Chapter

Elevated CO_2 Concentration Improves Heat-Tolerant Ability in Crops

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Abstract

The rising concentration of atmospheric carbon dioxide (aCO_2) and increasing temperature are the main reasons for climate change, which are significantly affecting crop production systems in this world. However, the elevated carbon dioxide (CO_2) concentration can improve the growth and development of crop plants by increasing photosynthetic rate (higher availability of photoassimilates). The combined effects of elevated CO_2 (eCO_2) and temperature on crop growth and carbon metabolism are not adequately recognized, while both eCO_2 and temperature triggered noteworthy changes in crop production. Therefore, to increase crop yields, it is important to identify the physiological mechanisms and genetic traits of crop plants which play a vital role in stress tolerance under the prevailing conditions. The eCO_2 and temperature stress effects on physiological aspects as well as biochemical profile to characterize genotypes that differ in their response to stress conditions. The aim of this review is directed the open-top cavities to regulate the properties like physiological, biochemical, and yield of crops under increasing aCO_2, and temperature. Overall, the extent of the effect of eCO_2 and temperature response to biochemical components and antioxidants remains unclear, and therefore further studies are required to promote an unperturbed production system.

Keywords: elevated CO_2, heat stress, physio-biochemical mechanisms

1. Introduction

Climate change in the form of increasing temperature and increasingly variable rainfall patterns threatens the production of the crop [1, 2]. Therefore, elevated CO_2 (eCO_2) absorption may indorse plant growth, whereas increased temperature is repressive for C_3 plants. Both CO_2 and temperature caused significant changes in crop productivity. The collaborative properties of eCO_2 and increased temperatures on the crop growth and carbon metabolism are not well known.

The fluctuating climatic surroundings are predictable to upsurge the atmospheric CO_2 (aCO_2) meditation, temperatures and modify the rainfall outline. The aCO_2 meditation is prophesied to range 550 ppm by 2050, and possibly surpass 700 ppm by the end of the present century [3]. These fluctuations are expected to disturb the creation and output of cultivated crops, and stimulus the upcoming food safety. The influence analysis of climate alteration on worldwide food construction reveals a 0.5% failure by 2020 and 2.3% by 2050 [4]. The progress of climate arranged germplasm to counterbalance these wounded is of the highest reputation [5].

The eCO_2 is significant abiotic stress and has a noteworthy fertilization encouragement on crops. Widespread preceding educations have described that eCO_2 meaningfully enhanced the water use efficiency (WUE), reduced transpiration frequency, abridged maize growth rate, and augmented plant height, leaf number, leaf area, growth frequency, and overall yield [6]. Furthermore, the cumulative of aCO_2 disturbs precipitation equilibrium, which can alter the periodic precipitation circulation [7]. It has been predicted that this result would carry about a 10% upsurge or decline in water capitals in several areas [8]. The raised temperature, i.e., heat stress (HS) damage growth and physiological ailments, and consequentially reduce yield [9]. Increased temperature due to eCO_2 has a primary effect on the food grain invention reliant on the places. With the rising temperature by 1.0–2.0°C in tropical and subtropical states and the food grain manufacture in India is predictable to decline up to 30% [9].

The C_4 grass maize (*Zea mays* L.) is the third most vital food crop worldwide in the relation of the invention, and its claim is prophesied to rise by 45% from 1997 to 2020 [10]. Educations with maize retort to dual the ambient CO_2 presented variable possessions on growth fluctuating from no inspiration of yield [11] to 50% stimulation [12]. The growth and productivity of maize are expected to be pretentious by raised aCO_2 and temperature. Raised temperature severely disturbs the growth, and yield of maize plants [13]. There is unpredictable information on the properties of eCO_2 on the vintage of maize changing from slight positive consequence [14], no consequence [15] to rice harvest by 50% [16].

Record of the experimentations on the influences of eCO_2 and temperature on the crop yield, though, used measured atmosphere amenities like phytotron and plant growth cavities or crop growth reproduction models [13, 17]. Determination of the impact of raised CO_2 on the photosynthesis tolerance to severe HS is vital to expect the plant replies for universal warming since photosynthesis is sensitive to severe HS and aCO_2 upsurges slightly [18, 19]. Further, flowering is a critical element for plant generative achievement and seed-set. The increase in temperature and eCO_2 is the main climate revolution issues that might influence plant suitability and associated flowering actions. Resolving the influence of these ecological issues on the flowering actions like time of days to anthesis and flowering (duration from germination till flowering) is serious to appreciate the acclimatization of crops in altering climate [20].

