Carbon dioxide and photosynthetic limits

Grant Kinkead
Independent Researcher, Melbourne, VIC, Australia
grant@kinkead.au

***Abstract*—Carbon dioxide is the substrate used for Rubisco-mediated carbon fixation, but increasing its availability does not ensure a proportional increase in photosynthesis. This paper examines when additional carbon dioxide can increase photosynthetic opportunity and why the response subsequently becomes limited by other factors. The evidence indicates that carbon dioxide can relieve a substrate constraint when light, temperature, water status, nutrition and plant physiological capacity are sufficiently favourable. Its effect is conditional because each of these factors can independently limit assimilation or restrict the use of newly fixed carbon. Evidence on light response, vapour pressure deficit, nutrient supply and root-zone oxygenation also demonstrates nonlinear crop behaviour and shifting constraints. Consequently, carbon dioxide enrichment should be interpreted as one component of coordinated environmental management rather than as a universal productivity input. The paper synthesises the mechanisms underlying conditional carbon dioxide response, the evidence for diminishing returns and acclimation, and the limitations that should guide practical interpretation and future validation [1], [2], [3], [4].**

I. Introduction

Carbon dioxide availability can limit photosynthesis because carbon dioxide is the substrate for Rubisco-mediated carboxylation. When carbon dioxide supply constrains this reaction, a greater supply can increase the opportunity for carbon fixation. Yet this biochemical role does not make carbon dioxide an independent determinant of plant performance. The plant must also capture sufficient light, maintain suitable metabolic activity and possess the physiological capacity to use the assimilated carbon. Evidence on elevated carbon dioxide responses identifies interactions with light, nitrogen, drought, heat and photosynthetic pathway, indicating that the magnitude and persistence of response depend on the wider growth environment [3], [5].

The management problem is therefore not whether carbon dioxide can influence photosynthesis, but whether it is the active limiting factor under a particular set of conditions. Artificial-lighting research indicates that gains from lighting depend on adequate carbon dioxide, water, nutrients and other conditions. A crop may receive more photosynthetic radiation without a corresponding increase in assimilation if carbon dioxide or another requirement is limiting. Conversely, increased carbon dioxide may offer little benefit where light is insufficient or where downstream plant capacity is constrained. These dependencies make carbon dioxide response a system property rather than a property of concentration alone [2], [6].

This paper provides an evidence-based explanation of carbon dioxide and photosynthetic limits. It first defines the scope of interacting limitation, then examines the mechanisms by which carbon dioxide can relieve or cease to relieve photosynthetic constraints. It next synthesises evidence on nonlinear responses to associated environmental variables and identifies practical limitations on generalisation. The central argument is that carbon dioxide enrichment can increase photosynthetic opportunity only when light, temperature, water status, nutrition and plant capacity permit its use. Excessive light may itself impose stress, with responses differing among species, cultivars and environmental conditions, reinforcing the need for coordinated interpretation [2], [7].

II. Background and Scope

A useful basis for interpreting carbon dioxide enrichment is that plant responses to inputs are commonly bounded. Reviews of nutrient solution production report heterogeneous crop outcomes and concentration-dependent nutrient effects, including phytotoxicity in some circumstances. This evidence is not a direct carbon dioxide treatment, but it demonstrates why greater input availability should not be treated as an inherently positive or indefinitely scalable condition. The relevance to carbon dioxide lies in the requirement to identify the active limitation, the crop response range and the conditions under which an apparent benefit is reduced or reversed by another constraint [8], [9].

Nutrient strength provides a related example of conditional plant response. Soilless cultivation literature describes inhibitory effects at higher nutrient strength or electrical conductivity while also recognising the importance of adequate nutrient delivery. A crop supplied with additional carbon dioxide still requires nutrient-supported photosynthetic capacity and growth processes to use the added carbon. However, increasing nutrient supply cannot itself resolve inadequate carbon dioxide, poor water status or unsuitable temperature. The limiting factor may therefore shift as environmental conditions change, which means carbon dioxide response cannot be inferred from nutrient supply or concentration in isolation [10], [11].

Prior work on elevated carbon dioxide provides the direct physiological context for this analysis. Carbon dioxide responses vary with light, nitrogen availability, drought, heat and photosynthetic pathway, and these factors influence both immediate assimilation and longer-term plant adjustment. This scope excludes universal concentration prescriptions because the available evidence does not support a single response threshold across crops and environments. Instead, the synthesis focuses on the relationship between carbon dioxide availability and the conditions that determine whether its addition relieves

a photosynthetic constraint or simply exposes another limiting process [3], [12].

