

Review

Climate Change and Its Impact on Crops: A Comprehensive Investigation for Sustainable Agriculture

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Abstract: 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. Hence, current and future climate change factors pose a challenge to sustainable agriculture. Photosynthesis is the primary biochemical trait of crops that are affected by abiotic stress and elevated CO₂ (eCO₂). Under eCO₂, the C₃ legumes could perform better photosynthesis over C₄ grasses. The associated elevated temperature promotes the survival of the C₄ crop (maize) over C₃ plants. In the American *Ginseng*, the elevated temperature promotes the accumulation of phytochemicals. Under less water availability, poor transpirational cooling, higher canopy temperatures, and oxidative stress will attenuate the stability of the membrane. Altering the membrane composition to safeguard fluidity is a major tolerance mechanism. For protection and survival under individual or multiple stresses, plants try to undergo high photorespiration and dark respiration, for instance, in wheat and peas. The redox status of plants should be maintained for ROS homeostasis and, thereby, plant survival. The production of antioxidants and secondary metabolites may keep a check on the content of oxidating molecules. Several adaptations, such as deeper rooting, epicuticular wax formation such as peas, and utilization of non-structural carbohydrates, i.e., wheat, help in survival. In addition to yield, quality is a major attribute abridged or augmented by climate change. The nutrient content of cereals, pulses, and vegetables is reduced by eCO₂; in aniseed and *Valeriana* sp., the essential oil content is increased. Thus, climate change has perplexing effects in a species-dependent manner, posing hurdles in sustainable crop production. The review covers various scientific issues interlinked with challenges of food/nutritional security and the resilience of plants to climate variability. This article also glimpses through the research gaps present in the studies about the physiological effects of climate change on various crops.

Keywords: climate change; eCO₂; photosynthesis; yield; nutrient; quality; sustainable agriculture

1. Introduction

Changing the climate scenario is imposing more challenges on crop production and medicinal plant productivity due to its adverse impacts on soil and plant processes. A detailed understanding of the mechanisms affecting these processes is highly pertinent for

researchers, policymakers, as well as farmers. Consequently, in recent decades, widespread research has been devoted to crop productivity under climate change involving field and modeling experiments. We are focusing on plant physiological processes affected by climate change scenarios. A meta-analysis of the literature for 55 rice and 60 wheat varieties showed that the yield losses due to water deficit stress would be 25.4 and 27.5%, respectively [1]. Even though elevated CO₂ (eCO₂) can increase crop yield, such as soybeans, the effect will be attenuated by intensified drought [2]. A combined stress experiment of eCO₂ with canopy warming of 2 °C in a rice-wheat rotation system exhibited multiple physiological effects. An elevated temperature with CO₂ (500 ppm) resulted in a significant reduction in C:P and N:P ratios and an increase in the C:N ratio, indicating the altered nutrient status of tissues [3]. Thus, climate change can indirectly influence the nutritional security of the feeding population.

Climate change imposes abiotic stress in combination rather than in solitude. Experiments in chickpeas under drought along with a high temperature showed that combined stress impaired the membranes and stomatal conductance. Chlorophyll content, PSII activity, and Rubisco activity were also severely compromised [4]. Several genotypes with high and low temperatures and drought tolerance were identified in this crop. The gene pyramiding of the corresponding Quantitative trait locus (QTLs) can impart multiple stress tolerance in chickpeas [5]. Studies in sorghum showed that drought, in concert with salinity stress, leads to reduced water retention, increased reactive oxygen species (ROS) accumulation, afflicted pigment levels, and inhibited plant growth. For survival, plants accumulated the compatible osmolyte proline [6]. Water logging can also act in concert with salinity. A comparative study between two medicinal species, namely *Plantago maritima* L. (salt-tolerant) and *Plantago media* L. (salt-sensitive), showed several adverse effects on plant health in the sensitive type. In the tolerant variety, ascorbate peroxidase activity was induced in addition to catalase-peroxidase [7].