2. Interaction of eCO_2 with high-temperature stress and other factors to climate change

The impacts of eCO_2 and stress factors on crops have been made using controlled atmosphere amenities like plant growth cavities or crop growth reproduction models in many studies [13]. The eCO_2 contributes to global warming, causing alterations in the precipitations, water scarcity and changes at temperatures in several regions affecting the growth and development of crop plants [3]. However, the interactive effects of eCO_2 and environmental stress conditions on the crop growth and carbon metabolism are not well predictable. The interactions between eCO_2 and stress factors are critical to photosynthesis performance. It has been reported how stomata react to eCO_2 levels, but the effects on photosynthesis performance of other environmental factors are poorly understood [21].

Numerous studies showed the combining impacts of eCO_2 and drought and revealed that the machines are different from singular eCO_2 and drought. The impact of combined eCO_2 and drought are varying with crop stage such as during vegetative stage, and it restricted the shoot development, decreased leaf area, diminished mobilization of nutrients due to weak root growth, reduced stomatal closure, transpiration, and relative water contents (RWC). However, it enhances the resource use efficiencies of the plant, including WUE, light use efficiency (LUE), and nutrient use efficiency (NUE) at a certain level [22, 23]. Similarly, eCO_2 and drought affect reproductive growth severely such as the impacts on the pollen abortion, pollination, flower formation, panicle length, panicle weight, seed formation, seed size and, yield potential of important agriculture crops [22].

Altering climate, counting eCO_2, increasing temperatures, changing precipitation designs have influenced terrestrial environment assembly and function, carbon and water balance, and finally production of crops [24, 25]. Several experiments have described the biological replies to CO_2 enhancement and their communication with ecological alteration at different levels [26]. The temperature has an important role in plant growth and development and regulates the several functions and enzymatic reactions in plants. Although, the increased value of temperature causes several abnormalities in plants such as reduces the chlorophyll contents, leaf growth, fresh and dry biomass, photosynthesis, and stomata limitations, inhibits the functions of several temperature-sensitive enzymes such as ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). Impacts of eCO_2 and temperature combined stresses are very destructive at the reproductive phase. They may cause reduced pollination, spike sterility, less filling of grain, reduction of grain size and number, test weight, and yield potential of major crops [22].

It has been reported that eCO_2 promotes an initial stimulation of photosynthesis by an increase of substrate or RuBisCO carboxylation activity and self-consciousness of RuBisCO oxygenation, which might ultimately underwrite for advanced biomass in cereal crops [27, 28]. Nevertheless, growth responses over the long-standing under eCO_2 conditions include a reduction of photosynthesis measurements and several regulatory mechanisms to avoid potential damage by this condition. A regulatory mechanism to maintain the growth and expansion of plants consists of the equilibrium among manufacture and removal of reactive oxygen species (ROS) at the intracellular level. This balance is continued by both enzymatic and non-enzymatic antioxidant defense systems [29–31].

The enzymatic machinery involves numerous antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), guaiacol peroxidase (POX), peroxiredoxins (Prxs), and enzymes of the ascorbate-glutathione (AsAGSH) cycle. The AsAGSH includes different enzymes like ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) [30, 32]. Modifications of this enzymatic antioxidant component have been reported in studies of cereal crops under eCO_2 conditions with contradictory results. Thus, the response of these antioxidants components is unclear with studies that find to increase [33], decreases [34], or no consistent alterations [35].

Besides, plant cells have non-enzymatic components that involve ascorbate and glutathione (GSH) along with phenolic acids, flavonoids, carotenoids anthocyanins, and phenolic composites. The free hydroxyl groups on the phenolic rings or the chromanol rings of these non-enzymatic compounds are responsible for their antioxidant properties [36]. The ring hydrogen atom can be given to free radicals, dropping and counteracting ROS. The phenolic compounds can lose a hydrogen atom which develops a free radical that is directly non-reactive by character delocalization in the entire ring assembly [28, 37]. Several studies reported only an increase in some of the individual phenolic compounds in cereal crops under high CO_2 conditions [38].

