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ELEVATED ATMOSPHERIC CO_2 AND CROP NUTRITIONAL QUALITY: MECHANISMS, INTERACTIONS WITH CLIMATE STRESSORS AND IMPLICATIONS FOR GLOBAL FOOD AND NUTRITION SECURITY

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ABSTRACT
Rising atmospheric CO_2 is widely recognized for its potential to enhance crop productivity. However, increasing evidence indicates that elevated CO_2 (eCO_2) can simultaneously reduce the nutritional quality of both staple and horticultural crops, an aspect often overlooked when crop responses are evaluated primarily in terms of yield. This review synthesizes current knowledge on the effects of eCO_2 on crop nutritional composition, with particular emphasis on findings from Free-Air CO_2 Enrichment (FACE) and Open-Top Chamber (OTC) studies. Across diverse crop groups, eCO_2 has been associated with reductions in protein, iron and zinc concentrations, together with alterations in vitamins, carbohydrates, lipids and secondary metabolites. These findings suggest that nutritional changes under eCO_2 are not confined to cereal grains but occur across a wide range of food crops. The review further examines the interactive effects of eCO_2 and other climate-related stressors, including heat, drought, salinity, tropospheric ozone, waterlogging, biotic stresses, UV-B radiation and limitations in nitrogen and phosphorus availability. Such combined stresses can modify, exacerbate or occasionally offset nutritional responses, thereby more closely reflecting the complex environmental conditions crops are likely to experience under future climate scenarios. The implications of these changes for human nutrition and global food security are also discussed. Declining nutrient concentrations under eCO_2 may increase the risk of protein and micronutrient deficiencies, particularly among populations that rely heavily on plant-based staple foods and have limited opportunities for dietary diversification. Overall, the available evidence indicates that nutritional decline under eCO_2 is a direct effect of rising CO_2 rather than merely a secondary consequence of increased biomass production. Therefore, nutritional quality should be incorporated as a core parameter in climate–crop research and evaluated alongside yield performance. Such an approach is essential to ensure that gains in agricultural productivity are not achieved at the expense of food nutritional value and human health.

KEYWORDS: Elevated CO_2, crop nutritional quality, micronutrient deficiency, climate stressor interactions, food and nutrition security

1. INTRODUCTION

Cereal and legume crops remain the primary sources of dietary protein and micronutrients for a large proportion of the global population, particularly in regions where access to diverse diets and animal-based food is limited. More than two billion people are estimated to live with hidden hunger, a state of micronutrient deficiency that persists even when energy intake is sufficient. Part of this burden is traced to breeding and production systems that have rewarded yield far more than nutrient density in staple crops (Yılmaz & Yılmaz, 2025). Under changing atmospheric conditions, agricultural research and policy have largely continued this yield-centred approach, often treating nutritional composition as a secondary consideration. Consequently, a significant gap persists in our understanding of how rising atmospheric CO_2 influences the food system beyond its effects on crop productivity. Evidence accumulated over the past decade suggests that this knowledge gap has important implications for human nutrition and food security. eCO_2 has been shown to reduce the concentrations of protein, iron and zinc in staple crops, thereby diminishing nutritional quality independently of changes in yield (Ujiie et al., 2019). These effects are not limited to cereal crops. Studies on horticultural and fruit crops have reported similar alterations, including increased carbohydrate accumulation accompanied by changes in vitamin and mineral composition, indicating that the nutritional impacts of eCO_2 occur across diverse crop groups rather than being confined to grain physiology (Doddrell et al., 2023). Consequently, several researchers now regard nutrient decline under eCO_2 as a direct effect of rising atmospheric CO_2 rather than merely a secondary consequence of biomass dilution or interactions with other environmental stresses (Ter Haar et al., 2025).

Because staple and horticultural crops constitute major components of human diets and are often difficult to replace in populations that depend predominantly on plant-based foods, reductions in their nutritional quality have consequences that extend beyond agriculture to public health and food security. Modelling studies project that CO_2-induced decreases in the availability of protein, iron and zinc could hinder progress in addressing global malnutrition, even if overall food production continues to increase (Beach et al., 2019). This concern is further amplified by evidence suggesting that anticipated nutritional declines may intensify existing malnutrition burdens and impede progress toward international food and nutrition security targets, including the Sustainable Development Goals (Ekele et al., 2025). Collectively, these findings underscore the need for systematic, dedicated evaluation of nutritional impacts, rather than treating them as an incidental outcome within yield-focused research (Ainsworth et al., 2025).

This imbalance between yield-centred and nutrition-centred assessments carries important implications for further research agendas. Studies reporting crop performance under elevated CO_2 conditions without accompanying nutritional analyses risk providing an incomplete and potentially misleading assessment of future agricultural outcomes. A coordinated research framework that recognizes nutritional composition as a primary outcome, alongside yield, is therefore essential to address this knowledge gap and to guide policies that proactively mitigate nutritional decline rather than merely respond to its consequences (Ebi et al., 2021).

The present review focuses specifically on the nutritional implications of elevated CO_2-induced changes in crop quality, distinguishing itself from previous reviews that primarily emphasize the physiological, biochemical and genetic mechanisms underlying crop responses. It examines the magnitude and consistency of nutrient declines across major crop groups, their implications for human nutrition and food security and the rationale for establishing nutritional quality as a standard reporting metric in climate–crop research, with equal importance accorded to yield.

2. Importance of nutritional quality changes under elevated CO_2

Elevated CO_2 (eCO_2) can reduce the concentrations of important nutrients, particularly protein, iron and zinc, in staple crops, potentially affecting human nutrition, especially in populations that depend heavily on plant-based diets (Ujiie et al., 2019). Alterations in plant stoichiometry under eCO_2 may create an imbalance between carbon assimilation and nutrient uptake, contributing to reductions in crop nutritional quality and potentially affecting the quality of the food supply (Ebi et al., 2021). Elevated atmospheric CO_2 is also associated with dilution of elemental nutrients across major crop species, indicating that increases in food production may not necessarily translate into improved nutritional security. This may increase the risk of micronutrient deficiencies and hidden hunger (Ter Haar et al., 2025).