Climate change has many antagonistic effects on plants by creating several stresses. Research on the presence of various secondary metabolites recognizes medicinal and aromatic plants. An elevated temperature influences the production of secondary metabolites, such as volatile plant metabolites (VPM) [8]. Stress can alter different metabolic pathways, resulting in the production of different metabolites' by-products. For instance, the ultraviolet-B induces changes in the phenylpropanoid pathway and essential oil production in *Curcuma* sp., namely, *C. longa* L. and *C. cassia* Roxb. [9]. In the medicinal crop *Cornus officinalis* Sieb. et Zucc., bioactive compound accumulation strictly depends on weather conditions [10]. Similar is the case with the production of food grains [11] and grain legumes [12]. Thus, climatic variability impedes crop productivity and quality (Table 1).

Despite the various stress effects, some crops are better adapted to changing climatic scenarios than others. Their various indispensable metabolic activities are least affected and make them better-suitable over others. These crops and some genotypes of susceptible crops are the light in the darkness of climate change for feeding the world's booming population. For sustaining agriculture, food, and nutritional security, the selection of crops which can be better adapted to changing climatic scenarios is essential. A thorough understanding of the mechanisms underlying tolerance and susceptibility will lead us in the direction of breeding climate-resilient crops and achieving the goal of sustainable agriculture. This article clearly mentioned the pros and cons of different climatic and weather factors on the morpho-physiological attributes of agricultural, horticultural, and medicinal plants. The novelty of this paper is to examine and indicate the research gaps in the field of climate change research. Very few attempts were made for the study of climate change effect on high-altitude medicinal plant. So, in this review article, we addressed all the benefits and drawbacks of climate change in the survival and productivity of diverse crop plants of agriculture, horticulture and medicinally important.

Table 1. The effect of various environmental conditions on physiological and biochemical attributes at cellular and plant levels determines tolerance or sensitivity.

Trait	Species	Change (+/−)	Effect of Change on the Plant (+/−)	Reference
Elevated CO₂				
Photosynthesis	Legumes	+	+	[13]
Photosynthetic acclimation	Tomato	+	−	[14]
Yield	Wheat, rice	+	+	[15]
Levels of PSI and PSII		+	+	
Stomatal conductance	<i>P. kurroa</i>	+	+	[16]
Lipid peroxidation	<i>A. balfourii</i> , <i>A. hetrophyllum</i>	+	−	[17]
Antioxidant activity	Soybean	+	−	[18]
Productivity	Maize; Sorghum	−	−	[19]
Growth rate	<i>S. barbata</i> , <i>S. lateriflora</i>	+	+	[20]
Total biomass	<i>T. vulgaris</i> , <i>T. hyemalis</i>	+		[21]
Essential oil content	Soybean	−	−	[18]
Iron assimilatory genes	Wheat, rice, legumes, vegetables	−		[22]
Nutrient content in edible produce	Herbal plant species	+		[23]
Medicinally important metabolites, vitamins				
Elevated temperature				
Photosynthesis	Rice	−	−	[24]
Respiration rate	Rice	+	−	[25]
Non-structural carbohydrate in stem	Rice	−	−	[26]
Activity of NADH dehydrogenase, cytochrome c oxidase, ATPase	Rice	+	+	[27]
Photosynthesis	<i>P. quinquefolius</i>	−	−	[28]
Transpiration rate		+	−	
Water use efficiency	<i>P. hexandrum</i>	−	+	[29]
Canopy temperature depression	Soybean	−	−	[30]
Epicuticular wax	Pea	+	+	[31]
Dark respiration	Wheat	−	+	[32]
Respiration		+	+	
Photorespiration	Cowpea	+	+	[33]
Electron transport rate		−	−	
Carboxylation efficiency		−	−	
Oil quality	<i>B. napus</i>	−	−	[34]
Seed yield		−	−	
Growth and multiplication	<i>P. polyphylla</i> , <i>S. chirayita</i>		+	[35]
Linalool concentration	<i>H. spicatum</i>	+		[36]
Low temperature				
Mitochondrial respiration	Pea	+	−	[37]
Malondialdehyde content		+	−	
Osmolytes	Rye grass (<i>L. chinensis</i>)	+	+	[38]
Antioxidants		+	+	
Drought				
Chlorophyll content	<i>P. polyphylla</i>	−	−	[39]
Light compensation point		+	−	
Chlorophyll fluorescence	<i>V. trifolia</i>	+	−	[40]
PSII activity		−	−	
Membrane stability index		−	−	
Malondialdehyde content	Rapeseed	+	−	[41]
ROS accumulation	Maize hybrids	+	−	[42]
Oxidized/reduced glutathione ratio		−	−	
NADP/NADPH ratio	Chinese cabbage	−	−	[43]
CAT and POD activities	<i>D. moniliforme</i>	+	+	[44]
Leaf and root protein content	<i>Picrorhiza</i> sp.	−	−	[45]
ROS homeostasis	Mustard	−	−	[46]
Salinity				
Biomass and oil yield	Canola	−	−	[47]
Membrane stability index		−	−	
Malondialdehyde content	Pistachio	+	−	[48]

