

Research progress on the cellular and molecular mechanisms of carbon dioxide The fertilisation effect on the Plant Photosynthesis

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Abstract. Plants display improved photosynthetic functionality through the carbon dioxide fertilisation effect under environments with higher atmospheric CO₂ concentrations. Various technical constraints remain regarding omics-based research exploring photosynthetic control mechanisms under CO₂ enrichment. Future research must combine multiple experimental factors, high-speed phenotype analysis features, and imaging systems to learn about dynamic controlling operations. This research creates an extensive conceptual framework to promote future investigations about Plant adaptive mechanisms, agricultural improvement, and ecosystem direction at elevated atmospheric CO₂ concentrations.

Keywords: High concentration of CO₂; Photosynthetic regulation mechanism; Multi-omics integration technology; Plant adaptability research.

1. Introduction

The global atmospheric CO₂ levels have increased dramatically since pre-industrial times, when they reached 280 ppm, to exceed 415 ppm in 2024 because of human-made emissions [1]. The dramatic increase in CO₂ concentrations has become the leading cause of worldwide climate change while transforming essential ecological processes throughout all terrestrial environments. Academic and scientific interest around the carbon dioxide fertilisation effect (CFE) has strengthened because researchers recognise this phenomenon as both a biological mechanism and a controller of vegetation carbon cycle patterns [2] [3].

The CFE improves photosynthetic carbon assimilation through increased Calvin - Benson cycle substrate availability, which benefits C₃ plants because their Rubisco enzyme shows high CO₂ affinity [4]. The carbon fertilisation effect impacts primary metabolic activities and plant morphology, transpiration, biomass distribution, and competitive plant interactions at different biological levels [5]. Academic research in plant biology, combined with ecological and scientific investigations of environmental change, requires an immediate focus on understanding CFE mechanisms because climate change is accelerating. At the same time, atmospheric CO₂ interacts with plant responses [6].

The main impact of CO₂ enrichment on organisms appears through its regulation of photosynthetic activity. The fertilisation effect boosts Rubisco carboxylation efficiency through increased intercellular CO₂ levels, improving carbon fixation and decreasing photorespiration losses in C₃ plants [7]. The increase in CO₂ levels leads to limited stomatal closure that reduces water loss through transpiration and enhances water-use efficiency by 30% in specific environments [8]. The physiological adjustments result in temporary increases of net primary productivity and changes in biomass allocation patterns, mainly in nitrogen-rich or well-irrigated environments [9].

At an ecological range, CO₂ fertilisation affects species combinations, competitive systems, and natural carbon reservoirs. Changes in photosynthetic efficiency impact functional plant groups differently between C₃, C₄, and CAM species, which alters successional patterns and vegetation structure [10]. Ecosystem resilience and plant performance show nonlinear and threshold effects when CO₂ enrichment occurs with other environmental stressors like temperature, water availability, and nutrient limitation [11]. Complex system dynamics demonstrate the requirement for uniting

physiological knowledge within ecosystem prediction models that track the long-term effects of climate change on land masses [12].

Researchers have extensively investigated the macroscopic effects of CO₂ fertilisation that led to biomass increase and yield variability, but the systematic analysis of its cellular and molecular pathways remains insufficient [13]. Researchers need to study these detailed mechanisms because they help forecast Plant adaptive actions when environmental conditions change in predicted climate patterns, specifically when light, water, nutrients, and temperature coexist [14]. The diverse reaction patterns across different species and developmental states make it difficult to apply CO₂ findings across populations; therefore, additional integrated physiological and genomic studies are required [15].

Researchers have combined recent discoveries about Plant molecular and cellular reactions to CO₂ increase to produce this review, which examines photosynthetic process control, chloroplast developmental patterns, gene functional changes, enzymological activities, and regulatory hormonal networks. The paper first explores the significance of photosynthesis to plants for growth and development, then presents its biological importance.

2. The Role of Photosynthesis in Plant Growth and Development

2.1 Contribution to Stress Tolerance and Water Use Efficiency

The specialised Kranz anatomy of C₄ plants creates spatial separation between CO₂ fixation and the Calvin cycle, reducing photorespiration and increasing CO₂ levels at the Rubisco active site [16]. C₄ plants like maize and sorghum show stronger photosynthetic capabilities at high temperatures combined with reduced water supply than C₃ species do.

