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1 **Feeding the world: impacts of elevated [CO₂] on nutrient content**
2 **of greenhouse grown fruit crops and options for future yield gains**
3

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13 **Running title:** Impacts of elevated [CO₂] on fruiting crops
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23 **Abstract**

24 Several long-term studies have provided strong support demonstrating that growing crops under
25 elevated [CO₂] can increase photosynthesis and result in an increase in yield, flavour and
26 nutritional content (including but not limited to Vitamins C, E and pro-vitamin A). In the case
27 of tomato, increases in yield by as much as 80 % are observed when plants are cultivated at
28 1000ppm [CO₂], which is consistent with current commercial greenhouse production methods
29 in the tomato fruit industry. These results provide a clear demonstration of the potential for
30 elevating [CO₂] for improving yield and quality in greenhouse crops. The major focus of this
31 review is to bring together 50 years of observations evaluating the impact of elevated [CO₂] on
32 fruit yield and fruit nutritional quality. In the final section, we consider the need to engineer
33 improvements to photosynthesis and nitrogen assimilation to allow plants to take greater
34 advantage of elevated CO₂ growth conditions.

35
36 **Keywords:** Photosynthesis, fruit, quality, climate, nutrition

INTRODUCTION

Elevated $[\text{CO}_2]$ ($e[\text{CO}_2]$) has been shown to significantly improved light saturated photosynthetic carbon assimilation rates (A_{sat}) by increasing the efficiency of Rubisco CO_2 assimilation (carboxylation) over the alternate RuBP oxygenation (O_2 assimilation), which results in enhanced growth and yield ^{1,2} (Figure 1).

The majority of research evaluating the impact of $e[\text{CO}_2]$ on fruit crop production has been carried out in controlled environment conditions (chambers), polytunnels and commercial greenhouses where crops are grown in $e[\text{CO}_2]$, and focus almost exclusively on soft fruit such as strawberry, tomato and cucumber. Early work in the 1980's suggested that $e[\text{CO}_2]$ increased the average yield of all plants tested by approximately 30%, with optimal $[\text{CO}_2]$ concentration for growth and yield in the range of 700 to 900 ppm with concentration in excess of 1000 ppm having a negative impact on plant growth and yield ³⁻⁶. In the case of vegetable crops, much of the work has been carried out in controlled environments, in which elevated $[\text{CO}_2]$ (800–900 ppm) increased lettuce, carrot, and parsley yield by 18%, 19%, and 17%, respectively in greenhouse grown crops. However, the yields of leek, chinese cabbage and celery were not significantly affected by increases in growth $[\text{CO}_2]$ concentration ⁷. A meta-analysis of 107 selected articles showed that $e[\text{CO}_2]$ results in an increase in vegetable number (yield) by on average 32% and vegetable mass by 11% ⁸. Furthermore, a meta-analysis of 57 articles consisting of 1,015 observations found that $e[\text{CO}_2]$ has both positive and negative impacts on vegetable quality. For example, whilst concentrations of fructose (+14.2 %), glucose (+13.2 %), total soluble sugar (+17.5 %), total antioxidant capacity (+59.0 %), total phenols (+8.9 %), total flavonoids (45.5 %), vitamin C (+9.5 %), and calcium (+8.2 %) increased in the edible part of vegetables, protein (-9.5%), nitrate (-18.0%), magnesium (-9.2 %), iron (-16.0 %), and zinc (-9.4 %) decreased ⁹. Moreover, a meta-analysis of legumes found a reduction in zinc and iron (and in non-legumes a reduction in protein) when plants were grown under $e[\text{CO}_2]$ (see

63 Myers et al ¹⁰). In 2018, Zhu et al ¹¹ confirmed these results, and moreover demonstrated that
64 rice grown under $e[\text{CO}_2]$ showed consistent declines in the quantities of vitamins B1, B2, B5,
65 and B9 and, an increase in vitamin E. Finally, studies have shown that grains (wheat, rice, and
66 barley), legumes, and maize-have a 4-10% reduction in iron concentrations of when grown
67 under $e[\text{CO}_2]$ (~550 ppm)¹². These results shown that $e[\text{CO}_2]$ can positively and negatively
68 impact on legumes, grain and vegetables on a crop-by-crop basis and simultaneously alter
69 quality attributes in the same harvestable material.

