

Elevated CO₂ in Combination with Heat Stress Influences the Growth and Productivity of Cereals: Adverse Effect and Adaptive Mechanisms

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CONTENTS

7.1	Introduction	126
7.2	Impact of Climate Change on Escalating Temperature and eCO ₂	127
7.3	Influence of eCO ₂ and Temperature on Physiological Traits of Cereal Crops	127
7.3.1	C ₃ Cereal Plants and eCO ₂	129
7.3.2	C ₄ Cereal Plants and eCO ₂	129
7.4	Effect of eCO ₂ and Temperature on Cereal Crops: Seed Germination and Seedling Growth	131
7.5	Influence of eCO ₂ and High Temperature Stress during Flowering and Grain Filling Periods in Rice	132
7.5.1	High Temperature Stress	132
7.5.2	Effect of Elevated CO ₂ on Rice	133
7.5.3	Effects of Elevated CO ₂ and Heat Stress on Rice	133
7.6	Elevated CO ₂ and Heat Stress Effect on Maize	134
7.7	Elevated CO ₂ and Heat Stress Effect on Wheat	135
7.8	Elevated CO ₂ and Heat Stress Effect on Sorghum	136
7.9	Elevated CO ₂ and Heat Stress Effect on Barley	137
7.10	Adaptations to Elevated CO ₂	138
7.10.1	Adaptations of Photosynthesis to Elevated CO ₂	138
7.10.2	Adaptations of Antioxidant Systems to Elevated CO ₂	139
7.10.3	Changers in Key Metabolites, Hormones, and Gene Expressions under Elevated CO ₂	139
7.10.4	Effect of eCO ₂ on Stomatal Development	140
7.10.5	Effect of Elevated CO ₂ on Stomatal Conductance	140
7.10.6	High CO ₂ Improves Water-Use Efficiency	141
7.11	Challenges to Improving Production with Elevated CO ₂ and Heat Stress	141
7.11.1	Strategies and Challenges for Improving Crop Production	142
7.11.1.1	With Elevated CO ₂	142
7.11.1.2	Under Heat Stress	142
7.12	Conclusion	143

7.1 Introduction

The global picture on climate change has been terrifying. Apart from the controversial ozone layer depletion, there is increased radiation, global warming, incidences of excessive or sparse rainfall, flood, drought, desertification, melting of arctic ice, rise in sea level, tsunami, and possible armageddon, etc. being experienced with loss of agricultural and water resources (Raza et al. 2019b, 2020). The unabated loss of global agricultural and water resources poses a significant threat to world peace and togetherness. Yet, these losses cannot be made up when the world is languishing under the effects of hunger and starvation, especially in Sub-Saharan Africa, Asia, and Latin America, where most of the world's citizens reside. Most of the time, what breeds civil conflicts and unrest is a struggle for scarce natural resources, especially land, food, clothing, and shelter. As the saying goes, 'A hungry man is an angry man' (Igboji et al. 2018). Changing climate is possibly the most nagging and imperative environmental issue on the world's priority list. The earth's systems of air, water, and land have always been dynamic as studies of ancient climates show that there have been alternating periods of global warmth and global chill at various times. However, it's now that ample proofs are testifying to the fact that human actions are altering or possibly rushing climate change (Raza et al. 2019).

The global temperature level has increased by 0.6°C in the previous 130 years. Whereas carbon dioxide (CO₂) concentrations in the air have increased by about 25% in the past 200 years, a cumulating effect from about 280–356 ppm. Methane (CH₄) concentrations in the air have crumpled during the past 100 years. Collectively taken, CO₂, CH₄ and N₂O are greenhouse smokes/gases which comprise reradiation of heat energy released from the ground's outward and which is making the earth hotter. The gas levels are increasing mostly due to human activities associated with energy production, transportation, and farming. The fossil fuel-linked emissions account for 65% of the extra transience degree attributable to atmospheric contamination and 70% of anthropogenic atomizers' environment preservation (Lelieveld et al. 2019). The rank of the gas ordered by percentage of emission due to human-induced universal heating is CO₂ (70%), CH₄ (20%), and N₂O plus other gases (10%). It is supposed that particles in the air, for instance, from engineering activities or volcanic eruptions, imitate rays and harvest a chilling outcome. A doubling of CO₂ levels would theoretically lead to an average global temperature rise of 1–2 °C even if all other factors remain the same (Anderson et al. 2016). But in reality, other factors will also change in response to the rising temperature and may show some negative (bad) and positive (good) fallouts. For example, water vapour in the atmosphere increases as temperature rises (Hudson Institute 1999). Information on the opposing influences of climate alteration on the growth and production of crops because of the elevated CO₂ (eCO₂) concentration and elevated temperature (eT) is obstinately illuminating the necessity for the advancement of tools to measure the response of crops owing to climate alteration aspects (Mina et al. 2019). Most of the physiological traits of crops are adversely affected by changing precipitation, a higher level of CO₂ and rise in temperature (Lawlor and Mitchell 2000; Raza et al. 2019; EL Sabagh et al. 2020). Such adverse effects on crops are usually referred to as the changing environment induced stresses (Raza 2020). It is reported that the increased temperature to 30 °C during floret development can cause sterility in wheat (Saini and Aspinall 1982). Schlenker and Roberts (2009) reported that maize yield could be increased up to 29°C but beyond that it decreases. It is established by Lobell et al. (2011) that the increase of temperature by every 1°C negatively impacts the yield of maize. The model projects carried out in India show that a rise of 2°C in temperature stops the optimistic signs of crop performance, like crop quality, from the greater level of CO₂. For example, the yield of wheat is anticipated to be lessened by 19.04%, consequent upon the mutual effect of rising temperature and CO₂ concentration to 4.5°C and 390–630 ppm, respectively (Verma and Misra 2018). Therefore, this chapter discussed the importance of eCO₂ and temperature on cereal crops' physiological traits, so as to understand the subject matter and accelerate work on addressing the critical challenges.

7.2 Impact of Climate Change on Escalating Temperature and eCO₂

The projected rise in average temperatures anywhere up to 3.7 degrees (IPCC 2007) by the end of the present era might have a substantial influence on crops vernalization (Adhikari et al. 2016; Ali et al. 2016). Rising temperature is also affecting barley phenology particularly pollination, flowering time (Amasino 2010), and grain filling by both disturbing the degree of growth and expansion precisely and persuading eCO₂ beneficial offsets (Robredo et al. 2007; Smith et al. 2011; Moore and Lobell 2014). Studies of Wallwork et al. (1998a) and Singh et al. (2008) evidenced the product degradation of endosperm storage when the high temperature (up to 35 degrees) for five days was applied to malting barley plants during grain-filling. Furthermore, a sign of endosperm cell wall and crushed cell layer (CCL) progress were highly sensitive to maximum heat, and the compact width of the CCL caused incomplete hydrolysis of b-glucans. Contraction of 11–75% in the movement of enzymes under study following exposure to extreme temperatures is evident (Wallwork et al. 1998b). Meanwhile, the development of the embryo significantly increased in heat-treated seeds than that in the normal condition seeds.

Higher CO₂ (>1000 ppm) might potentially progress yield of important crops (Körner 2006), like amongst species of C₃ plants which are likely to inherit such an advantage. The shared effect on flowering time and grain filling needs systematic evaluation (Fuhrer 2003; Lee 2011). Lee (2011) reported that by rising of temperature by 4°C, the time of flowering was advanced by 31 and 50 days for *Setaria viridis* and *Chenopodium album*, respectively.

Stomatal conductance unerringly alters plant water contents and photosynthesis. Its effects also improved with growing temperature notwithstanding the decline in leaf water probable, upsurge in transpiration, and upsurge in intercellular CO₂ meditation, and was decoupled by photosynthesis (Urban et al. 2017). It was observed that control on stomatal inaugural under eCO₂ was not altered by temperature; however, their amalgamation meaningfully enhanced entire-plant functioning (Habermann et al. 2019).

Although rising atmospheric CO₂ levels are identified with increased photosynthesis and production of biomass, the signs of crop performance, like crop quality, on plants' chemical composition requires study (Erbs et al. 2015). The conclusion reached from the FACE (free air CO₂ enrichment) facility in California, USA, suggested that when eCO₂ touched 680 ppm on a grassland environment, forbs flowering was accelerated by 2–4 days. Whereas, in the dominant grasslands, flowering time of grasses were delayed by 2–6 days (Cleland et al. 2007). However, the peak inspected concentration of CO₂ at 3000 ppm (ambient +4°C-day/5°C-night) significantly stimulated biomass production of barley (Juknys et al. 2012). The maximum biomass accumulation was observed under the shared effect of temperature and eCO₂ for tomato and barley.

Ko et al. (2019) had run the DSSAT CERES-barley crop model to simulate the yields potential of multiple barley cultivars, and reported reasonable increases under demonstrative attentiveness pathways 4.5 (RCP 4.5) and quick increases under the RCP 8.5 scenario. In the context of future scenarios, it is very important to develop barley varieties adaptive to forthcoming environments with calls for better-quality yield under weather warming and eCO₂ scenarios. Augmented temperature may defend the nutritional excellence of crops under upcoming eCO₂ meditations (Kohler et al. 2019). The mixture of eCO₂ with eT usually reinstated seed iron and zinc meditations gained under usual CO₂ and temperature environments, signifying that the possible danger to human nourishment by growing CO₂ meditation may not be complete.

