide concentrations, high temperature and associated climate change over the next century are likely to impact both agricultural production and food quality.

Salinity is one major challenge faced in vegetable production which poses water stress to the plant. Salt stress caused reduction in growth and stomatal conductivity. It is noticed that salt affected plants exhibit lower transpiration and cell water potential. Onions are susceptible to saline soils, while cucumber, brinjal, pepper, and tomato are moderately sensitive to salinity (De la Peña and Hughes,2007). Salinity causes a significant reduction in germination percentage and rate, root and shoots length and fresh root and shootweight in cabbage (Jamil and Rha, 2004).

Impact on pests and diseases in vegetables

Theecology and biology of insect pests are affected by climate change (Jat *et al.*, 2011).Being cold-blooded, insects are extremely sensitive to temperature. Rising temperatures will result in longer breeding seasons and higher reproduction rates. Studies showed that increased temperatures will hasten the growth of the Colorado potato beetle, European corn borer, onion maggot, and cabbage maggot (Newton *et al.*, 2011). Studies on aphids and moths have demonstrated that rising temperatures can enable insects to achieve their minimum flight temperature earlier, enhancing their ability to disperse (Zhou *et al.*,2014). Some insects with short life cycles, including aphids and diamondback moths reproduce more often and finish their life cycles early under increased temperature therefore create more generations every year (FAO, 2009). High air temperatures enhance insect growth and oviposition rates, insect outbreaks and the introduction of invasive species but they also reduce the fungi's capacity to control insects through biocontrol, the reliability of economic threshold levels, insect diversity in ecosystems, and parasitism (Das *et al.*, 2011).

Changes in temperature and precipitation patterns may have an impact on the host plant's physiology and resistance as well as the growth stage, development, and pathogenicity of infectious pathogens (Mboup *et al.*, 2012). Faster disease cycles are brought on by airborne infections at higher temperatures, which also increases their survivability due to the decrease in frost (Boonekamp, 2012). According to Harvell *et al.*,(2002) it is anticipated that the effects of plant infections will increase with climate change because thelow temperatures and extended winters in northern latitudes, which now restrict the survival, generations per year, reproduction rate, and activity of a majority of diseases attacking crops during the growing season.

Conclusion

The impact of climate change is a long-term concern, but it demands immediate action because greenhouse gases are accumulating in the atmosphere and there is the possibility of global temperatures rising by more than 2°C. It has been noted that the development of plants under increased carbon dioxide concentrations of 475–600 ppm results in an average 40% increase in leaf photosynthetic rates.Increased CO_2 stimulates the accumulation of soluble sugar in plant’s edible portions.Vegetables are highly susceptible to unpredictable weather conditions and are highly perishable. They are sensitive to environmental extremes*viz.*, high temperatures and limited soil moisture.Major challenges faced by vegetable farmers are crop failures, low yield, decreased quality, and increase in pest and disease incidence.High temperaturereduces the netassimilation rate, induce denaturation of proteins and programmed cell death in some cells or tissues. It causes decreased ion flux, leakage of electrolytes, changes in relative water content, the production of toxic compound and disruption of homeostasis, ultimately reduce cell viability. So any changes in long-term mean annual temperatureand extreme temperatureevents willprobably have a tremendous effect onphysiological responsesof crops and ultimatelyaffect the quality of food produced. Germination, vegetative stage, reproductive stage and the yield are all impacted by high temperature stress and it is critically necessary to find innovative ways to adapt crops to these changes. High temperatureinduced by climatic fluctuations are an important threat for plant growth, development and quality of agricultural produces. Adaptableness to environmental changes generally derive from a large set of genetic traits affecting physio-morphological, biochemical and agronomic parameters. Therefore to mitigate the adverse impact of climatic change on productivity and quality of vegetable crops identification of genotypes with higher yield and good quality parameters at high temperatures is becoming increasingly necessary for future breeding programs.

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