The adaptive mechanism of stomata depends on their ability to adjust their functionality through aperture control. Plants facing CO₂ elevation and drought conditions maintain sufficient photosynthetic CO₂ levels after restricting stomatal aperture to decrease water loss. The adjustment enables plants to improve their intrinsic WUE by 15 – 30% based on species and environmental conditions [17]. Research demonstrates that C₄ plants can quickly decrease their stomatal conductance under vapour pressure deficit conditions without affecting their net CO₂ uptake, showing carbon gain separates from water loss [18].

The photosynthetic regulation under stress shows a strong link between physiological factors such as abscisic acid (ABA) signalling and anatomical elements. During periods of drought, ABA concentration rises, which prompts stomata to close and activates genes responsible for tolerance to dehydration while operating, and sugar molecules are generated by photosynthesis [19]. By integrating structural adaptations, metabolic flexibility, and signalling networks, photosynthesis enables plants to mitigate environmental stress while maintaining productive carbon metabolism. The abovementioned traits serve vital functions in personal plant existence and create stable agricultural yields despite climatic instability.

2.2 Integration with Nitrogen Metabolism and Environmental Signals

Photosynthesis is a tightly controlled metabolic network with nitrogen metabolism that aims to achieve balanced carbon – nitrogen assimilation. GS is a prominent enzyme within this cross-talk pathway that converts ammonium and glutamate into glutamine using ATP. The metabolic reaction functions as a bridge that links photosynthesised carbon molecules with processes of nitrogen assimilation [20]. Research shows that GS activity matches photosynthetic abilities and biomass development, particularly when N sources vary.

The Calvin – Benson cycle suffers from decreased carboxylation efficiency while photorespiration increases when plants experience nitrogen deficiency because this deficiency reduces Rubisco content. Photosynthetically fixed carbon moves toward amino acid synthesis and photorespiration pathways when plants experience such conditions, which reduces growth efficiency [21]. The synthesis of

amino acids and indirect Calvin cycle support occurs through redox and carbon status feedback loops that moderate nitrate accumulation, activating enzymes like NR and NiR [22].

Environmental light signals control photosynthetic efficiency by influencing pigment production, photosystem operation, and Rubisco activation mechanisms. The combination of red light improves the chlorophyll a/b ratio and PSII efficiency, yet blue light activates Rubisco activase to enhance CO₂ fixation [23]. The acidification of chloroplasts, non-photochemical quenching, and phytochrome-mediated gene expression are influenced by far-red and UV light. The mechanisms unite to prove how photosynthesis functions as an integrated system that reacts to both resource availability and surrounding light signals. This dynamic coordination allows plants to optimise resource utilisation and maintain metabolic homeostasis under variable environmental conditions.

2.3 Ecosystem-Scale Implications of Photosynthesis

Through photosynthesis, plant growth sustains at different levels as the process regulates atmospheric carbon fluxes and facilitates belowground carbon allocation. The primary method of carbon capture through photosynthesis creates terrestrial carbon reserves while controlling global carbon cycling patterns. Plants distribute fixed carbon through their tissues, but most of it exits the Plant through deposited litter, root exudates, and symbiotic behavioural patterns with other organisms [24].

The arbuscular mycorrhizal fungus (AMF) can remarkably advance photosynthetic efficiency across ecosystems as it enters mutualistic relationships with every second plant species inhabiting terrestrial land areas. The photosynthetic capacity of host plants increases through AMF because these fungi improve water and nutrient uptake, especially phosphorus, and control stomatal conductance and chloroplast stability [25]. The photosynthetic net rate of poplar trees grows 18 – 42% higher after they receive AMF inoculation because the trees maintain increased intercellular CO₂ concentrations, and PSII shows better photochemical efficiency [26]. Tree growth increases through supported biomass development while the rhizosphere receives more stable carbon deposition.

The carbon content in soil experiences increased stabilisation because AMF create physical aggregations and chemical bindings of organic matter. The glomalin compounds released by hyphal networks and other compounds help create soil macroaggregates, which result in 20 – 40% higher soil carbon content in certain ecosystems [27]. The increase in photosynthesis delivers additional advantages to the plant system by strengthening soil ecology and sustaining it against drought conditions while preserving long-term carbon storage. These research findings demonstrate how photosynthesis drives ecosystem function by using aboveground and belowground network connections as a key factor in reducing the effects of climate change.

3. The Mechanism of Action of the Carbon Dioxide Fertilization Effect at the Cellular and Molecular Levels

Plants exhibit multiple physiological and biochemical reactions because of the carbon dioxide fertilisation effect, which produces large-scale morphological growth and ultrastructural changes in genetics and enzyme activity down to the cellular level. The adaptive response of plants depends on hormonal communication and resource-based allocation that determines their capacity to adapt to environmental changes.