7.3 Influence of eCO₂ and Temperature on Physiological Traits of Cereal Crops

Every passing decade is becoming more warmer than the previous one since 1850 (IPCC 2013). Melting of ice, increasing sea level, and continuous greenhouse gas emissions are making the situation worse (Nastis et al. 2012). Under such circumstances, global food security has become a complex challenge, especially in developing countries (Tyfield 2011; Mendelsohn 2014; De Laurentiis et al. 2016).

Changing climatic conditions are directly associated with the crop’s productivity (Jones 2013), especially cereals crops that face unpredictable challenges due to increasing levels of CO₂ in the air and increased temperature of the earth (Raza et al. 2019, 2020; Raza 2020). Most of the physiological traits of crops are adversely affected by changing precipitation patterns, a higher level of CO₂, and increased temperature (Lawlor and Mitchell 2000). Such adverse effects on crops are usually referred to as the changing environment induced stresses. Some of the negative effects of changing climate on cereal crops are provided in Figure 7.1.

For a better understanding of crop response towards eCO₂ and eT, characterization of stomata is a key physiological trait (Lobell et al. 2013). These stomata are directly in contact with atmospheric CO₂ (aCO₂) level, which is negatively associated with rice’s stomata density. The stomata size has shown positive correlation with eCO₂ concentration in the atmosphere (Franks et al. 2009). Mesophyll cells and inner lateral walls of epidermal guard cells of stomata are specialized in sensing the CO₂ concentration (Tubiello and Ewert 2002; Attri and Rathore 2003). The higher atmospheric temperature usually caused stomatal closure in cereal crops when water evaporation is increased (Figure 7.2). Such a cereal plant strategy played a decisive role in leaf moisture conservation (Bernacchi et al. 2007). Lower latent heat loss due to stomatal closure also increased the leaf’s surface temperature in conditions of eCO₂ (Kimball and Bernacchi 2006). It has been observed that low conductance of stomata also disturbs the photosynthesis rate, which is a key factor for low carbohydrate accumulation in the C₄ cereal seeds and poor productivity of crops. Xu et al. (2011) and

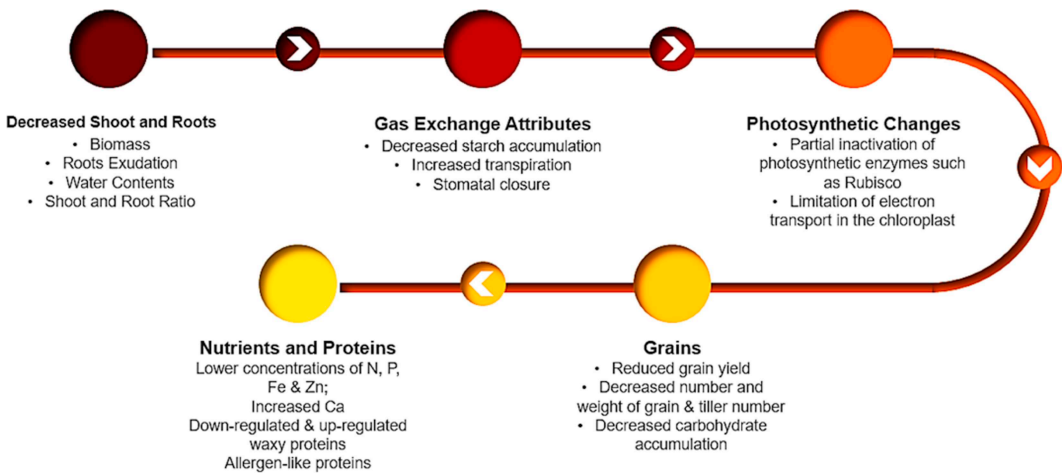


FIGURE 7.1 Different negative possessions of eCO₂ and temperature on cereals crops.

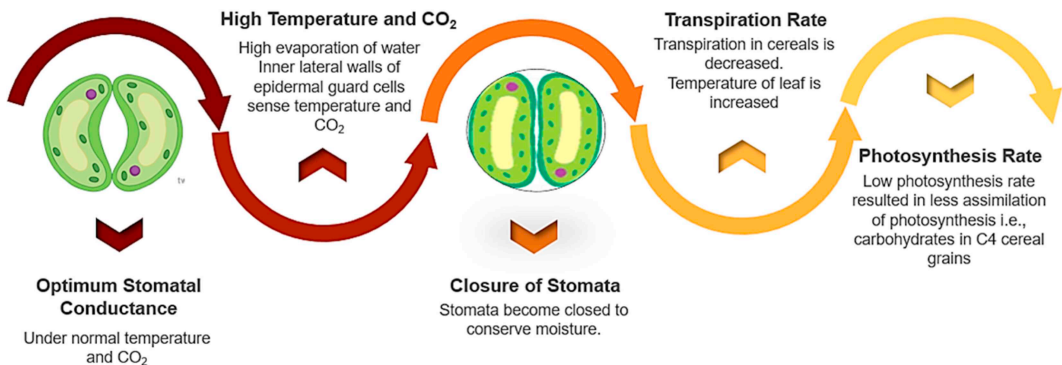


FIGURE 7.2 Stomatal responses of cereals towards eCO₂ and temperature.

Lobell et al. (2013) observed a significant reduction in maize plants' stomata conductance under temperature conditions seen to hover in the range of 36–42°C.

At the same time, Chavan et al. (2019) found that eCO₂ improves the adverse influence of heat stress on wheat functioning, nonetheless without affecting grain harvest. In non-heat stressed plants, eCO₂ enhances CO₂ adaptation rates (+36%) evaluated at growth CO₂, notwithstanding having down-regulated the photosynthetic potential. Heat stress compact assimilation rates (–42%) in atmospheric carbon dioxide (aCO₂) but not in eCO₂ resulted in full-fledged plants since CO₂ threatened photosynthesis via rising ribulose biphosphate rejuvenation scope and decreasing photochemical injury under heat stress (Chavan et al. 2019).

7.3.1 C₃ Cereal Plants and eCO₂

If there is short-term exposure to CO₂, crops have been observed to display an increase in the rate of photosynthesis (Moore et al. 1998; Xu and Shen 2002; Von Caemmerer and Furbank 2003). However, long-term exposure to high CO₂ concentration may acclimatize the crop to its environment with prolonged growth at elevated atmospheric CO₂ or they may become insensitive (Delucia et al. 1985; Arp 1991; Farage et al. 1991; Lin et al. 1997). A higher level of CO₂ in the air increased the accumulation of carbohydrates in C₃ cereals as a result of occurrence of successive acclimation of photosynthetic capacity (Myers et al. 2014). In contrast, during prolonged exposure of crop to elevated CO₂, Rubisco becomes deactivated, indicating that cereal crops do not necessarily behave in predictable ways like showing an ideal acclimation response towards a high level of CO₂ (Makino 1994).

7.3.2 C₄ Cereal Plants and eCO₂

A wide range of adaptation mechanisms have been documented so far in C₄ cereal plants vis-à-vis exposure to a higher level of CO₂ viz. (a) Rubisco in the bundle sheath cells (Ziska and Bunce 1997), (b) CO₂ saturation effect (Ziska and Bunce 1997), (c) Adjustment of direct CO₂ and bundle sheath leakiness (Watling et al. 2000), (d) C₃-like photosynthesis in early C₄ leaves (Ziska et al. 1999) and (e) Lower stomatal conductance (Ainsworth and Rogers 2007).

Upsurge in the respiration of plants as compared to photosynthesis caused a decline in a net gain of carbon under high temperature (Valentini et al. 2000). In C₃ cereal crops, i.e., rice and wheat, the rate of photosynthesis becomes maximum when the temperature ranges between 20 and 32°C. The respiration rate becomes non-linearly rapid from 15 to 40°C and, then, eventually becomes linearly decreased (Porter and Semenov 2005). In chloroplast, limited activity of electron transport chain and deactivation of rubisco activase have been seen to decrease the potential photosynthesis of cereal crops in the face of heat levels increasing due to high temperature (Joshi and Karan 2013). Modification in kinetic constants of rubisco have been noted to disturb the CO₂/O₂ ratio in cereal plants with results including decreased solubilization of CO₂ and increased photorespiration (Crafts-Brandner and Law 2000). Such conditions also minimized the carboxylation in plants at eT (Andersson and Backlund 2008; Zahoor et al. 2016). The photosystem II of cereal crops exhibited maximum sensitivity towards high temperature-induced stress, as it does not show signs of being disturbed until the temperature of leaf touches 40°C or more (Markelz et al. 2014). Depending upon the cultivar of cereal crops, an increase of 0.5–1.7°C in leaf temperature has been documented under conditions of twice the concentration of CO₂ as normal. The increase in leaf temperature can also be a high of 3°C under specified weather conditions. In addition to the above facts, the longevity of proteins and chlorophyll in crops is also curtailed under high atmospheric temperature which also caused a significant decrease in the high photosynthetic capacity of cereal crops (Paul et al. 2014).

