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Rising CO₂ and ecosystem sustainability: The role of carbon fertilisation

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Abstract

Globally, plant functioning and ecosystem processes are changing due to rising atmospheric CO₂ concentrations. The carbon fertilization effect is the term used to describe how elevated CO₂ usually improves photosynthesis, increases water-use efficiency, and stimulates biomass accumulation. However, there are significant differences between species and ecosystems in the intensity, duration, and ecological significance of this response. While changes in soil microbial activity can affect nutrient cycling, decomposition, and organic matter stability, nutrient limitations, especially those related to nitrogen and phosphorus, frequently limit plants' ability to convert surplus carbon into long-term growth. Forests, grasslands, croplands, wetland systems, and arid landscapes each display distinct sensitivities to elevated CO₂ depending on hydrology, soil fertility, dominant vegetation types, and disturbance regimes. Although enhanced CO₂ can support higher productivity, greater vegetative cover, and improved drought tolerance in some systems, it may also reduce plant nutrient concentrations, alter competitive dynamics, and weaken ecosystem stability. In agricultural systems, increased carbohydrate accumulation under elevated CO₂ frequently results in nutrient dilution, posing risks to food quality and human nutrition. At the same time, potential gains in carbon sequestration depend on long-term storage in wood, roots, and soil organic matter, which remain uncertain under variable climate and nutrient conditions. Reliable management strategies such as improved nutrient stewardship, soil carbon-building practices, and development of CO₂-responsive cultivars are essential to harness benefits while minimizing ecological trade-offs. A deeper integration of experimental findings, long-term monitoring, and ecosystem modelling is needed to better predict how rising CO₂ will shape sustainable terrestrial systems in the future.

Keywords: CO₂ fertilisation, elevated CO₂, carbon sequestration, soil organic carbon, photosynthesis, sustainable ecosystem

1. Introduction

In recent decades, greenhouse gasses and global warming have attracted a lot of interest worldwide. Fossil fuel consumption, deforestation, agricultural activities, and cement manufacturing are the main causes of the rise in atmospheric CO₂ concentrations, and they all have a substantial impact on the atmosphere's CO₂ concentration (Nunes 2023) ^[1]. According to [Yuan et al. \(2024\)](#) ^[2], the atmospheric CO₂ concentration has surpassed 400 parts per million, surpassing its natural variability and causing concerns about unpredictable alterations in the carbon cycle that might have a substantial influence on the climate and the ecosystem. According to current estimates, if significant steps are not taken to limit GHG emissions, concentrations will continue to rise to 500-1,000 ppm by the year 2100 (Nordhaus 2018) ^[3].

Increased photosynthetic absorption of CO₂ by leaves and improved water-use efficiency (WUE) are the results of the CO₂ fertilization effect caused by the growing atmospheric CO₂ concentration (Gonsamo et al. 2021) ^[4]. However, comparatively little research has been done to investigate the possible benefits of climate change, despite the fact that many studies have looked at its negative effects. The possibility that increased CO₂ levels could potentially boost crop yields is one noteworthy possible benefit. Through photosynthesis, plants fix and use CO₂, and a number of studies have indicated that rising atmospheric CO₂ concentrations may promote plant growth, which in turn may increase agricultural output. This phenomena, referred to as the carbon fertilization effect (Taylor and Schlenker 2023) ^[5], emphasizes how important it is to comprehend how higher CO₂ levels benefit agricultural systems (Liu and Lu 2024) ^[6].

The term “CO₂ fertilization” comprises two effects of elevated ambient CO₂ on the plants physiology (Fig.2). Firstly, stimulating carbon assimilation under elevated CO₂ in the interior of leaves, which leads to increased plant productivity and biomass (Leakey *et al.* 2009; Fatichi *et al.* 2016) [7, 8]. Additionally, leaves adjust to the CO₂-rich environment by reducing their stomatal conductance and possibly their stomatal density over time, as indicated by in situ observations. As a result, the loss of water due to transpiration reduces, leading to improved water-use efficiency (the ratio of carbon uptake to transpiration rate) (Ukkola *et al.* 2016; Fatichi *et al.* 2016) [9, 8]. Theoretically, both impacts should lead to an increase in leaf area, particularly in conditions where water availability limits plant growth (Ukkola *et al.* 2016) [9]. Rise in atmospheric CO₂ can result in greater terrestrial carbon storage, specifically through photosynthesis, alterations in land use, vegetation and soil reactions to ongoing warming, and variations in the water cycle (Rodrigues *et al.* 2023) [10].

Photosynthesis is the main process that shifts carbon to the soil, whereas atmospheric CO₂ can dissolve in soil water in somewhat limited quantities (Kell 2011) [11]. Thus, the net primary productivity of an ecosystem, defined as the difference between carbon gained via photosynthesis and carbon lost through respiration, mainly dictates the carbon accumulation rate within the ecosystem. As respiration progressively rises over time, the accumulation of carbon in an ecosystem declines. Elevated CO₂ concentrations promote carbon's entry into ecosystems, leading to the storage of carbon and nitrogen in organic matter and durable plant biomass. Nevertheless, the global C balance shows a net absorption of CO₂ by land ecosystems, which explains the phenomenon known as “missing carbon” or fugitive CO₂.

An increase in atmospheric CO₂ content (eCO₂) causes plants to absorb more net photosynthetic carbon through metabolic processes, which enhances net primary production (NPP) or the CO₂-fertilization effect. The latter is more noticeable in C₃ species, and estimates of the increase in light-saturated photosynthesis range from 14% (Lee, 2011) [12] to 26-31% (Ainsworth and Rogers, 2007) [13]. When there are significant sinks for carbon (such as reproductive organs or belowground storage organs), the growth of C₃ plants whose photosynthesis is CO₂-limited usually reacts to increased CO₂ more strongly than that of C₄ plants. C₄ plants typically react more as a result of higher water use efficiency (WUE).

However, only with optimal soil resources (such as water and nutrients), which control plant growth rate and active carbon (C) sinks, can NPP rise (Reich *et al.* 2006) [14]. Only with nutrient supplementation, especially in resource-limiting conditions, has the response of C₄ plants been demonstrated (Markelz *et al.* 2011) [15]. This kind of reaction is anticipated since, according to Liebig's “rule of minimum,” maximizing the benefits of the easily accessible resources requires others. When there are substantial sinks for carbon (such as reproductive organs or belowground storage organs), the growth of C₃ plants whose photosynthesis is CO₂-limited generally reacts more strongly to increased CO₂ than that of C₄ plants.

2.1 Effect of CO₂ fertilisation on plant growth and development

- **Physiological changes associated with CO₂ fertilisation**
Although altering the degree of stomatal opening is another strategy, C₃ plants primarily sense and react to elevated CO₂ in the atmosphere by increasing the carboxylase activity of RuBisCO (Long *et al.* 2004) [16]. RuBisCO, an

enzyme that crops use to fix CO₂ during photosynthesis, is in touch with the intercellular air space via stomata. Because RuBisCO concentrations in mesophyll chloroplasts are not saturated with atmospheric CO₂, C₃ plants can directly use atmospheric CO₂ through RuBisCO carboxylation. In contrast to C₃ plants, C₄ plants have CO₂ concentrations that are several times greater than the environment (i.e., the CO₂ concentrations in RuBisCO situated at bundle-sheath are near saturation). Thus C₄ plants are unable to increase the utilization rate of CO₂ through carboxylation in RuBisCO (Taylor and Schlenker 2023) [5]. Instead, C₄ plants respond to CO₂ only by adopting the degree of stomatal opening, which changes their water use efficiency.

- **Enzyme activity changes associated with CO₂ fertilisation**

The [CO₂] in the chloroplast and the catalysis of the main CO₂-fixing enzyme Rubisco, in particular its carboxylation efficiency (k_{cat}/K_c21%O₂) and specificity for CO₂ rather than O₂ (S_{c/o}), affect photosynthetic CO₂ assimilation (Badger and Sharwood 2023) [17]. Though it exhibits catalytic inefficiencies that require plants to expend a substantial amount of energy and nitrogen (N) to produce copious pools of Rubisco in order to maintain adequate rates of carbon (C) fixation, Rubisco catalyzes the assimilation of CO₂ by the carboxylation of ribulose-1,5-bisphosphate (RuBP) in the Calvin cycle (Galmés *et al.* 2019) [18]. Accordingly, Rubisco's subpar catalytic efficiency has been characterized as a possible target for enhancing photosynthesis (Iñiguez *et al.*, 2021) [19].

