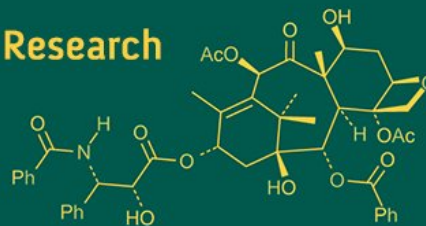


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Stress biology of crops under elevated CO₂ and warming: Implications for productivity and resilience

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Abstract

Climate change brings two forces that shape how crops grow, yield, and feed people: rising CO₂ in the atmosphere and rising temperatures. On its own, extra CO₂ tends to help plants. It speeds up photosynthesis, adds biomass, and lets crops use water more efficiently, an effect most visible in C₃ species like wheat and rice, since they fix carbon more effectively and partially close their stomata, cutting water loss. Canopies fill out, leaves grow larger, and flowering gets pushed back slightly. Heat works against this. Once temperatures climb too high, plants rush through their growth stages, the grain-filling period shrinks, and core physiological processes break down. Reproductive growth takes the hardest hit, with fewer fertile spikelets, fewer grains, and lower yield overall. Combine rising CO₂ with heat stress and the outcome is not simply additive; the two interact in complicated ways, and heat usually cancels out much of what CO₂ would have gained alone. So, yields still tend to fall even when CO₂ alone should have helped. Grain quality suffers too, since higher CO₂ often dilutes protein and micronutrients like iron and zinc, a real concern for nutrition, not just total harvest. Crops don't respond the same way, either. C₃ plants are more sensitive to CO₂ than C₄ plants such as maize, largely because of how they photosynthesize. Nitrogen availability shifts things further, since plants lacking nitrogen cannot fully capitalize on extra CO₂. No single fix solves this. Better nutrient management helps. So does breeding cultivars built to withstand heat. What it takes is treating environment, physiology, and field management as one system if crop productivity and food security are going to hold up as the climate keeps changing.

Keywords: Elevated CO₂, Heat stress, Crop productivity, Crop resilience, Photosynthesis, Grain quality

Introduction

Carbon dioxide is a greenhouse gas that helps regulate Earth's temperature and drives essential biological processes like photosynthesis and respiration in plants. Over the last 150 years, atmospheric CO₂ concentrations have climbed from roughly 280 to about 416 ppm, mostly because of industrialisation and fossil fuel burning. That rise has strengthened radiative forcing in the atmosphere and pushed climate change forward, which is why cutting CO₂ emissions matters so much for limiting human driven climate impacts going forward (Kuttippurath *et al.*, 2022) ^[1]. Between 2015 and 2024, global average surface temperatures rose about 1.24 °C above pre industrial levels, driven largely by human activity; the pace has picked up alongside intensified agricultural practices, and the increase traces mainly back to high greenhouse gas emissions, so where things go from here will depend on how well those emissions get managed in the coming decades (Forster *et al.*, 2025) ^[2]. As a result, crop productivity and overall farm output face growing risk from climate factors such as rising heat, shifting rainfall patterns and higher CO₂ levels. Current projections put CO₂ somewhere between 550 and 700 ppm by 2050, with global temperatures potentially climbing another 2 to 4 % by the end of the century. Temperatures and CO₂ together shape how crops grow, develop, and ultimately yield. C₃ plants, for instance, can lose up to half their biomass when exposed to low CO₂ conditions of around 180 to 220 ppm (Sabagh *et al.*, 2020) ^[3]. Under elevated CO₂ on the other hand, crops usually respond fairly well, though exactly how much depends on the experimental setup being used. Rice tends to respond more strongly in glasshouse settings than under FACE or OTC methods. Soybean, also a C₃ crop, grains around 40 % in yield under FACE conditions, while wheat grains roughly 47 % under OTC conditions instead (Ziska *et al.* 2007) ^[4].

Elevated CO₂ generally boosts yield related traits across crops, but again, temperature and exposure length both change the outcome considerably. Under normal temperatures, elevated CO₂ raises spikelet density and lifts yield by about 16.2 %; under high heat, that same gain drops to around 10.1%. At normal temperatures, elevated CO₂ clearly improves rice yield, but rising heat flips that effect into a negative one. Higher temperatures cut into spikelet number and shorten the grain filling window. So, when CO₂ and heat rise together, their effects largely cancel each other out, leaving yield roughly unchanged overall (Hu *et al.*, 2021) ^[5]. On the greenhouse gas side, methane (CH₄) and nitrous oxide (N₂O) emissions tend to rise during short term exposure to elevated CO₂ meaning under five years, but that pattern reverse once exposure runs past ten years (Yu *et al.*, 2022) ^[6]. Plants grown under elevated CO₂ also tend to grow more overall, showing more root and shoot biomass, taller stems, more tillers per plant and a noticeably larger leaf area than plants grown under normal ambient conditions. Yield typically peaks somewhere around 600 to 699 ppm, then starts falling beyond that point. Under elevated CO plants also shifts more resources toward root growth rather than shoot growth (Wang *et al.* 2015) ^[7, 8].