Under elevated temperature and CO₂ induced stress, the accumulation of toxic compounds i.e., reactive oxygen species (ROS), is increased. High ROS-induced oxidative damage in lipids, DNA, and proteins which are synthesized in peroxisomes, chloroplasts, and mitochondria is well documented (Hasanuzzaman et al. 2020). These ROS caused peroxidation of lipid membrane in cereal

crops at the cellular level, especially in wheat and rice (Király and Czövek 2002; Shah et al. 2011). Antioxidants malondialdehyde (MDA), ascorbic acid (AsA), and glutathione (GSH) contents are also increased under high-temperature stress which played a vital role in detoxification of ROS. Synthesis of scavenging enzymes, i.e., superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxiredoxin (PrxR), and glutathione peroxidase (GPX), also acts as an imperative signalling molecule in minimizing the toxic effects of ROS (Savicka and Škute 2010; Hasanuzzaman et al. 2013, 2020).

Furthermore, accumulation of endogenous stress ethylene in cereal crops under abiotic stress i.e., high temperature, is a well-known fact. Stress conditions stimulate the methionine to convert into S-adenosyl-Met. Activation of enzyme ACC synthase changes into S-adenosyl-Met into ACC. This ACC is then catalyzed by ACC oxidase, with resulting biosynthesized stress generating ethylene (Glick et al. 1998). Higher biosynthesis and accumulation of ethylene ultimately induced negative changes in the crops' development phases and decreased plant growth (Arshad et al. 2008). Higher accumulation of stress ethylene in plant roots plays a decisive role in decreasing the root elongation. It promotes the thickness of plant roots via accumulation of dead cells in the root cortex. Such accumulation of dead cells in the root cortex results in the formation of lysigenous aerenchyma. In the region of hypocotyls, stress ethylene also decreases the cell division. Low cell division eventually results in poor elongation of roots and shoots in plants (Skirycz et al. 2011).

Matile et al. (1997) also observed a similar reduction in the synthesis of chlorophyll in plants as a result of higher biosynthesis of ethylene under stress, and they suggested that the outburst of ethylene under stress condition degraded the lipid which resulted in the loss of chloroplast cell membrane integrity. In chloroplast, the chlorophyllase (chlase) gene becomes stimulated by higher ethylene (Figure 7.3) accumulation which starts degradation of the lipid as it comes in contact with chlorophyll (Matile et al. 1997). However, scientists have observed that a low level of ethylene in plants also played an important role in decreasing the adverse signs of ROS under temperature trauma (Overmyer et al. 2003).

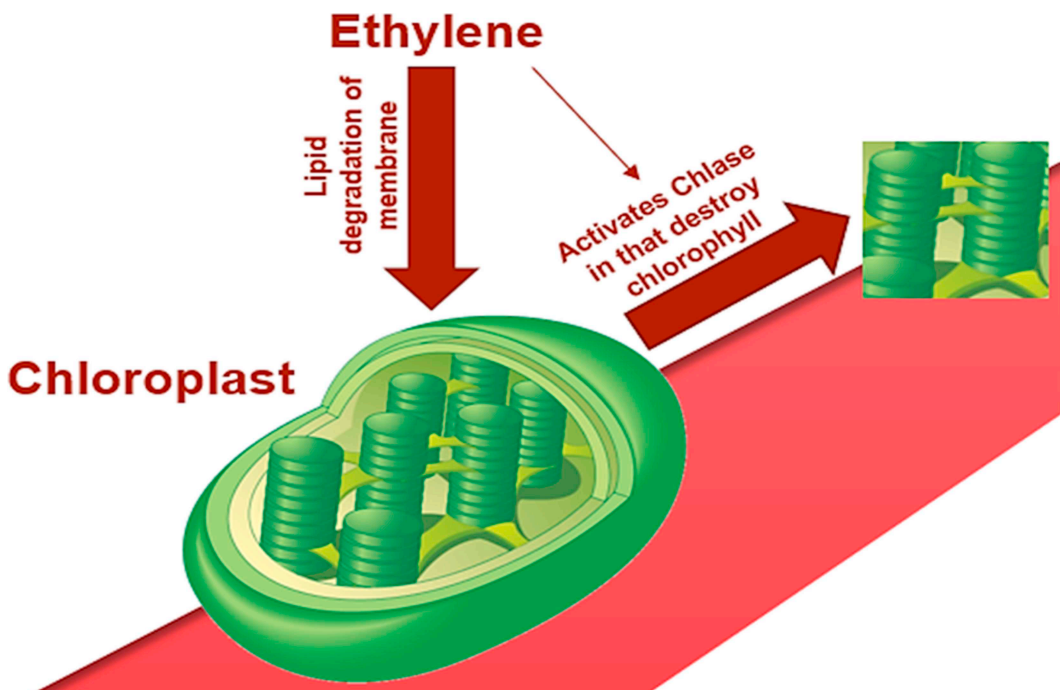


FIGURE 7.3 Stress ethylene and degradation of chlorophyll under high temperature induced stress.

7.4 Effect of eCO₂ and Temperature on Cereal Crops: Seed Germination and Seedling Growth

The effects of eT on physiological traits of the root, stem, and leaf area of three cereal crops, i.e., maize, rice, and sorghum at two weeks after germination, were monitored by Iloh et al. (2014) in Nigeria. They observed a reduction in germination speed as temperature regimes were raised. The shoot and root lengths of those crops were decreased with increasing temperature. However, the maize root length is decreased from 13.10±1.5 cm to 3.80±0.5 cm with increasing temperature from 40 to 50°C, respectively. Rice had a decrease in leaf length of 6.70±1.0 cm to 4.20±1.5 cm at 50°C. Iloh et al. (2014) reported that sorghum was severely affected by the elevated temperature among the crops studied. Their findings suggest growth stagnation of rice, maize, and sorghum with rises in temperature (Table 7.1).

Mina et al. (2019) evaluated the effects of eT and eCO₂ on maize genotypes' health index and generated crop health index (CHI) for maize cultivars (PEHM5 and CM119) in response to eT and eCO₂. In an open field experiment, in open-top chambers, PEHM5 and CM119 maize cultivars during their growth were subjected to two levels of CO₂ (400 ppm) which is ambient and eCO₂ (550±20 ppm), and three temperatures (ambient, ambient + 1.5°C and ambient + 3°C). These workers monitored the reply of maize plants to temperature and eCO₂ using 13 stress pointer constraints— morphological, physiological, and biochemical at three growth phases – vegetative, tasselling, and dent. The scientists' data to define minimum dataset (MDS) receptive to mixtures of temperature and eCO₂ actions via PCA is shown in Table 7.2. According to these findings, out of 13 pointers, total dry weight, relative leaf water content, and photosynthetic degree had advanced incidences for MDS at all the three phases. After generating CHI results, it was reported that CHI for maize plants under changed handlings was wide-ranging in 0.14–0.93. The normal CHI under different handlings were meaningfully connected to the harvest of both maize genotypes with R² of 0.82 and 0.90, correspondingly. The authors found that upsurge in temperature had a damaging consequence on CM119 and PEHM5 maize plants, with least mean CHI of 0.20–0.53 (Mina et al. 2019).

TABLE 7.1

The Effects of Elevated Temperature on Maize after 2 Weeks of Exposure (Adapted from Iloh et al. 2014)

Physiological Parameter (cm)	RCO	RCI	RCII	RCIII	RCIV
Rice					
Length of root	8.30±1.0	7.10±1.5	7.60±2.9	6.50±1.5	5.80±0.1
Length of leaf	8.20±0.1	6.70±1.0	5.80±0.6	4.90±3.2	4.20±1.5
Width of leaf	0.70±0.1	0.50±0.1	0.50±0.1	0.20±0.1	0.20±0.1
Length of stem	6.80±0.3	5.90±0.5	5.30±0.5	4.0±0.5	3.00±0.1
Sorghum					
	SCO	SEI	SEII	SEIII	SEIV
Length of root	8.90±2.3	6.30±1.3	6.10±1.9	5.50±1.6	1.50±0.1
Length of leaf	11.10±0.6	8.80±2.2	7.70±0.4	6.90±2.5	5.80±1.1
Width of leaf	0.50±0.1	0.20±0.0	0.03±0.1	0.30±0.1	0.10±0.1
Length of stem	8.60±2.2	5.00±0.4	4.20±0.9	4.0±2.3	3.40±0.5
Maize					
	MCO	MEI	MEII	MEIII	MEIV
Length of root	16.3±1.0	13.10±1.5	11.6±2.9	8.50±1.5	3.80±0.5
Length of leaf	19.90±1.6	15.40±3.6	11.60±1.7	9.70±3.2	5.80±1.1
Width of leaf	1.30±0.1	1.20±0.1	1.00±0.1	0.90±0.1	0.50±0.1
Length of stem	7.80±0.3	6.90±0.8	5.30±0.8	4.0±0.4	4.0±0.7

Note: MCO, control experiment at 37°C, MEI experiment at 40°C heat stress; MEII experiment at 42°C heat stress; MEIII experiment at 45°C heat stress; MEIV at 50°C heat stress; SCO, control experiment at 37°C, SEI experiment at 40°C heat stress; SEII experiment at 42°C heat stress; SEIII experiment at 45°C heat stress; SEIV at 50°C heat stress; RCO, control experiment at 37°C, RCI experiment at 40°C heat stress; RCII experiment at 42°C heat stress; RCIII experiment at 45°C heat stress; RCIV at 50°C heat stress.