Furthermore, crop growth responses to eCO_2 rely on the tissue category, developmental stage as well as strength and duration of these conditions which also depend on the diversity of apparatuses of construction and purification of ROS, and the result of free radicals on antioxidants [39]. Several studies have reported a high production of hydrogen peroxide (H_2O_2) after exposure of crops to eCO_2, and the concentration of H_2O_2 is dependent on the duration of these conditions. Besides, H_2O_2 production differed among various cellular compartments [40]. The outcome of elevated aCO_2 meditation on growth and various antioxidant actions is superior in C_3 plants to C_4 plants [41, 42]. For example, rice as a C_3 plant is further sensitive to the variations of the aCO_2. However, there are inconsistent studies on the impacts of eCO_2 on the antioxidant responses and yield of rice changing from the reduction of the growth responses [43] to increment of antioxidants components and enhancement of growth [44, 45].

Kumar et al. [46] reported that rice plants under eCO_2 conditions showed modifications in electrolyte leakage, leaf water potential, proline, CAT, and POD activity as compared to ambient CO_2, which assisted the plant to battle contrary effects of stressful environments. Thus, these authors suggest that undesirable possessions on rice yield subsequent from abiotic stress conditions may be moderated by the eCO_2 meditations [46]. In agreement, leaves of a susceptible wheat cultivar (*Triticum aestivum* L.*cv*. Yitpi) infected with Barley yellow dwarf virus-PAV (*PadiAvenae* virus) and grown under eCO_2 presented that the eCO_2 conditions may decrease the oxidative stress caused by virus infection [47]. Nevertheless, more evidence for direct communicating possessions of eCO_2 and biotic and abiotic stress conditions in cereal crops is necessary.

3. eCO_2 mitigates oxidative stress in plants

Various environmental stresses induce the production of ROS, which triggers oxidative stress in plants [30, 48, 49]. The most common ROS are $O_2^{\bullet-}$, $^{\bullet}OH$, and H_2O_2. In response to stressful conditions, H_2O_2 is mainly synthesized by photorespiration, beta (β)-oxidation, or due to the activity of nicotinamide adenine dinucleotide phosphate (NADPH) oxidase [30, 50]. The eCO_2 can efficiently reduce the ROS level by increasing RuBisCO carboxylation along with reducing photorespiratory H_2O_2 production. Several reports have provided indications regarding the eCO_2 influences on the mitigation of abiotic stress in plants [30, 51, 52]. Elevated CO_2 known to be induced plant growth by supplying additional Carbon (C) sources, subsequently alleviates abiotic stress in plants. Although the elevated CO_2 mediated particular physiological and molecular mechanisms related to abiotic stress alleviation are still to be explored. In the physiological aspect, supplying extra C by eCO_2 leads to induce stomatal closing, improves WUE that protect drought stress in plants [53]. However, abiotic stress-induced ROS (e.g., $O_2^{\bullet-}$, $^{\bullet}OH$, and H_2O_2) and cellular oxidative damages (e.g., protein oxidation, lipid peroxidation) are involved in non-stomatal factors with metabolic changes [30, 54].

A systematic study of recently published articles addressed the two major hypotheses such as enhancement of antioxidant (antioxidant hypothesis) and reduction of stress impact (relaxation hypothesis) by reducing ROS generation in the plant under stressful conditions [30, 51, 55]. Several reports have been found in favor of the relaxation hypothesis in plants in response to eCO_2 under stressful conditions. The ROS level was found to be reduced by eCO_2 in plants under drought, and heat stresses through increasing RuBisCO carboxylation as well as reducing the level of photorespiratory H_2O_2 [51]. In the same study, glycine/serine (Gly/Ser) ration, glycolate oxidase (GO), and hydroxypiruvate reductase (HPR) level were evaluated as an indicator of photorespiration, which was found to be decreased in response to eCO_2 under drought and heat stresses. In barley, these all parameters were found at a lower level in response to eCO_2 [56]. Moreover, reduced photorespiration is correlated to the decreased level of NADPH oxidase. Therefore, a combined effect of lower photorespiration and NADPH oxidase responses may lead to reduce H_2O_2 in plants.