The molecular effects of CO₂ enrichment involve altering the patterns of gene expression dedicated to carbon metabolic processes, light-harvesting components, and stress response mechanisms. Rubisco and PEPC undergo both transcriptional and post-translational modification and metabolic feedback-based regulation. CO₂ serves simultaneously as a signalling molecule that affects plant physiology through an integration process between calcium-dependent pathways and hormonal transduction systems. The current research elaborates on the complex molecular procedures that elevated CO₂ levels affect plant functions while demonstrating how these cellular mechanisms relate to genomic control for improving crops and adapting plants to climate change [28].

3.1 Cellular-Level Mechanisms of CO₂ Fertilization

Atmospheric CO₂ levels that rise above normal levels trigger cellular-level physiological changes, boosting carbon assimilation efficiency and optimising resource consumption. The most rapid physiological response involves stomatal conductance regulation. The increase in atmospheric CO₂ levels results in reduced stomatal aperture among various C₃ plants without substantial impacts on their CO₂ absorption efficiency. The adjustment leads to better intrinsic water-use efficiency, and scientists have recorded this effect in wheat, soybean, and rice [29]. The process of CO₂-sensitive guard cell turgor regulation occurs through abscisic acid (ABA) accumulation and reactive oxygen species (ROS) signalling [30].

Elevated CO₂ concentrations modify chloroplast structure and the number of chloroplasts present in plant tissues. CO₂ enrichment stimulates chloroplast multiplication, resulting in advanced thylakoid membranes and enhancing photosynthetic capacity for every unit of leaf surface [31]. The chloroplasts under elevated CO₂ levels contain more starch granules and larger grana structures, improving their photochemical and carbohydrate storage capabilities [32]. The development of cells and organs receives stimulation from environments enriched with CO₂. High carbon availability activates cell cycle regulators and cyclin-dependent kinases in the apical meristems of roots and shoots to increase their mitotic activity [33]. Research shows that Arabidopsis and tomato seedlings exhibit increased leaf area and root elongation after CO₂-responsive upregulation of CYCD3;1 and CDKA;1 [34].

The distribution of auxin and cytokinin hormones depends on CO₂ levels because the gas affects their biosynthesis process, which controls cell expansion and differentiation patterns. The roots of rice plants exposed to elevated CO₂ levels accumulate more auxin in their tips, which leads to better lateral root development and improved nutrient absorption capabilities [35]. The ability of plants to modify their cellular structures at this scale lets them acquire carbon but also stay flexible during environmental changes.

3.2 Molecular-Level Regulatory Mechanisms of CO₂ Fertilization

The molecular processes of CFE reorganise various genetic directives while affecting enzyme operations and signalling pathways to optimise photosynthetic mechanical functions. The Calvin - Benson cycle is a primary target for CO₂-induced transcriptional regulation through genes that encode ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Accumulated evidence demonstrates that elevated CO₂ levels lead to increased *rbcL* and *rbcS* gene expression in C₃ species, including Arabidopsis, rice, and wheat, and this prompts higher production of Rubisco protein and faster carboxylation rates [36], [37].

Photosynthetic enzyme activity and enzyme stability become modulated by post-translational modifications when plants experience CO₂ enrichment. Under changing CO₂ and light environments, Rubisco activase functions as a molecular chaperone that requires redox-sensitive thiol modification and phosphorylation for proper activation [38]. The activity of sucrose-phosphate synthase (SPS) enzymes, which participate in sucrose biosynthesis, depends on phosphorylation events that respond to both carbon status fluctuations and circadian signal changes [39].

Diverse genes that participate in chlorophyll biosynthesis, light-harvesting complexes, and antioxidant defence systems experience effects from increased CO₂ amounts. DNA sequencing studies indicate that CO₂ enrichment leads to increased expression of *psbA*, *psbD*, and *LHCB* and chloroplast-localised *APX* and *SOD* genes, which enhance photoprotection and electron transfer efficiency [40].

Through genetic control mechanisms, elevated CO₂ levels modify photosynthetic gene expression, metabolic gene expression, and alter enzyme activities through post-translational modifications and interact with calcium-ion-based and hormone-mediated signal transduction pathways. Research needs further investigation regarding how different species react to changes in CO₂ conditions, how signals respond to these changes, and what lasting effects result from regulatory shifts.