TABLE 7.2

Principal Components/Indicators Parameters Response to eCO₂ and Temperature on the Vegetative Stage in PEHM5 Maize Genotype (Aadapted from Mina et al. 2019)

PCs	PC1	PC2	PC3
Eigen value	4.162	2.256	1.805
% variance	34.687	18.796	15.042
Cumulative %	34.687	53.483	68.526
Factors loading: Eigenvector			
Plant height	0.727	0.313	-0.259
Stem girth	0.777	-0.394	0.042
Leaf Area	0.398	0.036	-0.206
Relative Leaf Water Content (RLWC)	-0.085	0.083	0.750
Photosynthetic rate	-0.368	0.549	-0.154
Stomatal conductance	0.845	0.234	0.295
Transpiration rate	0.826	0.410	0.116
Total dry biomass	0.926	0.447	0.337
Total chlorophyll content	0.109	-0.550	0.632

7.5 Influence of eCO₂ and High Temperature Stress during Flowering and Grain Filling Periods in Rice

7.5.1 High Temperature Stress

High temperature stress is a serious threat to sustaining yield and grain quality of rice. Increasing eCO₂ is prophesied to improve photosynthesizing efficiency ensuring higher biological and grain yield. Contrary to this, both high-temperature stress and a higher level of eCO₂ are believed to decline the rice grain quality. Though, the interaction between eCO₂ and high-temperature stress on rice grain harvest, quality characters, and predominantly inorganic configuration under normal field environment in cool environmental conditions are not yet fully disclosed (Chaturvedi et al. 2017). The progressive ineluctability of haphazardous atmospheric conditions leading to regularization of stress incidents among recent world climatic models averring in, for example, growing global temperature level causing an augmented regularity of heat stress incidents (Battisti and Naylor 2009). Rice is susceptible to high-temperature stress (Jagadish et al. 2010) and the forewarned variations in the present and upcoming climate profiles would adversely influence worldwide rice productivity (Teixeira et al. 2013) and grain quality (Lin et al. 2010) and, consequently, decreasing its commercial and nutritional status (Wang et al. 2011; Lyman et al. 2013). It was proposed that further research must be devoted to investigate high temperature stress differences among various types of rice varieties. The revolutionary rice-planting methods based on planting system changes in rice planting regions with extreme high temperature stress. At the same time, high temperature detection and indication systems must be upgraded to gain optimal high temperature stress management efficiencies (Wang et al. 2019). Contrarily, high-temperature stress revelation throughout reproduction and grain formation stages is known to decrease rice harvest by reducing the amount of fertile spikelets (Jagadish et al. 2010) and reduced grain formation period (Ahmed et al., 2015) along with damage of sink efficiency (Kim et al. 2011). Furthermore, leaf sensation, leading to reduction in net photosynthetic proficiency (Kim et al. 2011) and starch alteration enzymes action are evident under heat stress which caused deterioration in final grain yield in rice (Ahmed et al. 2015) and other major crops like maize and wheat (Hawker and Jenner 1993; Cheikh and Jones 2006).

7.5.2 Effect of Elevated CO₂ on Rice

Rice is a C₃ crop, therefore, it shows a positive response against eCO₂ and produces maximum yield in rice (Shimono et al. 2009). Yang et al. (2009) presented evidence in favour of eCO₂ at the rate 580 ppm having improved the rice yield up to 24–34% when all other environmental factors like irrigation, light, and temperature were kept optimum. Mittler and Blumwald (2010) and Jagadish et al. (2016) revealed that environment and climatic issues such as eCO₂ and eT might differ significantly and interrelate in fully open-air field environments upsetting several growth and developmental phases of crops. Yang et al. (2007) documented that eCO₂ harms the proportion of rice chopping in relation to head rice recovery because of accelerated crop health. Myers et al. (2014) observed a close relationship between eCO₂ and reduced grain protein content, as well as changes inside the composition of grain minerals. However, it was observed that wheat and rice grown in eCO₂ have reduced grain nutrient contents (Myers et al. 2014). Among the researchers, a few reported that eCO₂ reduces photorespiration, improves photosynthesis, and WUE and, thereby, increases rice grain yield (Bowes 1996; Leakey et al. 2009a; Ziska et al. 2012). Ainsworth and Bush (2011) revealed that encouragingly, photosynthetic efficiency and primary production at eCO₂ are unerringly correlated to the absorbing efficacy when using or storing additional non-structural carbohydrates (NSC), which otherwise could lead to the adaptation of photosynthesizing activity in the original tissue. Consequently, varieties with an increased absorber size and durability for storing or using photo assimilation will find this useful when exposed to eCO₂, reducing the adjustment of photosynthetic efficiency and maintaining maximum production at the leaf, side by side (Zhu et al. 2015).

7.5.3 Effects of Elevated CO₂ and Heat Stress on Rice

Climate change will have an impact on agricultural production. Though high temperatures can damage crops, the maximum CO₂ concentration will have a positive influence on crop evolution and productivity (Raza et al. 2019, 2020a, 2020b). Reports exist that vouch to the fact that the maximum concentration of eCO₂ in the atmosphere maximizes the potential yield of C₃ crops, especially of rice in high latitudes (Taylor et al. 2018). Rice is a necessary food crop with half of the biosphere's population being the staple food in the everyday diet where rice is taken every day (Maclean et al. 2002). It is also the staple food across Asia, where about half of the biosphere's poor people live, and the rest in Africa and Latin America. Different studies on rice have also shown that eCO₂ frequently increases the photosynthesis rate, plant weight, and grain harvest (Horie et al. 2000; Chakrabarti et al. 2012).

Elevated temperature causes a decrease in total dry matter, tiller impermanence, reduced number of panicles and grains per panicle, floret sterility, and grain weight which ultimately reduces the crop yield. The high-temperature stress of 3.9°C significantly reduces the grain and biomass yield of rice. An increase in daily average temperature from 28°C to 32°C significantly reduces the total dry biomass, root dry biomass, root extent, leaf area, and specific leaf part of rice (Rankoth and De Costa 2013; Raj et al. 2016). Cao et al. (2009) recognized that increase in temperature at flowering stage and early grain filling phase of various rice varieties showed lower photosynthetic efficiency in the crop. Moreover, eCO₂-facilitated variations in material sugar levels and a straight CO₂-ambitious controlling pathway connecting a key flowering gene (*MFT*) are strong indications that eCO₂ plays an important role in the flowering period regulation in crops. Increasing temperature and eCO₂ are main climate alteration influences that could disturb plant suitability and flowering-related procedures (Jagadish et al. 2016). Hussain et al. (1999) revealed that heat stress throughout grain filling primes will decrease application of extra NSC in the sink in spite of amplified integrate amount from leaves in response to eCO₂. For instance, high temperature condensed grain mass or grain starch level, even with developed sucrose source from basis tissue, has been found to exist exposed to below-eCO₂ in rice. Temperature and photoperiod are the two main powerful forces for crop growth. The optimal temperature for standard rice development is 27–32°C (Yin et al. 1996). Wahid et al. (2007) studied that elevated temperature disturbs nearly all the growth phases of rice from budding to maturing and

gathering. The developmental phase at which the plant is exposed to heat stress regulates the harshness of the likely injury to the crop.

Ziska and Teramura (1992) documented that the aCO₂ level is likely to enhance in the forthcoming years, which will have long-term effects on numerous plants. As a C₃ plant, rice will surely have advantage from this enhancement in CO₂, mostly through condensed photorespiration. A positive role of elevated CO₂ has also been delineated for biomass accretion, tillering, panicles per plant, and grain yield of rice. Maximum CO₂ levels will impact stomatal conductance positively by decreasing moisture loss through transpiration efficiency, thus improving WUE (Wassmann et al. 2009b). Therefore, it is evident that predictable increase in CO₂ concentration will be beneficial in several ways for rice development. However, the general impact is adverse when rise in CO₂ and temperature are taken into consideration simultaneously (Wassmann et al. 2009a). Kim et al. (1996) studied that rising of aCO₂ level is considered to exclusively exacerbate heat persuaded spikelet sterility because it causes stomatal conductance under increased aCO₂ owing to heat stress.

Anjum et al. (2008) revealed that high-temperature stress harmfully influences pollen cell microspore progressing into male barrenness. However, heat stress of above 30°C during floral growth can cause whole sterility reliant on genes (Kaur and Behl 2010). Heat stress adversely affects the grain formation stage that ultimately reduces grain yield (Farooq et al. 2011). Elevated temperature stress usually increases the degree of grain-filling and curtails the grain-filling time period (Dias and Lidon 2009a). But, the grain development rate and period over which it happened reduced in crops having dissimilar grain weight constancy (Vijayalakshmi et al. 2010).