Elevated CO₂ and rising temperature pull crop phenology in different directions. Elevated CO₂ tends to shorten the vegetative phase, while higher temperatures cut the grain filling period short, often leaving grains lighter. Elevated CO₂ also cuts both ways from crop performance and grain quality: it boosts growth and physiological activity overall, but it often drags down grain nutrition at the same time, lowering protein, amino acids, and mineral content. In rice specifically, elevated CO₂ increases chalkiness and changes grain size, shape, and cooking quality (Wang *et al.*, 2011) ^[9]. At the same time, it does improve water use efficiency, letting plants make better use of the moisture available. Even so, nitrogen supply needs to stay adequate under elevated CO₂ conditions to keep productivity up over time. Elevated ozone (O₃) works differently from CO₂ in this regard: exposure to it clearly hurts both yield and quality overall (Ainsworth, 2008) ^[10]. Elevated CO₂ can partly cancel out heat's downside, cutting nearly a third of the yield loss that a 1 °C temperature rise would otherwise cause on its own. But when elevated CO₂ and high heat hit at the same time, yield can still drop by around 14.8% regardless. Rising temperature speeds up crop phenology on its own too, shortening the growth period and in turn cutting into biomass and lowering the harvest index (Wang, 2018) ^[11]. Yield generally peaks somewhere around 500 ppm CO₂ past that point, plants start losing their ability to use the extra carbon well. Photosynthesis speeds up considerably under elevated CO₂, but heat can damage the photosynthetic machinery itself in the process (Baker & Allen, 1993) ^[12]. CO₂ and temperature interact together to shape the final yield outcome. High heat also suppresses two key enzymes, GBSS (granule-bound starch synthase) and SBE (starch branching enzyme), which lowers amylose content and hurts overall grain quality (Wang *et al.*, 2024) ^[13]. Cultivars vary quite widely in how they respond to elevated CO₂ - some gain about 13% in yield, others up to 26 % and some barely respond at all under the same conditions. That spread comes down largely to source-sink balance, which governs how well a given plant can put extra CO₂ to use for growth and yield formation (Hasegawa *et al.*, 2013) ^[14]). Traits that respond well to elevated CO₂ and happen to be heritable can

be bred deliberately into future cultivars. Genotypes with more biomass and a greater number of tillers before flowering tend to perform better under elevated CO₂ environments (Shimono, 2009) ^[15]. Elevated CO₂ changes grain nutrition in other ways as well: rice grown under such conditions tends to lose B vitamins, proteins, iron and zinc, while vitamin E by contrast tends to go up (Zhu *et al.*, 2018) ^[16]. Temperature shifts this picture further still. Combine elevated CO₂ with warm conditions and yield can rise by around 14.5% under cooler conditions instead, that same gain drops to about 7.8%. Getting the most out these responses ultimately comes down to solid nutrient management, and integrated approaches paired with higher fertilizer inputs tend to work best in practice.

Elevated CO₂ improves water use efficiency considerably, which matters most during dry seasons since it cuts down on water loss (Satapathy *et al.*, 2015) ^[17]. Other physiological efficiencies shift too, including radiation use efficiency (RUE). RUE generally rises under elevated CO₂, but it falls once crops face high temperatures instead and that drop shows up as reduced biomass accumulation and a lower harvest index overall (Cai *et al.*, 2016) ^[18]. How well plants actually use elevated CO₂ in the first place depends heavily on nitrogen availability. Without enough nitrogen on hand, plants struggle a bit to move excess CO₂ into mesophyll cells efficiently, though, mesophyll conductance improves noticeably and plants make far better use of the CO₂ available. Proper nitrogen application also helps the photosynthetic machinery adapt more effectively as climatic conditions shift (Xiong *et al.*, 2015) ^[19]. In rice specifically, elevated CO₂ raises amylose content, which makes grains firmer and less sticky, and it increases chalkiness by creating small air spaces inside each grain. Extra carbon also drives the formation of more starch granules than usual, which then takes longer to cook through (Patindol *et al.*, 2015) ^[20]. In C₃ crops like tea, elevated CO₂ speeds up CO₂ assimilation rates, producing more ATP and NADPH and boosting overall physiological performance (Ahmed *et al.*, 2020) ^[21]. Under elevated CO₂ conditions, plants can also start acting more like carbon sinks, pushing net assimilation rates considerably higher. At extremely high CO₂ concentrations, around 6000 ppm, transpiration drops by nearly 20% compared to levels at 400 ppm, which translates into roughly four times the water use efficiency (Levy *et al.*, 2025) ^[22]. Recent research has also looked closely at how elevated CO₂ and heat together affect legume nutrition, since legumes matter both for fixing atmospheric nitrogen and for serving as a major protein source (Shankar *et al.*, 2025) ^[23]. All of this ties back to climate tipping points, the stages where the systems start changing on its own and produces large, often permanent shifts. Global warming already sits around 1.1 °C above pre industrial levels, putting the global system close to some of these key thresholds, another 1.5 to 2 °C or more could set off changes that are far harder to reverse, which is why both cutting emissions and adapting matter so much going forward (McKay *et al.*, 2022) ^[24].

Impact of elevated CO₂ and temperature on crop growth and development

Elevated CO₂ counts as an abiotic stress, but it still helps crops in several ways, it often works almost like a fertiliser, cutting water loss through transpiration and improving how

efficiently plants use water, while also driving better overall growth: taller plants, more leaves, a bigger leaf area and in the end, high yield (Sabagh *et al.*, 2020) ^[3].