70 The aim of this review is to provide an overview of the current available data of the
71 impact of elevated $[\text{CO}_2]$ on fruiting crops production in commercial growing systems. This
72 paper examines these studies and the long-term implications of $e[\text{CO}_2]$ on the yield and quality
73 of fruit-required to feed a growing population. In the last section, we discuss the potential for
74 designing crops for these new growing environments and allowing them to take full advantage
75 of the introduced CO_2 , potentially increasing crop yield, reducing costs for commercial
76 producers, and improving quality of the final product providing high nutritional value to
77 consumers.

79 **IMPACT OF ELEVATED $[\text{CO}_2]$ ON YIELD AND QUALITY OF GREENHOUSE** 80 **GROWN CROPS**

81 **Impact of elevated $[\text{CO}_2]$ on solanaceous crops**

82 Commercially, tomato crops are grown in greenhouses with $e[\text{CO}_2]$, in some cases as
83 high as 2000 ppm. The effects of $e[\text{CO}_2]$ of fruit yield and quality has been extensively studied
84 (Figure 2). Under $e[\text{CO}_2]$, tomato fruit yield increases ranged from 7 % – 125 % with $[\text{CO}_2]$
85 ranged from 450 ppm – 1200 ppm compared with plants grown under $a[\text{CO}_2]$. An increase in
86 the quantity of non-reducing sugars (glucose and fructose) has been reported ¹³⁻¹⁷ and fully ripe
87 tomatoes grown in an $e[\text{CO}_2]$ were found to be preferable for consumption in sensory panels

88 ¹³. As liking sweetness has been shown to be a universal trait ¹⁸, it is possible that this increase
89 in sugar is responsible for preference of the carbon enriched tomato fruits. An increase in
90 vitamin C was also found between most studies ^{13,15,16,19}, potentially improving the health
91 benefit gains from consumption of carbon-enriched grown tomatoes (Table 1). Vitamin C is an
92 important dietary requirement and at high concentrations it has been used as a treatment for
93 cancer, arteriosclerosis, and cardiovascular diseases ²⁰⁻²². These results suggest that increasing
94 environmental [CO₂] could contribute to an increase in Vitamin C improving their nutritional
95 value for the consumer. However, growth at *e*[CO₂] does not have the same impact on all
96 species, as another studies in barley reported a significant decrease in Vitamin C content ²³
97 highlighting the species–species response differences to *e*[CO₂] and suggesting that high carbon
98 growth environments may not always provide the best outcome for the consumer even though
99 increases in yield maybe the producers primary concern (see Fenech et al. ²⁴ and references
100 therein).

101 Similarly, tomato fruit concentration of lycopene and β-carotene (pro-vitamin A) were
102 found to increase in response to *e*[CO₂] by as much as 30 % and 70 % respectively ¹³.
103 Rangaswamy et al. ²⁵ reported an increase in carotenoid (+20 %) and lycopene (+31 %) in the
104 fruits of tomato plants grown at 550 ppm [CO₂], however carotenoid content decreased (- 12%)
105 when the concentration was increased to 700 ppm, suggesting that the level of CO₂ enrichment
106 impacts fruit quality and careful consideration is needed to ensure an appropriate balance
107 between levels of *e*[CO₂] and final yield. Lycopene is an important phytonutrient, is sold
108 commercially as a dietary supplement, and has been reported to possess anti-cancer properties
109 and can improve cardiovascular health ^{26,27}.

110 β-carotene is the precursor for Vitamin A, also known as retinol. Vitamin A is an
111 essential micronutrient playing important roles in growth and development, vision ²⁸ and the
112 immune system ²⁹. More than a third of all pre-school children and a significant number of

113 pregnant women around the world are affected by Vitamin A deficiency, increasing the risk of
114 night blindness and miscarriage ^{30,31}. Importantly, most people suffering from a deficiency in
115 Vitamin A show no clinical symptoms resulting in a phenomenon termed ‘Hidden Hunger’ ³².
116 Production of crops with increased Vitamin A is therefore an important target for improving
117 the diet and health of these at-risk groups; enhanced uptake of carbon may be a useful approach
118 to achieve this. Increases in the Vitamin A precursor β -carotene has been observed in tomato
119 fruit grown under $e[\text{CO}_2]$ of 800-900ppm, in addition to a 28 % increase in vitamin C at ripe
120 stage and an ~8 % increase in total soluble solids (Table 1) (Zhang et al. ¹³, suggesting the under
121 these growth conditions, improved vitamin A and C and increased carotenoid content may be
122 attainable.