Future increases in atmospheric CO_2 concentrations are projected to reduce the global availability of key nutrients, particularly protein, iron and zinc, potentially constraining progress in reducing malnutrition despite increases in total food production (Beach et al., 2019). The decline in nutritional value under high CO_2 conditions, particularly through reductions in protein and micronutrient concentrations, highlights the need for comprehensive evaluation of eCO_2 effects on crop quality and long-term nutritional sustainability (Ainsworth et al., 2025). CO_2 enrichment can alter not only macro- and micronutrient concentrations but also crop yield and overall nutritional composition. In some crops, it may increase carbohydrate accumulation while modifying vitamin and mineral profiles, emphasizing the need to assess food quality alongside agricultural productivity (Doddrell et al., 2023).

The marked inter- and intra-specific variability in crop responses to eCO_2, both in the magnitude and direction of nutrient changes, further highlights the importance of systematic characterization of nutritional responses. Such information is essential for developing targeted adaptation strategies to maintain crop nutritional quality under future atmospheric CO_2 scenarios (Garmendia et al., 2022). Overall, increasing atmospheric CO_2 may enhance crop productivity in some cases, but this gain can be accompanied by reductions or alterations in nutritional quality. Therefore, evaluating both yield and nutritional composition is essential for understanding the implications of eCO_2 for food security and human dietary nutrition.

3. Experimental approaches for studying nutritional quality under elevated CO_2

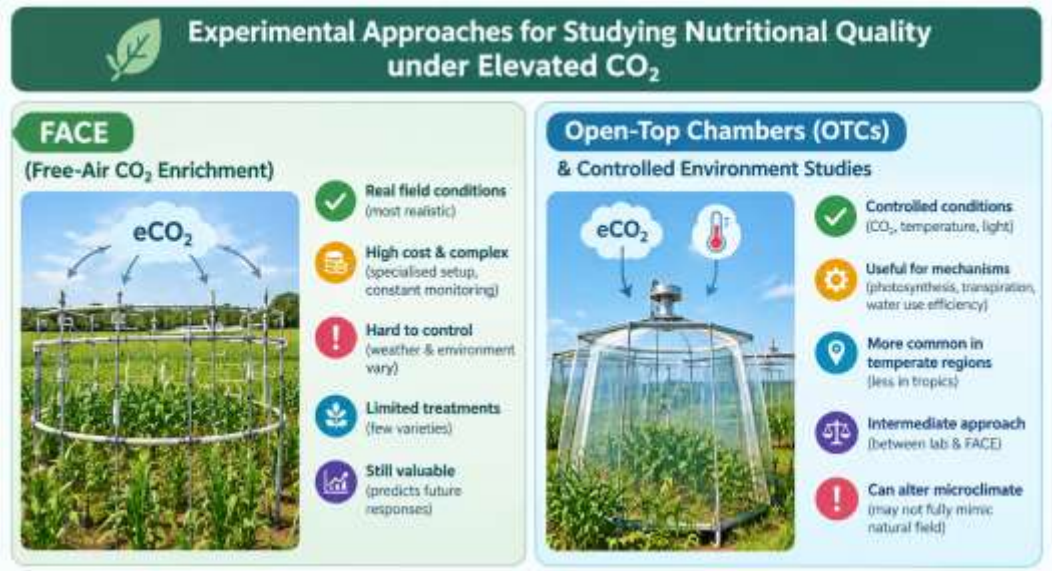


Figure 1. Experimental approaches for studying crop responses to elevated CO_2.

Comparison of free-air CO_2 enrichment (FACE), open-top chamber (OTC)and controlled-environment approaches used to investigate physiological, biochemical and nutritional responses of crops to elevated CO_2 and associated climate variables.

3.1 Free-Air CO_2 Enrichment (FACE) experiments

Free-Air CO_2 Enrichment (FACE) experiments provide a realistic approach for studying crop responses to elevated CO_2 (eCO_2) under near-field conditions (Figure 1). However, their operation is practically demanding and relatively costly. These systems require specialised infrastructure and continuous management to maintain elevated CO_2 concentrations across large agricultural areas. Moreover, natural fluctuations in environmental conditions introduce additional variables, making it difficult to distinguish the direct effects of eCO_2 from those arising through interactions with other environmental stresses (Ekele et al., 2025). Such variability can influence important physiological and biochemical processes, necessitating careful experimental design and rigorous statistical analysis to determine the effects of eCO_2 on crop nutritional quality.

A major limitation of FACE experiments is their operation at a large field scale, which involves high installation and operational costs and restricts the number of treatments or crop varieties that can be evaluated simultaneously (Kahn et al., 2022). Despite these limitations, FACE remains important for generating evidence under realistic field conditions and for improving predictions of crop responses to future atmospheric CO_2 concentrations. Compared with greenhouse and controlled growth chamber studies, FACE experiments provide a more representative assessment of plant and ecosystem responses under naturally fluctuating environmental conditions. Therefore, they are particularly valuable for understanding crop responses to future climate conditions (Knopf et al., 2024).

The practical challenges associated with establishing and maintaining FACE facilities, together with their high operational costs, limit their widespread implementation and the number of research questions that can be addressed (Feng et al., 2023). In addition, variations in pathogen populations and continuous crop improvement may influence the applicability of existing findings, as newly developed cultivars may respond differently to eCO_2 because of changes in plant traits and plant–microbe interactions (Bakker et al., 2023). Climate context also matters: over six decades, warming and drought in the world's top wheat-producing countries offset much of the yield benefit expected from rising CO_2 (Helman & Bonfil, 2022), so results from FACE sites in one climate may not transfer to others. Thus, although FACE experiments offer highly realistic conditions for evaluating crop responses to eCO_2, their high installation and maintenance costs and experimental complexity remain important limitations.

