Climate Change and Its Impact on Crops

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Plants are a highly advanced kingdom of living organisms on the earth. They survive under all climatic and weather variabilities, including low and high temperature, rainfall, radiation, less nutrients, and high salinity. Even though they are adapted to various environmental factors, which are variable, the performance of a crop will be compensated under sub/supra optimal conditions.

1. Photosynthesis

The changing climate is associated with an increase in the concentration of greenhouse gases (GHGs), having more significant implications on the major physiological processes in plants. Among these, the effect on the plants' photosynthetic rate is of profound importance as it directly contributes to the economic yield of the plant. Exposing C_3 plants to elevated CO_2 increases photosynthesis primarily due to increased activity of the enzyme Rubisco [1]. Despite the initial increase in photosynthesis at elevated CO_2 (eCO_2), various studies using growth chambers as well as FACE (Free Air CO_2 Enrichment) facilities showed that long-term exposure to eCO_2 incurred in attenuation of photosynthesis by a process called photosynthetic acclimation to elevated CO_2 (PAC). Increasing N supply was found to counteract the saturation effects of elevated CO_2 on photosynthesis and the source-sink imbalance in tomatoes [2]. An experiment was conducted on four perennial grassland species from four functional groups (C_3 grasses, C_4 grasses, forbs, and legumes) exposed to eCO_2 (ambient + 180 ppm) over two decades in a Minnesota FACE facility (BioCON). It showed that, among the four groups, the photosynthetic response of legumes was the best and that of C_4 grasses least under eCO_2 [3]. However, C_4 plants were found to respond to long-term exposure to eCO_2. The yields of wheat and rice were increased by CO_2 enhancement, but higher temperatures reduced their grain yield [4]. Under unstressed conditions, eCO_2 caused increased photosynthesis, boosting growth, aboveground biomass, and yield [5][6].

The carbon metabolism and photochemical reaction are the most affected plant processes under high-temperature stress. The high-temperature-induced inactivation of the PSII electron acceptor and donor leads to enhanced reactive oxygen species (ROS) production accompanied by a reduction in Rubisco activity [7]. A rise in temperature as high as 45 °C would result in complete inhibition of photosynthesis in rice and ultimately result in plant death if such a condition is sustained for more than 24 h [8]. Generally, plants experience much higher temperatures only for 1–2 h per day, and the leaf temperatures will be 5–10 °C lower than the ambient air temperature [9][10]. Studies in rice genotypes showed no noticeable change in the photosynthetic rate when exposed to 28, 34, and 38 °C but an increase in the respiration rate with increasing temperatures. Contrary to this, a high night temperature resulted in a significant yield loss in rice and wheat, which was attributed to higher dark respiration resulting in increased consumption of photoassimilates, thereby reducing the non-structural carbohydrates in the stem tissue [11][12]. Several findings show that C_4 plants exhibit more tolerance than C_3 plants to high-temperature regimes. The optimum temperature for photosynthesis in maize was 40 °C which suggested the possibility of overestimation of the negative impacts of global warming on the maize yield [13]. In hot climates, the main yield declining factor in rice might not be photosynthesis exclusively. For instance, rice under high temperatures exhibited higher respiratory enzyme activities (NADH dehydrogenase, cytochrome c oxidase, ATPase), increasing energy production efficiency at the onset of stress. The energy produced by enhanced respiration was supplied to maintenance rather than growth, thus decreasing the energy utilization efficiency and reducing yields [14].

Plant species and environmental variables influence the magnitude of photosynthetic CO_2 uptake. Increased atmospheric CO_2 at high temperatures promotes plant development by increasing photosynthetic rates. One of the most significant effects of eCO_2 is an increase in the number of proteins linked to PSI and PSII. Conversely, increased atmospheric CO_2 causes a decrease in stomatal conductance [15]. The photosynthetic rate of *H. spicatum* Sm. and *V. jatamansi* Jones decreases modestly after 5 days (2 and 9%, respectively) due to individual and combined heat and drought stress. It

declined severely under combined stress effects (89–95%) under drought (51–84%) and heat stress (64–77%) after 30 days of exposure [16]. Photosynthesis is reduced in *Panax quinquefolius* L. under high heat conditions [17]. In *Sinopodophyllum hexandrum* (Royle) Ying, 40 to 60% shade was found to be ideal for photosynthesis in abiotic stress trials [18]. A soil moisture deficit lowers chlorophyll content and the photosynthetic rate. The light saturation points decrease gradually while the light compensation point and dark respiration rate increase [19]. Differential expression of proteins involved in photosynthesis, transcription, metabolism, protein synthesis, defense response, signaling, transport, and cytoskeleton development was recorded in *P. kurrooa* Royle. It was accompanied by a reduced photosynthetic rate [20].