Table 1. Cont.

Trait	Species	Change (+/−)	Effect of Change on the Plant (+/−)	Reference
Yield	Elevated CO₂ + temperature			
	Wheat, rice	−	−	[15]
Photosynthetic rate Valerenic acid content	Drought + temperature			
	<i>H. spicatum</i> , <i>V. jatamansi</i>	−	−	[36]
	<i>V. jatamansi</i>	−		

2. Impact of Climate Change on Various Physiological and Biochemical Attributes

2.1. 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 C₃ plants to elevated CO₂ increases photosynthesis primarily due to increased activity of the enzyme Rubisco [49]. Despite the initial increase in photosynthesis at eCO₂, various studies using growth chambers as well as FACE (Free Air CO₂ Enrichment) facilities showed that long-term exposure to eCO₂ incurred in attenuation of photosynthesis by a process called photosynthetic acclimation to elevated CO₂ (PAC). Increasing N supply was found to counteract the saturation effects of elevated CO₂ on photosynthesis and the source-sink imbalance in tomatoes [14]. An experiment was conducted on four perennial grassland species from four functional groups (C₃ grasses, C₄ grasses, forbs, and legumes) exposed to eCO₂ (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 C₄ grasses least under eCO₂ [13]. However, C₄ plants were found to respond to long-term exposure to eCO₂. The yields of wheat and rice were increased by CO₂ enhancement, but higher temperatures reduced their grain yield [15]. Under unstressed conditions, eCO₂ caused increased photosynthesis, boosting growth, aboveground biomass, and yield [50,51].

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 ROS production accompanied by a reduction in Rubisco activity [52]. 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 [24]. 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 [53,54]. 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 [25,26]. Several findings show that C₄ plants exhibit more tolerance than C₃ 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 [55]. 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 [27].

Plant species and environmental variables influence the magnitude of photosynthetic CO₂ uptake. Increased atmospheric CO₂ at high temperatures promotes plant development by increasing photosynthetic rates. One of the most significant effects of eCO₂ is an increase in the number of proteins linked to PSI and PSII. Conversely, increased atmospheric CO₂ causes a decrease in stomatal conductance [16]. 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 [36]. Photosynthesis is reduced in *Panax quinquefolius* L. under high heat conditions [28]. In *Sinopodophyllum hexandrum* (Royle) Ying, 40 to 60% shade was found to be ideal for photosynthesis in abiotic stress trials [56]. 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 [39]. 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 [45].

The effect on *S. hexandrum* Royle was exposed to control and increased (650 ppm) CO₂ concentrations for four months in the open-top chamber (OTC) [57]. They observed that the photosynthetic rate increased while transpiration and stomatal conductance decreased dramatically. Using an OTC facility, [58] investigated the impact of eCO₂ (800 ppm) on the growth dynamics, structure, and function of *Ocimum sanctum* L. (Holy tulsī). The increased CO₂ concentration stimulates photosynthesis, intercellular CO₂ 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 CO₂ levels, namely at the control (360 ppm) and elevated (720 ppm) levels [59]. A studied FACE technique on *Isatis indigotica* Fort., an important Chinese medicinal plant, with an effect of enhanced CO₂ levels of 550 ppm, significantly increased photosynthetic rates and water usage efficiency (WUE), compared to controls, while the transpiration rate and stomatal conductivity decreased [60].