3.2 Open-Top Chambers (OTCs) and controlled environment studies

OTCs are widely used to study the effects of climate change on plants, with CO_2 the most frequently manipulated factor, followed by ozone and temperature (de Alencar et al., 2024). By providing a partially controlled field environment, OTCs allow the effects of elevated CO_2 on physiology and nutrient composition to be examined. In spinach grown in OTCs at 400 and 600 μmol mol^{-1}, elevated CO_2 raised photosynthetic rate, lowered stomatal conductance and transpiration, and reduced root and leaf macro- and micronutrient concentrations (Ahmad et al., 2024). OTC-based studies are more commonly conducted in temperate regions than in tropical regions, despite the potentially greater impacts of climate change in tropical areas, partly because of the practical challenges associated with their implementation (de Alencar et al., 2024).

In agricultural research, OTCs have been used to evaluate the effects of elevated CO_2 on crop performance (Ahmad et al., 2024). For example, OTCs have been used to assess changes in photosynthesis and growth under in situ warming conditions in desert species, particularly during the transition from wet to dry periods (Lin et al., 2024).

The ability to regulate environmental conditions within OTCs is particularly useful for understanding plant water-use efficiency because photosynthesis, transpiration and stomatal conductance are closely interconnected under changing climatic conditions (Pernicová et al., 2024; Wang et al., 2026b). Gas-exchange measurements conducted within these chambers enable researchers to examine the movement of carbon and water through leaves, providing important information on plant physiological responses and their implications at the ecosystem level (Busch et al., 2024). By regulating CO_2 concentration and temperature, researchers can investigate how plants adjust their physiological processes under environmental stress, thereby improving the understanding of plant resilience under future climatic conditions (Kiongo et al., 2025).

Plants adjust photosynthetic capacity to prevailing growth temperature over weeks to months, and this acclimation has been detected at canopy scale across more than 200 eddy-covariance sites (Liu et al., 2024). Experiments that sustain elevated temperature and CO_2 over long periods, such as OTC studies, are therefore needed to capture it. However, although OTCs provide greater environmental control than open-field experiments, the chamber structure itself can alter microclimatic conditions and therefore may not completely reproduce natural field conditions. Hence, OTC studies provide a useful intermediate approach between highly controlled growth chambers and large-scale FACE experiments, but their results should be interpreted considering the differences between chamber and natural field environments.

4. Impacts of eCO_2 on nutritional quality

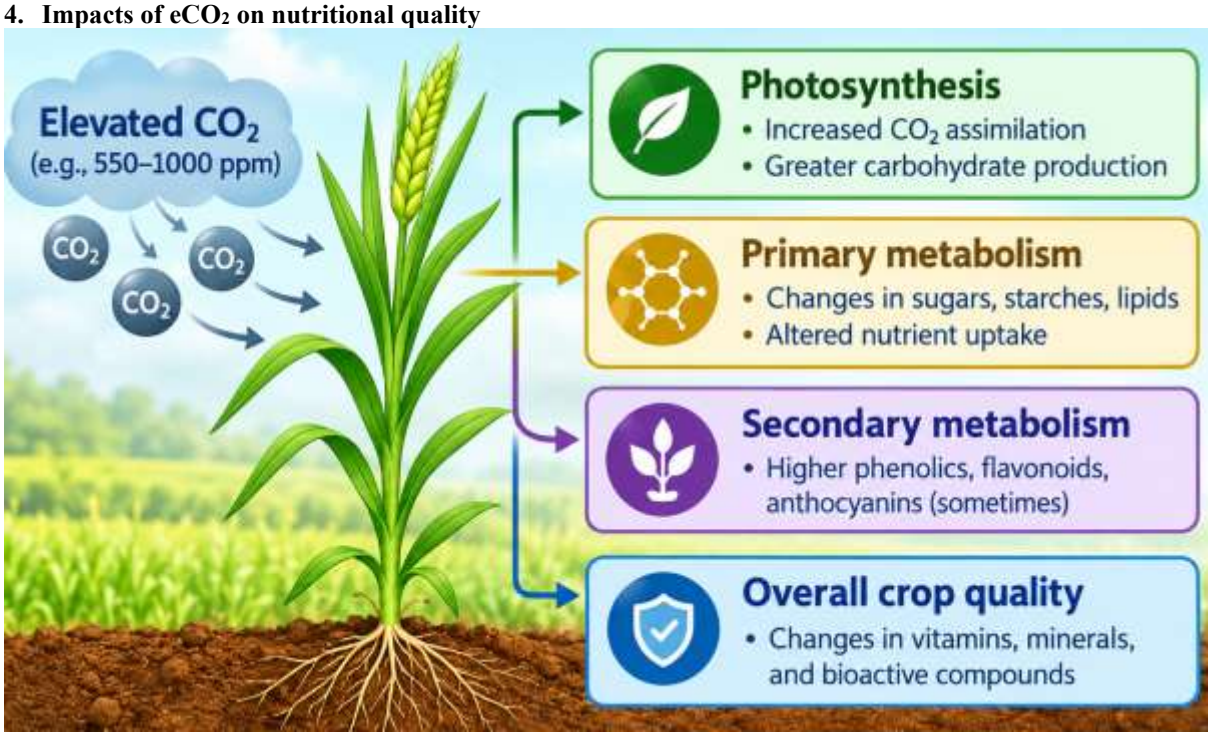


Figure 2. Overview of the effects of elevated CO_2 on crop nutritional quality.