According to Xu *et al.* (2013) [20], eCO₂ also markedly enhanced the abundance of genes related to labile C degradation and C and N fixation, such as RuBisCo, carbon monoxide dehydrogenase (CODH), propionyl-CoA/acetyl-CoA carboxylase (PCC/ACC), nifH, and nifS. It has been proposed that eCO₂ hinders N assimilation into protein by inhibiting leaf nitrate photo assimilation (Bloom, 2015) [21]. Increased CO₂ levels slow down photorespiration and limit the availability of cytosolic NADH, which is necessary for nitrate reduction (Bloom 2015; Vicente *et al.* 2016) [21, 22]. Decreased cytosolic NADH levels also reduce nitrate assimilation (Quesada *et al.* 2000) [23] and malate efflux via the dicarboxylic acid translocator from the chloroplast to the cytosol (Backhausen *et al.* 1998) [24]. In *Chlamydomonas*, nitrite is transported from the cytosol to the chloroplast by members of the nitrate assimilation related component 1 (Nar1) transporter family (Mariscal *et al.* 2006) [25].

The importance of studying root-shoot interactions in nitrate uptake and N dynamics has been demonstrated by recent studies in *Arabidopsis* (Jauregui *et al.* 2016) [26] and cucumber (Dong *et al.* 2017) [27]. Root nitrate absorption was favoured over leaf nitrate assimilation to offset the decline in total N metabolism in leaves under eCO₂. Inhibition of nitrate assimilation is more noticeable in leaves with increased competition for reductant and barriers to nitrate accessibility (Hawkesford *et al.* 2012) [28]. The tissue variation in nitrate assimilation in wheat under eCO₂ is not well supported. In order to maintain carbon-to-nitrogen (C/N) ratios, it is expected that increasing carbon and sugar availability under eCO₂ will activate N assimilation pathways. Alternatively, the C/N response occurs when an external sucrose supply inhibits nitrate-mediated seedling growth enhancement (Martin *et al.*

2002)^[29]. Additionally, a number of transcription factors (TF) have been recognized as crucial regulators of the Arabidopsis nitrate response (O'Brien *et al.*, 2016)^[30].

- **Gene expression regulating carbon allocation**

Additionally, a number of transcription factors (TF) have been found to be crucial regulators of the nitrate response in Arabidopsis (O'Brien *et al.* 2016)^[30]. The expression of nitrate-responsive genes is impacted by variations in the activity or expression levels of these TFs in response to nitrate. Additionally, the auxin sensor AFB3 exhibits calcium-independent transcriptional regulation in response to nitrate. It was demonstrated that CIPK23 phosphorylates the nitrate transceptor NPF6.3 (CHL1/NRT1.1), which inhibits the main nitrate response at low nitrate concentrations (Ho *et al.* 2009)^[31]. TaNAC4 and TabHLH1 were observed to be upregulated under nitrogen-deficient conditions in wheat (Mahmoud *et al.* 2020)^[32]. It was earlier stated that TaNAC2-5A is inducible by nitrate and plays a role in nitrate signalling by controlling the expression of nitrate transporters (He *et al.* 2015)^[33]. There is very little information regarding the impact of EC on nitrogen-responsive TFs and nitrogen signaling components in crop plants such as wheat. Adavi and Sathee 2021^[34], performed a study to explore how plant growth under EC influences (1) the shoot/root balance of nitrogen assimilation and (2) the transcript levels of nitrogen signaling and metabolism genes; two wheat genotypes, BT-Schomburgk (BTS, with high leaf NR activity) and Gluyas Early (GE, with high root NR activity) were utilized for this research. Increased atmospheric CO₂ reduces the activity of nitrate and ammonia assimilatory enzymes along with the expression of related genes. In N-deficient conditions, EC enhances the expression of genes involved in N assimilation and signaling; conversely, under high N availability, it disrupts gene expression, leading to a decline (Adavi and Sathee 2021)^[34]

- **Root growth dynamics**

In a future with high CO₂, belowground root mass may become an increasingly significant carbon sink due to carbon fertilization, where elevated CO₂ (eCO₂) increases biomass production. This sink is caused by both young forests' increasing root mass and mature forests' stocks and fluxes that are thrown out of balance by CO₂ (Ziegler *et al.* 2023)^[36]. However, greater reliance on soil nutrient availability results from increased growth under elevated CO₂ (Norby *et al.* 2016)^[37]. This is especially evident in agricultural studies because produce have lower nutritional value (Fernando *et al.* 2014)^[38]. According to Terrer *et al.* (2019)^[39], the availability of phosphate and nitrogen seems to be crucial for long-term growth response and could constitute a limiting factor in soils that aren't fertilized.

Root growth may become phosphate limited due to a close relationship between nitrogen levels and phosphate mobility in soils (Marklein and Houlton 2012; Edwards *et al.* 2006)^[40, 41]. Such nutrient constraints may limit the amount and duration of carbon fertilization of fine root growth, thereby limiting its long-term potential as a carbon sink (Terrer *et al.* 2019; Norby and Zak 2011)^[39, 42]. Plants may be able to get around some of the consequences of nutrient limitation through belowground colonization through root system growth. Competition for space may hinder such colonization in mature ecosystems; mycorrhizal fungal hyphae can help by reaching areas that roots cannot reach, and these microbial communities are

comparatively stable with eCO₂ (Norby and Zak 2011)^[42]. In general, it is difficult to determine the extent and timeframe of carbon fertilization of belowground root mass, especially in old forests, due to the challenges of non-destructive observation of below-ground systems (Felipe-Lucia *et al.*, 2018)^[43].

2.2 Soil-plant interactions

- **Microbial community feedbacks**

Free-air CO₂ enrichment (FACE) studies have been used to study the impacts of eCO₂ levels on soil ecosystems, and the results show that rising CO₂ has a major impact on soil organisms. However, conflicting findings have been found regarding microbial composition and function in relation to nitrogen and carbon cycling (Rosado-Porto *et al.* 2022)^[44]. It was discovered at the BioCON field experiment that ambient CO₂ (aCO₂) and eCO₂ have distinct microbial community structures (He *et al.* 2010)^[45]. On the other hand, several FACE studies have found no impacts of eCO₂ on the structure and activity of the soil microbiome. Marhan *et al.* (2011)^[46] reported that the abundances of nitrate-reducing bacteria and total 16S rRNA genes were influenced by sampling date and depth rather than CO₂. Dunbar *et al.* 2014^[47] described that neither bacterial nor fungal community structure nor composition were altered under eCO₂. According to Pujol Pereira *et al.* 2013^[48], eCO₂ had no discernible effects on soil C, N, or bacterial abundance. Although eCO₂ decreased the number of C and N functional genes, Butterly *et al.* (2016)^[49, 48] found no evidence of alterations in the organization of microbial communities. According to Rosado-Porto *et al.* (2022)^[44], changes in the microorganisms involved in the various processes of these cycles under elevated carbon dioxide have an impact on the dynamics of the nitrogen cycle in grassland soils. Increases in plant-derived ¹³C enrichment and the relative abundances of distinct phylogenetic clades comprising Bacteroidetes and Gemmatimonadetes in the bacterial community and Funneliformis associated with arbuscular mycorrhizas in the fungal community were correlated with the acceleration of phytate mineralization in the rhizosphere zones caused by elevated CO₂ (Jin *et al.* 2022)^[51].

Caravaca *et al.* (2022)^[52] grew *Nicotiana glauca* and *Mirabilis jalapa* in five different semiarid soils at ambient (410 ppm) or elevated (760 ppm) CO₂ levels in order to compare the effects of elevated CO₂ on the rhizosphere bacterial and fungal communities of two invaders with varying degrees of invasiveness. The genera *Sphingomonas*, *Stenotrophobacter*, and *Gaiella* were the most prevalent bacterial indicator species in the rhizosphere of *N. glauca* plants cultivated in an environment with higher CO₂.

- **Nutrient cycling modifications**

Future C sinks in global forests are primarily influenced by the CO₂ fertilization effect on net primary productivity (NPP), yet the projected C sinks with CO₂ enrichment are still debated because of possible constraints related to nutrient limitation as noted in Fig 3 (Wang *et al.* 2020)^[53]. Particularly the supply of nitrogen (N) and phosphorus (P) significantly restricts plant growth in global terrestrial forests, thus limiting the extent of NPP reactions to increasing CO₂ and climate warming (Du *et al.* 2020)^[54]. Du *et al.* 2025^[55] indicates that climate warming leads to a significant rise in nitrogen availability in typically

nitrogen-limited boreal and temperate forests, while resulting in a minor increase in phosphorus availability in typically phosphorus-limited tropical forests. Moreover, nutrient limitations differ among forest biomes and probably impose unique restrictions on the future reactions of NPP and C sinks to increasing CO₂ levels (Du *et al.* 2020, De sesto *et al.* 2024) [54]. Nutrient availability limits the ability and speed at which terrestrial plants absorb carbon (Goll *et al.* 2012) [56]. N and P are the nutrients that typically restrict plant growth (Du *et al.* 2020) [54]; therefore, they have been the focus of extensive research and large-scale modeling initiatives.