The effect on *S. hexandrum* Roylewas exposed to control and increased (650 ppm) CO_2 concentrations for four months in the open-top chamber (OTC) [21]. They observed that the photosynthetic rate increased while transpiration and stomatal conductance decreased dramatically. Using an OTC facility, [22] investigated the impact of eCO_2 (800 ppm) on the growth dynamics, structure, and function of *Ocimum sanctum* L. (Holy tulsi). The increased CO_2 concentration stimulates photosynthesis, intercellular CO_2 concentration, carboxylation efficiency, and mesophyll efficiency. The water use efficiency (in terms of transpiration and stomatal conductance) decreased with respect to control. The physiology of *Gynostemma pentaphyllum* Makino at two CO_2 levels, namely at the control (360 ppm) and elevated (720 ppm) levels [23]. A studied FACE technique on *Isatis indigotica* Fort., an important Chinese medicinal plant, with an effect of enhanced CO_2 levels of 550 ppm, significantly increased photosynthetic rates and water usage efficiency (WUE), compared to controls, while the transpiration rate and stomatal conductivity decreased [24].

The optimum temperature for photosynthesis was estimated in alpine and temperate populations of *S. hexandrum* Royle grown in environmentally controlled rooms with variable photosynthetically active radiation (PAR) levels and temperatures. Nonetheless, an increased transpiration rate and reduced water usage efficiency (WUE)were ascribed to the decrease in photosynthesis at higher temperatures, demonstrating that the species is susceptible to high temperatures [25]. Thus, the eCO_2 condition that is expected in the near future can provide yield increments in all crops. The detrimental effects come up when the greenhouse affects the temperature that attenuates photosynthesis in C_3 crops. Stresses such as drought also cause yield deterioration as assimilation and partitioning are affected. The combined stresses of high temperature and drought are most detrimental to individual ones.

2. Canopy Temperature and Transpiration

The elevated CO_2 and temperature have opposing effects on transpiration rates. Elevated CO_2 can reduce stomatal conductance, which in turn reduces the transpiration rates. The result is amplified by the elevated temperature expected to happen due to elevated CO_2 [26]. The cowpea is a drought-sensitive pulse crop. Under water-limited conditions, it could not restrict transpiration loss even beyond the soil moisture threshold. Specific tolerant genotypes were able to minimize stomatal conductance and transpiration, which help in their survival [27]. Studies from almond trees to elucidate the relationship between the Crop Water Stress Index (CWSI), transpiration, and canopy temperature revealed that water deficit stress increases proportionately with the transpiration rate and canopy temperature [28]. Canopy temperature depression (CTD) is the difference in temperature between the ambient microclimate and plant canopy, where a lower (more negative; cooler) value is healthier than the higher one. The soybean crop yield was reduced by 273 to 304 kg/ha when exposed to a 1 °C increase in CTD. The CTD and transpiration rate can estimate crop yield under elevated temperatures [29]. In pea plants under drought, the epicuticular wax was increased in tolerant varieties that reduced the associated heat stress due to reduced transpiration cooling [30].

Under high-temperature conditions, plant metabolism is prone to drastic changes. With the rising temperature, maintenance respiration costs rise [31][32], and plants attain more excellent whole-plant respiration rates on a daily basis. Plants that survive in low-light situations may become more reliant on non-structural carbohydrate reserves (NSC) under high temperatures [33][34]. The imposition of drought in *Vitex trifolia* L. increased chlorophyll fluorescence and impaired PSII activity [35]. Drought stress also caused a differential expression of proteins involved in metabolism, photosynthesis, transcription, protein synthesis, defense response, transport, signaling, and cytoskeleton development in *P. kurrooa* [20].