Elevated CO_2 influences photosynthesis, primary and secondary metabolism, nutrient acquisition and the accumulation of nutritional and bioactive compounds, thereby altering overall crop quality.

Elevated CO_2 reduces protein, iron and zinc concentrations across the major staple crops (Figure 2). Al-Hadeethi et al. (2019) pooled 542 observations from 135 studies and reported lower protein, Zn and Fe in wheat, rice, field peas and corn (Zn and Fe reductions of about 3–12%), with soybean the exception (Table 1). A rice systematic review described a later-consensus pattern of declining Fe and Zn despite earlier contradictory results (Chumley & Hewlings, 2020). A FACE-based dataset spanning seven global sites reached the same conclusion for C_3 crops broadly, with mid-century CO_2 concentrations lowering zinc and iron in the edible portion (Myers et al., 2014). In soybean, temperature modified the response. In a two-season T-FACE experiment, elevated CO_2 lowered seed Fe by 8.7% and 7.7% and, in one season, seed Zn by 8.9%, but combining CO_2 enrichment with warming largely restored both to ambient levels (Köhler et al., 2019). In a meta-analysis of 57 articles on vegetables, only Fe, Zn and Mg declined, Ca rose, and P, K, S, Cu and Mn were unchanged (Dong et al., 2018; Table 1).

Table 1. Mineral nutrient responses to elevated CO_2

Crop	Parameter	Change	Source
Wheat, rice, field peas, corn	Fe, Zn	Decline ~3–12% (soybean: no significant decline)	Al-Hadeethi et al., 2019
Rice	Fe, Zn	Declining (later-consensus pattern)	Chumley & Hewlings, 2020
C3 crops	Fe, Zn	Lowered at mid-century CO_2	Myers et al., 2014

Soybean	Fe	−8.7% and −7.7% across two seasons	Köhler et al., 2019
Soybean	Zn	−8.9% (one season; reversed by higher temperature)	Köhler et al., 2019
Vegetables	Fe, Zn, Mg, Ca	Fe −16%, Zn −9.4%, Mg −9.2%, Ca +8.2%; P, K, S, Cu, Mn unaffected	Dong et al., 2018
Wheat	Xylem sap Ca, Mg	Reduced, alongside transpiration flow	Houshmandfar et al., 2015
Wheat	K, Ca, Mg	Declined across leaves, stems, roots, grain (yield improved)	Li et al., 2016
Wheat–field pea–canola	N, P, Zn	−6%, −5%, −10% respectively	Jin et al., 2019
Wheat	N, Fe, S, Zn, Mg	Largest reductions of all minerals tested (range: no change to strong negative)	Broberg et al., 2017

Wheat's mineral response has been traced partly to xylem transport. Elevated CO_2 reduced both transpiration flow and the calcium and magnesium concentrations of the xylem sap in combined glasshouse and FACE experiments, with the authors noting that this points to a mechanism beyond reduced transpiration-driven mass flow alone (Houshmandfar et al., 2015). A companion study adding soil warming (+2.4 °C) to CO_2 elevation (700 µmol l^{-1}) found that grain yield improved while K, Ca and Mg accumulation and concentration declined across leaves, stems, roots and grain, attributed to lowered uptake via both decreased stomatal conductance and reduced xylem-sap mineral concentration (Li et al., 2016). A seven-year FACE rotation of wheat, field pea and canola across three contrasting soils found N, P and Zn concentrations reduced by 6%, 5% and 10% respectively, irrespective of soil, crop and year, with the N decline greater in canola and wheat than in field pea and with elevated CO_2 lowering grain nutritional value more in fertile than in infertile soils (Jin et al., 2019). A meta-analysis and response-function synthesis across the wheat literature found mineral responses ranging from no measurable change to strong negative effects, with the largest reductions in N, Fe, S, Zn and Mg and concluded that the spread of responses cannot be explained by a simple dilution model (Broberg et al., 2017). Mechanistically, reduced transpiration under elevated CO_2 appears to restrict mass flow of minerals from the roots, and CO_2-driven shifts in metabolite and enzyme concentrations may independently alter plant requirements for minerals used as protein cofactors (McGrath & Lobell, 2013).

Vitamin responses are less uniform. Ascorbic acid climbed 9.5% in the aggregate vegetable dataset, though the magnitude shifted with species, cultivar and growing conditions (Dong et al., 2018) and reviews of greenhouse fruit crops point to possible gains in vitamins C and E and pro-vitamin A alongside yield increases of up to 80% in tomato at 1000 ppm, though not consistently enough to state as a rule (Doddrell et al., 2023). Rice is the one crop with substantial B-vitamin data and the picture there is not encouraging: across 18 rice lines at two FACE sites in China and Japan (568–590 ppm), vitamin B1 fell 17.1%, B2 16.6%, B5 12.7% and B9 30.3%, with protein falling 10.3%, iron 8% and zinc 5.1%; vitamin B6 was unaffected and vitamin E rose in most lines, a split the authors linked to the nitrogen content of the molecules themselves (Zhu et al., 2018; Table 2). Whether comparable patterns hold for fruits or vegetables remains unknown, as no equivalent dataset exists.