123 Carotenoids are also the precursors of several flavour and aroma compounds. β -carotene
124 is cleaved by carotenoid cleavage dioxygenases CCD1 and CCD4 ^{26,33-35}, to form the aromatic
125 apocarotenoid β -ionone, which is important to tomato fruit flavour. Furthermore, lycopene,
126 shown to increase under $e[\text{CO}_2]$ is cleaved by CCD1 to form several important flavour and
127 aroma compounds including 6,10-dimethyl-3,5,9-undecatrien-2-one (pseudoionone; ³⁴, 6-
128 methyl-5-hepten-2-one (MHO; ³⁶ and geranial ³⁷. MHO has been shown to be an important
129 contributor to tomato fruit flavour ^{38,39} and has also been shown to accumulate in tomato fruit
130 with higher lycopene levels ⁴⁰. It is therefore apparent that growth in $e[\text{CO}_2]$ can increase a
131 range of key flavour and nutraceutical precursor compounds present in tomato fruit; this
132 phenomenon deserves further study, the optimal levels of $[\text{CO}_2]$ are currently not clear and
133 more work is needed to better understand the relationship between CO_2 assimilation carotenoid
134 content, flavour and overall quality (Table 2).

135 Similar results have also been found in pepper crops with yield increase of 12.9 % –
136 370.2 % was reported when grown at $e[\text{CO}_2]$ between 450 ppm – 1000 ppm (Table 2) with
137 most other studies reporting yield increases in the range of 12.9 % – 47.4 % in the absence of

138 other parameters ⁴¹⁻⁴⁷. However, it should be noted that growth at ~800ppm $e[\text{CO}_2]$ was found
139 to reduce sweet pepper total amino acid content by up to 29 %, including reductions in the
140 sweet tasting amino acids alanine and glycine, which could be detrimental to the perceived fruit
141 flavour ⁴². Yield was also found to vary with different irrigation programmes ^{41,48}, nitrogen
142 sources ⁴⁸, substrate salinity ^{42,44} and pruning regimens ⁴⁶. Given that previous work in tomato
143 has shown an increase in potential phytonutrients in fruit grown at 550 ppm and a decrease in
144 those grown at 700 ppm, further research is needed to better identify the specific quantity of
145 CO_2 fertilisation necessary for maximally improved yield in solanaceous crops, especially when
146 considering that CO_2 uplift is often accompanied by additional treatments, such as increased
147 nutrient and nitrogen (N) fertilisation (Figure 2).

148 In chili pepper, yield increases of 43.8 % – 142 % were reported for $e[\text{CO}_2]$ (in the range
149 of 500 ppm – 1140 ppm). These yield increases were in part attributed to an increase in the size
150 of fruits ⁴⁹. However, in controlled environments a 4°C increase in temperature decreased yield,
151 even at $e[\text{CO}_2]$ (750 ppm), ^{50,51}, indicating that carbon enrichment is not sufficient to rescue
152 yield where glasshouse facilities or growth tunnels experience periods of elevated temperature
153 in an extreme climate change scenario. Carbon-enriched growth was found to increase the
154 capsaicinoid content of fruits, resulting in an increase in Scoville Heat Units (SHU) ^{49,52}. This
155 approach therefore has potential for producing hotter varieties of chili, a growing and
156 competitive market. However, at the same time Vitamin C concentration decrease by up to
157 15.84 % ⁵³, reducing potential health benefits gained from growing chilli plants under $e[\text{CO}_2]$.
158 (Table 2).

159 These reports suggest that the effects of growing crops in $e[\text{CO}_2]$ can have both a
160 positive influence on yield and nutritional quality, however, growth at $[\text{CO}_2]$ levels above what
161 is optimum can negatively impact some quality traits.