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 [29]. Thus, the eCO₂ 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 C₃ 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.

2.2. Canopy Temperature and Transpiration

The elevated CO₂ and temperature have opposing effects on transpiration rates. Elevated CO₂ 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 CO₂ [61]. 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 [62]. 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 [63]. 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 [30]. In pea plants under drought, the epicuticular wax was increased in tolerant varieties that reduced the associated heat stress due to reduced transpiration cooling [31].

Under high-temperature conditions, plant metabolism is prone to drastic changes. With the rising temperature, maintenance respiration costs rise [64,65], 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 [66,67]. The imposition of drought in *Vitex trifolia* L. increased chlorophyll fluorescence and impaired PSII activity [40]. 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* [45]. Thus, we can infer from diverse species that drought and high temperatures can cause reduced transpiration in the long run, which can cause increased canopy temperatures and CWSI. As shown in soybeans, every degree in temperature has a proportionate compromise in stable crop productivity. Medicinal plants are susceptible to climate change. They contain many volatile aromatic compounds subjected to the alteration of secondary metabolite components, and in the concentration of secondary metabolites—the drought and upsurge of heat negatively influence medicinal plants. Only eCO₂ has a beneficial role in medicinal plant growth and other traits.

2.3. 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 [68]. Water stress resulted in a decreased Membrane stability index (MSI) in the spring rapeseed which was clearly shown by a higher malondialdehyde content [41]. It was demonstrated in canola that drought and salinity affect growth, biomass, and oil yield [47]. In pistachios, there is a significant increase in malondialdehyde content and poor membrane stability that attenuated its growth under salinity [48]. In fact, sodicity is a significant threat to crop production over salinity, as shown in quinoa [69].

The 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 (Figure 1). It would have a comparable effect with the senescence processes by free radicals on tissues owing to increased membrane rigidity [70]. Malondialdehyde is a stress sensitivity marker to recognize lipid peroxidation. It is an indicator of the extent of membrane damage [71]. The effect of eCO₂ on two high-altitude medicinal plant species (*Aconitum lethale* Griff. and *A. hetrophyllum*) exhibited increased lipid peroxidation [17]. 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.