3. Opportunities Associated with Carbon Fertilisation

3.1 Enhanced plant productivity

- **Crop yield potential under elevated CO₂ (eCO₂)**

An important factor contributing to rising CO₂ concentrations is the rise in extreme precipitation events and changing patterns (Zhang *et al.* 2021) [57]. On the other hand, eCO₂ can be helping plants (CO₂ fertilization effect). By altering leaf gas exchange, including net photosynthetic rate, transpiration rate, stomatal conductance, plant growth, and biomass, eCO₂ typically either promotes or inhibits plant growth, which ultimately affects WUE (Lawson and Blatt 2014) [58, 59]. Conversely, eCO₂ frequently causes stomatal closure, which lowers transpiration rate and may maintain a high plant water status and lessen the effects of drought (Tausz-Posch *et al.* 2015) [60]. In addition to decreasing water loss through partial stomatal closure, which lowers transpiration rates, this action raises canopy density and total yield (Gonsamo *et al.* 2021) [4]. According to a number of studies, the impact of eCO₂ on WUE can vary greatly among species, with C₃ plants often being more responsive than C₄ plants because of variations in their photosynthetic processes (Zhang *et al.* 2021) [57]. However, because of their effective stomatal control, C₄ species may exhibit higher WUE under eCO₂ in drought situations.

According to Bai *et al.* (2025) [61], eCO₂ raised maize, rice, and wheat yields by about 12%, 17%, and 22%, respectively. For these three crops, variations in biomass were responsible for 39%, 28%, and 43% of the yield response, respectively. While the belowground biomass had a greater impact in rice, the non-yield components of the aboveground biomass in maize and rice had direct effects and served as mediating variables. According to Manderscheid *et al.* (2014) [62], maize will only benefit from an increase in [CO₂] during droughts; it won't gain from an adequate supply of water. Reduced stomatal conductance, which may preserve soil water and postpone the beginning of drought stress, is thought to be the cause of the CO₂ fertilization effect of C₄ crops during drought (Ghannoum 2009) [63].

- **Water use efficiency**

According to El Masri *et al.* (2019) [64], WUE is the quantity of carbon that plants absorb for every unit of water lost. This physiological measure is predicated on the theoretical claim that stomata ought to function to reduce the quantity of water used for each unit of carbon acquired. Due to rising CO₂, water use efficiency (WUE), which measures the trade-off between carbon assimilation and water used or released as transpiration, has been seen to rise over the past few decades (Soh *et al.* 2019; Zhang *et al.* 2022) [65, 66]. The carbon fertilization effect, which is the

rise in photosynthesis and vegetation production brought on by rising atmospheric CO₂ concentrations, may be the source of an increase in WUE (Wang *et al.* 2020) [53] or by decreased transpiration rates caused by CO₂-mediated stomatal suppression or a combination of both. Plant characteristics such as leaf habit and biome type have been discovered to influence WUE gains in response to increasing CO₂ (Soh *et al.* 2019) [65]. However, despite a significant rise in WUE, previous research revealed little indication of a carbon fertilization effect in terms of tree development (van der Sleen *et al.* 2017) [67], suggesting a major influence of transpiration suppression. According to a review (Walker *et al.* 2021) [68] that synthesizes a variety of evidence for CO₂-fertilization, there is high confidence that global primary productivity and WUE have increased over the historical period (Mndela *et al.* 2022) [69], but due to the complexity of the issue, there is low to medium confidence in the magnitude and low confidence in how much such changes are attributable to rising CO₂.

- **Stomatal response to Elevated CO₂**

Although plant responses to elevated CO₂ vary, typically elevated CO₂ alters plant physiology and development via two mechanisms: (1) higher primary productivity and photosynthesis as a result of carbon fertilization; and (2) suppression of the rate of leaf transpiration due to a decrease in stomatal conductance and density caused by elevated CO₂ (Ahmad *et al.* 2024) [70]. At various temporal and spatial dimensions, both of these processes have the potential to directly or indirectly modify the hydrological cycle, including the water balance (Steinthorsdottir *et al.* 2012) [71]. Clarifying the stomatal response to CO₂ concentrations is essential to understanding stomatal physiology and gas exchanges between vegetation and the atmosphere. In order to adapt CO₂ absorption for photosynthesis and water release for transpiration, plants must control stomatal growth and behaviour to balance CO₂ and water exchange through the leaf epidermis in a changing environment (Lawson *et al.* 2014) [58, 59]. Increased CO₂ typically results in decreased stomatal conductance (Ainsworth and Rogers 2007; Gao *et al.* 2015) [13, 72], stomatal density (SD, *e.g.* Teng *et al.* 2009) [73], leaf transpiration (Katul *et al.* 2010), and canopy/ecosystem evapotranspiration (Bernacchi and VanLoocke 2015) [75]. Because the opposite reaction could happen when increased CO₂ combines with other climatic conditions, some research have questioned this response.

- **Enhanced drought tolerance in certain ecosystems**

According to Wang *et al.* (2022) [76], eCO₂ improved leaf water status during drought conditions rather than conserving soil water. This was demonstrated by a higher leaf relative water content (LRWC) and a less negative midday leaf water potential, which were caused by a decrease in stomatal conductance (gs) and an increase in the root to shoot ratio. However, the "water saving effect" and/or the "low intercellular CO₂ concentration (Ci) effect" are two ways that eCO₂ may interact with drought stress. According to the "water saving effect," which has been shown in both grasslands and forests, a lower gs under eCO₂ decreases plant transpiration, leading to a greater soil water content (SWC; Duursma and Medlyn 2011) [77]. SWC under eCO₂ was often higher than that under ambient CO₂ concentration (aCO₂), but the difference decreased when subjected to drought, according to Paudel *et al.* (2018) [78]. Through increases in photosystem II efficiency,

water use efficiency, antioxidative defense capacity, and nutrient uptake and allocation, eCO₂ improved mulberry plants' resistance to drought (Shi *et al.* 2025) ^[79]. Additionally, it was found that soybeans under drought stress had higher levels of malondialdehyde (MDA) accumulation and highly activated antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) to adapt and scavenge the free radicals caused by drought stress (Li *et al.* 2020, Zhang *et al.* 2024) ^[80, 57]. The higher WUE under eCO₂ suggests that plants may exhibit tolerance to future high CO₂ concentrations during drought circumstances (Zhang *et al.* 2021) ^[57]. Additionally, during drought stress, increased photosynthesis under eCO₂ causes a buildup of carbohydrates, which raises cell osmotic potential and facilitates osmotic correction. (Ulfat *et al.* 2021) ^[81].

3.2 Potential role in climate change mitigation

- **Carbon sequestration in vegetation and soils**

The growing atmospheric CO₂ had an effect on the carbon (C) source-sink interactions of terrestrial ecosystems, the biochemical pathway of plant nutrients, soil microorganism activity, and plant physiological processes (Dotaniya *et al.* 2016) ^[82]. While SOC has been demonstrated to grow, remain constant, or even decrease in elevated CO₂ (eCO₂) studies, plant biomass often increases (van Groenigen *et al.* 2014) ^[83]. Conflicting studies have assessed how rising CO₂ levels affect soil carbon stores, and it is inherently difficult to detect changes in soil carbon (Walker *et al.* 2021) ^[68]. In CO₂-enrichment experiments, plants associated with arbuscular mycorrhizae improve soil-carbon stocks more than those associated with ectomycorrhizae, claim Terrer *et al.* (2016) ^[84].

The quantity of carbon stored in plants and soil would eventually have to be traded off at the ecosystem-scale in a CO₂-enriched atmosphere. Bossio *et al.* (2020) ^[85] state that grasslands, shrublands, and other ecosystems with substantial soil-carbon stocks have a considerable possibility of acquiring more soil carbon when CO₂ levels rise. Bastos and Fleischer (2021) ^[86] found a coordinated increase in soil carbon storage and above-ground plant biomass caused by elevated CO₂. High CO₂ levels significantly affected soil microbial populations, increasing microbial biomass C and respiration rate by 15% and upregulating genes linked to carbon and nitrogen metabolism by 12%, according to a 2024 study by Tariq *et al.*

- **Forest biomass accumulation**

According to He *et al.* (2023) ^[88], CO₂ fertilization has dominated the forest biomass C sink during the past few decades. This paper is a crucial step in better understanding the crucial role that forests play in land-based policies for climate change mitigation. The general upward trend of tree-ring growth in recent decades, particularly in cold and nitrogen-poor conditions, is supported by enhanced nitrogen recycling through increased litterfall under rising atmospheric CO₂, according to Guo *et al.* (2022) ^[89]. According to Leuzinger *et al.* (2011) ^[90], older forests are unlikely to exhibit the CO₂-driven growth stimulation that is frequently observed in young, growing tree plantations or fertilized trees. According to Klein *et al.* (2016) ^[91], there is no proof that raising CO₂ levels over their current levels can boost Norway spruce above-ground productivity and growth. Important species- and tissue-specific reactions,

however, can still result in competitive advantages or disadvantages among species given the ubiquitous, ongoing rise in CO₂. By promoting mycorrhizal and root growth, increased CO₂ can improve plant nutrient usage efficiency and increase nutrient absorption, potentially leading to positive feedbacks in the long run (Norby *et al.*, 2024) ^[92]. Dawes *et al.* (2011) ^[93, 42] found no growth response to increased CO₂ in *Pinus uncinata* during a 9-year treeline FACE experiment in which trees grew at their lower temperature limit. However, in *L. decidua*, CO₂-induced growth stimulation persisted for at least the seventh year of treatment, suggesting that this species benefited from additional carbon even in the face of low growth temperatures.