Table 2. Vitamin responses to elevated CO_2

Crop	Parameter	Change	Source
Vegetables	Ascorbic acid	+9.5% (magnitude varies by species/cultivar)	Dong et al., 2018
Greenhouse fruit crops	Vitamin C, E, pro-vitamin A	Possible gains, not consistent; yield up to +80% in tomato at 1000 ppm	Doddrell et al., 2023
Rice	B1, B2, B5, B9	−17.1%, −16.6%, −12.7%, −30.3% respectively	Zhu et al., 2018
Rice	B6, E	B6 unaffected; E rose in most lines	Zhu et al., 2018
Rice	Protein, Fe, Zn	−10.3%, −8%, −5.1% respectively	Zhu et al., 2018
Sour orange	Ascorbic acid (juice)	+7% at 700 ppm vs. 400 ppm CO_2, OTC, 8-year trial	Idso et al., 2002
Barley	Ascorbic acid, glutathione	Declined in primary leaves under elevated CO_2	Robinson & Sicher, 2004
Lettuce	Vitamin C	Increased across three cultivars alongside chlorophyll; nitrate declined	Song et al., 2023
Carrot	Carotenoids (pro-vitamin A)	Increased; linked to upregulation of carotenoid biosynthesis genes	Song et al., 2021
Wheat	Multiple B-vitamins, minerals	Diminished under projected future climate (CO_2 + temperature + precipitation gradients, Ecotron study)	Cao et al., 2026

Carbohydrates generally move in the opposite direction to most other nutrients, though grain-level outcomes are messier than leaf-level ones. In rice grown season-long across 160–900 µmol CO_2 mol^{-1}, leaf sucrose and starch

concentrations rose with CO_2 during vegetative growth but tended to level off at higher concentrations, with the priority between carbon storage and export shifting with developmental stage (Rowland-Bamford et al., 1990). Field-grown wheat at elevated CO_2 likewise showed increased carbohydrate accumulation, accompanied by decreased transcript levels for photosynthetic genes (Nie et al., 1995). A three-year wheat FACE experiment found grain fructose concentration significantly increased with a positive trend for fructan. On a per-area basis, total and individual non-structural carbohydrates increased with the single exception of starch, while grain protein fell 7.4% and grain size distribution shifted toward smaller grains (Högy et al., 2009; Table 3).

Table 3. Carbohydrate and lipid responses to elevated CO_2

Crop	Parameter	Change	Source
Rice	Leaf sucrose, starch	Rose with CO_2; levelled off at higher concentrations	Rowland-Bamford et al., 1990
Wheat	Carbohydrate accumulation	Increased, with decreased photosynthetic gene transcripts	Nie et al., 1995
Wheat	Grain fructose, fructan, starch, protein	Fructose significantly increased, fructan positive trend, starch the sole NSC exception; protein −7.4%	Högy et al., 2009
Potato	Glucose, fructose, reducing carbohydrates, protein, K, Ca	Sugars increased (raising browning/acrylamide risk); protein and K declined, Ca trended down; dry matter and starch viscosity rose	Högy & Fangmeier, 2009
Soybean, 4-yr OTC, 2 cultivars	Seed yield, seed oil yield, crude oil content, SFA/UFA	Seed yield +18–54% (mean 31%); seed oil yield +32% on average — driven by the yield increase, not by higher oil concentration (crude oil content itself did not respond consistently); SFA declined, UFA/SFA ratio +1.9–6.0%	Wang et al., 2026a
Soybean, 13 genotypes, FACE	Soluble sugars, starch, phytic acid, protein	Sugars +9.1%, starch +16.0%, phytic acid +8.1%; protein −5.6%; strong genotype-dependent variation	Soares et al., 2021
Soybean, 4 cultivars	Crude oil, oleic, linoleic acid	Crude oil increased at maturity; oleic acid rose; linoleic acid cultivar-dependent	Li et al., 2018
Soybean	Oleic acid	More strongly regulated by temperature than by CO_2 alone	Thomas et al., 2003
Rapeseed	α-linolenic acid (ω-3), oil content	−45% and −10% respectively under CO_2 + temperature; oil yield loss −58%, ω-3 loss −77% (biomass-adjusted)	Namazkar et al., 2016

Fats show a fairly consistent qualitative shift toward less saturation and more unsaturation, even where the quantitative picture stays murky. Soybean data are split: a four-year open-top-chamber experiment on two cultivars found seed yield up 18–54% (mean 31%) and seed oil yield up an average 32%, while crude oil content did not respond consistently; saturated fatty acids generally declined and the UFA/SFA ratio rose significantly in every cultivar–year combination (1.9–6.0%), though the oleic/linoleic and ω-6/ω-3 ratios varied substantially by cultivar and year (Wang et al., 2026a). An earlier study found crude oil concentration increasing at maturity across four cultivars, with oleic acid rising and linoleic acid responding in a cultivar-dependent manner (Li et al., 2018), while a third experiment concluded that oleic acid is more strongly regulated by temperature than by CO_2 alone (Thomas et al., 2003). Mung bean moved in a nutritionally favourable direction, with palmitic and ω-6 fatty acid percentages falling and ω-3 percentage and the ω-3:ω-6 ratio rising in mature seed (Ziska et al., 2007). Rapeseed was the clearest exception to the generally mild picture: across five future-climate scenarios, oil content and quality were significantly reduced except under elevated CO_2 alone and combining elevated CO_2 with higher temperature cut α-linolenic acid (ω-3) by 45% and oil content by 10%, with estimated per-hectare losses of 58% for oil yield and 77% for ω-3 once seed biomass reductions were factored in (Namazkar et al., 2016).

Antioxidant compounds are where elevated CO_2's effects look most consistently positive. Total antioxidant capacity showed the largest gain in the Dong et al. (2018) vegetable dataset (+59.0%), followed by flavonoids (+45.5%) and total phenols (+8.9%), while anthocyanins were unchanged. Field and controlled-environment trials support this directly: strawberries grown at 300 and 600 μmol mol^{-1} above ambient gained ascorbic acid and glutathione, showed higher ratios of reduced to oxidised forms of both and accumulated anthocyanins, phenolics and specific flavonols, with elevated oxygen-radical absorbance across multiple reactive species (Wang et al., 2003). Two Malaysian young ginger varieties showed increases in flavonoids and phenolic acids when CO_2 was raised from 400 to 800 μmol mol^{-1}, with the response stronger in rhizomes than in leaves (Ghasemzadeh et al., 2010). Red-pigmented lettuce accumulated cyanidin, chlorogenic acid, conjugated caffeic and ferulic acids, quercetin and its glycosides, rutin, quercitrin and kaempferol under 700 ppm CO_2, maintaining higher antioxidant capacity than the green cultivar under all conditions tested (Sgherri et al., 2017).