Impact of elevated [CO₂] on rosaceous crops

Rosaceous crop research in this area has focused primarily on cultivated strawberry with a small number of studies on raspberry and Nashi pear (Table 3). This is likely due to the relatively smaller size and rapid growth of strawberry compared to other commercially important rosaceous fruit species, such as tree fruits, like apple and cherry, and woody stemmed shrub fruits, like raspberry and blackberry. This makes strawberry a convenient plant to study as a rosaceous model. Furthermore, greater production of strawberry fruits would not only increase profits for growers but also decrease costs for consumers, increasing the availability of healthier options. Better access to such products through economic growth is strongly correlated to reduced micronutrient malnutrition or “hidden hunger”⁵⁴.

In cultivated strawberry, fresh fruit yield increases ranged from 1.0 % – 62.0 % in plants grown under atmospheric $e[CO_2]$ of 450 ppm – 3000 ppm, while dry fruit yield increased by up to 120 % (Figure 2; Table 3). This has been directly linked to a 73 % increase in assimilation rate of CO₂ in strawberry leaves at optimal $e[CO_2]$ of 600 ppm⁵⁵⁻⁶⁰. Further investigation at a genetic level (through RNA seq analysis) revealed that 150 genes were upregulated in strawberry plants grown in an enriched-carbon atmosphere, with 14 of these being photosynthetic genes⁶⁰, suggesting that plants respond to these atmospheric increases by increasing their ability to assimilate the excess carbon.

Additional annual yield increases could be achieved by a two-week reduction in time to fruiting for plants grown in an enriched-carbon atmosphere^{58,61} increasing the field season and the period of productive (fruit) growth. Several fruit quality traits are also improved by growth at $e[CO_2]$; increases in reducing sugars, and therefore sweetness index, were reported^{62,63} alongside reductions in organic acids⁶². These increases in sugar-acid ratio is highly favourable for a more pleasant perception of strawberry flavour by the consumer¹⁸ and an increase in key volatile organic compounds, including furaneol, linalool and major esters, was also reported,

188 further enhancing the “strawberry” aroma ⁶². Growth in a carbon-enriched atmosphere therefore
189 strongly enhances strawberry flavour and increases vitamin C (an important nutritional
190 compound) by up to 13.3 % alongside other antioxidant compounds ^{64,65}. Growth in carbon-
191 enriched atmospheres therefore simultaneously improves yield, flavour and health benefits of
192 strawberry fruits, creating enormous potential for strategies involving enhanced photosynthesis
193 of strawberry plants, including genetic manipulation. The greatest reported increase in fresh
194 fruit yield where obtained when [CO₂] was kept between 600 ppm – 1000 ppm ⁵⁸, linking
195 greater carbon assimilation to increased fresh fruit yield in strawberry and demonstrating an
196 optimal degree of CO₂ fertilisation for strawberries (Table 3).

197 **Impact of elevated [CO₂] on cucurbitaceous crops**

198 Cucumber is the most studied fruit crop of the cucurbitaceae in relation to growth in
199 carbon-enriched atmospheres (Figure 2; Table 4). Improved carbon assimilation rates of up to
200 99 % and 112 % have been reported for cucumber and melon respectively when grown in
201 *e*[CO₂] ^{66,67}, demonstrating that growth in *e*[CO₂] improves photosynthesis of cucurbitaceous
202 crops.
203

204 In cucumber (*Cucumis sativus*), fruit yield increases for plants grown in enriched-
205 carbon atmospheres ([CO₂] = 450 ppm – 3000 ppm) ranged between 16.2 % and 41 % in the
206 absence of other parameters that could alter fruit yield. In high nitrogen supplemented
207 fertilisation, fruit yield was as high as 106 % when grown under *e*[CO₂] of 800 ppm ⁶⁸,
208 indicating the potential of increased nitrogen fertilisation alongside [CO₂] enrichment to unlock
209 the greatest yield increases in cucumber. Interestingly, when grown under *e*[CO₂] of 1200 ppm
210 with the addition of high nitrogen fertilisation treatment, studies found a yield increase between
211 71 % – 73 % ^{66,68}, which was lower than the 106% for plants grown at *e*[CO₂] of 800 ppm.
212 Concentrations of [CO₂] above optimal reduced stomatal density, stomatal conductance (*g_s*),