III. Core Concepts and Mechanisms

The mechanism of carbon dioxide limitation can be understood as a transition from substrate limitation to another form of limitation. Initially, additional carbon dioxide may permit greater Rubisco carboxylation when substrate availability is restrictive. As supply increases, the constraint may move to light capture, nutrient-supported photosynthetic capacity, water relations, temperature-sensitive metabolism or another component of plant function. Reviews also describe declining or acclimating responses to elevated carbon dioxide. Thus, an initial assimilation gain cannot establish that further enrichment will maintain the same effect, because crop type and environmental conditions influence both the size and duration of response [3], [13].

Crop responses to manipulated light quality illustrate the broader importance of interaction and nonlinearity. Lettuce studies have reported that fresh mass and quality responses to far-red radiation depend on the accompanying red and green light environment and on growing conditions. Although such findings do not directly measure a carbon dioxide dose-response relationship, they show that environmental inputs act through combinations rather than simple independent additions. Carbon dioxide enrichment should therefore be interpreted as an opportunity to relieve a constraint, not as a substitute for crop-appropriate light conditions or a guarantee of equivalent outcomes for biomass and quality [14], [15].

Light-response saturation further clarifies why carbon dioxide effects can diminish. Controlled-environment modelling has indicated that crop response to light may approach saturation while energy demand continues to rise. Where a light-related response has reached a practical limit, additional carbon dioxide may produce little benefit unless it becomes the factor that releases the prevailing constraint. Conversely, where carbon dioxide limits the use of existing light, additional carbon dioxide may allow greater assimilation. The implication is not a universal combination of light and carbon dioxide, but the need to evaluate both variables together in relation to measured crop response [16], [17].

IV. Evidence Synthesis

Water status modifies the conditions under which carbon dioxide can increase photosynthesis. Evidence on rising vapour pressure deficit describes nonlinear plant and transpiration responses, indicating that atmospheric demand cannot be assumed to produce a linear physiological effect. Carbon dioxide entry and water loss are both associated with stomatal behaviour, so unfavourable water relations can restrict the use of increased carbon dioxide availability. The same carbon dioxide treatment may consequently have different outcomes under different vapour pressure deficit conditions. This supports interpreting carbon dioxide opportunity alongside the plant water status that enables sustained gas exchange and carbon assimilation [4], [18].

Controlled-environment reviews similarly position carbon dioxide among interacting variables that include light, temperature and vapour pressure deficit. These sources emphasise contextual optimisation and trade-offs rather than a universal environmental recipe. This systems perspective is consistent with the evidence for shifting photosynthetic limits: improving carbon dioxide availability can only improve assimilation while carbon dioxide remains the operative constraint and while associated environmental conditions support its use. Carbon dioxide management is therefore better viewed as an iterative assessment of crop response than as an isolated input adjustment [19], [20].

Nutrient evidence adds an important distinction between photosynthetic capacity and other measures of plant response. Experimental work has shown that increased nutrient availability can increase photosynthetic capacity while a leaf-to-air carbon dioxide ratio remains unchanged. This finding supports the proposition that nutrient status can affect the capacity to use carbon dioxide without demonstrating that carbon dioxide is limiting under all nutrient conditions. It also cautions against assuming that one favourable indicator predicts every component of crop response. Carbon dioxide enrichment requires assessment against plant capacity and environmental context, not nutrient sufficiency alone [1], [21].

V. Practical Implications and Limitations

Practical interpretation should begin with the recognition that photosynthetic capacity and realised crop response are not interchangeable. Nutrient availability can change photosynthetic capacity, but nutrient effects may differ from effects on other physiological measures. Consequently, a nutrient-replete crop should not automatically be assumed to respond predictably to increased carbon dioxide. A sound assessment would consider whether the crop has suitable light, temperature and water conditions, then determine whether carbon dioxide is plausibly constraining assimilation under those conditions. This approach is more consistent with the available evidence than transferring a presumed enrichment response between contrasting crops or environments [1], [22].