Bioavailability adds a further layer of complexity in rice. Iron bioavailability in brown rice fell 22% under elevated CO_2, while calcium bioavailability rose 5–11% in the bran and husk fractions; phytic acid concentration and zinc bioavailability were unaffected and essential amino acids declined substantially — isoleucine by 40% in white rice, tyrosine by 57% in brown rice and phenylalanine by 23% in bran (Goufo et al., 2014). Loladze's (2014) analysis of 7,761 observations across 130 species placed the average decline at roughly 8% across the full set of minerals examined.

Nitrate showed the largest decline of any parameter in the Dong et al. (2018) vegetable dataset (−18.0%), followed by Fe (−16.0%), with protein at −9.5%. Kansas State trials on leafy greens found nitrogen loss especially pronounced in lettuce, where shoot nitrogen was reduced by more than 30% under elevated CO_2 alongside declines in potassium, phosphorus, sulfur, zinc, copper and magnesium, while total phenolics and antioxidant capacity rose in lettuce but were unaffected in spinach (Giri et al., 2016). A synthesis spanning 13 studies and 339 effect sizes confirmed protein declines in both spinach and kale, hitting spinach harder (Ekele et al., 2026). Arugula broke from this pattern: photosynthetic CO_2 assimilation increased at 800 versus 400 ppm regardless of nitrogen form, but nitrate assimilation and biomass were unaffected, with the extra photosynthate going to leaf structural compounds rather than antioxidants — increasing dry mass and diluting several mineral elements (Schmidt & Zinkernagel, 2021). Nitrogen responses are not fixed either. In Chinese cabbage, temperature determined both the size and the direction of the effects of elevated CO_2 and nitrogen form on yield and quality (Reich et al., 2016; Table 4).

Table 4. Secondary metabolites, antioxidants, amino acids and other quality responses to elevated CO_2

Crop	Parameter	Change	Source
Vegetables	Flavonoids, antioxidant capacity, phenols, anthocyanins	+45.5%, +59.0%, +8.9%; anthocyanins unchanged	Dong et al., 2018
Strawberry	Ascorbic acid, glutathione, anthocyanins, phenolics, flavonols	All increased; higher reduced:oxidised ratios	Wang et al., 2003
Ginger	Flavonoids, phenolic acids	Increased; stronger in rhizome than leaf	Ghasemzadeh et al., 2010
Red-pigmented lettuce	Cyanidin, chlorogenic/caffeic/ferulic acids, quercetin, rutin, kaempferol	Accumulated; antioxidant capacity higher than green cultivar	Sgherri et al., 2017
Brown rice	Fe bioavailability, Ca bioavailability	−22%; +5–11% (bran/husk); phytic acid, Zn bioavailability unaffected	Goufo et al., 2014
Rice	Isoleucine, tyrosine, phenylalanine	−40% (white rice), −57% (brown rice), −23% (bran)	Goufo et al., 2014
Multiple species (130)	Average mineral decline	~8% across all minerals examined	Loladze, 2014
Vegetables	Nitrate, protein	−18.0% (largest decline recorded), −9.5%	Dong et al., 2018
Lettuce	Shoot N, K, P, S, Zn, Cu, Mg	N reduced >30%; all others also declined; phenolics/antioxidant capacity rose in lettuce only	Giri et al., 2016
Spinach, kale	Protein	Declined in both; spinach hit harder	Ekele et al., 2026
Arugula	Photosynthetic CO_2 assimilation, nitrate assimilation, biomass, minerals	Assimilation increased; nitrate assimilation and biomass unaffected; dry mass increased, several minerals diluted	Schmidt & Zinkernagel, 2021
Chinese cabbage	Yield and quality effects	Size and direction determined by temperature	Reich et al., 2016

5. Interactive effects of elevated CO_2 with other climate stressors

5.1 Elevated CO_2 × Heat Stress

Elevated CO_2 often protects photosynthesis and promotes stomatal closure during heat stress, but the benefit is strongly dependent on species, growth temperature and acclimation. In tomato, elevated CO_2 increased P_n, Vcmax, Jmax and PSII efficiency under severe heat, while reducing photoinhibition, reactive oxygen species and redox imbalance (Pan et al., 2018). In wheat, it maintained photosynthesis and PSII efficiency during heat or combined drought–heat stress, although heat eliminated the grain-yield benefit of elevated CO_2 even while physiological and biomass benefits persisted (Abdelhakim et al., 2022; Chavan et al., 2019). Elevated CO_2 generally reduced

stomatal conductance; in tomato, RBOH1-dependent H_2O_2 signaling narrowed stomatal apertures, improving water retention and water-use efficiency (Zhang et al., 2018a; Ainsworth & Rogers, 2007). However, evidence is mixed: acute-heat experiments found improved photosynthetic thermotolerance in C_3 species but reduced tolerance in C_4 and some CAM species (Hamilton et al., 2008; Wang et al., 2008). Post-anthesis heat also weakened CO_2's protective effect in wheat, largely erasing the physiological, biomass and yield gains seen without heat stress (Zhang et al., 2018b).