213 the maximum carboxylation rate (V_{cmax}) and the maximum photosynthetic electron transport
214 rate (J_{max})⁶⁹. This suggests that an optimal concentration of atmospheric $[CO_2]$ exists for
215 maximum yield returns and deserves further investigation. There is large variation between
216 studies on how cucumber fruit quality is impacted by carbon-enriched growth. Fructose and
217 glucose were reported to increase by 6 % and 12 % in one study⁶⁸ and by 75 % and 73 %
218 respectively in another⁷⁰. The inorganic nutrient content of fruits was also reported to decrease
219 in fruits grown in $e[CO_2]$, however only phosphorus showed a significant reduction in multiple
220 cycles⁷¹. These data do suggest that $e[CO_2]$ may enhance fruit flavour and fruit yield at the
221 expense of nutritional value.

222 **Impact of elevated $[CO_2]$ on yield and quality of fruiting trees**

224 Sweet clonal cherry (*Prunus avium* L.) plants were grown for 19 months in climate-
225 controlled greenhouses at ambient (1994-358 ppm; 1995-360 ppm) or $e[CO_2]$ (700 ppm).
226 Elevated $[CO_2]$ treatment increased photosynthesis and dry matter production, leaf (55%) and
227 stem (61%), after two months at 700 ppm, however, this initial stimulation is not sustained.
228 Photosynthetic rates were less after 10 months of growth than after 2 months of growth, and
229 only small increases in dry mass are still evident after 10-months, suggesting that sweet cherry
230 acclimates to $e[CO_2]$ due to long-term exposure⁷². Due to the young nature of plants studied
231 compared with fully grown mature trees (deciduous tree 15-32 m in height and with a trunk up
232 to 1.5 m in circumference^{73,74}, no information is available to determine the impacts of $e[CO_2]$
233 on fruit yield or quality. In Nashi pear, a CO_2 -enriched atmosphere of 700 ppm increased fruit
234 weight, diameter and length along with a 22.5 % increase in Brix, (a key measure of sweetness
235 for marketable fruit⁷⁵). However, this also resulted in a reduction in fruit firmness
236 demonstrating that improvements in yield can be nullified by negative impacts on fruit quality
237 (Table 3).

238 While these studies are limited in, they do indicate the potential of CO₂-enriched growth
239 for improving photosynthesis, increasing yield and quality of tree crops. However, they also
240 suggest that some crops, especially perennial crops, may become acclimated to higher [CO₂]
241 and any gains may be lost over time.

242 243 **DOES INCREASING CARBON ASSIMILATION INCREASE ENVIRONMENTAL** 244 **TOLERANCES?**

245 The work presented above also suggest that increasing CO₂ uptake could have other
246 benefits. It is notable that growth of fruit crops in carbon enriched atmospheres has a similar
247 effect of protecting against environmental stresses, such as drought and elevated temperature,
248 that may become increasingly common due to climate change as plants genetically engineered
249 to increase carbon assimilation. For example, in melon (*Cucumis melo*), growing plants in
250 $e[\text{CO}_2]$ has been shown to mitigate yield losses from increased salinity⁶⁷, and in sweet pepper,
251 $e[\text{CO}_2]$ of 800 ppm was sufficient to rescue any significant yield loss of total and marketable
252 fruits from salinity stress (20 mmol L⁻¹ NaCl)⁴². It could be hypothesised that increasing CO₂
253 assimilation increases sugar and chlorophyll content triggering salt tolerance. However, it
254 should be noted that these results are not universally translatable. Gray et al.⁷⁶ demonstrated
255 in soybean that $e[\text{CO}_2]$ was insufficient to protect yields from drought conditions triggered by
256 higher temperatures demonstrating that benefits in some crops may not be translatable across
257 all crops of agronomical importance. Furthermore, in tomato plant Zhou et al.⁷⁷ showed that
258 plants grown in $e[\text{CO}_2]$ were more sensitive to combined drought and heat stress; $e[\text{CO}_2]$ drives
259 g_s and transpiration reducing net photosynthesis and therefore productivity, which is
260 concerning given that greenhouses tend to have elevated temperatures compared to the external
261 environment due to the nature of their construction, glass and metal, and therefore $e[\text{CO}_2]$ in
262 an enclosed system may negatively impact on yields if water supplies are limiting. This

demonstrates that irrigation within greenhouse environments is an essential element and adjusting water regimes to maintain productivity and optimise water-use efficiency.