Root-zone conditions also limit the value of aerial environmental adjustment. Under hypoxia, reduced oxygen availability affects energy generation and is associated with reduced nutrient uptake, stomatal conductance and carbon dioxide assimilation in aerial plant tissues. This does not establish atmospheric carbon dioxide as the direct mechanism of limitation, but it demonstrates that compromised root-zone function can reduce the plant capacity required to benefit from favourable carbon dioxide conditions. Carbon dioxide enrichment should therefore not be treated as a substitute for adequate root-zone oxygenation or as a remedy for physiological restrictions arising from hypoxic stress [23], [24].

The evidence also has boundaries that constrain strong recommendations. Far-red research has examined photosynthetic responses under controlled carbon dioxide conditions, but controlling carbon dioxide is not equivalent to testing carbon dioxide as a response factor. Light-spectrum studies

can therefore establish interaction context without defining a carbon dioxide enrichment curve. Similarly, photoperiod and temperature evidence identifies threshold-like biological responses but does not directly establish carbon dioxide saturation. Future validation should explicitly vary carbon dioxide while documenting light, temperature, water status, nutrition, crop identity and relevant root-zone conditions [25], [26].

VI. Conclusion

Carbon dioxide increases photosynthetic opportunity when substrate availability limits Rubisco-mediated carbon fixation and when the crop has sufficient light, suitable temperature, favourable water status, adequate nutrition and physiological capacity to use the additional carbon. The response eventually becomes limited when another process becomes more restrictive or when acclimation changes the relationship between carbon dioxide supply and assimilation. Evidence on light saturation, vapour pressure deficit, nutrient-dependent capacity and environmental interactions supports an interacting-limitation model rather than a universal enrichment target [1], [3], [4], [17].

The highest-value next work is controlled validation that treats carbon dioxide as an explicit response factor while measuring the environmental conditions most likely to alter the result. Such work should distinguish immediate photosynthetic response from longer-term crop outcomes and establish when light, nutrient supply, water status, temperature or root-zone function replaces carbon dioxide as the active limitation. Until these relationships are established for the relevant crop and conditions, carbon dioxide enrichment should be regarded as a conditional means of relieving photosynthetic limitation rather than as an independent solution [2], [23], [25].

Acknowledgment

The author used artificial intelligence tools to assist with manuscript drafting and revision, and with LaTeX and bibliography preparation. The author reviewed all AI-assisted output and remains responsible for the final content.

References

[1] J. A. Lankhorst, H. J. de Boer, D. C. Behling, P. L. Drake, E. A. Perkowski, and K. T. Rebel, "Nutrient availability increases photosynthetic capacity without altering the cost of resource use for photosynthesis," *AoB PLANTS*, 2025.

[2] S. Azizi, S. Aliniaeifard, S. Zarbakhsh, S. Esmaeili, K. Baghalian, and N. S. Gruda, "Photobiology, photosynthesis, and plant responses under artificial lighting in controlled environment agriculture," *Scientia Horticulturae*, 2025.

[3] Z. Xu, Y. Jiang, and G. Zhou, "Response and adaptation of photosynthesis, respiration, and antioxidant systems to elevated co2 with environmental stress in plants," *Frontiers in Plant Science*, 2015. [Online]. Available: https://doi.org/10.3389/fpls.2015.00701

[4] C. Grossiord, T. N. Buckley, L. A. Cernusak, K. A. Novick, B. Poulter, R. T. W. Siegwolf, J. S. Sperry, and N. G. McDowell, "Plant responses to rising vapor pressure deficit," *New Phytologist*, 2020.

[5] S. Scott and C. Villouta, "Dissolved oxygen limitation and pythium root rot in strawberry nft systems: Mechanisms, research gaps, and prospects for substrate-free production," *Frontiers in Plant Science*, 2026.

[6] I. A. Lakhiar, H. Yan, T. N. Syed, C. Zhang, S. A. Shaikh, M. Rakibuzzaman, and R. B. Vistro, "Soilless agricultural systems: Opportunities, challenges, and applications for enhancing horticultural resilience to climate change and urbanization," *Horticulturae*, 2025.

[7] J. Liu and M. W. van Iersel, "Photosynthetic physiology of blue, green, and red light: Light intensity effects and underlying mechanisms," *Frontiers in Plant Science*, 2021. [Online]. Available: https://doi.org/10.3389/fpls.2021.619987

[8] I. Szekely and M. H. Jijakli, "Bioponics as a promising approach to sustainable agriculture: A review of the main methods for producing organic nutrient solution for hydroponics," *Water*, 2022.