Flowering has been recognized as the phase most susceptible to heat stress, and the dominant ambient temperatures throughout anthesis have been correlated to reproductive offsets (Jagadish et al. 2007). At the plant level, a maximum CO₂ level improves photosynthetic rate, growth period, developmental phases, and yield of several growing crops, including rice (Ainsworth and Rogers 2007). So far, most of the researches with eCO₂ and rice have verified conservatively bred japonica (Yang et al. 2007) and Indica cultivars (De Costa et al. 2007). Nevertheless, recent hybrid rice genotypes display developed seedling vigour, degree of tillering, comparatively advanced growth degree, and advanced yield probable as compared to conventional inbred cultivars (Xie et al. 1996). Rise in temperature during flower initiation and grain formation stage is stated to decrease grain harvest and improve superiority in rice quality (Usui et al., 2014; Bahuguna et al. 2015). Elevated temperature stress-tolerant rice cultivar (NL-44) upheld advanced seed-set and pliability with starch metabolism enzymes on exposure to eCO₂ and high temperature simultaneously. Establishing rice genotypes with eCO₂ exposure integrated with greater tolerance to heat throughout the flowering and grain filling by givers such as NL-44 is capable of lessening the adverse effects of temperature, and support higher food availability efficiency in a global context, advancing from CO₂-rich surroundings (Chaturvedi et al. 2017).

7.6 Elevated CO₂ and Heat Stress Effect on Maize

Elevated CO₂ is a significant abiotic stress issue and leaves noteworthy fertilization signals on various crops. Early wide-ranging investigations on this concern for crops have described that eCO₂ suggestively enhanced WUE, reduced transpiration frequency, curtailed maize development retro and augmented plant height, leaf number, leaf zone, development rate, and harvest. In addition, increasing CO₂ disturbs rainfall stability, which can alter the periodic precipitation delivery (Easterling et al. 2000). It has been projected that this result would carry about 10% upsurge or decline in water resources at numerous zones (Wallace 2000). Elevated temperature causes heat damage and physiological syndromes resulting in condensed harvest (Johkan et al. 2011). Raised temperature due to eCO₂ also had a principal effect on food grain harvest reliant on the sites. With temperature upsurge by 1.0–2.0°C in tropical and subtropical states, such as India, food grain production is expected to decline by 30% (Johkan et al. 2011).

The C₄ grass maize is the third most important food crop globally because of harvest and its yield is presaged to jump by 45% from 1997 to 2020 (Young and Long 2000). Research on maize yield

responses to eCO₂ displayed changing signals of growth extending from no stimulus of biomass (Hunt et al. 1991) to 50% stimulation (Rogers and Dahlman 1993). High temperature unfavourably affects growth, yield, and crop quality of maize plants (Pathak et al. 2012). At the same time, maize does not respond without major signs to high temperature stress. The plant transduces the abscisic acid (ABA) signal to direct heat shock proteins (HSPs), which are molecular chaperones that contribute in protein refolding and deprivation triggered by high temperature. The HSPs can steady selective protein arrangements and tortuously provision constancy of thylakoid membrane construction, electron transportation, and secure carbon adjustment which may lead to greater photosynthesis (Tao et al. 2016). There is a lot of information on the effect of eCO₂ on maize yield varying from little optimistic consequence (Leakey et al. 2009a), no consequence (Kim et al. 2007) to upsurged harvest by 50% (Vanaja et al. 2015). Though there are several studies on the influences of eCO₂ and eT on maize yield, that used precise atmosphere amenities such as phytotron and plant growth cavities or crop growth reproduction copies (Pathak et al. 2012), still there are an inadequate number of investigations on the effects of eCO₂ level and temperature on this important crop under field environments. Consequently, there is a necessity to develop or to recognize cultivars which can accomplish healthier growth and productivity under presaged climatic variations (EL Sabagh et al 2020a). Further, there is a need to characterize maize genotypes that differ in heat tolerance at a molecular level and identification of candidate genes for heat stress tolerance in maize with the potential to assist maize breeding programmes.

7.7 Elevated CO₂ and Heat Stress Effect on Wheat

Rising CO₂ concentration is linked to the increased surface mean temperatures worldwide. As a result of changing climate, warm days are becoming warmer threatening global wheat production. Heat stress (HS) means that as the daily temperature rises above the threshold levels for plants (Wahid et al. 2007), it drastically affects agricultural productivity, (Asseng et al. 2015; Raza et al. 2019a; Salim and Raza 2020). Heat stress bounds the growth and development of plants through altering physio-biochemical processes (Wahid et al. 2007; Yildirim et al. 2018; EL Sabagh et al. 2019) and hindering photosynthesis (Sage and Kubien 2007; Farooq et al. 2011; Barutcular et al. 2017). Plants may adapt an HS-induced oxidative damage by triggering several survival mechanisms (Pan et al. 2018; Zhang et al. 2018).

The maximum degree of ribulose biphosphate (R_{BP}) carboxylation (V_{cmax}) is an exact reaction to temperatures of 40°C, but the highest degree of R_{BP} rejuvenation or electron transportation (E_{Trs}) usually causes shrinkages at lower temperatures of 33°C (Medlyn et al. 2002). The comparison of eCO₂ vis-à-vis remaining photosynthesis is superior at HS because of the conquest of photorespiration (Li et al. 2013). The eCO₂ may also upsurge the OTT of photosynthesis (Alonso et al. 2008; Ghannoum et al. 2010). At eCO₂, the reply of photosynthesis to eT conversions is progressively imperfect by E_{Trs} and Rubisco initiation (Sage and Kubien 2007). The OTT of photosynthesis reproduces that of E_{Trs} in plants grown at eCO₂. Beyond OTT, acclimation of photosynthesis to HS is linked with augmented electron transportation and/or eT constancy of Rubisco initiation (Sage and Kubien 2007).

Therefore, for the development of wheat varieties suitable to forthcoming climate changes, it is imperative to gain knowledge on how eCO₂ and HS interactively influence wheat yields. For confirmation of the hypothesis, Chavan et al. (2019) conducted a glasshouse trial with a modern, HYV wheat cultivar, 'Scout' at 419 μl l⁻¹ of aCO₂ or 654 μl l⁻¹ of eCO₂ through maintaining day/night temperature at 22/15°C, respectively. Around 50% of the wheat plants at anthesis stage were exposed to 40/24°C for 5 days for inducing by HS. Results of the study revealed that in control plants, eCO₂ improved (+36%) aCO₂ acclimatization rates measured at growth aCO₂ despite photosynthetic capacity being downregulated. HS condensed AsRat (-42%) in aCO₂- nonetheless not in eCO₂ fully fledged plants since eCO₂ sheltered photosynthesis by enhancing the capacity of R_{BP} rejuvenation and dropping photochemical injury under HS. The eCO₂ reduces the stomatal conductance and upsurses the photosynthesis by encouraging carboxylation and Rubisco oxygenation, recognized as photorespiration (Ainsworth and Rogers 2007; Leakey et al. 2009a).

7.8 Elevated CO₂ and Heat Stress Effect on Sorghum

Sorghum [*Sorghum bicolor* (L.) Moench.], a C₄ plant, is a tall cereal grain that is an important food and feed crop on a global scale grown particularly in the USA, Mexico, Sudan, and some developing countries of Africa and South Asia. It is a hardy crop that is best adapted to warm climates and is resilient to drought and heat because its large fibrous roots can reach far down into the soil to extract water. Growing temperature and eCO₂ are the main climate alteration factors that may adversely affect growth, development, and grain yield of sorghum. Future predictable variations in temperature could harshly impact sorghum yield worldwide. Several reproduction models predicted 7–17% yield reduction in sorghum in Asia and Africa (Butt et al. 2005; Tingem et al. 2008; Srivastava et al. 2010; Sultan et al. 2014).

The average optimal temperature for seed germination of sorghum ranges from 21–35°C, where optimal temperatures are 26–34°C for vegetative development and 25–28°C for reproductive development (Maiti 1996; Prasad et al. 2006, 2008). Higher temperature than optimum affects both vegetative and reproductive development of sorghum, and the influence of eT on the generative growth phase is more noticeable compared to vegetative phase (Prasad and Staggenborg, 2008; Nguyen et al. 2013; Singh et al. 2015). Previous studies have shown that increase in temperature enhances crop development rate resulting in earlier flowering, augmented leaf number, and leaf appearance rate, but with no result on leaf size. Though, there was a noteworthy reduction in plant height, pollen feasibility, grain number, individual grain heaviness, and grain yield (Prasad and Staggenborg, 2008; Nguyen et al. 2013). The result of eT (36–40°C) on sorghum leaf number plant⁻¹ seems to be slight, as reduction in leaf number is remunerated by an enlarged leaf amount axis⁻¹ (Jain et al. 2007; Van Oosterom et al. 2011).

Prasad et al. (2006, 2008) stated that sorghum is frequently cultivated in the regions where day/night temperatures are more than 32/22°C, as high-temperature throughout pre-anthesis (sporogenesis) reduces pollen feasibility and number of pollen grains, that results in reduced seedset. They also concluded that high temperature throughout the grain-filling phase declined separate grain extent owing to reduction of grain filling period that reduced the source and finally reduced grain size and yield. The eT>33/28°C throughout the initial phases of panicle growth persuade floret and embryo abortion (Downes 1972). Raised temperature throughout floret formation changes pollen morphology with adverse consequences on flowering, having an irregular exine wall, deterioration of tapetum cells, and sheath injury, foremost to pollen barrenness (Prasad and Staggenborg 2008; Djanaguiraman et al. 2014). Prasad et al. (2015) reported that anthesis period (5 days before and 5 days after) is very sensitive to elevated temperature stress producing supreme diminution in floret fruitfulness of sorghum. High temperature stress throughout floret expansion or grain filling phase of sorghum reduced floral fertility, grain mass, and grain mass per panicle. CO₂ is an important element that affects plant development mostly by its direct effect on photosynthesis and stomatal composition (Upreti et al. 2002; Shimono et al. 2013). The rising of CO₂ concentration due to climate change is extensively likely to enhanced photosynthesis resulting in increased yield and crop output in crop plants (Kant et al. 2012; Hasegawa et al. 2013; Hussain et al. 2016). The growth and developmental responses greatly vary with the growth stage of plants, e.g., a better response in early growth phases and a reduced response as plants enter the adult stage (Kramer 1981; Geiger et al. 1999). Chaudhuri et al. (1986) reported that sorghum grown at eCO₂ produced extra roots and shoots as compared to plants grown with ambient CO₂. eCO₂ may improve crop productivity and alter N level in different plant tissues of sorghum (Torbert et al. 2004).