It is also important to note that it is the increase in atmospheric [CO₂] that causes the increase in air temperature (along with associated stresses) by absorbing energy and preventing it from being radiated out into space (see ^{78,79}); as such one might view that the cause cannot mitigate its own effects, however, in some crops where both [CO₂] and temperature increase simultaneously, yields were maintained compared with data where temperature is increased in the absence of e [CO₂] leading to yield loss and these results cannot be ignored, but a better understanding of the impact of cause and effect climate change on crop yields needs to be researched, otherwise, the logic consequences would be further increase amounts of [CO₂] in the atmosphere to increase crop tolerance against the effects of ever-increasing temperatures.

Interestingly, some parallels do exist between photosynthetically genetically modified crops and increased tolerance to salinity. In *Arabidopsis*, over-expression of Sedoheptulose-1,7-bisphosphatase (SBPase), which enhances CO₂ assimilation rates by increasing the regeneration of the Rubisco substrate RuBP ⁸⁰, enhances salt tolerance through increases in sucrose, starch and chlorophyll content were reported ⁸¹. This suggests that increasing photosynthetic rates, either through increasing the availability of [CO₂] for photosynthesis or increasing the plants' ability to assimilate [CO₂] under ambient conditions could have a similar protective effect. It would be interesting to explore if increased carbon assimilation rates, through atmospheric manipulation or genetic modification, can have a positive impact on crop resistance to high salt environments and other abiotic stresses in large field trials or commercial greenhouses. There is currently evidence that over-expressing the Calvin-Benson cycle (CBC) enzyme SBPase can increase tolerance to chilling stress in tomato ⁸² and the expression of the cyanobacterial CBC bifunctional fructose-1,6-bisphosphatases/Sedoheptulose-1,7-bisphosphatase enzyme in soybean prevent yield loss under high temperature ⁸³. Köhler et al.

288 ⁸³ concluded that the manipulation of CO₂ uptake could mitigate against the effects of global
289 increases in temperature under $e[\text{CO}_2]$. This may be deemed especially important given the
290 expected impact of global climate change. This suggests that increasing carbon assimilation
291 through manipulation of photosynthesis ^{84,85} can have similar outputs to improved
292 photosynthesis through growth in an enriched carbon atmosphere and further demonstrates the
293 viability of this approach for improvement of yield and quality in fruiting crops. This must be
294 studied considering the recent work showing that improved carbon assimilation also results in
295 improved nutrient uptake and an increase in NUE ⁸⁶.

296 297 **FUTURE OPPORTUNITIES**

298 As [CO₂] surpasses 550 ppm, A_{sat} will be limited by the rate of RuBP regeneration rather
299 than Rubisco activity suggesting there is scope to improve plant photosynthesis to increase
300 yield in greenhouse environments where CO₂ is routinely increased to 1000 ppm or more for
301 short periods of time. These short time-periods are furthermore unpredictable and chaotic given
302 that greenhouses must be vented, due to external environmental conditions, to maintain, as close
303 as possible, optimal growing conditions i.e temperature and humidity inside the growth facility.
304 Furthermore, the [CO₂] dosing capacity must be economically beneficial, especially given the
305 chaotic nature of CO₂ loss to the environment during periods of venting. As dosing increases,
306 costs go up accordingly determined by the cost of CO₂. Moreover, at some point, there is a
307 price limit where the supplemental cost of CO₂ increases to a point where costs cannot be
308 recovered by the selling price of the product. In the last year, CO₂ costs have increased for £100
309 per tonne to as much as £3000 per tonne ^{87,88}. Therefore, future options that maximize the ability
310 of the crop to take full benefit of the $e[\text{CO}_2]$, or maintaining higher yields when CO₂ costs are
311 unmanageable become more important.