- **Long-term carbon storage in forest ecosystems**

Elevated CO₂ can increase forest carbon storage in two ways: increased wood output and deeper or mineral-associated SOC (Fig. 4) (Norby *et al.* 2024) ^[92]. In forests with enough N/P and low disturbance risk, CO₂-driven production is more likely to lead to long-term carbon storage. Active management, such as stopping deforestation, reducing the risk of fire, and maintaining nutrient cycles, strengthens the sequestration effect (Richy *et al.* 2024) ^[94]. If more of the extra fixed carbon is absorbed by long-lived woody biomass (stems, coarse roots), carbon can be stored for decades or even centuries. According to recent research, certain old forests have increased woody biomass under increasing CO₂, which is a favourable route for long-term storage (Norby *et al.* 2024) ^[92]. Increased root exudation, leaf litter, and root formation are frequently caused by elevated CO₂; if stable, these inputs can raise soil organic carbon (SOC) (Schufft *et al.* 2025) ^[95]. Although process models based on FACE data indicate that CO₂ fertilization can increase forest C stocks for decades to centuries, estimates of century-scale sequestration are highly uncertain due to assumptions about nutrient limitation, turnover rates, disturbance, and acclimation (Walker *et al.* 2015) ^[96]. Root growth and decomposer activity may be significantly impacted by increases in soil pCO₂ (Johnson and Henderson 2018) ^[97]. Increasing atmospheric [CO₂], increasing temperature, elevated nitrogen deposition and intensified management will change this C store (Hyvönen *et al.* 2007) ^[98].

3.3 Support for degraded ecosystem restoration

- **Increased vegetative cover**

Vapor pressure deficit (VPD), or rising atmospheric dryness, can restrict photosynthesis and lower vegetation output. In the meanwhile, carbon dioxide (CO₂) fertilization and global warming can both be advantageous to plants. According to Song *et al.* (2022) ^[99], the decrease in global SIF (or GPP) caused by rising VPD was similar to the rise caused by warming, but it was significantly smaller than the increase caused by elevated CO₂ concentration. In water-limited habitats, the growing response of LAI to SM is consistent with the CO₂ fertilization effect on WUE, suggesting that a given amount of SM has sustained higher levels of photosynthetic foliage over time (Gonsamo *et al.* 2021) ^[4]. The annual sequestration of 112-169 PgC (1PgC = 1015g carbon) by terrestrial vegetation is essential to the global carbon recycling process. Vegetation carbon sequestration varies under different land management practices (Sha *et al.* 2022) ^[100]. Higher CO₂ increases the rate of photosynthesis

(carbon fixation) in many plants (Taub 2010) ^[101]. With more photosynthate (sugars) available, plants often grow more producing more leaves, stems, roots, overall biomass. Elevated CO₂ dramatically increased the aboveground biomass and net photosynthetic rates of annual ryegrass by 14.5% and 25.3% under sufficient P supply (0.5mM), respectively (Li *et al.* 2016) ^[102].

- **Soil carbon rebuilding**

Jastrow *et al.* 2005 ^[103] revealed the potential for mineral soils in diverse temperate ecosystems to store additional C in response to CO₂ enrichment. The natural processes of photosynthesis and humification of biosolids added to the soil are the foundation for carbon sequestration in terrestrial ecosystems (soil and biota) (Lal 2009) ^[104]. In high CO₂ environments, increased soil microbial activity brought on by higher biomass carbon inputs may hasten the decomposition of soil organic matter (SOM) (Maity *et al.* 2020) ^[105]. Increased inputs of readily biodegradable and soluble carbon may also encourage macro-aggregation and protect SOC within aggregates (Ghiat *et al.* 2021) ^[106]. While substrates with a lower C:N ratio may encourage microbial respiration because of their greater capacity for carbon metabolism, substrates with a wider C:N ratio may show slower respiration processes under increasing CO₂, helping to stabilize organic carbon in the soil (Al Maliki *et al.* 2017) ^[107]. A labile pool with a high turnover rate is created by removing CO₂ from the atmosphere through plant photosynthesis, transferring CO₂ from the atmosphere to plant biomass, and transferring organic carbon from plant biomass to the soil (Kuzakov *et al.* 2019) ^[108]. The potential for terrestrial C uptake to reduce rising atmospheric CO₂ concentrations has been questioned since it has been proposed that a higher rate of C flux through the soil compartment as a result of elevated CO₂ concentrations limits C sequestration in terrestrial ecosystems.

4. Challenges and Limitations

4.1 Nutrient constraints

- **Decline in plant nutrient contents under eCO₂**

Elevated CO₂ enhances carbon assimilation and reduces stomatal conductance, which results in increased seed yield, whereas root biomass showed no significant change. However, concentrations of several seed nutrients, particularly iron (Fe), zinc (Zn), manganese (Mn), boron (B), phosphorus (P), potassium (K), and magnesium (Mg), declined at maturity (Kaur *et al.* 2025) ^[109]. Reductions in micronutrients content of C₃ grains and legumes under elevated CO₂ may exacerbate essential micronutrient deficiencies worldwide, potentially affecting nearly 2 billion people in both developing and developed countries (Tulchinsky, 2010) ^[110]. Soybean cultivars differ markedly in their biomass and yield responses to eCO₂ (Sanz-S  ez *et al.* 2017) ^[111], and some genotypes also exhibit reductions in seed mineral content, including Fe and Zn, in eCO₂ conditions (Myers *et al.* 2019) ^[112].

- **Downregulation and acclimation of photosynthesis**

Photosynthetic down-regulation under elevated CO₂ (eCO₂) concentrations could be linked to the reduced nitrogen (N) availability after long-term exposure to eCO₂ (progressive nitrogen limitation, PNL) or leaf N dilutions resulting from excessive accumulation of non-structural carbohydrates (Byeon *et al.* 2021) ^[113]. Under conditions of high fruit load, photosynthetic rates declined

by approximately 4% in eCO₂ greenhouses, without showing significant differences in the biochemical parameters of photosynthesis (Hassan and Ito 2023) ^[114]. In *Pyrus*, drought-induced suppression of photosynthetic acclimation to elevated CO₂ was primarily associated with reduced stomatal conductance, decreased mesophyll diffusional efficiency, thinner mesophyll layers, and smaller mesophyll cells (Hao *et al.* 2023) ^[115]. Even when photosynthesis per leaf was reduced, plants grown under elevated CO₂ compensated by developing a larger total leaf area. This increase more than offset the decline in leaf-level photosynthesis, resulting in greater carbon uptake, faster growth, and higher overall biomass (Wang *et al.* 2022) ^[116, 76]. At very high CO₂ levels (720 ppm), key processes such as photosynthesis, carbon fixation, and carbohydrate production remained active at the gene-expression level, despite reductions in chlorophyll content and the accumulation of carbohydrates in leaves (Kim *et al.* 2022) ^[117]. In addition, plants exposed to elevated CO₂ appear to adjust their hormonal balance, with increases in auxin and bioactive cytokinins (including zeatin and isopentenyl adenine). These hormonal changes may slow leaf aging and improve nitrogen recycling within the plant, helping to sustain carbon assimilation even under biochemical constraints (Torralbo *et al.* 2025) ^[118].

- **Nitrogen and phosphorus limitations**

Because elevated CO₂ stimulates photosynthesis and subsequent growth responses, it is anticipated that elevated CO₂ will significantly increase plant phosphorus needs. Increases in rooting depth and changed root shape are two factors that contribute to elevated CO₂ altering P acquisition (Jin *et al.* 2015) ^[119]. Increased allocation of labile carbon belowground, which promotes microbial turnover of organic matter and mobilization of chemically bound P, is likely how CO₂ fertilization increases nutrient availability, especially for phosphate, in P-limited soils. eCO₂ has been linked to accelerated nutrient turnover rates in the first six months of the experiment, with higher N (+175%) and P (+211%) mineralization rates compared to ambient rings, though these effects were temporary (Hasegawa *et al.* 2016) ^[120]. According to Liu *et al.* (2013) ^[121], increased CO₂ and N addition may help tree species overcome P constraint since they have a stronger effect on P dynamics than N in subtropical forests. Plant P absorption may decrease under eCO₂ due to intense competition with microorganisms, as shown by Ben Keane *et al.* (2023) ^[50]. This could have consequences for the productivity of P-limited ecosystems in the future as a result of climate change. This is supported by the fact that ecosystem responses differ depending on the type of soil: aboveground biomass rose by 16 percent in a limestone grassland while microbial biomass P stayed the same, while aboveground productivity and P uptake decreased by 11 and 20 percent, respectively, in an acidic grassland, while microbial P immobilization increased by 36 percent.