Canopy characteristics

Elevated CO₂ tends to boost plant growth in fairly noticeable ways, particularly when it comes to height and canopy development. Plant height rises in both maize and rice, with gains around 3.35% and 4.84% and under certain other conditions those gains climb even higher to 7.47% and 8.84% (Xie *et al.*, 2020) ^[25]. Canopies also grow taller during the vegetative stage under elevated CO₂. through that advantage tends to shrink a bit by the time the crop nears harvest (Knopf *et al.* , 2024) ^[26]. Leaves respond well too, across a range of different crops, with leaf area increasing enough to capture more light and support noticeably stronger growth overall. Tomato, for instance, shows that a 21.2% jump in leaf area 110 days after transplanting, while maize, sugarcane, and sorghum post gains of roughly 50%, 30% and 25% respectively at the anthesis stage (Rangaswamy *et al.*, 2021) ^[27]. Taken together, these results point clearly to elevated CO₂ giving vegetative growth a real boost, especially early on in a crop’s overall development.

Photosynthesis and gas exchange traits

As CO₂ levels rise, photosynthesis generally improves significantly across most crops. Every 100 ppm increase in CO₂ can lift the photosynthesis rate by about 15.5% (Wang *et al.* 2020) ^[28]. That happens mainly because elevated CO₂ raises intercellular CO₂ concentration, by around 15.74% and pushes the net photosynthetic rate up by nearly 20%. The effect tends to show up more strongly in C₃ plants, which gain roughly 10 to 14 %, compared to C₄ plants, where the increase is smaller, around 2 to 3% (Li *et al.*, 2019; Vijayalakshmi *et al.*, 2023) ^[29, 30]. Elevated CO₂ also helps plants hold onto water, cutting stomatal conductance by about 5.52% and transpiration by around 9.40%. Heat works against this, pushing stomata to open wider and increasing water loss, while drought tends to suppress both. Combine heat and drought with elevated CO₂, and the CO₂ can partly offset their damage; it improves photosynthesis and water use efficiency while still keeping stomatal conductance down, which in the end helps handle stress better and keep growing (Li *et al.*, 2019; Vijayalakshmi *et al.* 2023; Roy *et al.*, 2024) ^[29, 30, 31]. Table summarises the main physiological responses of crop to eCO₂, temperature, and their combined effects.

Table 1: Effect of eCO₂ and temperature on crop physiological processes

Process	Effect of eCO ₂	Effect of temperature	Combined effect	Reference
Photosynthesis	Increased	Decreased	Variable	Wang <i>et al.</i> , 2020 ^[28]
Respiration	Slight increase	Increased	Net carbon loss	Wang, 2018
Transpiration	Decreased	Increased	Balanced effect	Vijayalakshmi <i>et al.</i> , 2023 ^[30]
Biomass accumulation	Increased	Reduced	Slight increase or neutral	Knopf <i>et al.</i> , 2024 ^[26]
Phenology	Slight delay	Accelerated	Shortened duration	Jing <i>et al.</i> , 2024 ^[32]
Reproductive development	Improved	Reduced	Reduced	Wang <i>et al.</i> , 2024 ^[13]

(eCO₂ - elevated CO₂)

Biomass

Elevated CO₂ generally helps plants grow better, lifting both leaf biomass and rootshoot ratio, by about 15.04% and 8.08% respectively (Li *et al.*, 2019) ^[29]. Plants grown under high CO₂ also tend to pack on more biomass overall, around 21.73% more than plants grown under ambient conditions (Knopf *et al.*, 2024) ^[26]. That response isn’t exactly uniform across every plant type, though C₄ plants usually show little or no real improvement under elevated CO₂ (Roy *et al.*, 2024) ^[31]. Temperature changes this picture too. Shoot biomass rises about 20% under ambient conditions but only around 14% once temperatures climb (Hu *et al.*, 2022) ^[33]. Specifically, at 35 days after emergence, plants grown under higher heat showed greater biomass than those under normal conditions. Under elevated CO₂, plants tend to send more biomass toward tubers, leaving less for leaves and stems. By 58 days after emergence, biomass had grown further under both elevated CO₂ and higher temperature. When high temperature showed up on its own, though, leaf growth dropped off in later stages, likely from the added stress that heat puts on the plant (Lee *et al.*, 2020) ^[34]. Overall, growth under elevated CO₂ isn’t just a carbon story, either, it depends heavily on nutrients, nitrogen especially. With enough nitrogen on hand, plants make better use of the extra CO₂ and grow more, building up more biomass. Without it, plants can’t take full advantage of that extra CO₂, so the growth benefit gradually fades over time (Maschler *et al.*, 2022) ^[35].

Plant phenology: Daytime temperature and atmospheric CO₂ both shape crop phenology (Wang *et al.* 2019) ^[36]. Plants need a certain amount of accumulated heat, usually measured as growing degree days, to shift from one growth stage to the next. As temperature climb, development speeds up, pushing flowering and heading earlier, and that effect gets stronger when higher CO₂ is added into the mix. Elevated CO₂, on its own, tends to work the other way, nudging flowering slightly later and stretching out the growth period, which in turn supports better growth and yield. That delay in flowering can actually help crops cope with stress and adjust as conditions shift (Fotopoulos *et al.*, 2016) ^[37]. In maize specifically, higher temperatures hurt biomass accumulation, anthesis and silking but elevated CO₂ can partly cancel out that damage, helping the crop keep growing and developing even under stress (Vanaja *et al.*, 2024) ^[38]. Legumes respond somewhat differently depending mostly on their growth stage, with the strongest effects showing up early on. Elevated CO₂ tends to support better and can push flowering earlier, though exactly how much varies from one legume to another. Temperature, meanwhile, has the stronger pull here, since higher temperatures shorten the growth period more directly. Put together, eCO₂ and temperature don’t produce one consistent outcome; it comes down to the specific crop and growing conditions (Adireddy *et al.*, 2024) ^[39]. Table lays out a clearer comparison of yield responses and the key physiological mechanisms across different CO₂ and temperature regimes.