[9] C. E. Boyd, C. S. Tucker, and B. Somridhivej, "Alkalinity and hardness: Critical but elusive concepts in aquaculture," *Journal of the World Aquaculture Society*, 2016.

[10] A. Tuxun, Y. Xiang, Y. Shao, J. E. Son, M. Yamada, S. Yamada, K. Tagawa, B. Baiyin, and Q. Yang, "Soilless cultivation: Precise nutrient provision and growth environment regulation under different substrates," *Plants*, 2025.

[11] B. M. Eldridge, L. R. Manzoni, C. A. Graham, B. Rodgers, J. R. Farmer, and A. N. Dodd, "Getting to the roots of aeroponic indoor farming," *New Phytologist*, 2020.

[12] P. Sambo, C. Nicoletto, A. Giro, Y. Pii, F. Valentinuzzi, T. Mimmo, P. Lugli, G. Orzes, F. Mazzetto, S. Astolfi, R. Terzano, and S. Cesco, "Hydroponic solutions for soilless production systems: Issues and opportunities in a smart agriculture perspective," *Frontiers in Plant Science*, 2019. [Online]. Available: https://doi.org/10.3389/fpls.2019.00923

[13] C. D. Mihaela Constantin and M. Oprea, "Thermodynamic analysis of oxygenation methods for stationary water: Mathematical modeling and experimental investigation," *Thermo*, 2025.

[14] L. Corbesier and G. Coupland, "Photoperiodic flowering of arabidopsis: integrating genetic and physiological approaches to characterization of the floral stimulus," *Plant, Cell & Environment*, 2005.

[15] N. Kelly and E. S. Runkle, "Dependence of far-red light on red and green light at increasing growth of lettuce," *PLOS ONE*, 2024. [Online]. Available: https://doi.org/10.1371/journal.pone.0313084

[16] S. Zhen and B. Bugbee, "Substituting far-red for traditionally defined photosynthetic photons results in equal canopy quantum yield for co2 fixation and increased photon capture during long-term studies: Implications for re-defining par," *Frontiers in Plant Science*, 2020. [Online]. Available: https://doi.org/10.3389/fpls.2020.581156

[17] M.-H. Talbot and D. Monfet, "Analysing the influence of growing conditions on both energy load and crop yield of a controlled environment agriculture space," *Applied Energy*, 2024.

[18] P. Kusuma and B. Bugbee, "Improving the predictive value of phytochrome photoequilibrium: Consideration of spectral distortion within a leaf," *Frontiers in Plant Science*, 2021. [Online]. Available: https://doi.org/10.3389/fpls.2021.596943

[19] P. L. Palsha, M. W. van Iersel, R. W. Dickson, L. Seymour, M. Yelton, K. Qin, and R. S. Ferrarezi, "Strategic light use efficiency optimization of hydroponic lettuce exposed to different photosynthetic photon flux densities," *Agronomy*, 2024.

[20] C. Vatistas, D. D. Avgoustaki, and T. Bartzanas, "A systematic literature review on controlled-environment agriculture: How vertical farms and greenhouses can influence the sustainability and footprint of urban microclimate with local food production," *Atmosphere*, 2022.

[21] S. D. Jackson, "Plant responses to photoperiod," *New Phytologist*, 2009.

[22] L. Balázs, Z. Dombi, L. Csambalik, and L. Sipos, "Characterizing the spatial uniformity of light intensity and spectrum for indoor crop production," *Horticulturae*, 2022.

[23] J. Jethva, R. R. Schmidt, M. Sauter, and J. Selinski, "Try or die: Dynamics of plant respiration and how to survive low oxygen conditions," *Plants*, 2022.

[24] A. Fussy and J. Papenbrock, "An overview of soil and soilless cultivation techniques-chances, challenges and the neglected question of sustainability," *Plants*, 2022.

[25] S. Zhen, M. van Iersel, and B. Bugbee, "Why far-red photons should be included in the definition of photosynthetic photons and the measurement of horticultural fixture efficacy," *Frontiers in Plant Science*, 2021.

[26] G. Vicentini, M. Biancucci, L. Mineri, D. Chirivı, F. Giaume, Y. Miao, J. Kyozuka, V. Brambilla, C. Betti, and F. Fornara, "Environmental control of rice flowering time," *Plant Communications*, 2023.