312 Araus et al ⁸⁹, noted that canopy photosynthesis holds a crucial place in a context of
313 yield gains through photosynthetic improvement, which requires additional factors including

314 the availability and uptake of nutrients, such as nitrogen, irrigation, the transport of
315 photoassimilates and sink-source balance. As such, in addition to improving photosynthetic
316 rates via CO₂ supplementation, the improvement of other plant processes such as N uptake,
317 non-foliar photosynthesis, stomatal function, and rubisco(activase) thermotolerance so that
318 crops are better adapted for growth in [CO₂] enriched environments such as greenhouses are
319 discussed below (Figure 3). These works will also need to account for changes to the landscape
320 of greenhouse crop cultivation, such as a move to vertical farming, changes in growth medium
321 from soil to substrates such as coir (derived from coconut husks) or rockwool⁹⁰. It is estimated
322 that more than 50 % of strawberry production occurs in substrate rather than soil⁹¹. Coir is
323 often used as it has been shown to retain water more efficiently than soil, so strawberry plants
324 require less frequent watering improving water use efficiency. Coir also has a high level of
325 aeration, which is ideal for strawberries' whose root systems require a lot of oxygen. More
326 recent developments in hydroponics⁹² and aeroponics⁹³, will impact on irrigation, fertiliser
327 regimes and N uptake.

328 *Nitrogen use efficiency (NUE)*

329
330 With regards to fruit quality, this is a complex trait that may not be simply attributed to
331 enhanced carbon assimilation. More research is needed to link increased assimilate, with
332 assimilate distribution and transport, NUE to better understand the sink-source relationship in
333 any given crop, which can vary significantly across varieties and crop types. NUE is determined
334 by yield per unit of available N in the growth medium (i.e often coir in greenhouse grown
335 crops). Plants with higher NUE may allocate N toward both the photosynthetic complexes (i.e
336 N is major component of chlorophyll; total N allocated to Rubisco $18.2 \pm 6.2\%$; ⁹⁴) and/or
337 toward the development of additional sinks. The second definition of NUE could be described
338 as the efficiency with which N is applied to soils, (through artificial means in greenhouse crops),

339 is taken up by plants and converted to usable products (i.e. biomass, grain yield). This can be
340 manipulated through breeding to identify new varieties with high NUE uptake from selected
341 growing mediums or through engineering nitrogen symbiosis (Figure 3). Recently, scientists
342 reported the engineering nitrogen-fixation into non-legume cereal crops by enabling them to
343 interact with soil bacteria to convert N from the air into ammonia fertiliser ⁹⁵. These works
344 could firstly reduce the reliance on commercial synthetic fertilisers and secondly provide
345 alternate sources of N that along with improvements to carbon assimilation, foliar or non-foliar,
346 co-contribute to improving photosynthesis and yields in crops (Figure 3).

347 A recent review has identified a number of targets in the literature to improve N uptake,
348 assimilation and remobilisation through genetic manipulation (see ⁹⁶ for review). One of these,
349 the over-expression of the nitrate transporter (NRT2.3) was shown to increase nitrate
350 concentrations in tomato increasing biomass and fruit weight ⁹⁷. More recently, the transcription
351 factor DREB1C has been identified as a regulator of NUE by controlling the expression of
352 several important growth-related genes including the rubisco small subunit 3 (RBCS3), nitrate
353 transporters (NRT1.1B, NRT2.4), nitrate reductase (NR2) and the flowering regulator (FTL3).
354 Once over-expressed (OE), OsDREB1C increased the abundance of photosynthetic pigments,
355 plants were shown to have about one-third more chloroplasts, 38% more rubisco and improved
356 photosynthesis and N uptake. The OE of OsDREB1C resulted in a >40% increase in grain
357 yield in elite rice varieties and an ~20% increase in wheat yields, while in Arabidopsis, a
358 significant increase in biomass ⁹⁸. Many of these identified genes have potential for improving
359 NUE in fruiting crops grown in *e*[CO₂]. A recent report of a large grain rice cultivar, Akita 63,
360 having a high yield due to an enlarged sink capacity without and photosynthesis improvement.
361 However, this work demonstrated that source capacity was strongly limiting the yield potential
362 under high N fertilization. These authors suggested that enhancing photosynthesis is an
363 important step to further increase yield of current high-yielding cultivars ⁹⁹. This work can be

364 extrapolated that engineering NUE and photosynthesis in plants grown at $e[\text{CO}_2]$ could provide
365 a step-change in yields in greenhouse cultivated crops.