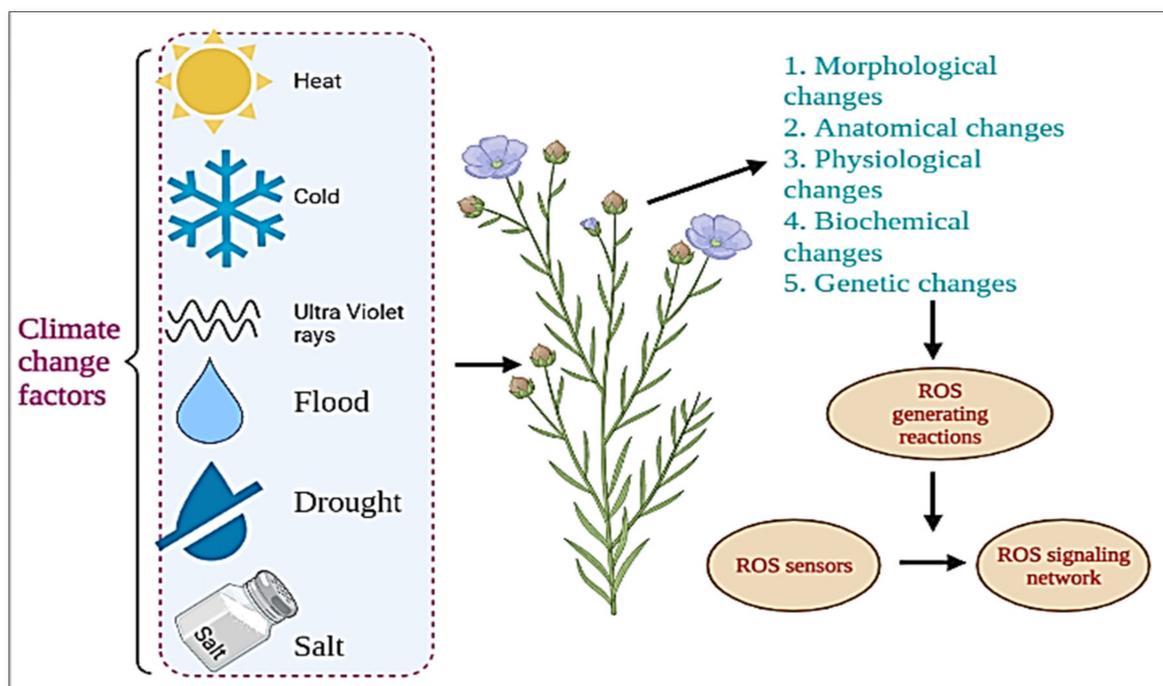


Figure 1. Depicting the effects of climate change (in the form of the different factors, such as heat, cold, ultraviolet rays, flood, drought, and salinity stress) on the medicinal plants resulted in morpho-anatomical and physio-biochemical changes, which further lead to the ROS production. ROS production is sensed by ROS sensors which will activate the ROS signaling network. ROS generation is harmful to the plants, and ROS finally leads to the death of the plants (created with BioRender.com).

2.4. Photorespiration and Respiration

There is no conclusive evidence on the relation between $e\text{CO}_2$ and the respiration rate in plants, and it remains unaffected, declines, or increases depending on the species. Experiments correlating with $e\text{CO}_2$ and photorespiration showed a decrease in the latter. Nevertheless, this relation is not linear as the regeneration step of the Calvin cycle becomes saturated [72]. 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 [73]. Numerous studies proved that short-term exposure to $e\text{CO}_2$ increases photosynthesis by minimizing energy wastage in photorespiration [50].

Under elevated temperatures, both respiration and photorespiration are increased. In cowpeas, the increase in these pathways helps the plant to survive extreme weather conditions [33]. Similar observations on the hike in mitochondrial respiration and photorespiration were observed in wheat under high temperatures (40–60 °C) [74]. Field-grown wheat exposed to 25 °C was acclimated to reduce dark respiration, leading to lesser yield loss [32]. In pea seedlings, drought stress led to a significant reduction in mitochondrial respiration, and its recovery was hastened by chilling stress of 15 °C [75]. Thus, global warming can bring down the net carbon gain by rising plant respiration rates [37]. Even though respiration is not significantly affected by $e\text{CO}_2$, 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.

2.5. Redox Status

The redox status of a plant cell and tissue is determined by the accumulation of ROS and its counteraction by antioxidant enzymes and scavengers. ROS is categorized into

two, namely non-radicals and free radicals. Non-radicals are stable or relatively stable compounds. They generally have stable valency as there are paired electrons in their orbital. They can react with molecules and leading to the formation of free radicals. Free radicals are highly reactive unstable molecules owing to an unpaired electron in their outermost orbital [76] (Table 2; Figure 1).

Table 2. Types of most common reactive oxygen species (ROS) generated in plants (adopted from [76]).

Molecule Name	Formula	Half-Life
<i>Non-radicals</i>		
Hydrogen peroxide	H ₂ O ₂	Stable
Singlet oxygen	¹ O ₂	10 ^{−6} s
Ozone	O ₃	Stable
Organic peroxide	ROOH	Stable
Hypochlorous acid	HOCl	Stable (min)
Hypobromous acid	HOBr	Stable (min)
<i>Free radicals</i>		
Superoxide	O ₂ ^{•−}	10 ^{−6} s
Hydroxyl radical	OH [•]	10 ^{−10} s
Alkoxy radical	RO [•]	10 ^{−6} s
Peroxy Radical	ROO [•]	17 s
Nitric oxide	NO [•]	2 ms
Nitrogen dioxide	NO ₂ [•]	

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 [42]. Antioxidant activity in soybean roots was negatively affected by eCO₂ (800 ppm), as shown by the downregulation of 10 different putative peroxidase genes, one *FER1* gene, and glutathione pathway genes (*GSTU4*, 7, 8, and 19) [18]. 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 [38]. The water deficit stress showed a significant alteration in ROS homeostasis in mustard that curtailed its yield [46]. Similarly, when exposed to drought stress, Chinese cabbage resulted in a decrease in oxidized/reduced glutathione and NADP/NADPH ratios [43].