4. Problems in Current Research

The study of elevated CO₂ impacts on plant photosynthesis has made substantial progress, yet research on carbon dioxide fertilisation effect (CFE) faces multiple methodological, conceptual, and practical barriers. Research papers focus on controlled environment experiments, but these systems fail to replicate realistic natural ecosystems and their long-term variations. Omics-based research has exposed numerous candidate genes and pathways affected by CO₂ enrichment, but scientists need to finish validating these components and connecting them to integrated regulatory systems [41].

Various essential regulatory factors, including non-coding RNAs, epigenetic modifications, and hormonal communication, perform inadequately in the present CO₂ response modelling systems. Ecosystem assessments continue to face difficulties when applying laboratory research to practical tactics for crop improvement and carbon sequestration strategies. The incomplete understanding calls for accurate research methods, unifying analytical approaches, and ground-based field tests. As described in the subsequent sections, three main research gaps prevent a complete understanding and practical application of CO₂ fertilisation effects.

4.1 Methodological Limitations

The current research on CFE faces a significant obstacle because existing observation methods struggle to achieve precise measurements of cellular and subcellular changes. The technical difficulty of observing chloroplast morphological changes, including volume alterations, thylakoid rearrangement, and starch accumulation under different CO₂ concentrations, becomes especially challenging when studying living organisms. The structural data provided by confocal and electron microscopy cannot replace the non-invasive real-time analysis of photosynthetic organelle behaviour because these techniques lack the necessary temporal resolution [42].

Omics technologies, including transcriptomics, proteomics, and metabolomics, have greatly expanded our understanding of CO₂-responsive pathways. However, studies with these methods encounter substantial background interference, plenty of erroneous results, and minimal experimental test repeatability. Many speculated regulatory factors remain unsupported because the functional validation of differential genes or proteins is insufficient. The current methods to unify multi-omics datasets create fragmented and unclear regulatory networks because they stay at an early stage of development [43].

There is a significant deficiency in converting laboratory experimental findings into practical applications. Research demonstrating elevated CO₂ performance and biomass production through photosynthesis mainly happens under tightly controlled environments of constant light and optimal temperatures with abundant nutrients. Laboratory conditions favour exposure to constant environmental factors for field crops and wild species, yet these conditions regularly diminish or prevent the benefits obtained through laboratory testing. Growth chamber studies that show positive CO₂ effects fail to produce similar results when field experiments are conducted under conditions of nitrogen deficiency or drought stress [44]. The methodological problems combine to decrease the reliability and reproducibility of findings related to CFE. Research in these three areas needs to progress to deal with these problems.

4.2 Mechanistic Gaps in Regulatory Networks

The identification of many genes and proteins which respond to CO₂ remains inadequate to explain the regulatory mechanisms which control the photosynthetic responses to elevated carbon dioxide levels. A lack of clarity exists regarding the mechanisms which regulate the upstream factors that control changes in the expression of genes like *rbcL*, *LHCB*, or *SPS*, according to findings from various research studies [45]. Environmental CO₂ changes lead to correlative relationships between physiological changes rather than establishing mechanistic explanations of the causal chain.

Researchers have insufficiently explored the connection between several signalling pathways, which currently include carbon status signals alongside light quality signals, nutrient availability

signals, and hormonal cues signals. The physiological connections between CO₂ signalling and ABA or auxin pathways have been documented, yet researchers have not identified the specific molecular points where these pathways meet [46]. The incomplete understanding of how plants respond to diverse signals when conditions in the field change prevents accurate prediction of how they will interact with multiple signals.

Research about non-coding RNA regulation of CO₂-responsive gene expression remains severely underdeveloped, especially regarding microRNAs (miRNAs), long non-coding RNAs (lncRNAs) and circular RNAs (circRNAs). Scientists have established plant development and stress adaptation regulation through these molecules, but their role in CFE-related transcriptional control remains an underdeveloped area of research [47]. Scientific studies have revealed that miR156 and miR172 family members influence vegetative phase changes through carbon signals, though researchers have not commented on elevated CO₂ environments. Addressing these mechanistic blind spots is essential for building predictive models of CO₂ responsiveness and for designing molecular interventions aimed at enhancing photosynthetic resilience under climate change.

5. Future Research Directions

A thorough understanding of plant CO₂ responses depends on considering various environmental elements such as temperature, light, water, and nutrients simultaneously. The relationship between CO₂ enrichment and abiotic stressors will determine how plants perform photosynthetically and survive within natural and managed ecosystems because of more severe climate change predictions. This chapter outlines three strategic directions to guide future inquiry, aiming to deepen mechanistic understanding, improve model accuracy, and facilitate the translation of research findings into practical solutions for crop resilience and ecological sustainability.