Table 2: Response of crop yield to eCO₂ and temperature under different environmental conditions

Condition	Yield response	Key physiological mechanism	Reference
180-220 ppm CO ₂	Marked yield reduction (50%)	Limited carbon availability restricts photosynthesis and biomass formation	Sabagh <i>et al.</i> , 2020 ^[3]
450-550 ppm CO ₂	Moderate yield increase (10-15%)	Improved photosynthetic rate and reduced photorespiration enhance carbon gain	Ainsworth, 2008
600-700 ppm CO ₂	Highest yield response	Balanced source-sink relationship and efficient carbon utilisation	Wang <i>et al.</i> , 2015 ^[7, 8]
>700 ppm CO ₂	Yield decline begins	Sink limitation leads to carbohydrate accumulation and feedback inhibition	Wang <i>et al.</i> , 2015 ^[7, 8]
eT (+2 to +4 °C)	Yield reduction (20-30%)	Faster crop development shortens grain filling and reduces assimilate accumulation	Wang, 2018
eCO ₂ +aT	Yield increase (14%)	Enhanced photosynthesis and better carbon assimilation efficiency	Cai <i>et al.</i> , 2016 ^[18]
eCO ₂ +eT	Yield reduction (10-16%)	Heat stress disrupts reproductive development and partially overrides CO ₂ benefits	Wang <i>et al.</i> , 2024 ^[13]

(et-elevated temperature, At-ambient temperature, eCO₂- elevated CO₂)

Defence response

Elevated CO₂ does more than change how crops grow; it also shifts pest interactions and plant defences. Sap sucking pests like aphids tend to multiply more under higher CO₂, while leaf feeding insects often see their numbers drop instead. In tea, elevated CO₂ lowers caffeine content, and that makes the plant easier prey for tea aphids, driving up infestation. Reduced transpiration adds to the problem by keeping leaf water content higher, which helps pests survive even better. Lower caffeine also leaves plants more open to diseases like anthracnose and dieback. Applying caffeine externally can push back against this, boosting plant defence by triggering jasmonic acid production through the lipoxygenase pathway (Ahammed *et al.*, 2020) ^[21]. Elevated CO₂ reshapes plant biochemistry more broadly too, cutting caffeine while raising defence compounds such as salicylic acid and jasmonic acid (Li *et al.* 2019) ^[29]. It also helps plants handle stress by cutting down reactive oxygen species (ROS). That happens because RuBisCO carboxylation increases while photorespiration drops, which together reduce how much H₂O₂ forms. Elevated CO₂ also dials down NADPH oxidase activity in mitochondria and chloroplasts, limiting ROS production and giving plants a much better shot at coping with stress (Sabagh *et al.*, 2020) ^[3].

Effect of elevated CO₂ on C₃ and C₄ plants

When it comes to photosynthetic pigments, elevated CO₂ doesn't treat C₃ and C₄ plants the same at all. At around 1000 ppm, C₃ plants react quite strongly, whereas C₄ plants show little to no response at all, thanks to their own built-in CO₂ concentrating mechanism. C₄ plants naturally carry more chlorophyll, and that acts almost like a protective, energy-efficient system, keeping photosynthesis steady even when CO₂ climbs high. C₃ plants, by comparison, are far more sensitive to rising CO₂ levels. Push concentrations too high and their photosynthetic machinery starts to break down, leaves age faster, and chlorophyll content drops,

which eventually caps photosynthesis. At 1000 ppm, for instance, photosynthesis in C₃ plants jumps by about 96.8%, but that gain reverses hard at extreme levels, falling 14.1% at 3000 ppm and 46.7 % at 5000 ppm. C₄ plants, true to form, show little response at 1000 ppm thanks to their CO₂ concentrating mechanism (Wang *et al.*, 2015) ^[7, 8]. Elevated CO₂ also shifts pigment composition. In C₄ plants, chlorophyll b converts into chlorophyll a, raising the chlorophyll a/b ratio, a shift that usually signals stress and aging. At the same time, intercellular CO₂ concentration rises even as transpiration falls off. Stomatal conductance generally drops at higher CO₂ levels, around 3000 ppm, in both plant types, though it stays fairly stable at 1000 ppm. C₄ plants also tend to run a lower stomatal conductance than C₃ plants overall. Water use efficiency tells a fairly similar story here: C₄ plants typically run about 2.1 times more efficient than C₃ plants, though that edge shrinks at extremely high CO₂, like 5000 ppm. At first, elevated CO₂ helps photosynthesis in both types, driven by better PSII efficiency and stomatal behavior, but at very high concentrations those same systems start failing. Photochemical quenching rises at 1000 ppm but falls at 5000 ppm in both C₃ and C₄ plants (Wang *et al.*, 2015)^[7, 8]. CO₂ enrichment also cuts membrane damage in C₃ plants, helping them tolerate stress better (Vijayalakshmi *et al.*, 2023) ^[30]. Because their photosynthetic pathways differ, C₃ plants show a clearer CO₂ fertilization effect, usually translating into bigger yield gains than C₄ plants see (Ter Haar *et al.* 2025) ^[40]. Under combined stress, drought plus elevated CO₂, C₄ plants tend to show lower stomatal conductance and photosynthetic rates than C₃ plants do (Shankar *et al.*, 2025) ^[23]. Elevated CO₂ and temperature together can also affect crops unevenly, sometimes cutting photosynthesis in C₄ plants more than in C₃ plants (Roy *et al.*, 2024) ^[31]. Table lays out in more detail how C₃ and C₄ crops compare physiologically and in yield under elevated CO₂ conditions.