Watling et al. (2000) conducted a study on sorghum using CO₂ at the rate 350 (ambient) or 700 (raised) μmol mol⁻¹ on key rudiments of the C₄ pathway, and they observed a 2-fold decline in the width of the package sheath cell wall in plants grown at raised CO₂ relative to ambient CO₂. They also reported both carboxylation proficiency and CO₂-soaked degree of photosynthesis which was lesser in plants fully-fledged at raised CO₂ relative to ambient CO₂. 49% decrease was observed in phosphoenol pyruvate carboxylase (PEPC) content of leaves (area basis) in the plant developed in raised CO₂ against eCO₂, but no alteration in Rubisco was found. There was a 3-fold upsurge in C-isotope taste in leaves of plants grown in eCO₂, and bundle sheath leakiness was projected to be 24 and 33%, for the ambient and eCO₂-grown plants, respectively.

During the anthesis phase, eCO₂ has been described to increase tissue temperature by dropping the dangerous temperature verge, subsequent in advanced spikelet infertility in sorghum (Prasad et al. 2006). The positive response of leaf carbon exchange rate (CER) to eCO₂ was better in young leaves as compared to that in the old leaves. In young leaves, eCO₂ improved Rubisco movement at 30/20°C and 36/26°C, while PEPC action was not exaggerated by eCO₂ at 30/20°C but was slightly improved at 36/26°C. Leaf CER and Rubisco action were improved by eCO₂ at the early phases of leaf ontogeny for the sorghum (Prasad et al. 2009).

Prasad et al. (2009) stated that vegetative growth and dry matter production of sorghum were significant at high day/night temperatures (36/26°C) as compared to a cooler temperature (30/20°C) with eCO₂, however, economic yield losses were greater with the combination of high temperatures with eCO₂ than at ambient CO₂. The improvement in CER and up-regulation of Rubisco action of the mid-section of leaf rudiments of sorghum were found to be better at early phases of leaf growth which may underwrite to the better nonsexual development and dry mass construction experiential at eCO₂ and high temperatures. Prasad et al. (2006) investigated the communication of eCO₂ at dissimilar levels of temperatures on sorghum, and found that no substantial changes occur in seed figures or seed extent at ambient (350 μmol mol⁻¹) or eCO₂ (700 μmol mol⁻¹) in augmented day/night temperatures of 36/26°C. However, the percent seed-set was decreased under eCO₂ than ambient CO₂ at either 32/22 or 36/26°C resulting in decreased yield by 40–100% and of harvesting index by 24%. In the semi-arid tropics, where sorghum is presently fully fledged throughout the rainy period, the cruel crop-season temperatures were previously approaching or had crossed over these optimal temperatures (Prasad et al. 2006; Singh et al. 2014).

7.9 Elevated CO₂ and Heat Stress Effect on Barley

Barley (*Hordeum vulgare* L.) is a more or less climate-adaptable crop cultivated worldwide and with a global yield recently recorded as reaching 149 million tonnes. It is used in multiple food preparations, beverages, animal feeds, and has other uses (Calvo et al. 2017; EL Sabagh et al. 2019). On the other hand, increasing atmospheric CO₂ levels is the main reason for rising average surface temperatures worldwide as well as the main reason behind the prolonged duration of, rate of recurrence in, and intensity of a heatwave. Elevated CO₂ and rising temperatures are the key climate change aspects that might distress plant suitability, flowering grain filling, and yield of barley (Jagadish et al. 2016). Excessively higher temperature in the warmer regions of the world during the crop growth period is threatening the yield potential of barley globally. (Savin et al. 1996; Passarella et al. 2005). Flowering and grain filling stages are critical determinants for plant reproductive outcome and seed-set. Numerous studies have examined the response of barley to eCO₂ (Pritchard et al. 1999; Smith et al. 2011; Jagadish et al. 2016). Increasing the temperature by 2°C can improve the agronomic parameters (plant height, dry matter quality and ear length) of highland barley, but no significant impact of temperature on barley harvest was observed as a result of eCO₂ while raising the temperature by 4°C will seriously disturb the normal growth and harvest of highland barley (Liu et al. 2018). Globally, the daily temperature is considered as the most important factor upsetting grain quality (Taub et al. 2008) in the majority of cereal growing regions. Research (Senghor et al. 2017) findings revealed that the short-term periods of extreme temperature throughout flowering and grain filling can reduce grain size, weight, yield, and quality of crop (Passarella et al. 2005, 2008; Senghor et al. 2017). Flowering and grain filling periods are controlled by a compound signalling system including the modulation of ecological spurs (i.e., temperature, photoperiod) and endogenous genetic behaviours (Passarella et al. 2002). A study of Clausen et al. (2011) has revealed that CO₂ levels above the existing ambient concentration normally enhanced the growth and yield of C₃ crop species. Further, similar trends could stimulate future harvest, except snowballing climate change effects such as escalating temperatures, erratic rainfalls, and atmospheric interference. Existing variation in the stimulation in the harvest at eCO₂ concentrations has been detected in many cereals, including barley (Clausen et al. 2011). Although, field trials of Chavan et al. (2019) revealed that

eCO₂ alleviated the damaging impacts of heat stress at the anthesis stage on wheat photosynthesis. However, grain harvest was condensed by high temperature in both eCO₂ handlings.

7.10 Adaptations to Elevated CO₂

The changes in climate, including eCO₂, increasing temperature, and changed rainfall have extreme influences on vegetation function and crop yields affecting sustainable food production (Lobell et al. 2011; Ruiz-Vera et al. 2013; Lavania et al. 2015) and causing exacerbated impacts when above climate vicissitudes are joined with other ecological boundary conditions, such as limited or toxic nutrition status (Peñuelas et al. 2012; Xu et al. 2013a, 2013b; Wang et al. 2015).

Rising aCO₂ has a significant influence on almost all important biological procedures such as photosynthesis, respiration, hormone signalling, and antioxidant defence, as well as other significant tributary metabolic processors in crop plants (Matros et al. 2006; Peñuelas et al. 2013; Singh and Agrawal 2015). CO₂ has direct impacts on plant metabolism predominantly through its role in photosynthesis, while it indirectly influences plant performance by its effects on atmospheric temperature and ground water status. It is well understood that the adaptations to eCO₂ are mainly due to changes in primary metabolic processors and associated physiological functions.

7.10.1 Adaptations of Photosynthesis to Elevated CO₂

The elevated aCO₂ concentration accelerates the rate of photoassimilation in the leaves of many plants, which enhances plant growth leading to increase in crop yield (Long et al. 2004, 2006). Contrary to this, rising CO₂-mediated photoassimilation stimulates transcriptional upregulation of genes associated with respiratory pathways (Fukayama et al. 2011; Markelz et al. 2014). However, photosynthetic down-regulation was detected with long-term exposure to eCO₂ (Darbah et al. 2010). The long-term impact of CO₂ enrichment has been more pronounced on C₃ species as compared to C₄ species. This photosynthetic down-regulation is said to be due to limited ATP production, which is not sufficient for RuBP regeneration, as ATP produced in respiration processes and consumed more with eCO₂ (Watanabe et al. 2014) causes an undesirable reaction to result during photosynthesis. This shows the close connection among the photosynthetic and respiratory processes (Moroney et al. 2013; Watanabe et al. 2014).

Increased aCO₂ concentrations depicted increased levels of soluble sugars and starch in plant leaves, indicating that photoassimilation increases under eCO₂ concentrations (Teng et al. 2006). However, the extent of the response to eCO₂ differs with the plant functional types and plant groups, for example, extreme response for trees and C₃ grasses, reasonable for C₃ shrubs, and minimum for C₄ grasses (Ainsworth and Long 2005; Ainsworth and Rogers 2007) and their environmental conditions such as nutrient and water availability.

The eCO₂ inhibits the oxygenation of RuBP by down-regulating the affinity of O₂ to Rubisco while up-regulating the carboxylation of RuBP by facilitating CO₂ affinity resulting in stimulation of photosynthesis (Kane et al. 2013; Moroney et al. 2013). Reports showed photorespiration caused approximately 30% loss of the carbon fixed by photosynthesis with the rising temperature. Nonetheless, the CO₂ fixing can be increased >50% when suppressing the oxygenation reaction, as the carboxylation reaction occurs (Long et al. 2006) showing high adaptations to increased CO₂ concentrations.