4.2 Negative impacts on food quality

- **Reduced protein, micronutrient concentrations**

Interactions between elevated CO₂ and N and P fertilisation significantly influenced shoot biomass at anthesis and straw biomass at harvest maturity. When fertiliser supply was limited, biomass yield showed little respond to CO₂ level (Chakwizira *et al.* 2022) ^[122]. In contrast, under optimum fertiliser rates, both shoot and straw yield

increased (10.0–34.0%) as CO₂ levels rose. Across multiple experiments, grain yield increased by about 15.6% with increasing CO₂, which resulted in grain nutrient concentration declining (3.0–13.0%) with increasing CO₂. Notably, micronutrients and vitamins that are already commonly deficient in human diets such as folate, iron, and zinc—are among the most negatively affected by rising CO₂ (Bailey *et al.* 2015) ^[123]. The response effect of seed weight to eCO₂ is variable and influenced by the nutrient availability, particularly nitrogen. Similarly, seed germination responses are variable, while seed vigour that indicates the strength of a seed usually is reduced under eCO₂ (Lamichaney and Maity 2021) ^[124]. Joshi *et al.* 2010 ^[125] revealed that Fe and Zn concentrations in wheat grains varied across locations and years and are influenced by elevated temperature and availability of Zn in 30–60 cm soil depth.

- **Impacts on human nutrition and food security**

Current evidence suggests that long-term exposure to eCO₂ has limited effect on overall soil N availability. However, important risks remain, including decreasing soil phosphate (P) availability and increased greenhouse gas emissions (methane [CH₄], nitrous oxide [N₂O]), challenging food security sustainability, global food security inequity will likely worsen (Wang *et al.* 2025) ^[126]. For wheat (*Triticum aestivum* L.) which is a major food crop worldwide, reductions in grain nitrogen content under elevated CO₂ raise concerns for human protein consumption (Table 1.), especially in developing countries where cereals are major components of the diet (Ainsworth and Long 2021) ^[127]. Evidence also shows that weeds can respond more than crops to rising CO₂, with consequences for crop production (Ziska *et al.* 2022) ^[128]. Sionit 1981 noted that leaves developing in elevated CO₂ exhibited increased carbohydrate levels, higher C:N ratios, and reduced nitrogen concentrations. In soybean, cultivars grown in fields subjected to higher temperatures and increased CO₂ demonstrated lower levels of seed Fe and Zn, yet high temperatures combined with elevated CO₂ levels did not exhibit reductions compared to control conditions (Kohler *et al.* 2019) ^[129]. Wang *et al.* (2019) ^[130] stated that warming might only partially counteract the effect of increased CO₂ on grain protein levels, while sacrificing grain yield, failing to completely alleviate the adverse impacts of climate change on agricultural output. Smith and Myers (2018) ^[131] conducted a worldwide evaluation of increased CO₂ effects on the consumption of iron, zinc, and protein in 151 countries, considering age and gender, while maintaining fixed diets and omitting other climatic influences that could impact food production. The adverse impacts of high CO₂ levels on rice, maize, and wheat—the three most commonly eaten staple crops suggest a rise in global food insecurity as atmospheric CO₂ concentrations increase (Dakora *et al.* 2025) ^[132].

4.3 Ecosystem imbalance and biodiversity concerns

- **Altered species competition**

Whilst growth promotion is a common outcome associated with high CO₂ (eCO₂), it is not necessarily a reflection of enhanced long-term carbon sequestration in plant biomass. Whilst growth may be promoted, a potential trade-off could occur if growth rate accelerations, in response to eCO₂, are associated with decreased plant survival chances or shorter life spans (Maschler *et al.* 2017). Notably, a majority of the

available CO₂ enrichment experiments on perennial plant types have not been of sufficient duration to accurately determine trends in plant survival across all life stages, which currently makes it impossible to determine the accurate impact of eCO₂ on plant survival, aside from its impact on young plant life stages. Agricultural plant growth experiments exposed to eCO₂ have indicated accelerated leaf senescence for annual crop species (Sakai *et al.* 2001) ^[133]. Yet, what may occur is a more rapid depletion of carbon sinks in plant biomass exposed to eCO₂, which may be misinterpreted as a reduction in plant life-span, specifically among perennial plant types. Another essential aspect, regarding plant life-span, is the duration of carbon turnover in deceased plant life, which defines plant carbon turnover (Raich and Schlesinger 1992) ^[134]. This defines the rate of carbon return to the environment, as well as life-span over which plant nutrients remain sequestered in organic form, preventing plant uptake (Adams *et al.* 1970) ^[35].

- **Shifts in ecosystem structure and function**

In an eight-year experiment within a C₄ agroecosystem (maize), elevated CO₂ significantly altered both the functional and phylogenetic structure of soil microbial communities (at both 0–5 cm and 5–15 cm depth). Exposure to eCO₂ increased the abundance of genes involved in carbon (C), nitrogen (N), and phosphorus (P) cycling indicating increased microbial functional potential (Xiong *et al.* 2015) ^[135]. A recent meta-analysis (2024) spanning many studies reported that eCO₂ generally increases microbial biomass C and soil respiration (~ +15%) and upregulate genes / enzyme activities associated with carbon acquisition and cycling (~ +12% for C acquisition enzymes), but observed a decline (~ 5%) in nitrogen-acquiring enzyme activity. This suggests a shift in balance: more emphasis on C processing at the expense of nitrogen acquisition (Fig 5.). Additionally, fungal-to-bacterial ratios increased under eCO₂. Such microbial shifts can strongly influence decomposition dynamics, organic matter turnover, nutrient availability, and thus influence long-term soil carbon storage and soil fertility (Tariq *et al.* 2024) ^[187]. Under eCO₂, the “active microbiome” in soils may shift new microbial taxa may become more dominant compared to ambient-CO₂ conditions (Rosado-Porto *et al.* 2023) ^[136]. In a 25 year grassland global change experiment, researchers found that while species diversity under ambient conditions continued to support productivity and stability, the positive influence of diversity on ecosystem stability weakened under treatments combining elevated CO₂ and nitrogen enrichment (Butler *et al.* 2025) ^[137].

4.4 Soil and microbial constraints

In many forests and grasslands, P (in addition to N) limits the capacity of plants and soil microbes to utilize extra C. Rising CO₂ levels can raise plant P demand and intensify competition between plants, microbes and mycorrhizal fungi for scarce P sometimes weaken the overall net CO₂ fertilisation effect (Jiang *et al.* 2024) ^[138]. eCO₂ often increases carbon concentrations in plant tissues and roots relative to N and P changing substrate quality entering the soil (higher C:N and altered C:P). Soil microbes are highly sensitive to these substrate stoichiometry: when N or P availability are limited, microbial decomposition can slow or shift toward nutrient acquisition processes such as “nutrient mining” (accelerated SOM turnover and priming), or microbes may become C-rich but nutrient-poor. These

stoichiometric shifts feedback to plant nutrition and CO₂ fertilisation persistence (Huang *et al.* 2015) ^[139]. eCO₂ effects are strongest in the rhizosphere and surface soil but can extend deeper via increased root penetration. Because deeper SOM pools often behave differently (sometimes greater stabilization or altered turnover), so whole-profile C outcomes depend on root dynamics and soil mineralogy.