Table 3: Comparative response of C₃ and C₄ crops under elevated CO₂

Parameter	C ₃ crops	C ₄ crops	Physiological effect	Reference
Photosynthetic response	High (10-14%)	Low (2-3%)	C ₃ plants are CO ₂ -limited, C ₄ have CO ₂ concentrating mechanism	Li <i>et al.</i> , 2019 ^[29]
Photorespiration	High (reduced under eCO ₂)	Negligible	Rubisco oxygenation in C ₃ pathway	Vijayalakshmi <i>et al.</i> , 2023 ^[30]
Yield response	Significant increase	Minimal response	Greater carbon fixation in C ₃ plants	Ter Haar <i>et al.</i> , 2025 ^[40]
Stomatal conductance	Strong reduction	Moderate reduction	CO ₂ -induced stomatal closure	Roy <i>et al.</i> , 2024 ^[31]
Water use efficiency	Moderate increase	Higher baseline	Lower transpiration in C ₄ crops	Wang <i>et al.</i> , 2015 ^[7, 8]
Stress tolerance	Moderate	Relatively higher	Better thermal stability in C ₄ pathway	Roy <i>et al.</i> , 2024 ^[31]

Interactive effects of elevated CO₂ and high temperature

A 1 to 2 °C rise in global temperature is expected to hit crop production hard, with projections pointing to as much as a 30% drop in food grain yield overall. Drought combined with elevated CO₂ brings a mix of problems for plants: smaller leaf area, disrupted nutrient movement, restricted stomatal movement, and lower transpiration and relative water content. But this particular combination isn't all bad; it also tends to improve water use efficiency, light use efficiency, and nutrient use efficiency, and shifts more biomass toward reproductive parts instead (Sabagh *et al.*, 2020) [3]. Stomatal traits also shift under these combined conditions too. Stress alone usually raises stomatal frequency, but when heat and drought hit together with elevated CO₂, stomatal frequency actually drops instead. Elevated CO₂ on its own can widen stomatal area somewhat, but heat and drought combined, whether under ambient or elevated CO₂, still shrink stomatal size overall (Vijayalakshmi *et al.*, 2023) [30]. Yield tends to follow a fairly similar pattern here overall. Elevated CO₂ alone can lift yield by roughly 13%, while high temperature alone can cut it by about 23% instead. Put both together, and heat stress wins out in the end, dragging final yield down by around 12% compared to current ambient conditions (Cai *et al.*, 2016) [18]. Grain quality suffers too, especially in rice. High temperature combined with elevated CO₂ tends to hurt

nutritional quality, mainly by pushing up the share of chalky grains. Heat on its own raises respiration and cuts photosynthetic activity, which lowers carbohydrate availability even at ambient CO₂. Elevated CO₂, though, boosts photosynthesis, supplying more carbohydrates to support pollen development along with carbon and nitrogen metabolism (Shankar *et al.*, 2025) [23]. When elevated CO₂ and high heat act together, CO₂'s benefits usually shrink. Elevated CO₂ under ambient temperature can lift yield by about 14 %, while elevated temperature under ambient CO₂ can cut yield by around 26 % instead. Combine both of these factors, and the net effect still lands negative overall, around a 16 % yield loss compared to current ambient conditions (Wang *et al.*, 2024) [13]. Figure 1 shows how climate change plays out across crop yield and grain quality more broadly. This combination generally drags down nitrogen content, mineral composition, and overall grain nutrition, since the downsides of warming tend to outweigh whatever benefits elevated CO₂ offers in return. Roy *et al.* (2024) [31] found that plants grown in open-top chambers show a noticeably higher photosynthetic rate, lower stomatal conductance, and better water use efficiency overall. Table summarizes in more detail how eCO₂ interacts with several major stresses, and Figure 2 shows the combined effects of elevated CO₂ and heat stress on crop physiology and yield outcomes.