3. Stability of Membranes

Under heat stress, the membrane fluidity is affected, and the effects are more severe with the damage to thylakoid membranes. The major factor that reduces maize yield under high temperatures is damage to chloroplast membranes [36]. Water stress resulted in a decreased Membrane stability index (MSI) in the spring rapeseed which was clearly shown by a higher malondialdehyde content [37]. It was demonstrated in canola that drought and salinity affect growth, biomass, and oil yield [38]. In pistachios, there is a significant increase in malondialdehyde content and poor membrane stability that

attenuated its growth under salinity [39]. In fact, sodicity is a significant threat to crop production over salinity, as shown in quinoa [40].

Some study shows that a low temperature-induced transitions in the membrane lipid phase, which lead to a loss of membrane stability and physiological dysfunction. The revelation is that chilling stress elicits a complex membrane retailoring response that leads to enhanced fluidity at lower temperatures. Membranes change their physical features, having a function in cold stress tolerance. Poor membrane integrity may potentially play a role in the development of irreparable harm during low-temperature stress. It would have a comparable effect with the senescence processes by free radicals on tissues owing to increased membrane rigidity [41]. Malondialdehyde is a stress sensitivity marker to recognize lipid peroxidation. It is an indicator of the extent of membrane damage [42]. The effect of eCO_2 on two high-altitude medicinal plant species (*Aconitum lethale* Griff. and *A. hetrophyllum*) exhibited increased lipid peroxidation [43]. Salinity, water deficits, and high as well as low temperatures are causing adverse effects at sub-cellular levels by affecting membrane fluidity. Reduced membrane fluidity hampers all the cellular vital functions, especially in chloroplasts and mitochondria. Accumulation of ROS and lipid peroxidation negates the tolerance mechanisms and crop production.

4. Photorespiration and Respiration

There is no conclusive evidence on the relation between eCO_2 and the respiration rate in plants, and it remains unaffected, declines, or increases depending on the species. Experiments correlating with eCO_2 and photorespiration showed a decrease in the latter. Nevertheless, this relation is not linear as the regeneration step of the Calvin cycle becomes saturated [44]. High temperatures affect photosynthesis by affecting the structure of thylakoids, altering the excitation energy distribution, and influencing the activity of the Calvin cycle and other metabolic processes such as photoinhibition, photorespiration, and product synthesis [45]. Numerous studies proved that short-term exposure to eCO_2 increases photosynthesis by minimizing energy wastage in photorespiration [5].

Under elevated temperatures, both respiration and photorespiration are increased. In cowpeas, the increase in these pathways helps the plant to survive extreme weather conditions [46]. Similar observations on the hike in mitochondrial respiration and photorespiration were observed in wheat under high temperatures (40–60 °C) [47]. Field-grown wheat exposed to 25 °C was acclimated to reduce dark respiration, leading to lesser yield loss [48]. In pea seedlings, drought stress led to a significant reduction in mitochondrial respiration, and its recovery was hastened by chilling stress of 15 °C [49]. Thus, global warming can bring down the net carbon gain by rising plant respiration rates [50]. Even though respiration is not significantly affected by eCO_2, photorespiration is negated. Conversely, a high temperature causes a hike in respiration and photorespiration. Photorespiration provides ample protection against environmental stresses, though its benefits on sustainable crop production must be explored.

5. Redox Status

Studies on three maize hybrids subjected to different water statuses (100, 80, 60, and 40% of field capacity) showed that drought conditions caused oxidative stress, which elevated ROS production, reducing the growth and yield of all maize hybrids studied [51]. Antioxidant activity in soybean roots was negatively affected by eCO_2 (800 ppm), as shown by the downregulation of 10 different putative peroxidase genes, one *FERI* gene, and glutathione pathway genes (*GSTU4*, 7, 8, and 19) [52]. Low-temperature stress exposure to rye grass (*Leymus chinensis* Tzvelev) resulted in elevated malondialdehyde content and cellular damage. To counteract the effects, osmolytes and various antioxidants were accumulated. The osmolytes can save the cells from reducing the water potential, while antioxidants will maintain redox homeostasis [53]. The water deficit stress showed a significant alteration in ROS homeostasis in mustard that curtailed its yield [54]. Similarly, when exposed to drought stress, Chinese cabbage resulted in a decrease in oxidized/reduced glutathione and NADP/NADPH ratios [55].