The restricted photorespiration at eCO₂ reduces the H₂O₂ productions, which protects the chloroplasts by oxidative stress (Watanabe et al. 2014; Zinta et al. 2014) implying photorespiration has a defensive role contrary to photooxidation (Zinta et al. 2014). Photosynthetic responses to eCO₂ may be to weaken when interacting with other abiotic factors such as water deficit (Xu et al. 2014), N deficit (Markelz et al. 2014) and raised temperature (Ruiz-Vera et al. 2013). Under CO₂-enriched environment, more carbohydrate accumulates due to increase in size of starch granules and number of chloroplasts (Teng et al. 2006, 2009). However, high carbohydrate accumulation damages chloroplasts which reduces photosynthetic capacity (Aranjuelo et al. 2011) under CO₂-enriched environment.

7.10.2 Adaptations of Antioxidant Systems to Elevated CO₂

Rising CO₂ up-regulates the antioxidant pathways such as polyphenols, ascorbate, alkaloids, and antioxidant defence activities including CAT and SOD which results in decreased cellular ROS levels (Mishra and Agrawal 2014; Zinta et al. 2014; Raza et al. 2020; Hasanuzzaman et al. 2020). Kumari et al. (2013) reported that ascorbate and phenol levels were increased in *Beta vulgaris* under eCO₂. The up-regulated ascorbate, GSH activities, and their redox position were reported in *Lolium perenne* and *Medicago lupulina* (Farfan-Vignolo and Asard 2012). The up-regulation of ascorbate synthesis was activated by enhanced photoassimilation at eCO₂ (Zinta et al. 2014; Ali et al. 2016). The declined oxidative stress at eCO₂ was detected in *Zingiber officinale* (Ghasemzadeh et al. 2010), *Catharanthus roseus* (Singh and Agrawal 2015), *Caragana microphylla* (Xu et al. 2014), *Vigna radiata* (Mishra and Agrawal 2014), and *Arabidopsis thaliana* plants (Zinta et al. 2014).

The plant antioxidant defence systems are closely related with carbon metabolism (Smirnoff and Wheeler 2000) where ascorbate synthesis has been drastically activated by enhanced carbohydrate biosynthesis because of eCO₂ (Smirnoff and Wheeler 2000; Zinta et al. 2014). The degree of mitigation of oxidative stress, extent of response, and magnitude of damage may vary with crop genotypes, varieties, growth stages, abiotic and biotic factors, and their interactions (Hodges and Forney 2000; Gill and Tuteja 2010; AbdElgawad and Asard 2013; Kumari et al. 2013; Zinta et al. 2014). Zinta et al. (2014) stated the constant transcription expression levels of ROS regulatory enzymes in *Arabidopsis* at increased CO₂ were below optimum water status, while O₃ partially suppressed the transcription expression levels of antioxidant metabolism at eCO₂ in soybean (Gillespie et al. 2012).

The impacts of oxidative damages caused by severe abiotic stresses such as drought (Xu et al. 2014; AbdElgawad et al. 2015), high temperature (Zinta et al. 2014; AbdElgawad et al. 2015), O₃ pollution (Kumari et al. 2013), and salinity (Pérez-López et al. 2009) could be mitigated by CO₂ fertilization. The CO₂-mediated up regulation of sugar production and sugar-derived reactive carbonyls were triggered in wheat plants under extreme environmental conditions (Takagi et al. 2014).

7.10.3 Changers in Key Metabolites, Hormones, and Gene Expressions under Elevated CO₂

Since early times, it has been reported that eCO₂ can influence primary and secondary metabolic processes and their compositions in plants (Lavola and Julkunen-Tiitto 1994; Lavola et al. 2013). At eCO₂, up-regulated accretion of carbon compounds is linked with up-regulation of phosphoglycerate mutase, and down-regulation of the adenosine diphosphate glucose pyrophosphatase protein which is responsible for the equilibrium among the carbon sink and basis in wheat plants (Aranjuelo et al. 2011). The decreased N compounds, increased total non-structural carbohydrates (starch and sugar) (Luo et al. 2004; Markelz et al. 2014), and steady whole structural carbohydrates (including cellulose, lignin, and lipids) (Markelz et al. 2014) were detected as present under CO₂ fertilization. However, Ribeiro et al. (2012) detected enhanced nitrogen assimilation in CO₂-rich atmosphere, while Guo et al. (2013) reported increased phloem amino acid contents in *Medicago truncatula* with eCO₂.

Secondary metabolites (phenylpropanoids, tannins, triterpenoids, phenolic acids, and alkaloids) were reported to increase with rising CO₂ (Matros et al. 2006; Ghasemzadeh et al. 2010; Lavola et al. 2013). For instance, huge accumulation of phenylpropanoids, chlorogenic acid, and scopoletin coumarins in tobacco leaves (Matros et al. 2006)-triggered levels of kaempferol and fisetin in ginger (Ghasemzadeh et al. 2010) were explored under CO₂ fertilization. CO₂ fertilization triggered the salicylic acid (SA) (Zavala et al. 2013) and brassinosteroids (BRs) levels (Jiang et al. 2012), but decreased jasmonates (JA) and ethylene meditations (Zavala et al. 2013; Vaughan et al. 2014). Enhanced auxin levels, decreased ABA, and constant cytokinins were observed in *Pinus tabulaeformis* disclose to enriched CO₂ environments, counteracting impacts of O₃ thereby stabilizing damage (Li et al. 2011). Ribeiro et al. (2012) found incorporating carbohydrate and inorganic nitrogen metabolism was associated with gibberellic acids with eCO₂. Thus, CO₂ fertilization is useful in replacing certain metabolic bioprocesses in the low-gibberellin crops.

The changed expressions of different genes in various crops have been reported with eCO₂. The overexpression of Rubiscoactivase in rice showed the reduced photoassimilation with CO₂-rich environments (Fukayama et al. 2011). The diminished Rubisco gene expressions were reported in N-deficient environments at eCO₂ (Leakey et al. 2009b; Markelz et al. 2014). The gene expression of PS II, D1 protein has been down-regulated with eCO₂ in high temperature environments in certain rice cultivars but not in others, indicating genotypic dependence (Gesch et al. 2003).

Mature wheat plants at senescence stage showed up-regulation of nitrogen remobilization genes and down-regulation of carbon remobilization genes (Buchner et al. 2015). The down-regulated photosynthetic gene expressions due to extreme weather events can be repaired by eCO₂ (Zinta et al. 2014). Winter wheat (*Triticumaestivum*) at low temperatures exhibited higher expressions of many genes with eCO₂ (Kane et al. 2013). A knockout mutant *bou-2* encoding mitochondrial carrier gene, *BOUT DE SOUFFLE (BOU)* in *Arabidopsis* showed halted growth at ambient CO₂ but not with eCO₂ (Eisenhut et al. 2013). High expressions of respiratory genes have been reported in deficient and optimum N environments with eCO₂ in *A. thaliana* plants (Markelz et al. 2014).

7.10.4 Effect of eCO₂ on Stomatal Development

Elevated CO₂ decreases both stomatal thickness and catalogue in a number of species, although cultivar or species-specific responses are also observed (Bettarini et al. 1998; Luomala et al. 2005; Field et al. 2015; Caldera et al. 2016). Stomatal development under eCO₂ is controlled by *HIC* (*High Carbon Dioxide*) that encodes a putative 3-ketoacyl coenzyme A synthase (KCS) (Gray et al. 2000). The *HIC* mutant showed an increase in stomatal density with eCO₂, indicating that *HIC* is a negative regulator of CO₂-dependent stomatal development. In addition to the transcriptional level regulation, post-transcriptional regulatory components are also involved in stomatal development. For instance, a naturally occurring *Arabidopsis* mutant, 28y, showed an augmented stomatal thickness and index. Through map-based cloning, *ARGONAUTE1 (AGO1)* was recognized as the causal mutation and it acts downstream of *TMM* (Yang et al. 2014). *AGO1* is a RNA-binding protein and its role in RNA silencing and post-transcriptional gene regulation is well established. In addition to *AGO1*, other mechanisms of the microRNA pathway, such as *HYL1* and *HEN1*, were also identified to participate in the establishment of stomatal patterns (Jover-Gil et al. 2012). Overall, these studies suggest that transcriptional and post-transcriptional gene regulatory factors control stomatal development and patterning. However, their role in controlling stomatal development under high CO₂ still requires further investigation. Jasmonic acid (JA) deficient mutant *fad-4* and ethylene insensitive mutant *ein-2* were found to be impaired in stomatal development at high CO₂ (Lake et al. 2002). As JA and ethylene are mainly involved in defence responses to pathogens, it could be interpreted that CO₂ signalling and defence signalling pathways cross-talk. Further, systemic signalling from mature to young leaves control stomatal density in the developing leaves under high CO₂, although the nature and identity of such signals are not known (Lake et al. 2001). Differentiation and distribution of stomata are controlled differentially at the adaxial and abaxial surfaces, as surface-specific molecular regulators can also influence stomatal responses to high CO₂ (Driscoll et al. 2006; Soares et al. 2008).