Specific findings [17] reported the effects of eCO₂ on two high-altitude medicinal plant species (*A. lethale* and *A. heterophyllum*), increasing antioxidant activity. Under eCO₂, increased carbon availability may enhance the concentration of antioxidant molecules, which can possibly ameliorate the defense mechanism against oxidative damage [77,78]. The activity of the Superoxide dismutase (SOD) enzyme was enhanced under eCO₂ in two *Aconitum* species studied. Conversely, peroxidase (POD) activity under eCO₂ decreased in two *Aconitum* sp. In *A. lethale*, there was a decline in POD activity (81%) under eCO₂, whereas, in *A. heterophyllum*, the decline recorded (35%) was much lower [17]. Antioxidant concentration in plants is a conventional criterion for evaluating a plant's therapeutic potential. Stress stimulates the generation of ROS, and antioxidant enzyme activity rises to counteract these hazardous molecules. The inactivation or denaturation of enzymes may cause inhibition of enzyme activities under high heat conditions. Catalase (CAT) and POD activities of *Dendrobium moniliforme* Sw., a widely grown medicinal crop, were significantly elevated during the early stages of drought stress to protect the plants against ROS damage [44,76] (Figure 2). These studies confirm that various types of ROS are accumulated from various cellular compartments under abiotic stresses. The action of antioxidant enzymes and metabolites counterbalances its uncontrolled accumulation. Compared to sensitive crops, tolerant crops can maintain ROS homeostasis and cellular physiology.

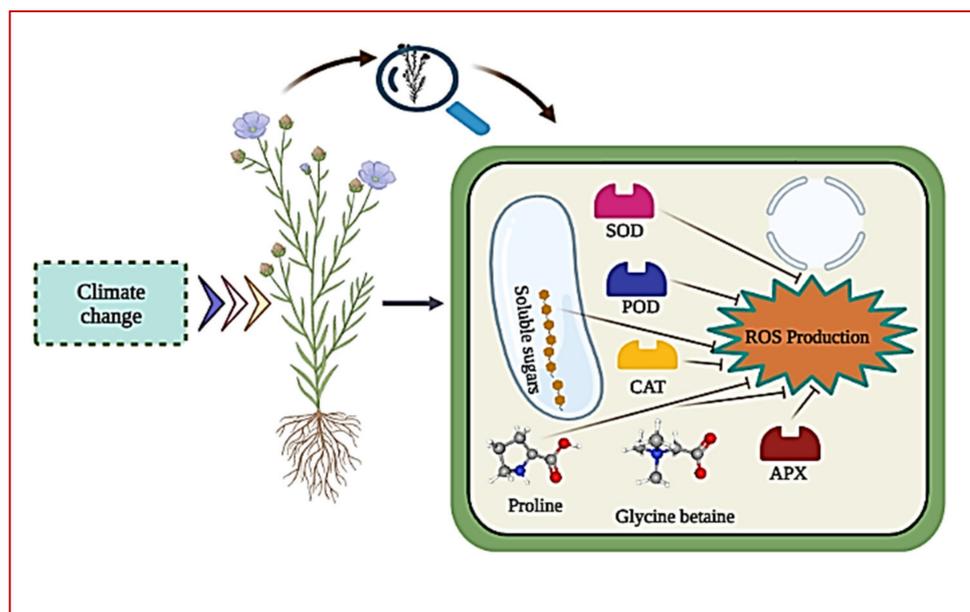


Figure 2. Depicting the changes in plant cellular metabolism. Climate change influences the production of ROS. Osmolytes (proline, glycine betaine) and antioxidant enzymes (SOD, POD, CAT, and APX), and water-soluble sugars help to denature ROS (created with BioRender.com).