According to the antioxidant approach, the availability of additional C by eCO_2 enhances antioxidant molecules, which increase ROS scavenging activity as well as protects grapevine and tomato plants from abiotic stress induced-oxidative damages [57, 58]. More specifically, higher C availability due to eCO_2 may enhance the supply of defense molecules, which improve protection against oxidative injury (antioxidant hypothesis) under stressful conditions in plant cells. However, changes in antioxidant levels are not specific, or C_3 or C_4 based metabolism, or not for a particular group of species. It has been reported in C_4 plants that photorespiration mildly active, in which eCO_2 reduces ROS level as well as oxidative injury without alteration of antioxidants level. It suggests a distinct non-stomatal process that except antioxidant defense or reduces photorespiration processes. Besides, several reports have provided the evidence regarding eCO_2 reduces NADPH oxidase activity and ROS formation in mitochondria and chloroplast in plants [59, 60], but the activity of beta (β)-oxidation is still to be explored.

The ascorbate-glutathione (ASC-GSH) cycle is one of the major mechanisms for stress-induced H_2O_2 regulation. However, only limited reports have been found concerning eCO_2 mediated changes of ASC-GSH cycle components in plants under stress conditions. For example, HS alleviated through enhancement of DHAR, MDHAR, APX, and GR in tomato [58]. Similarly, GR and APX were found to be increased by eCO_2 in wheat under ozone stress [61]. Also, responses of ASC-GSH cycle components varied based on the plant species and experimental set-up. Therefore, additional studies are needed concerning the eCO_2 mediated oxidative stress alleviation as well as enhancement of ASC-GSH cycle components in plants under abiotic stresses.

4. eCO_2 improves photosynthesis under high temperature

Several researchers on the consequences of eCO_2 and stress factors on crops have been made using monitored situation amenities like plant growth chambers, free-air concentration enrichment (FACE) experiment, open-top chamber (OTC) or stimulated crop growth models [13]. The eCO_2 contributes to global warming causing alterations in the precipitations patterns, water scarcity, flood, and changes at extreme temperatures in several regions affecting the growth and development of plants [3]. However, the interactive effects of eCO_2 and environmental stress conditions on the development of crops and metabolism are not well documented. It has been shown the average reduction of stomatal conductance (20–30%), stomatal density (5–7%), stomatal developments, and increment in WUE (8–18%)

under eCO_2 conditions. However, these changes vary with the crop species, developmental stages, nature of stressors and duration, surrounding environments, and plant attributes [62]. Likewise, the interactions between an eCO_2 with stress factors are crucial to understanding the photosynthesis performance. Therefore, there is a considerable deviation in the light-saturated photosynthetic assimilation rate under eCO_2 rely upon the plant type, plant functional traits, micro or surrounding environment, and resource availability. For instance, the stimulation in photosynthetic assimilation rate under eCO_2 is varied from 30 to 80% (strong stimulations in C_3 species as compared to C_4) in FACE experiment or pot conditions but diminished in field conditions because of the integration of other multiple stressors such as drought, heat, flood and nutrient deficiencies.

In this regard, several studies were conducted to observe the combining effects of eCO_2 and drought and reveals that the growth mechanisms are distinct to the singular eCO_2 or drought. The combined stress resulted in the longer retention time of dissolved organic carbon (accumulation of soil organic C), induce invertase and catalase activity in the soil, and ameliorate stress conditions via improving plant physiological traits and activates feedback mechanisms [63]. Further, it limits the activity of some antioxidant enzymes such as proline and MDA content and stimulates others such as SOD, CAT, and GPX [46, 64]. Abscisic acid, calcium-dependent protein kinase and glutathione *S*-transferase (GST) play an important role in the amelioration of drought stress responses by inducing signaling mechanisms under the combined form. Conclusively, it is suggested that drought and HS generate ROS, and affect the antioxidant defense mechanism of plants, which might be ameliorated by the eCO_2 via stimulation of antioxidant defense enzymes [51, 62]. Similarly, eCO_2 combined with drought and HS regulates the sugars (starch, sucrose) and amino acids (alanine, pyruvate, arginine, glutamate) and secondary metabolites (coumaric acid, salicylic acid) metabolism, protective proteins and readjusted the metabolic, redox, and osmotic equilibrium of plants under combined eCO_2 and drought [65, 66].