7.10.5 Effect of Elevated CO₂ on Stomatal Conductance

The impact of eCO₂ on stomatal conductance (gs) is widely studied using a wide range of experimental systems such as growth rooms, open top chambers (OTC), and FACE (free-air CO₂ enrichment) (Bunce 2001a; Seneweera et al. 2001; Uprety et al. 2002; Long et al. 2004; Ainsworth and Rogers 2007). Although gs response varies between experimental systems, high CO₂-induced stomatal closure is frequently observed. The duration of CO₂ exposure also influences stomatal responses, where short-term exposure to eCO₂ has a larger impact. In contrast, plants exposed to eCO₂ for an extended period of time shows a certain degree of stomatal acclimation. The exact mechanisms underlying this stomatal acclimation to high CO₂ are yet to be fully understood. Stomatal conductance also relies on the

aerodynamic properties, and changes in the stomatal conductance unequivocally translate to a change in transpiration. Besides CO₂, aerial environmental factors such as temperature, photosynthetic photon flux density (PPFD), and water vapour pressure difference (VPD) also affect stomatal conductance (Bunce 2004). The unique combinations of these factors influence stomatal conductance in a species-dependent manner (Bunce 2001b). The reduction of stomatal conductance caused by eCO₂ is greater in monocots (~ 42%) compared to dicots (~28%), and C₄ species have faster g_s response compared to C₃ species (Vodnik et al. 2013). Early reports highlighted the association among temperature-dependent photosynthetic potential and stomatal conductance (Wong et al. 1979). Further studies have shown that stomatal conductance is not firmly related to the photosynthetic potential, and decreases in Rubisco gratified condensed both guard cell and mesophyll photosynthesis with no seeming result on stomatal conductance (Von Caemmerer et al. 2004). This is contrary to the usual detected association between photosynthetic potential and stomatal conductance when the photosynthetic capacity is manipulated via antisense RNA technology. Also, CO₂-induced oscillations of g_s are known to be triggered by sudden changes in other environmental factors (Kaiser and Kappen 2001). Thus, it is of particular interest to know how the relative reduction in stomatal conductance at eCO₂ for a given species varies with other environmental factors.

7.10.6 High CO₂ Improves Water-Use Efficiency

Loss of water from aerial parts of plants during CO₂ uptake is inevitable. The proportion of the rate of left CO₂ assimilation (A_n) to transpiration (E) (A_n/E) for a given period of time throughout photosynthesis is usually demarcated as plant water-use efficiency (WUE). Plants with greater WUE fix more carbon per unit water lost, which is advantageous for survival in dry or drought-stressed environments. An improved formula for WUE was described later as a function of rate of A_n to leaf stomatal conductance (g_w), that is A_n/g_w, referred as physiological water-use efficiency (Feng 1999). Several lessons have designated an important upsurge in WUE in increasingly lean water seasons due to the soaring atmospheric CO₂ concentration from the year 1900 to present (Mccarroll and Loader 2004; Gagen et al. 2011). Examination of isotope timetables in tree jewels indicated an extensive upsurge in tree WUE over 40 years and found that WUE augmented by 20.5%, on an average, though stem development did not show any significant change (Peñuelas et al. 2011). Studies on angiosperm and conifer tree species showed a dynamic reduction of water loss in angiosperms, while conifers were found to be insensitive when exposed to eCO₂ (Brodribb and Mcadam 2013). A meta-analysis of statistics from 13 lasting (>one year) field-created investigations on European forest tree species with eCO₂ indicated an important reduction (21%) of stomatal conductance, and the response to CO₂ was significantly greater in new deciduous trees compared to coniferous trees. This response is extremely consistent in trees under water stressed conditions in long-term studies (Medlyn et al. 2001). Overall, high CO₂ improves WUE in a broad range of species, suggesting that it is a generally observed phenomenon.

7.11 Challenges to Improving Production with Elevated CO₂ and Heat Stress

Global climate change projections expect a rise in atmospheric CO₂ concentration up to 700 ppm and that in temperature by approximately 4.8°C by the end of the 21st century, respectively (Sultana et al. 2009). The aggravated levels of atmospheric CO₂ have outperformed during the pre-industrial phase, i.e., approximately 40% (IPCC 2013). Besides, it is believed that in the second half of the century, it can increase twice over the existing level (Jia et al. 2015). The preeminent CO₂ amount in the environment received a lot of attention because of its detrimental impacts on food crops. Similarly, the other constraint, i.e., heat stress, has also induced innumerable perturbations in the form of morpho-physiological responses that cannot even be ignored due to the consequent productivity loss. Therefore, this section is particularly based on the challenges that are faced frequently when researchers are exploring productivity improvement possibilities.

7.11.1 Strategies and Challenges for Improving Crop Production

After the perusal of literature, the details of strategies adopted for the improvement of crop productivity and challenges with enhanced CO₂ concentration and incidents of heat stress are summarized in the following subsections.

7.11.1.1 With Elevated CO₂

The relevant and recent reports on elevated CO₂ level are comprehensively addressed as below:

- According to the viewpoints of Hatfield et al. (2011), high amount of CO₂ has positive effects on plant growth and development along with the improvement in water use efficiency. In contrast, it is a challenge to predict whether these positive faces of elevated CO₂ can persist even with other changing environmental factors like temperature, precipitation, and interaction with biotic stress factors (weeds, insects, diseases, etc.).
- Due to the limited efficiency of the C₃ photosynthetic pathway, the growth and development of crop plants are adversely affected. In this context, the existence of CCM is reported in some algae along with micro-autotrophs and cyanobacteria (Beardall and Raven 2017). In this mechanism, Rubisco accelerates the process of carbon assimilation via highly proficient CCM that enhances the CO₂ concentration around Rubisco. However, innumerable contravenes are present, for example, comprehension of bicarbonate transporters' activation and energization processes, issues related to C₃ chloroplast, carboxysomal Rubiscos' chaperone requirements, etc. (Price et al. 2011; Breuers et al. 2012).
- As the source and sink association regulates biomass accumulation and crop yield, so it was recently chronicled that a thermostable Rubisco can be engineered via modifying Rubisco's small and large subunits (Peterhansel and Offermann 2012).
- As per the adjudications of Erb and Zarzycki (2016), it was revealed that this concern can be overcome via improving Rubisco efficiency, applying CCM, instituting bypasses' of photo-respiration, etc.
- It was reported that C₃ crop plants can be benefited from the enhanced CO₂ because of their photosynthesis responsiveness to CO₂. Besides, there are other challenges, and the major one is the requirements of greater sink capacity (Dingkuhn et al. 2020).
- The outcomes from the study of Eshete et al. (2020) indicated that the aggravated levels of CO₂ negatively impacted the production of both traded and non-traded crops. Therefore, the Ethiopian Government has inaugurated a strategy to relegate the emission of CO₂, i.e., climate-resilient green economy (CRGE).

7.11.1.2 Under Heat Stress

The temperature beyond the physiologically optimal limit that disturbs normal plant growth and development is referred to as high temperature, whereas extremely high temperatures are referred to as heat stress. Many conventional and modern strategies were employed to resolve heat stress-induced damages to environment. On contrary, there are several challenges that are yet to be resolved and addressed to deal with heat stress as summarized below:

- There are numerous loopholes in the complete mechanism of heat tolerance, thereby, the number of management strategies is limited to precise phenotyping techniques. Furthermore, the emphasis should be laid on crop diversity, identification, and selection of superior adaptive characters. The integration of molecular breeding, functional genomics, and transgenic techniques can make a difference, so that, reinforced with the facilities on next-generation phenomics (Jha et al. 2014).
- The incidences of high-temperature variations are reported to be associated with considerable floret-fertility loss that ultimately causes yield reduction. The prompt elevation in night-time

temperature is reported to mediate the narrowing of diurnal temperature amplitude that is another budding challenge to sustainable crop productivity (Prasad et al. 2017).

- An inclusive account of conventional as well as modern approaches to deal with heat stress has been addressed by Fahad et al (2017). It was reported that the identification of lines with superior characters via applying breeding techniques is the easiest option (Ehlers and Hall 1998). Heat tolerant plants are characterized via *the* minimization of photosynthetic damages along with the biosynthesis of protective compounds (Bita and Gerats 2013). Furthermore, the reproductive phase of plants is reported to be more vulnerable, therefore, many challenges are still there viz., improved photosynthetic rate, fruit setting, thermostability imparting to membranes, etc. (Fahad et al. 2017). Apart from this, the effectiveness of any method and/or strategy cannot be applied to all crops as it is under study.
- Heat stress is recorded to affect wheat plants adversely along with grain filling which, subsequently, causes a reduction in crop yield. Thus, a deep understanding of metabolic dynamics is essential to achieve heat stress-mediated consequences (Abdelrahman et al. 2020).

7.12 Conclusion

It can be easily inferred that climate change is a complex phenomenon that needs patience to solve. When the going gets tough, only the tough get going. Hence, this chapter is a welcome call to understand threats on cereal crops that feed more than 90% of world citizens with over 90% of them residing in Africa, Asia, and Latin America whose lands are severely threatened by rising temperature, as carbon dioxide exacerbates global warming and climate change. Constant research and applications are needed to address these issues in agriculture and the environment. Therefore, this research work discussed the importance of eCO₂ and temperature on cereal crops' physiological traits so as to understand the problem in hand and accelerate efforts at addressing the critical challenges facing us – not only they who must daily deal with it but also they who are responsible for solving it. It is well understood that the adaptations to eCO₂ are mainly due to changes in primary metabolic processors and associated physiological functions.

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