Table 4: Interaction of eCO₂ with major stresses

Stress factor	Effect under stress	Effect under eCO ₂	Reference
Drought	Reduced growth and yield	Improved water use efficiency	Sabagh <i>et al.</i> , 2020 ^[3]
Heat stress	Reduced yield and fertility	Limited compensation	Cai <i>et al.</i> , 2016 ^[18]
Heat + drought	Severe yield loss	Minimal recovery	Vijayalakshmi <i>et al.</i> , 2023 ^[30]
Nitrogen deficiency	Reduced productivity	Limits CO ₂ utilization	Xiong <i>et al.</i> , 2015 ^[19]
Elevated ozone	Reduced photosynthesis	Partial protection	Ainsworth, 2008

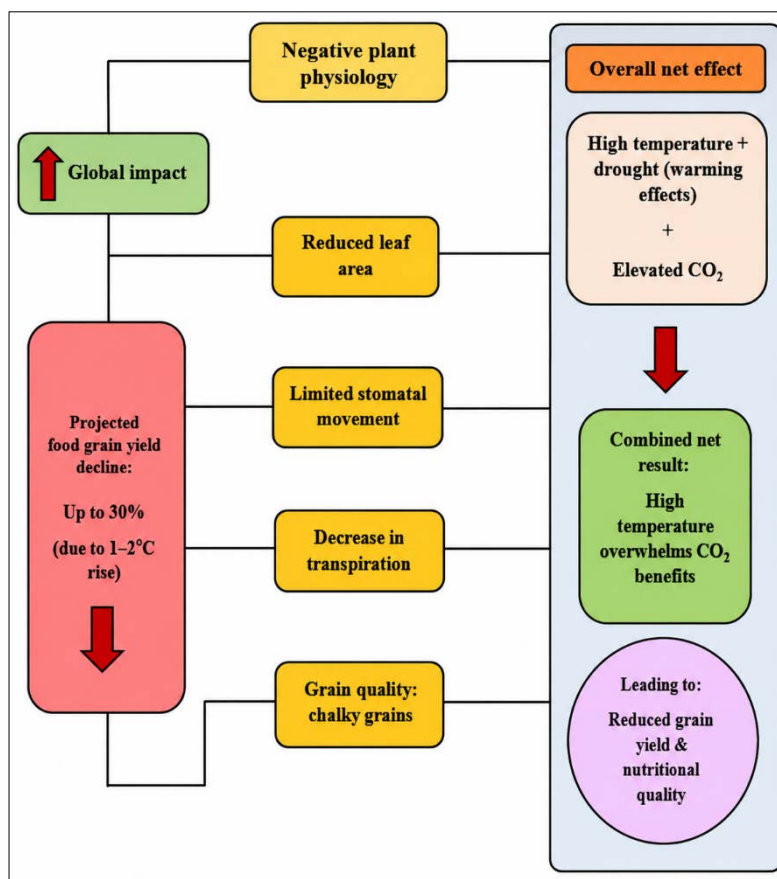


Fig. 1: Schematic representation of the impact of climate change on crop yield and grain quality

Effect of elevated CO₂ and temperature on reproductive traits, yield and grain quality

Elevated CO₂ generally helps plants grow and can push grain yield up, but that gain usually comes at the direct cost of overall grain quality. Grains grown under elevated CO₂ tend to turn chalkier and lose protein along with key nutrients like iron and zinc. Starch composition shifts as well, which can change how the grain actually cooks and tastes (Wang & Liu, 2021) [41]. Heat stress does even more damage overall, since it disrupts photosynthesis and grain filling directly, dragging down both yield and grain quality. Combine elevated CO₂ with heat stress, and the damage gets noticeably worse, especially for grain nutrition and quality (Wang & Liu, 2021; Mariem *et al.*, 2021) [41, 42]. Elevated CO₂ can also help reproductive processes along, improving pollen viability, germination, and pollen tube growth, which lifts yield in crops such as rice, maize, and ragi, and improves seed set in green gram. These gains shrink noticeably once heat and drought stress get added, since both conditions work directly against reproductive development and yield formation (Vijayalakshmi *et al.*, 2023) [30]. Drought layered on top of elevated CO₂ can cause pollen abortion, poor pollination, spikelet sterility, and reduced grain formation, all of which end up lowering yield overall. It also cuts grain quality in legumes, lowering key nutrients like phosphorus, sulphur, iron, and zinc (Sabagh *et al.* 2020) [3]. On the yield side, elevated CO₂ can raise grain yield by about 7.6% and grain number per square meter by around 12.87%, though this does vary quite a bit by cultivar; Hyvega, for instance, actually shows a slight yield decline of about 2.5% along with a lower harvest index (Knopf *et*

al., 2024) [26]. Cooking and grain quality shift under these conditions too. Elevated CO₂ can improve rice cooking quality by changing starch characteristics, producing better texture, thicker consistency, and slightly firmer cooked grains thanks to higher amylose content. It can also improve oil quality in crops like Brassica, yielding larger grains with a healthier fatty acid profile (Upriety *et al.*, 2010) [43]. High temperature works against these gains, disturbing starch formation and increasing chalkiness, which leaves cooked rice harder and less palatable. When elevated CO₂ and high temperature hit together, heat's downsides usually win out, lowering both cooking quality and nutritional value (Chen *et al.*, 2021; Chaturvedi *et al.*, 2017) [44, 45]. Elevated CO₂ under ambient temperature can lift yield by roughly 10%, but under warming conditions, that same gain shrinks to only about 4% (Jing *et al.*, 2024) [32]. Elevated CO₂ alone can boost yield and some quality traits, but combined with heat and drought stress, the outcome usually tips toward a net decline in grain quality, which is exactly why crop improvement work needs to factor in these combined climate effects together. Higher CO₂ helps plants grow faster and raises yield, but it also tends to lower produce quality. Protein, iron, and zinc typically drop, and shifts in starch can change cooking quality. Add high temperature and drought into the mix, and things get worse still: heat stress disrupts photosynthesis, hurts grain filling directly, and drags down both yield and quality. Elevated CO₂ does offer some benefits, but stress conditions cancel out most of those benefits (Ekele *et al.*, 2025) [46]. Table sums up how grain quality and nutritional traits shift under eCO₂ and temperature.