5. Carbon Fertilisation across Ecosystems

5.1 Agricultural systems

The study by Chakwizira *et al.* (2024) ^[140] indicated that elevated concentrations of atmospheric CO₂ increased grain yield by 15.6%, but this increase was associated with a decrease in grain nutrient concentrations of 3-13%. This decrease was mainly ascribed to the 'nutrient dilution effect', where the increase in carbohydrate content in the grain contributed to the decrease in nutrient concentrations. In general, the availability of fertilizer had a bigger effect on crop responses than CO₂ enrichment, and nitrogen deficiency was more potent than phosphorus deficiency. The responses of crops to elevated CO₂ concentration from growing season ambient concentrations of CO₂ (350-400 ppm) towards elevated concentrations (550-800 ppm), particularly when nitrogen fertilizer is sufficient, increase biomass and grain growth in temperate cereals as evident from controlled-environment experiments, including glasshouse experiments and free-air CO₂ enrichment experiments, depending on the availability of nitrogen fertilizer (Ainsworth and Long 2021) ^[127]. Several factors, including reduced nitrogen influx in roots and lower transport from roots to shoots, have been advocated as possible causes for the decrease in the nitrogen and protein contents of elevated-CO₂-grown shoots and grain in wheat experiments (Gojon *et al.* 2022; Shi and Bloom 2021) ^[141, 142]. In general, the growth of total plant dry matter under eCO₂ is less than nitrogen influx, and thus lower nitrogen concentrations per unit dry matter—an effect also known as nitrogen 'dilution'. This could be due to high storage of 'non-structural carbohydrates', including 'soluble sugars and starch', and other compounds like 'structural carbohydrates', 'organic acids', and 'lignin', as shown in other studies by Andrews *et al.* in 2020 and Krämer *et al.* in 2022) ^[143, 144].

Apart from nitrogen, several other major nutrients and minerals, including Phosphorus, Potassium, and Sulfur, and also Calcium and Magnesium, also exhibited similar decrease in concentrations in vegetative growth and grain of CO₂-enriched wheat as examined by Fernando *et al.* 2012 ^[145] and other studies as shown in the study by Chakwizira in 2024. These stimulated changes due to elevated CO₂ concentration on these several other mineral nutrients cannot be attributed solely due to 'carbon dioxide dilution effects on carbohydrate concentrations'. To support this, it was found that the concentrations of K, Ca, and Mg in the xylem sap were lower in wheat cultivars growing under high CO₂ concentrations (Houshmandfar *et al.* 2015; Li *et al.* 2016) ^[146, 102]. There were also differences in nutrient harvest index, also referred to as shoot nutrient allocation to the harvest index, under high CO₂ concentrations. The impact of CO₂ concentrations on wheat cultivars is therefore very significant in terms of plant physiology, grain yield, and quality (Wang *et al.* 2022) ^[116, 76]. In wheat cultivars, the reduction in grain protein content under high CO₂ concentrations will impact bakery quality and end use (Fernando *et al.* 2014; Panozzo *et al.* 2014) ^[38, 147]. The reduction in the protein content was attributed to the direct effect of starch overaccumulation in the wheat grain caused by CO₂ concentrations ((Panozzo *et al.* 2014) ^[147]. The study by

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5.2 Arid and semi-arid ecosystems

Yang *et al.* 2025 ^[148] revealed that simulated tree growth was more dependent on climate trends than on atmospheric CO₂ concentration. Their mechanistic analysis indicated that the regulation of stomatal conductance under water limited condition positively affected tree growth in the arid region, but produced the opposite response in the semi-arid environments. Although intrinsic water-use efficiency (iWUE, estimated from tree-ring $\delta^{13}\text{C}$) has increased by 29% and 44%

since 1900 CE in the arid and semi-arid regions, respectively, but did not translate radial tree growth. CO₂ fertilization effect was found to increase productivity in tropical forests through increased assimilation and light use efficiency (Yang *et al.* 2016) ^[149]. Elevated CO₂ (eCO₂) typically reduces stomatal conductance, allowing plants to meet photosynthetic carbon demands more efficiently and earlier, which leads to improved water use efficiency (eWUE). This makes plants exposed to elevated CO₂ to be more resistant to drought/water stress. Deep-rooted vegetation, i.e. broad-leaf evergreen trees, and deciduous broad-leaf trees thrive under elevated CO₂ concentration through enhanced water use efficiency and carbon assimilation (Geremew *et al.* 2022) ^[150]. The improved WUE resulting from carbon fertilization and higher rain under warming will supersede the increased evapotranspiration water loss due to radiative effects (Dubey and Ghosh 2023) ^[151].

5.3 Grasslands and savannas

Rising atmospheric CO₂ levels are shaping the dynamics of tropical savanna vegetation. While C₃ trees and grasses generally show strong positive growth responses to CO₂ fertilization, whereas responses to CO₂ by C₄ grasses are more variable (Del Toro *et al.* 2024) ^[152]. The changes in carbon dynamics within grassy-dominated ecosystems are changing, due to not only the indirect effects of anthropogenic climate change but also the direct effects of increasing atmospheric CO₂ (Bond and Midgley 2012) ^[153]. Models projections suggest that continued increasing atmospheric CO₂ will result in the expansion of C₃ vegetation at the expense of the C₄ grasslands (Still *et al.* 2019) ^[154], and CO₂ fertilization has been proposed as a key mechanism underlying the widespread encroachment C₃ woody plants into C₄-grass-dominated savannas (Stevens *et al.* 2017) ^[155], with knock-on impacts on herbivores, fire, and the carbon cycle. In experimental settings, C₄ grasses can be highly responsive to CO₂ concentrations both in and out of competition with C₃ plants (Pan *et al.* 2022) ^[156], especially when grasses are water limited. Multi-decadal observational data are needed, yet observations of grass biomass or community change often record patterns that are difficult to attribute to changing CO₂ as opposed to other drivers. For instance, long-term monitoring datasets give some indication that grass biomass may be increasing in C₄ savannas in the tropics (Staver *et al.* 2018) ^[157] but attributing this to CO₂ fertilization has been a challenge. Variations in rainfall, CO₂ fertilization, and fire and grazing patterns have all been connected to an increase in the density of woody stems in savannas. CO₂ functions as a fertilizer for plant development when its concentration in the atmosphere rises. As anticipated from the CO₂ fertilization effect on water usage efficiency and plant development, there will eventually be greater amounts of plant leaf materials as transpiration decreases with increasing CO₂ concentration. Woody vegetation invasion is typically linked to increasing patterns in growth in shallow-rooted plants (Geremew *et al.* 2022) ^[150].

5.4 Forest ecosystems

The equilibrium between positive (such as increased photosynthesis as a result of rising atmospheric CO₂ concentrations) and negative (such as increasing drought and wildfire frequency and severity) drivers determines the net forest carbon sink (Hogan *et al.* 2024) ^[158]. According to Davis *et al.* (2022) ^[159], whereas other environmental conditions produced a combination of both positive and negative impacts, rising carbon dioxide had a substantial and persistent beneficial

effect on wood volume. Although other reasons, such as nutritional constraint, may have outweighed the potential advantages of rising CO₂ levels, warming-induced stress was invoked in the majority of surveyed case studies to explain growth decline (Silva and Anand 2012) ^[195]. Over the past few decades, CO₂ fertilization has dominated the forest biomass C sink (Table 2), which is a crucial step in comprehending the crucial role that forests play in land-based climate change mitigation programs (He *et al.* 2023) ^[88]. Globally, the CO₂ suppression effect on stomatal conductance (28%) was comparable to the CO₂ fertilization effect on photosynthesis (23%). According to Zhang *et al.* (2022) ^[66], the stomatal suppression effect controlled the EWUE trend over tropical forests, whereas the fertilization effect prevailed over semi-arid environments. A crucial knowledge of the Amazon rainforest's evolution in the face of more frequent and severe extreme climate events is provided by rising CO₂, which affects forest carbon dynamics and vulnerability (Yao *et al.* 2024) ^[160]. The effects of elevated CO₂ (eCO₂) on carbon sequestration can be divided into two categories: indirect effects, such as partial stomatal closure and consequently increased water use efficiency (WUE; CO₂ physiological forcing), and direct effects, such as higher leaf carboxylation rates, which may result in a higher leaf area index, higher tree productivity, and increased biomass (also referred to as CO₂ fertilization) (Smith *et al.* 2020) ^[161]. McDowell *et al.* (2022) ^[162] have suggested that eCO₂ has a favorable influence on increasing tree loss; nevertheless, it has been difficult to show a meaningful association between eCO₂ and carbon loss (Hubau *et al.* 2020) ^[163]. Although extreme water stress can counteract the anticipated CO₂ fertilization effects, Fatichi *et al.* (2016) ^[8] found that indirect effects on production from eCO₂ tend to be more noticeable in ecosystems with limited water supplies (Kolby Smith *et al.* 2016) ^[164].