5.2 Elevated CO_2 × Drought

Elevated CO_2 generally increases plant water-use efficiency and can improve drought water status, but its effect on osmotic adjustment is inconsistent. A 54-study meta-analysis found elevated CO_2 increased leaf-level WUE by 29.3% under well-watered conditions, while under drought it slightly reduced photosynthesis by 8.3% (Li et al., 2021). Controlled studies found higher WUE under elevated CO_2 in peach (51% well-watered, 63% under stress) with no CO_2–drought interaction on biomass (Centritto, 2002) and in sunflower (230% and 380% increases) without preventing drought-related metabolic limitations (Tezara et al., 2002). Evidence for osmotic adjustment is mixed: enhanced in wheat, alongside improved drought avoidance and tolerance mechanisms (Wall et al., 2006); a broader review flags plant water relations under elevated CO_2 as an area of continuing uncertainty (Wullschleger et al., 2002).

5.3 Elevated CO_2 × Salinity Stress

Elevated CO_2 generally improves salinity tolerance through strengthened osmotic adjustment and antioxidant protection, but responses are species- and genotype-dependent. In Aster tripolium, elevated CO_2 enhanced salinity tolerance via increased photosynthesis, water-use efficiency and investment in compatible solutes and protective proteins, though this was not converted into extra biomass (Geissler et al., 2010). In barley, elevated CO_2 shifted the relative contributions of osmolyte accumulation versus cell wall elasticity to salt tolerance (Pérez-López et al., 2010). In Miscanthus, elevated CO_2 reduced Na^+ concentration and favored Na^+: K^+ maintenance, genotype-dependently (Liang et al., 2022). Tomato tissue Na^+ and Na^+: K^+ still rose under salinity even with elevated CO_2, though elevated CO_2 eased growth inhibition via increased photosynthesis and altered primary metabolism (Brito, 2020); a review emphasizes species/cultivar dependence generally (Pérez-López et al., 2012).

5.4 Elevated CO_2 × Tropospheric Ozone

Elevated CO_2 can offset ozone's damage to photosynthesis and biomass, but protection is incomplete and context-dependent. Field-grown wheat showed CO_2 protection through reduced ozone uptake and compensatory photosynthetic substrate (McKee et al., 2000). Across six perennial species spanning C_3 and C_4 photosynthetic pathways, elevated CO_2 eliminated ozone-induced reductions in photosynthesis and relative growth rate (Volin et al., 1998) and ameliorated ozone's negative effects on soybean biomass and development (Miller et al., 1998). Evidence is not uniform: ozone substantially reduced forest net primary production's responsiveness to elevated CO_2 in young aspen, birch and maple stands (King et al., 2005) and elevated CO_2 failed to ameliorate ozone's effects on carbon allocation in pine and birch grown in symbiosis with a mycorrhizal fungus (Kytöviita et al., 1999).

5.5 Elevated CO_2 × Waterlogging Stress

Elevated CO_2 does not uniformly offset waterlogging. Waterlogging forces roots to switch from respiration to low-yield alcoholic fermentation and plants compensate either by cutting energy-dependent processes like root growth and nutrient uptake or by consuming more carbohydrate per unit time (Kreuzwieser et al., 2004; Bailey-Serres & Colmer, 2014; Kreuzwieser & Rennenberg, 2014). In wheat, elevated root-zone CO_2 under hypoxia alleviated photosynthetic and chlorophyll declines in the waterlogging-tolerant genotype (Savannah) but not the sensitive genotype (Bayles); elevated CO_2 alone reduced root growth in both (Huang et al., 1997). In poplar, low oxygen and high CO_2 reduced root water flux non-additively (Smit & Stachowiak, 1988). Elevated CO_2 combined with microbial inoculation mitigated soybean waterlogging effects, though broader evidence remains limited (Shimoia et al., 2024).

5.6 Elevated CO_2 × Biotic Stress

Elevated CO_2 alters resistance/susceptibility to biotic stress in highly context-specific ways. High CO_2 primed SA-linked defenses and increased Arabidopsis resistance to bacterial and fungal challenge, an effect linked to redox signaling rather than stomatal closure (Mhamdi & Noctor, 2016), while elsewhere elevated CO_2 increased pathogen aggressiveness — twice-ambient CO_2 increased anthracnose fecundity over repeated infection cycles (Chakraborty & Datta, 2003; Pangga et al., 2011) and produced host morphological changes favoring infection (Lake & Wade, 2009). In soybean at 550 vs 419 ppm, plants were less susceptible to Pseudomonas syringae, more susceptible to two viruses and a fungus and unchanged toward an oomycete (Bredow et al., 2025). Reviews report broadly variable, patho system-specific outcomes: altered hormone signaling with conflicting fungal-immunity effects (Kazan, 2018); a survey of phytohormone-mediated resistance in C_3 crops finding elevated CO_2 typically raises constitutive/induced salicylic acid while suppressing jasmonate (Bazinet et al., 2022); a dedicated review of eCO_2 and fungal pathogen immunity concluding effects are pathosystem-specific with no universal direction predictable (Smith & Luna, 2023); and a review of insect–plant–pathogen interactions under future climate (Trębicki et al., 2017).

5.7 Elevated CO_2 × UV-B Radiation

Elevated CO_2 and UV-B jointly increase secondary-metabolite investment, but CO_2 can moderate UV-B-induced flavonoid production while enhancing tannins. In silver birch, UV-B increased phenolics and PAL activity;

elevated CO_2 increased enzyme activities and tannins under UV-B while dampening the flavonoid response (Lavola et al., 2000). Reviews support CO_2/UV enhancement of phenolic compounds generally, while noting effects are species- and chemical-type-specific (Bidart-Bouzat & Imeh-Nathaniel, 2008; Qaderi et al., 2023).