Specific findings [43] reported the effects of eCO_2 on two high-altitude medicinal plant species (*A.lethale* and *A. hetrophyllum*),increasing antioxidant activity. Under eCO_2, increased carbon availability may enhance the concentration of antioxidant molecules, which can possibly ameliorate the defense mechanism against oxidative damage [56][57]. The activity of the Superoxide dismutase (SOD) enzyme was enhanced under eCO_2 in two *Aconitum* species studied. Conversely, peroxidase (POD) activity under eCO_2 decreased in two *Aconitum* sp. In *A. lethale,* there was a decline in POD activity (81%) under eCO_2, whereas, in *A. heterophyllum,* the decline recorded (35%) was much lower [43].

6. Yield

Studies in wheat by [58] on the effect of eCO$_2$ (605 ppm) on grain yields recorded an increase in grain number and yield by 26%. Experiments in the FACE facility on eighteen C$_3$/C$_4$ crops for studying the effects of temperature, drought, ozone levels, and nitrogen treatments spreading across 14 sites from five continents revealed metadata of physiological and yield responses. A comparative increase in yield of 18% by an elevation of 200 ppm CO$_2$ when no other stresses were given was recorded. In the C4 crops—maize and sorghum—, lower productivity was observed only under eCO$_2$ conditions, though, in combination with drought stress, it availed relatively stable productivity [59]. Global warming can lower the net carbon gain by amplifying plant respiration rates, which would lead to a decline in the production/yield of crops and could even cause the invasion of weeds, pathogens, and pests [50][60]. For instance, in the case of wheat, an increase in temperature by 1 °C could decline the yields by 3 to 10% [61]. In paddies, the moisture deficit situation can directly link to the drop in yield [62]. As a direct effect of climate change, the cereal yield is affected by heat and water stresses, with a significant influence on fertilizer supply, pathogens, and pests indirectly [63].

An evaluation of the effect of two temperature statuses (23 and 29 °C) and water levels (90 and 30% water holding capacity) and their combinations in *Brassica napus* L., in different stages of growth, showed that the electron transport rate and the carboxylation efficiency significantly lowered under heat stress. Decreased seed yield by 85.3 and 31% under heat and drought stress, respectively, was recorded. It dictates that heat stress negatively impacts yield and oil quality more than drought stress [64]. In rice, drought stress at the flowering stage strongly influenced the physiological traits and yield by reducing the grain yield by more than 20% [65]. A similar trend was seen in seven maize hybrids, where the detrimental impact of drought on yield was well illustrated [66]. A decrease in grains in safflower occurred when different levels of water stress, by altering the time of irrigation, were imposed. The decreased test weight proportionately went with the increasing irrigation interval [67].

7. Quality

The eCO$_2$ resulted in decreased nutrient content in C$_3$ plants such as wheat (N, Ca, S, Mg, Mn, Al, Fe, Zn), rice (N, S, Fe, Zn, Mn, Cu), legumes (S, Fe, Zn, Cu), and vegetables (N, Mg, Fe, Zn) resulting in the dietary deficiency of nutrients [68]. Under eCO$_2$, the tissue nutrient content was found to be diluted. In addition to the excess carbon becoming fixed in the biomass disproportionately, the transpiration-driven mass flow of nutrients is hampered, reducing the concentration of nutrients [69]. On the assessment of the effect of eCO$_2$ (800 ppm) in soybeans by [52], the expression of iron assimilatory genes and various nutrient transporters was downregulated, which resulted in a lower mineral concentration inthe leaf and seed. The eCO$_2$ (655 ppm) in aniseed (*Pimpinella anisum* L.) resulted in increased essential oil content in mature seeds as the production of precursors, namely shikimic and cinnamic acids, was induced [70]. Similarly, eCO$_2$ (627 ppm) was found to improve the levels of soluble sugars, starch, organic acids, phenol content, flavonoids, and vitamins A and E in several herbal plant species [71]. Rice was exposed to flooding and drought stress, and there was no significant impact on the nutritional quality but was compromised with kernel chalkiness in grains [65]. Chemical content variations in food crops may pose more implications for human health than are typically recognized [72][73]. Increased environmental pressures may cause changes in chemical content in some species, potentially altering the quality or even the safety of medical products.

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