5.5 Wetlands and peatlands

Peat has been impacted by recent increases in atmospheric CO₂, according to several observations. C accumulation rates: (i) photosynthesis was the primary driver of variation in acrotelm peat accumulation (Charman *et al.* 2013) ^[165]; (ii) peat C accumulation in Alaskan mires increased approximately threefold over the course of the twentieth century (Loisel and Yu, 2013) ^[166]; and (iii) variations in leaf area index were the primary driver of variation in net ecosystem exchange between mires. (Lund *et al.* 2013) ^[193]. Elevated CO₂ often stimulates photosynthesis and above- and below-ground productivity in peatland/wetland plants (including vascular plants and, to varying degrees, Sphagnum), but the response is highly conditional on water table, nutrient status (especially N and P), and vegetation shifts (Fenner *et al.* 2007) ^[167]. Increased plant production under elevated CO₂ can increase carbon inputs to peat, but can also alter redox conditions, rooting and oxygen transport and therefore change decomposition and methane (CH₄) fluxes sometimes increasing CH₄ emissions or, via "oxygen priming", increasing aerobic decomposition (Kao-Kniffin and Zhu 2013) ^[168]. Nutrient supply (N, P) and hydrology (water-table depth) are the main moderators that determine whether elevated CO₂ results in net C sequestration or in increased GHG emissions (CO₂ + CH₄). Recent syntheses emphasise that peatland responses are spatially variable and that some peatlands may already be losing their sink function under changing climate (Mander *et al.* 2025) ^[169].

6. Management Strategies to Maximise Benefits

6.1 Nutrient management (N, P, micronutrients)

- **Focused nutrient application:** The application rates of N and P to be based on soil test levels and estimates of biomass production in eCO₂ environments; increase seasonal fertilizer application rates if soil analysis indicates deficiencies and biomass increase is detected in higher CO₂ levels (Wang *et al.* 2025) ^[126].
- **Divide applications and timing:** Divide N into applications (or apply fertigation) synchronized with crop uptake to minimize losses and sustain available N during peak growth under eCO₂. Implement advanced-efficiency N products when suitable (nitrification inhibitors, controlled-release N) to prolong N availability and minimize emissions, during extended uptake periods caused by increased growth.
- **Precision P placement and banding:** Band P near seed/roots to increase early P uptake (critical when eCO₂ stimulates early growth). Low-P soils may require starter phosphorus or rock phosphate and biological approaches (mycorrhiza). (Wang *et al.* 2019) ^[130]. Organically or recycle nutrient sources integrate mineral fertilizers with composts, manures, or biochars to improve nutrient availability and mitigate the fertilizer pulse applied in monocultures (Ng *et al.* 2023) ^[170].

6.2 Soil carbon enhancement approaches

- **Biochar:** Increasing soil carbon enhances soil aggregation improves water holding capacity, and improves cycling. Which in turn ensures continuous plant growth due to higher CO₂ concentrations. Studies have also shown that biochar, conservative tillage practices, and organic amendments are viable alternatives in plant growth due to their climatic-dependent interactive effects (Ng *et al.* 2023) ^[170]. Align biochar feedstock and pyrolysis parameters with soil requirements (for example use alkaline biochar for soils); combine with compost or mineral fertilizers to prevent temporary nitrogen immobilization; apply at feasible agronomic rates (trial, with 5-20 t ha⁻¹ depending on cost-effectiveness). Track phosphorus and micronutrient behaviour since biochar may adsorb or release nutrients (Pei *et al.* 2020) ^[171].
- **Conservation tillage (no-till / reduced till):** Decreases SOC mineralization enhances surface SOC accumulation and boosts aggregate stability; additionally it improves water retention potentially enhancing CO₂ advantages in water- environments. Meta-analyses consistently indicate SOC increases compared to tillage although the extent varies with climate, residue handling and sampling depth (Srivastava 2025) ^[172]. Management tips: combine no-till with residue retention, cover crops and crop rotations (otherwise SOC gains can be small). Watch for stratification of nutrients (surface accumulation) and adapt fertilizer placement accordingly.

6.3 Plant breeding and biotechnology

- **Carbon-efficient cultivars:** Target traits: improved photosynthetic capacity per leaf area (e.g., Rubisco kinetics, mesophyll conductance), lower respiratory losses, improved water-use efficiency (because eCO₂ reduces stomatal conductance), and improved harvest index under higher biomass. Field evaluation under elevated CO₂ (FACE or chamber) is essential because genotype × CO₂ interactions are common (Tausz *et al.* 2013) ^[173].

Enhanced sink strength traits

- **Root traits:** Deeper and finer root systems for soil C inputs and nutrient foraging (enhance belowground sinks).
- **Storage sinks:** Larger grain-filling capacity, greater stem carbohydrate storage or stronger partitioning to harvestable organs.
- **Biotechnological strategies:** Alter sugar transporters boost the capacity of storage enzymes. Adjust signalling mechanisms that regulate the source-sink equilibrium. Selecting for robust sinks enhances the likelihood that additional photosynthate is converted into yield instead of temporary non-harvest biomass (Tausz *et al.* 2013) ^[173].

Landscape-level and ecosystem-based management

CO₂ fertilisation effects and carbon sequestration are scale-dependent landscape planning maximises co-benefits (biodiversity, fire resilience, water regulation) while reducing leakage (i.e., carbon gains in one field causing losses elsewhere) (Denney *et al.* 2025) ^[174].

- **Mosaic governance and land integration:** Merge zones of high-yield cropping (where focused nutrient and sink control enhances CO₂ accumulation) with protected regions (forests, riparian zones, rehabilitated grasslands) that sequester carbon over periods and offer ecosystem benefits. Landscape optimization methods (LP models, prioritization) assist in balancing timber/food output, against carbon storage. (Hundal *et al.* 2024) ^[175].
- **Agroforestry and woody perennials:** Integrate trees or hedgerows to create long-lived biomass sinks and microclimatic buffers can substantially increase landscape carbon storage and stabilize gains from CO₂ fertilisation (Kay *et al.* 2019) ^[176].
- **Nutrient-flow regulation:** Synchronize nutrient distribution throughout the terrain to prevent runoff concentration areas that could diminish enduring soil improvements and damage downstream habitats. Encourage the use of buffer zones. Wetlands to capture nutrients and sequester carbon (Hundal *et al.* 2024) ^[175].
- **Fire and disturbance planning:** In fire-prone systems, reduce wildfire risk through landscape fuel management; large fires can negate decades of sequestration. Prioritize fire-resilient species and mosaic fuel breaks (Hundal *et al.* 2024) ^[175].

7. Future Perspectives

- Advantages of CO₂ fertilisation are limited by factors like nutrient supply, water scarcity and the nature of the ecosystem.
- Future investigations must connect divide between controlled trials such as FACE (Free-Air CO₂ Enrichment) and actual ecosystem reactions where biotic and abiotic stresses occurs.
- Regenerative farming practices like cover crops, reduced tillage, varied crop rotations, agroforestry and organic matter additions can boost ongoing productivity in conditions of increased CO₂.
- Future Earth system models will aid in forecasting how increased CO₂ interacts with warming changed precipitation and nutrient cycles to influence terrestrial carbon sinks.
- Extended records from carbon flux towers, soil observatories, remote sensing platforms and coordinated ecological networks will assist in capturing processes such as soil carbon buildup, nutrient reduction and changes, in vegetation.