2.6. Yield

Studies in wheat by [79] on the effect of eCO₂ (605 ppm) on grain yields recorded an increase in grain number and yield by 26%. Experiments in the FACE facility on eighteen C₃/C₄ 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 CO₂ when no other stresses were given was recorded. In the C₄ crops—maize and sorghum—, lower productivity was observed only under eCO₂ conditions, though, in combination with drought stress, it availed relatively stable productivity [19]. 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 [37,80]. For instance, in the case of wheat, an increase in temperature by 1 °C could decline the yields by 3 to 10% [81]. In paddies, the moisture deficit situation can directly link to the drop in yield [82]. 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 [83].

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 [34]. In rice, drought stress at the flowering stage strongly influenced the physiological traits and yield by reducing the grain yield by more than 20% [84]. A similar trend was seen in seven maize hybrids, where the detrimental impact of drought on yield was well illustrated [85]. 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 [86].

Experiments [20] on *Scutellaria barbata* D. Don. and *S. lateriflora* L. with CO₂ concentrations of 400, 1200, and 3000 ppm found that eCO₂ of 1200 ppm resulted in an increase in the growth rate and total biomass in both species when compared to 400 and 3000 ppm. Growth and morphogenesis in the *O. basilicum* L. (great basil) plant, where CO₂ enrichment

improved growth dynamics (plant height, collar diameter, branches, leaves number, root length, above and below-ground biomass) and structure (leaf shape, size, area, and leaf area index) were investigated when compared to ambient [58]. Leaf and root proteome studies in *Picrorhiza* sp. under drought stress showed an array of perturbations. It reduced leaf protein content by 24 and 37% on a fresh and dry weight basis, respectively. Drought stress increased root protein content by 12% on fresh weight and decreased by 9% on dry weight basis [45].

For flowering and blooming, several therapeutic herbs require a chilling temperature. The secondary metabolite output from therapeutic herbs is reduced with rising temperatures. Under elevated temperatures, the production of *Delphinium himalayai* Munz. was significantly hampered. *P. polyphylla* prefers warmer temperatures to flourish, and there was a positive trend in output, indicating that climate change has a favourable impact. The population of *Swertia chirayita* H. Karst. with an increased temperature has risen in recent years [35]. Drought stress during the first year of plant growth significantly raised the amount of valerenic acid in *V. jatamansi* Jones, whereas combined heat and drought stress significantly decreased it. Heat stress reduced valerenic acid production in the aerial component, implying organ-specific changes in the plant metabolism under stress. The Linalool concentration in *H. spicatum* increased modestly in drought and several folds with increased exposure to heat stress [36]. *Thymus vulgaris* L. and *T. hyemalis* R. Morales showed an increase in essential oil content when exposed to 500 ppm CO₂ [21,87]. These findings show the negative impacts of abiotic stresses on yield, irrespective of species. The compromised traits can be revamped by eCO₂ in varying degrees.

2.7. Quality

The eCO₂ resulted in decreased nutrient content in C₃ 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 [22]. Under eCO₂, 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 [88]. On the assessment of the effect of eCO₂ (800 ppm) in soybeans by [18], the expression of iron assimilatory genes and various nutrient transporters was downregulated, which resulted in a lower mineral concentration in the leaf and seed. The eCO₂ (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 [23]. Similarly, eCO₂ (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 [89]. 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 [84]. Chemical content variations in food crops may pose more implications for human health than are typically recognized [90,91]. Increased environmental pressures may cause changes in chemical content in some species, potentially altering the quality or even the safety of medical products.