The impact of combined eCO_2 and drought are varied with crop stage such as during the vegetative phase decreased the shoot elongation and leaf area, diminished mobilization of nutrients due to weak root growth, reduced stomatal conductance by increasing stomatal resistance and stomatal movements, plant hydraulic conductance, aquaporins, and reduce transpiration and RWC. However, at certain levels, it enhances the biomass allocations to the reproductive part, improves resource use efficiencies of plants including WUE, LUE, and NUE [67]. Similarly, eCO_2 and drought affect reproductive growth severely such as its impacts on the assimilate partitioning, pollen abortion, pollination, flower formation, panicle length, panicle weight, productive tiller number, seed formation, seed size, and yield potential of important crops [22, 68]. Besides the yield potential, eCO_2 decreased the grain quality via affecting macro- and micro-nutrients content such as phosphorus (P), Sulphur (S), and Iron (Fe), Zinc (Zn) contents of dryland legumes, which further associated with yield dilutions [23].

Several findings have stated the biological responses to CO_2 enhancement and their communication with conservation alteration at diverse levels [26]. In these aspects, the temperature has an important role in plant growth and development and regulates the several functions and enzymatic reactions in plants. Although, the increased value of temperature cause several abnormalities in plants such as change the emission of volatile organic compounds, reduce nitrogen uptake, chlorophyll contents, leaf growth, fresh and dry biomass, photosynthesis, and stomata limitations (by membrane damage and photosystem II (PSII) activity), enhance the activity of mitochondrial electron transport, stress proteins and plant growth regulators, limitation of several temperature-sensitive enzymes such as RuBisCO.

The combined effects of eCO_2 and temperature stresses are very destructive at the reproductive phase. They may cause changes in flowering time, pollination, spike sterility, less filling of grain, reduction of grain size and number, test weight, grain quality, and yield potential of major crops [20, 22, 69].

Besides the drought and HS (major), other stressors also interact with the eCO_2 under field conditions and influence the plant growth and development. For instance, eCO_2 and salt stress conditions influence the nitrogen metabolism, water balance, photosynthetic inhibitions, nutrient deficiency or toxicity, stomatal conductance, carbohydrate metabolism, phenolic enrichments, and generation of secondary metabolites [63, 70]. Similarly, limited nitrogen supply under eCO_2 modifies the C/N ratio, nitrogen metabolism, protein supply, protein structure, gene expression, sugar metabolism, and decreases antioxidant enzyme, amino acid synthesis, photosynthetic pigments, and elevated ROS, which influence the redox equilibrium and leads to early senescence in plants [71]. Likewise, under N limitations, the photosynthetic rate is more affected in C_3 species (because of more N requirement for RuBisCO synthesis), and eCO_2 could help in mitigation of N limitations by reducing photorespiration, elevating starch level, increase chloroplast size, higher stomatal resistance, mitochondrial respiration, metabolites and dilution of chlorophyll concentrations [62]. Therefore, the eCO_2 and stressors impacts have differed than singular stress, and up to a certain level of eCO_2 try to recover plants via inducing defense machinery, feedback mechanisms, activating secondary messenger signaling, and expression of stress proteins.

5. eCO_2 improves yield under high temperature

By the end of the 21st century, CO_2 is expected to rise from the current level 370 $\mu mol \cdot mol^{-1}$ to 540–970 $\mu mol \cdot mol^{-1}$, and about to grasp 550 $\mu mol \cdot mol^{-1}$ near 2050 and 750 $\mu mol \cdot mol^{-1}$ in 2100. In the meantime, Earth's global temperature will rise by about 2–4°C [72]. The increased concentration of CO_2 in the atmosphere would increase the temperature of Earth that is why global heating will develop, the most important aspect of upcoming climate variation. The relations between the temperature and CO_2 will have an intense effect on global agricultural production and the Earth's environment [73]. The rise in the atmospheric temperature and CO_2 would also accelerate the procedure of growth in plants [58, 74].