Table 5: Effect of eCO₂ and temperature on grain quality and nutritional traits

Trait	Effect of eCO ₂	Effect of eT	Combined effect	Reference
Protein content	Decrease (5-15%)	Decrease	Significant decline	Zhu <i>et al.</i> , 2018 ^[16]
Iron and zinc	Reduced concentration	Reduced	Marked reduction	Shankar <i>et al.</i> , 2025 ^[23]
Starch content	Increased	Altered synthesis	Imbalance in composition	Wang <i>et al.</i> , 2024 ^[13]
Chalkiness	Increased	Increased	High chalkiness	Chen <i>et al.</i> , 2021 ^[44]
Amylose content	Slight increase	Reduction	Variable	Patindol <i>et al.</i> , 2015 ^[20]
Vitamin content	Reduced (B vitamins)	Slight effect	Decline	Zhu <i>et al.</i> , 2018 ^[16]
Cooking quality	Slight improvement	Deterioration	Overall decline	Wang and Liu, 2021 ^[41]

Effect of elevated CO₂ and temperature in vegetable and legume crops

There is an evident impact of elevated CO₂ on the nutritional and biochemical composition of vegetables. It usually promotes accumulation of soluble sugars in edible parts, and also produces more compounds in leaves, such as triose phosphates, antioxidants, total phenols, flavonoids, ascorbic acid and chlorophyll b. Leafy vegetables usually accumulate more soluble sugars than fruits, roots or stem-modified vegetables, since carbohydrate transport within the plant is sometimes limited. This increase in sugars is usually accompanied by a decrease in protein content with increasing CO₂. Under eCO₂, nitrate levels in vegetables are generally lower. This is predominantly because the plant uses nitrogen more efficiently for assimilation rather than storage as nitrate. The mineral composition also varies with decreases of elements such as magnesium, iron and zinc, while calcium levels may increase (Dong *et al.*, 2018) [47]. The effects become more complex when eCO₂ is combined with high temperature (eT +eCO₂), especially in legumes. The protein content is reduced even more, raising concerns of possible protein deficiencies on a wider scale. The kernel

oil content also decreases. On the positive side, there is an increase in ash content and crude fibre. Under these combined conditions, most of the key macro and micro nutrients such as nitrogen, phosphorus, calcium, magnesium, iron, zinc, manganese, copper and sulphur are reduced. Another important effect is on cooking quality, when exposed to high temperature and CO₂ simultaneously, the cooking time increases steeply to around 13 minutes from 3.35 minutes in normal condition, this response may be dependent on the genotype (Shankar *et al.*, 2025) [23]. High temperature and elevated CO₂ may increase some biochemical traits, but their combined effect tends to decrease nutritional quality. Good management is essential to improve vegetable production under eCO₂. Plants require more nutrients, especially nitrogen. S0 ;, balanced fertilization becomes important. It also needs good temperature, enough light and enough water. CO₂ alone cannot get over heat and drought stress. The increase in yield is primarily due to the number of fruits, not their size. Natural CO₂ under greenhouse conditions with proper ventilation can be more sustainable (Dong *et al.*, 2020) [48]. Legumes normally respond with good growth, increased

nodulation and in some cases higher yield to eCO₂. This response is not consistent and may in some cases lead to a reduction in leaf growth or yield. High temperature has

more adverse effect causing decline in seed germination, poor growth and flowering and subsequently lower yield (Adireddy *et al.*, 2024) [39].