5.1 Interdisciplinary and Multi-Scale Research

To comprehensively understand the carbon dioxide fertilisation effect (CFE), future research must adopt a multi-scale systems approach that integrates cellular mechanisms, whole-plant physiology, and ecosystem-level responses. While significant insights have been gained at the molecular level, these findings often lack contextualisation within broader ecological dynamics. The gap must be bridged through an organised system that establishes associations between gene regulation and metabolic pathways and phenotypic traits and population-level outcomes across different CO₂ environments [48].

One promising direction involves the development of integrative modelling platforms that couple omics data with physiological measurements and environmental inputs.

5.2 Design for Complex Environmental Interactions

Gradual manipulation of field CO₂ concentrations and programmable variations in temperature, humidity, and nitrogen levels provide valuable experimental data for analysis. Research with factorial designs helps scientists locate critical points where the performance of photosynthesis and growth shows nonlinear responses and functional trade-offs. High temperatures have been proven to eliminate CO₂ fertilisation benefits by speeding up photorespiration and damaging photosystem II, especially in C₃ crop species [49]. Experimental protocols that include stress factors enable researchers to evaluate CFE stability more accurately when studying climate change effects.

Repeating cycles of cyclic treatment with full or partial heat waves and dry periods helps scientists observe changes in plant adaptation that standard conditions would otherwise hide. The validation of laboratory discoveries in natural ecosystems depends heavily on extensive field trials conducted with FACE facilities. Studies must add sensors and automation systems to their existing trials to monitor photosynthetic rate, chlorophyll fluorescence, stomatal aperture, and soil moisture in real-time [50]. Such experimental approaches, which accept complex conditions instead of simplifying

them, will create better ecologically realistic knowledge about how plants adapt their physiology as CO₂ levels rise and environmental stress increases.

5.3 Development and Application of Emerging Technologies

Developing emerging technologies enables researchers to solve multiple technical challenges in CO₂ fertilisation studies. High-throughput phenotyping platforms represent a practical solution for studying elevated CO₂ effects on plants across diverse environments because they measure various plant traits across significant plant populations. Combining automated imaging and spectral sensors with these systems enables the detection of minor trait variations, including stomatal conductance, chlorophyll content, and canopy temperature, leading to more effective genotypic CO₂ responsiveness identification [51].

In parallel, gene-editing technologies such as CRISPR/Cas9 allow for targeted modification of regulatory genes involved in photosynthesis, carbon allocation, and hormone signalling. Scientists now possess the capability to enhance photosynthetic efficiency through genetic modifications of Rubisco activase genes combined with carbon-sensing kinase regulation under high-CO₂ environments. Research initiatives explain how individual cell types and organelles adapt their operational function under CO₂-rich environments and how these functional changes affect whole-plant physiology [52]. Combined with environmental simulation systems and automated data acquisition, these tools support experimental designs that are both mechanistically informative and scalable to real-world conditions.

6. Conclusion

The research examined cellular and molecular processes of the carbon dioxide fertilisation effect (CFE) on plant photosynthesis while demonstrating the multifaceted influence of increased CO₂ on Plant biological and ecological phenomena. Elevated CO₂ affects plants through two levels of influence: it regulates cell-based chloroplast architecture and stomatal behaviour, and it modifies the entire molecular network, including gene expression and signal transduction mechanisms, which ultimately affect plant functions and production rates. The physiological changes lead to better photosynthesis, improved water conservation abilities, and better hormone regulation and stress tolerance [53].

Despite considerable progress, significant challenges remain. As outlined in Chapter 4, current research is constrained by methodological limitations, incomplete mechanistic models, and a persistent disconnect between laboratory insights and field-level applicability. The gaps that exist control our ability to produce complete predictions or accomplish engineering of plant reactions to elevated atmospheric CO₂ when environmental factors present complex and fluctuating conditions. Several uncertainties exist about species-specific responses, ecosystem feedback mechanisms, and the extended ecological effects of carbon dynamic changes [54].

The field of science requires future researchers to adopt interdisciplinary approaches, multiple research scales, and technological innovations to make progress. This research advance leads to developing climate-safe agricultural plants and improved carbon storage techniques, which provide the basis for policy measures about food stability and sustainable ecosystems.

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