Climate change impacts on crop growth are becoming global concerns. They are particularly important for food supply and sustainable agricultural development [75, 76]. CO_2 concentration and temperature are two key factors affecting crop growth, development and yield [77]. Combined or individual possessions of temperature increase and eCO_2 meditation change on crop growth and yield during the recent decades have been observed [78]. For instance, the modeled improvements in soybean absorption of CO_2 with an increase in the growing season temperature, and aCO_2 hindered the photorespiration by 23–48%, which depends on the future climatic conditions [79].

The growth and distribution of crops are reduced by environmental factors like CO_2 and temperature. The production of the biomass of modern C_3 plants was decreased by 50% when it was grown at a low concentration of CO_2 (180–220 ppm), while the other conditions were optimal. Crops need the almost dual amount of water at 2°C increase in temperatures at a higher elevation of agricultural plains. Elevated CO_2 concentration increases the yield of the crop once the substrate for the photosynthesis process of leaf and the incline of CO_2 absorption of air increases. C_3 plants are more benefitted at eCO_2 than C_4 plants [80]. However, the doubling of CO_2 does not deteriorate the adverse effects of high temperature on the reproductive growth of crops or fiber quality. Therefore, increased CO_2 concentration is associated with higher temperatures, crop yield, and quality that reduce particularly in areas where current temperatures are near to optimal [81].

Elevated CO_2 resulted in major changes in morpho-physiological restrictions. Besides, eCO_2 along with atmospheric temperatures during the phenological stages of rice cultivars showed contrasting results of the time of flowering and maturation such as eCO_2 in combination with the lower atmospheric temperature that stopped flowering g in the CR-1014 cultivar while with the higher temperature increased grain yield the in Naveen cultivar [82].

Growth and photosynthesis of C_3 crops are enhanced when it is grown at a high level of CO_2, although, the degree of stimulation differs with temperature among cultivars as well as species. The probable decline in the transpiration process due to the partial closure of stomata in the eCO_2 level is largely invalid by the energy balance between the crop and its environment, which could result in total water use in similar climate conditions. The yield of seeds is increased by an increase in the CO_2 under the ideal temperature. On the other hand, at supra-optimal temperature, the yield of seeds is decreased under both raised and ambient CO_2. The yield of kidney bean decreased in that region where temperatures are at or above optimal conditions in combination with increased CO_2 concentration [83].

The effects of HS on the grain and biomass yield of plants depend on the duration and magnitude of HS. HS at the vegetative phase decreased the grain and biomass yield mostly by increasing plant growth and dropping the time obtainable to capture possessions, and also by dropping the rate of photosynthesis [84]. At the anthesis or flowering phase, HS decreases the amount of grain due to pollen abortion. In contrast, at the grain-filling phase, HS decreases the heaviness of grain by restraining the translocation of integrating, and margarine the period of grain-filling [85, 86].

Notably, eCO_2 may lessen the harmful influence of heat stress on the grain and biomass yield by inspiration of photosynthesis, defense of the photosynthetic devices from HS injury, and improvement in the water status of plants owing to reduced transpiration. Moreover, high levels of hexoses and sucrose in plants with eCO_2 are related to increase fertile florets and dry spike mass [87], and osmotic modification [88], which can develop heat stress tolerance [89]. It is hypothesized that HS at anthesis has a drastic impact on the grain yield and plant biomass, but it has a less impact eCO_2 than ambient CO_2 [90].

6. Conclusion

It is very important to know that the impacts of climate change on crop growth are becoming global concerns. Interactive effects of eCO_2 and environmental stress conditions on crop growth and carbon metabolism are not well predictable. The influence of eCO_2 with the connection of temperature is considerable on crops under stress environments. The CO_2 concentration improves the productivity of crops because of improved carbon exchange rates, and superior vegetative and reproductive growth. In contrast, crop productivity is decreased with increased temperatures. Hence, there is a need to develop genotypes that are different intolerant to various environments or to identify genotypes that perform better under predicted climate change. In this review, cereal genotypes have been characterized by differing responses to eCO_2 and HS and identified the mechanisms of tolerance to HS. It can promote the crop potential to assist the breeding program for the development of new genotypes tolerance to HS.

Conflicts of interest

The authors declare no conflicts of interest.

Disclosure statement

Authors declare that no conflict of interest could arise.

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