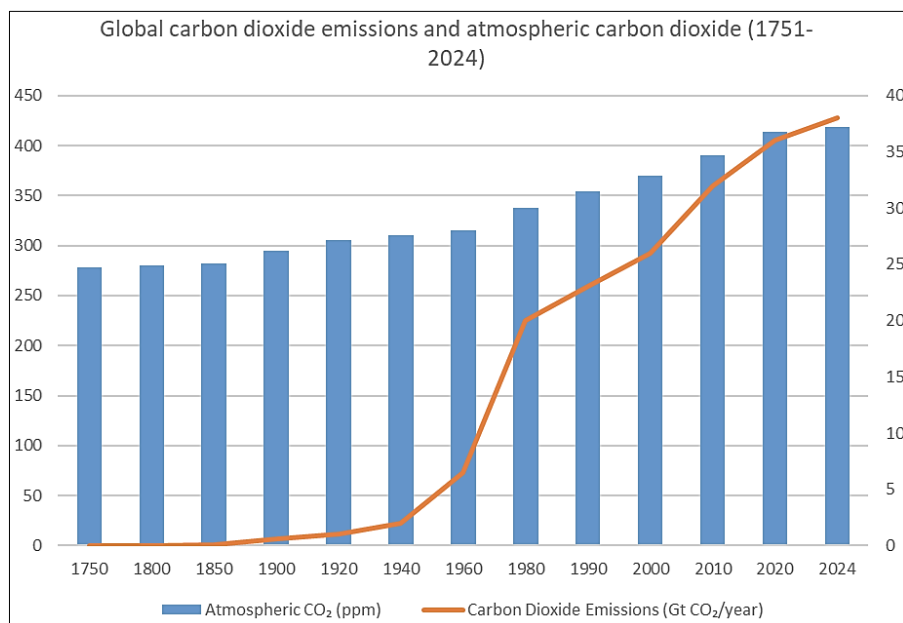


Fig 1: Global CO₂ emission and Atmospheric carbon dioxide



Fig 2: Carbon fertilisation

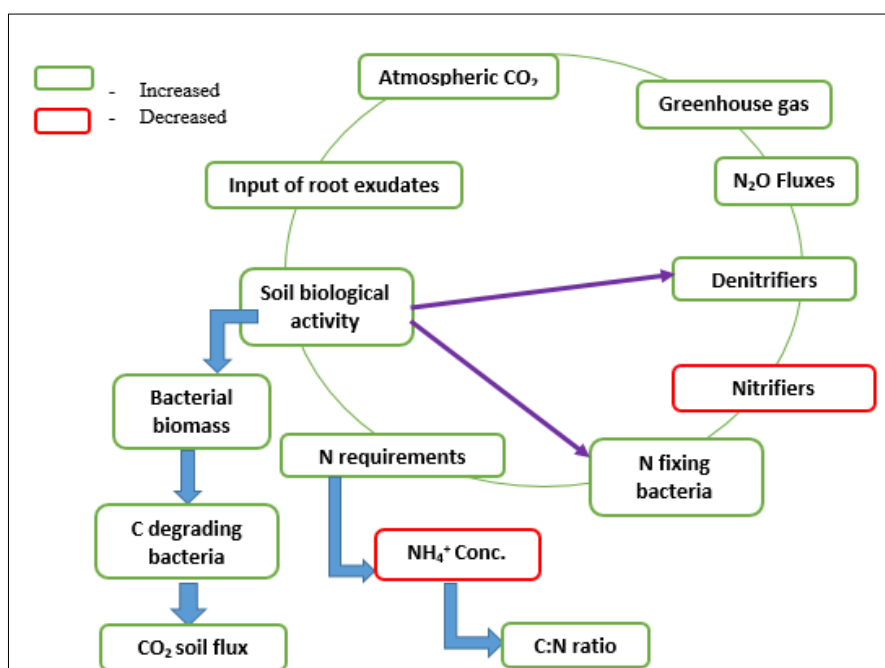


Fig 3: Nutrient cycling and Carbon fertilisation

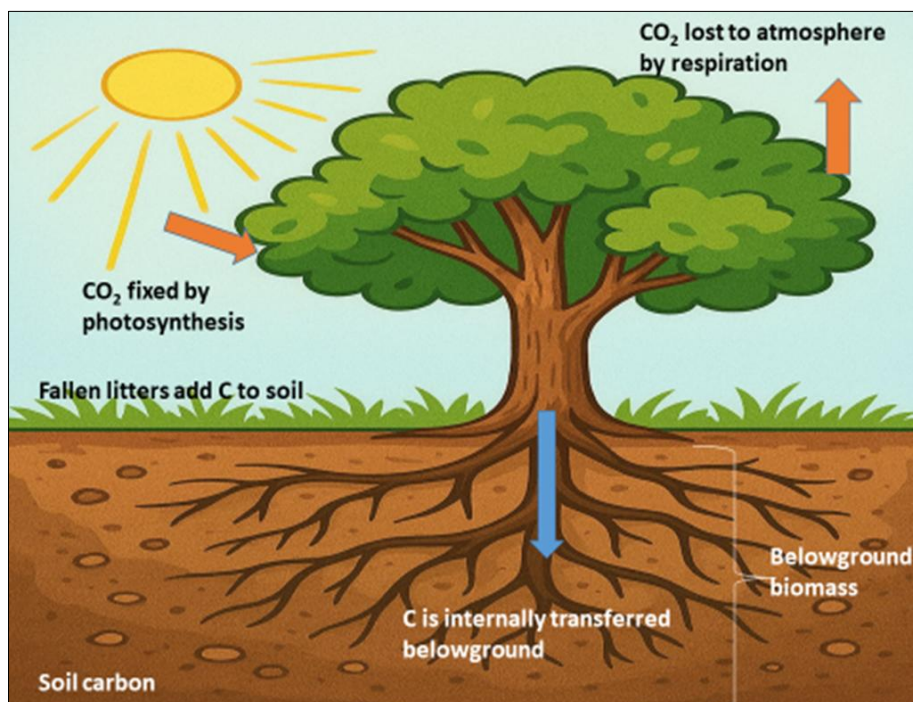


Fig 4: Elevated CO₂ and Carbon sequestration

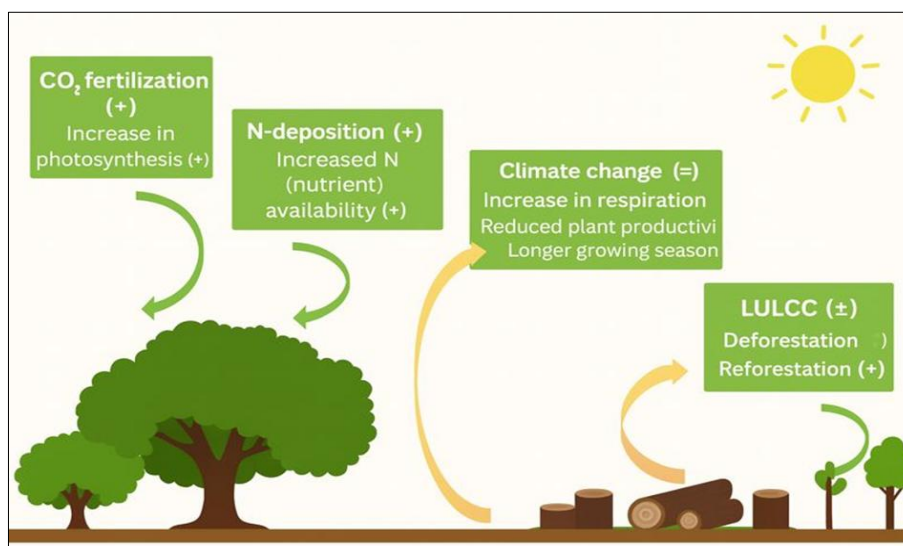


Fig 5: Schematics of CO₂ fertilization

Table 1: Effect of eCO₂ on human nutrition

Crop	Yield Change (%)	Protein Content	Mineral concentration	Implications	References
Wheat	↑ 10-15	↓ 7-10%	↓ Zn, Fe	Food quality risk	Dubey <i>et al</i> 2015
Rice	↑ 8-12	↓ 20.5%	↓ Fe	Hidden hunger	Liu <i>et al</i> 2017
Soybean	↑ 15-20	Slight↓	Variable	Mixed outcomes	Lenka <i>et al</i> 2017
Potato	↑ 25	↑ 13.9%	↓ Zn	Food quality	Liu <i>et al</i> 2025
Lettuce	↑ 18%	-	↓ Zn, Fe	Nutrient decline	Sgherri <i>et al</i> 2017
Carrot	↑ 19	↓ 20.5%	↓ Fe	Nutritional quality	Dong <i>et al</i> 2018
Parsley	↑ 17%	-	-	Food quality	Dong <i>et al</i> 2018
Tomato	↑ 15%	↓ 10.5%	↓ Zn	Accumulation of antioxidants	Zhang <i>et al</i> 2014

Table 2: Effect of carbon fertilisation across different ecosystems

Ecosystem Type	Productivity Response	Carbon Storage	Nutrient Limitation	aClimate Feedback	References
Forests	Moderate-high	High	N, P limitation	Net sink (variable)	Walker <i>et al</i> 2021
Grasslands	Moderate	Medium	N limitation	Short-term sink	Siddig and Warrag 2023
Agroecosystems	High (with inputs)	Low-medium	Managed nutrients	Management-dependent	Yu <i>et al</i> 2021
Wetlands	Variable	High	Oxygen limitation	CH ₄ trade-offs	Valach <i>et al</i> 2021
Arid and Semi-arid	Moderate	Low- medium	N, P limitation	Management-dependent	Jensen <i>et al</i> 2024

8. Conclusion

Carbon fertilisation offers meaningful opportunities to enhance plant growth and strengthen terrestrial carbon sinks, but its benefits are neither uniform nor guaranteed over time. Nutrient limitations, declining plant nutrient quality, altered microbial functioning, and ecosystem feedbacks can restrict long-term productivity gains. Sustainable use of this phenomenon requires management strategies that support nutrient balance, soil carbon protection, biodiversity, and climate resilience. As CO₂ levels continue to rise, combining improved field practices with advanced modelling and long-term monitoring will be vital for predicting ecosystem trajectories and safeguarding food and ecological security. Responses vary widely across ecosystems such as forests, grasslands, croplands, peatlands, and arid regions, where nutrient constraints—especially nitrogen and phosphorus often limit long-term gains. Ultimately, carbon fertilisation should be viewed not as a stand-alone solution, but as one component within broader climate-smart ecosystem management.

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Authors' contributions

- **Vishakha Bandgar:** Conceptualization, methodology, literature search, writing - original draft.
- **Bhimrao Kamble:** Data curation, visualization, writing - review & editing.
- **Ritu Thakre:** Supervision, critical revision.
- **Shriganesh Shelke:** Provided technical guidance, manuscript proofreading.
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The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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