5.8 Elevated CO_2 Under Combined Heat and Drought

Elevated CO_2 generally mitigates physiological and yield losses under combined heat and drought, but it does not reliably prevent reproductive or final-yield losses. In wheat, elevated CO_2 increased grain yield by 20.8%, while post-anthesis heat and drought reduced yield by 21.3–65.2% (Li et al., 2019). Another wheat study found improved water-use efficiency and physiology but no improvement in final yield under combined stress during anthesis (Abdelhakim et al., 2022). Elevated CO_2 improved photosynthesis and reduced oxidative damage in Arabidopsis (Zinta et al., 2014) and alleviated reversible photosynthetic damage in tomato, though growth benefits were inconsistent (Zhou et al., 2020).

5.9 Elevated CO_2 Under Nitrogen and Phosphorus Limitation

Elevated CO_2 can stimulate growth, but nutrient limitation constrains this and reduces nutritional quality. A 46-study meta-analysis found CO_2 enrichment lowers plant N more than P, significantly reducing the N:P ratio. Nitrogen addition increases P uptake under elevated CO_2, but P addition does not affect N (Huang et al., 2015). In soybean, the degree of CO_2-driven biomass stimulation depended on the severity of phosphorus deficiency and was essentially eliminated under the most severe P stress (Singh et al., 2014). Earlier controlled-environment work found CO_2 enrichment increased growth and seed yield of non-nodulated soybean even under substantial nitrogen or phosphorus limitation, though the very lowest nutrient levels blunted the response (Cure et al., 1988a, 1988b). Low nitrogen intensifies photosynthetic acclimation to elevated CO_2 (Stitt & Krapp, 1999). In vegetables, a meta-analysis found elevated CO_2 increased sugars but decreased protein, nitrate, iron, zinc and magnesium (Dong et al., 2018).

5.10 Multi-Factor Stress Combinations

Multi-factor stress reduces crop productivity more severely and less predictably than single stressors. CO_2 fertilization does not reliably offset combined heat and drought, and salinity can intensify damage. In rice and maize, four- and five-stress combinations reduced seedling survival to ~75% and ~60% (Sinha et al., 2023; Swentowsky, 2023). Arabidopsis showed stronger impairment under combinations, particularly with salinity (Secomandi et al., 2025). Tomato heat–salinity co-exposure impaired growth more than either stress alone (Rodrigues et al., 2023). A recent review examines combined abiotic stress complexity broadly (Khan et al., 2025). Field-scale evidence for the full CO_2 × heat × drought × salinity combination remains insufficient.

6. Implications of elevated CO_2 induced nutritional changes for human health and food security

Elevated atmospheric CO2 exerts a measurable effect on the nutritional composition of crops, with direct implications for human health and food security. Staple crops grown under elevated CO2 show a significant decrease in the concentrations of protein, iron and zinc, even where biomass accumulation increases (Ujiie et al., 2019). This pattern reflects a broader decoupling of yield from nutritional value: increases in food production under a higher-CO2 atmosphere do not necessarily translate into improved nutritional security and in several documented cases actively work against it (Ter Haar et al., 2025). As these nutrients play a central role in dietary nutrient uptake, their reduction contributes to worldwide micronutrient deficiency, particularly among populations that depend largely on plant-based diets (Yılmaz & Yılmaz, 2025).

This effect is not confined to staple cereals. Vegetable and fruit crops grown under elevated CO2 also show increased soluble sugar content alongside altered vitamin and mineral profiles, indicating that the decline in nutritional quality extends across crop types rather than being limited to grain-bearing species (Doddrell et al., 2023). Particularly in low- and middle-income countries, where dietary diversity is often constrained and staple crops make up a disproportionate share of caloric and nutrient intake, these shifts in crop nutritional quality increase the risk of undernutrition and interrupt progress toward international food and nutrition security targets, including the Sustainable Development Goals (Ekele et al., 2025).

The scale of this challenge has prompted calls for a dedicated research and technology agenda addressing crop nutritional quality under rising CO2, rather than treating it as a secondary outcome of yield-focused breeding and agronomy (Ebi et al., 2021). This is reinforced by the broader observation that the relationship between rising CO2 and crop performance is not uniformly beneficial: while elevated CO2 can support productivity gains in some contexts, its effect on nutritional composition raises the question of whether current cropping systems are, on balance, adequately positioned to meet future nutritional demand under a changing atmosphere (Ainsworth et al., 2025).

7. Conclusion

Rising atmospheric CO_2 concentrations exert a measurable and systematic influence on the nutritional composition of staple and horticultural crops, reducing concentrations of protein, iron and zinc independently of concurrent gains in yield. This decline is not merely a by-product of increased agricultural productivity; but a distinct consequence of elevated CO_2, compounding the already substantial global burden of micronutrient deficiencies. The implications extend far beyond agricultural production. Continued reductions in protein and micronutrient availability threaten to impede progress in addressing malnutrition, even as overall food production increases, thereby placing additional pressure on efforts to achieve international food security goals. Populations

that rely heavily on plant-based staple foods and that have limited capacity to compensate for nutrient losses through dietary diversification, are likely to be disproportionately affected. Consequently, food security strategies focused primarily on production volume may be insufficient to address this emerging quality-driven dimension of food insecurity.

These findings have important implications for future research and policy. Crop improvement programmes and climate adaptation strategies that prioritize yield alone risk creating food systems that appear resilient by conventional measures while gradually eroding the nutritional value of the food they produce. Addressing this challenge requires sustained, interdisciplinary collaboration among crop physiologists, nutrition scientists, agronomists and policy makers, rather than treating nutritional outcomes as a secondary consideration. Nutritional quality must therefore be incorporated as a standard reporting metric in climate-crop research and evaluated with the same rigor as yield. Continued reliance on production based indicators alone risks overstating the resilience of agricultural systems to rising CO_2 concentrations while underestimating their consequences for human nutrition. Closing this knowledge gap is essential to ensuring that future food systems remain not only productive, but also nutritionally secure under a changing atmospheric environment.

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