The temperature considerably influences chemical composition, for instance, in *Arnica montana* L. [92]. On the other hand, the relationship between altitude and the chemical content in bush tea does not appear to be related to temperature [93]. Medicinal quality will not necessarily improve if montane species whose chemical content is impacted by temperature migrate to higher elevations and hence remain in the same temperature regime, but populations that persist at their original altitudes may fall in quality. Further research must fully comprehend the links between therapeutic potency and elevation in different species. As proven for American ginseng, high temperatures, akin to drought stress, can result in an elevated concentration of secondary metabolites due to drastically lower biomass [28]. When compared to ambient circumstances, eCO₂ increased the essential oil content of *V. jatamansi* (17.7%) while the elevated temperature lowered (4.3%). Under Himalayan conditions, an increase in air temperature may not be advantageous to the essential oil

content and quality of *V. jatamansi* in the near future [94] (Figure 1). Nutritional security in terms of mineral and metabolite content is the next level of focus after attaining food security for agronomic, horticultural, and medicinal crops. The eCO₂ can give contrasting results in various species, as the bioactive compounds and oils are increased, while mineral nutrient levels are reduced. Developing crops with higher secondary metabolites with lesser compromise in mineral element content can ensure promising sustainability from agricultural fields.

3. Conclusions

In this article, we illustrated the effect of climate change on various types of cultivated crops. The diverse climatic and environmental attributes have a bearing on the primary as well as secondary metabolism. Understanding the mechanisms underlying tolerance and susceptibility is key to achieving sustainable agriculture. The increased concentration of CO₂ in the atmosphere produces a fertilization effect on crops. The metabolites of medicinal value and oil content increased under eCO₂ conditions. Conversely, the nutritional quality in terms of mineral nutrient content is compromised. The eCO₂ can raise the atmospheric temperature in future climatic scenarios. The hike in temperature can reduce the growth and yield of cereals, pulses, and oil seed crops. Yet, certain medicinal plants such as *P. polyphylla* and *Swertia chirayita* H. Karst. flourish better under increasing temperatures. The plant adapts several mechanisms to survive under high temperatures. Increased deposition of epicuticular wax, transpirational cooling, increased photorespiration, etc. are some of the strategies employed by plants to suit the changing climatic parameter. Low temperatures can damage the membrane by affecting its fluidity and associated lipid peroxidation. The plant tries to cover up the damage by accumulating compatible osmolytes and antioxidants and maintenance of membrane fluidity.

Drought stress also poses a multitude of biochemical and physiological effects on plants. It affects the chlorophyll content, photosynthesis, and yield in all crop species. Water deficits also afflict the oil content and protein. Salinity also imparts similar outcomes in various crops. A major issue in the changing climate is the simultaneous exposure to multiple abiotic stresses. The photosynthesis and metabolite yield of different medicinal plants have been afflicted under drought stress acting together with high temperatures. The mechanisms of survival under such situations are yet to be deciphered. The various QTLs associated with tolerance to abiotic stresses have been identified. Pyramiding those QTLs can assist in the development of climate-ready crops for the future.

4. Further Research

The literature survey showed that there is significant paucity in the understanding of multiple abiotic stresses [95]. This poses a serious research gap in developing climate-ready crops. Under natural systems, drought is associated with higher canopy temperatures; waterlogging precedes drought; salinity comes alongside drought; and low temperature with water scarcity, among several others. Hence, such studies need ample research attention. The crosstalk between various responses to climate-change-associated abiotic stresses is not entirely understood. These areas can be explored for the research activities of research graduates and scientists globally.

The use of microorganisms may boost plant growth in adverse environmental conditions. Microbial applications can stimulate plant growth, antioxidant production, and nutrient uptake, leading to organic farming in the future world [96]. From the previous works performed by Patni et al. research team [97–100], climate change has many influences on the secondary metabolites production, upregulation, modifications, and alterations. On the other hand, all the secondary metabolites have some role in medical research, pharmaceutical, cosmetics, and organic products. So, advanced biotechnological approaches and metabolite studies using different climatic factors can boost those industries. Studies are less abundant on climate change effects on medicinal plants. The high-altitude plants are less known to researchers. The collection of high-altitude plants is also challenging. Mostly,

high-altitude medicinal plants are endangered plants. Fewer attempts were performed on their metabolic profiling and other physiological parameters. Ultimately, such efforts pave the way for sustainable agriculture upon incorporating the traits in popular cultivars in a location-specific manner.

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