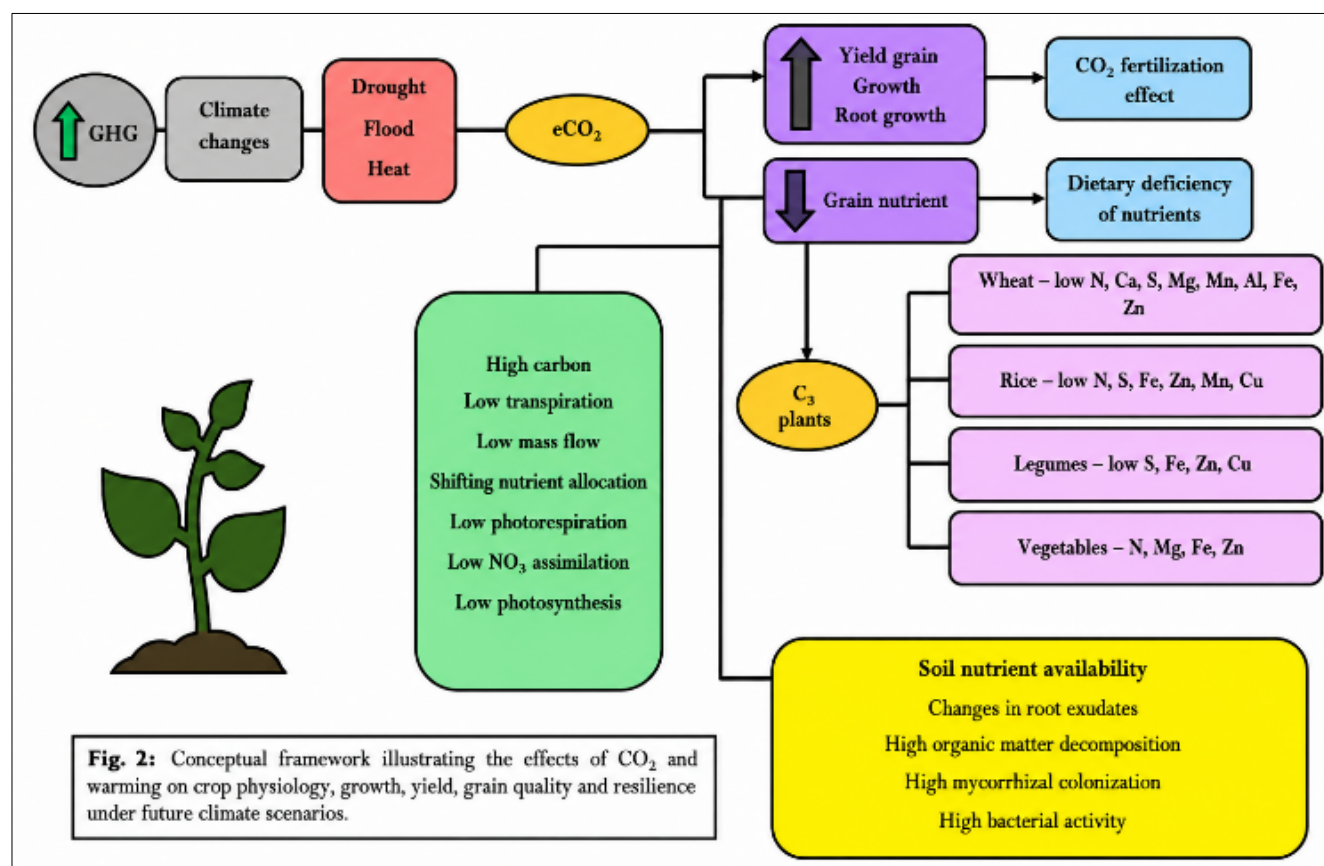


Fig 2: Conceptual framework illustrating the effects of CO₂ and warming on crop physiology, growth, yield, grain quality and resilience under future climate scenarios.

Conclusion

Elevated CO₂ has a significant effect on the growth and productivity of crops and can often improve plant growth by improving photosynthesis, biomass and water use efficiency. These gains are not consistently dependable, especially when coupled with stresses like extreme heat and drought, which can lower yield, compromise grain quality and interfere with reproductive processes. Responses also vary between crops, with C₃ crops generally responding more than C₄ crops. Also, there are some problems like reduced nutrient content in grains which raises concern about food quality. Understanding of these interactions is necessary to develop climate-resilient crops and effective management strategies to maintain agricultural productivity under future climatic circumstances.

Future prospects

Studies show that eCO₂ can mitigate the adverse effects of drought and heat stress by improving plant water relations, enhancing photosynthetic efficiency and regulating metabolic responses, thereby supporting better growth and productivity.

Future research needs to focus on studying more crops across different regions and improving crop models to better understand real-world interactions. This will help reduce uncertainties and support better decision making and agricultural adaptation strategies under climate change.

Rising CO₂ levels may help to reduce some of the negative effects of heat and drought leading to improvements in crop

and tree growth. This can help to maintain productivity and reduce soil carbon loss and can be a practical approach for improving sustainability under changing climate conditions. The impact of eCO₂ on grain quality depends on its interaction with the environment, crop variety, and management practices. Grain quality is influenced by components like protein, starch and lipids and their interactions. Elevated CO₂ often reduces essential nutrients like iron, calcium, magnesium and zinc, which may affect human nutrition. These effects can be managed through proper nutrient management and suitable cultivar selection. Future research should focus on developing crops that maintain yield and quality under rising CO₂ conditions.

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List of abbreviations

Sl. No.	Abbreviation	Full form
1.	CO ₂	Carbon Dioxide
2.	eCO ₂	Elevated Carbon Dioxide
3.	eT	Elevated Temperature
4.	aT	Ambient Temperature
5.	C ₃	C ₃ Photosynthetic Pathway Plants
6.	C ₄	C ₄ Photosynthetic Pathway Plants
7.	FACE	Free- Air CO ₂ Enrichment
8.	OTC	Open Top Chamber
9.	GHG	Greenhouse Gas
10.	CH ₄	Methane
11.	N ₂ O	Nitrous Oxide
12.	O ₃	Ozone
13.	ROS	Reactive Oxygen Species
14.	RUE	Radiation Use Efficiency
15.	WUE	Water Use Efficiency
16.	ATP	Adenosine Triphosphate
17.	NADPH	Nicotinamide Adenine Dinucleotide Phosphate
18.	GBSS	Granule-Bound Starch Synthase
19.	SBE	Starch Branching Enzyme
20.	LAI	Leaf Area Index
21.	DAE	Days After Emergence
22.	DAS	Days After Sowing
23.	NO ₃ ⁻	Nitrate
24.	PSII	Photosystem II
25.	RuBisCO	Ribulose-1,5-bisphosphate Carboxylase/Oxygenase
26.	ppm	Parts Per Million
27.	°C	Degree Celsius