366 *Genetic variation in photosynthetic traits in crops and wild relatives*

368 Methods of improving these traits including breeding, by exploiting the potential of crop
369 wild relatives as a source of new traits, and/or the genetic manipulation/genome editing of
370 specific traits. There is already evidence that substantial genetic variation exists within wild
371 relatives of fruiting crops ¹⁰⁰⁻¹⁰², which are now studied as a source of crop improvement in
372 various breeding programs ¹⁰³. Further evidence that even in elite material, significant variation
373 is observed in photosynthetic traits. For example, V_{cmax} , J_{max} and A_{sat} , indicators of
374 photosynthetic potential, have been shown to vary by as much as 30% in the flag leaves of
375 recent breeding lines of spring and winter wheats ¹⁰⁴⁻¹⁰⁶. Similarly, several quantitative trait loci
376 for photosynthetic efficiency have been identified in elite rice material, including the
377 identification of important transcription factors ^{107,108}. This work in wheat and rice is promising,
378 demonstrating the potential for breeding new varieties better adapted to changing growth
379 conditions, however it is unclear if such strategies will work in horticultural crops. In the case
380 of tomato, there is considerable variation within the wild and elite varieties to suggest that such
381 breeding strategies could be used to enhanced yield and quality ^{109,110}. See Sharwood et al ¹¹¹
382 for review (Figure 3).

383 In transgenic rice, overproducing Rubisco, increases the biomass production and yield
384 under high N fertilization in paddy fields suggesting that the development of new rice varieties
385 with both high photosynthesis and large sink capacity is essential ⁹⁹. Furthermore, genes
386 encoding thermostable variants of Rubisco activase (thermos-Rca) have been identified in wild
387 rice relatives. When over-expressed in domesticated rice, thermostable-Rca was sufficient to
388 enhance carbohydrate accumulation and improve yields after periodic exposure to elevated

389 temperatures (+45°C) throughout the vegetative phase ^{112,113}. Thermostable Rca have been
390 identified in Thermophilic cyanobacteria, bacteria that thrive in high-temperature
391 environments, making them a potential source of novel genes for engineering crops for growth
392 at higher temperatures ¹¹⁴. Improving the thermal tolerance of rubisco activase, either through
393 breeding with wild populations or genetic engineering, could aid greenhouse grown crops better
394 tolerate the elevated temperatures that often occur during the growing season (Figure 3).
395

396 *Genetic engineering of photosynthetic traits in crops*

397 Increasing the expression of enzymes and/or proteins involved in the regeneration of
398 RuBP, CO₂ transport or chloroplast electron transport have previously been shown to enhance
399 photosynthetic efficiency and increases in yield ^{84,85,115-117}. However, once again, it cannot be
400 ignored that much of this work has focused on non-fruiting crops, such as Arabidopsis, tobacco,
401 wheat and rice, (see Simkin et al. ⁸⁴ for review), grown in controlled conditions, performed in
402 pots, in soil or in the field with controlled irrigation, which is not typical of global agriculture.
403 Furthermore, work carried out in tomato, over-expression of sedoheptulose-1,7-
404 bisphosphatase, involved in RuBP regeneration, did not report on fruit yield ⁸². These data
405 indicating that more work is required to understand how these manipulations would impact
406 fruiting crops grown in tightly controlled environments.

407 One potential target for genetic manipulation is the starch synthesis enzyme adenosine
408 diphosphate glucose pyrophosphorylase (AGPase); increasing AGPase activity has potential to
409 increase starch accumulation for growth. Increased accumulation of starch has been shown to
410 have little negative feedback on photosynthesis ¹¹⁸ and increased AGPase activity in the
411 chloroplast would increase the strength of the transient starch pool, which acts as a sink in the
412 chloroplast. Reduced sink capacity does induce negative feedback on photosynthesis and can
413 limit photosynthesis even in favourable conditions (e.g. elevated [CO₂]) ¹¹⁹, suggesting that

414 increasing the sink may allow for greater CO₂ assimilation in supplemented [CO₂] growth
415 environments.

416 Although genetic manipulation has the potential to further increase yields in crops
417 grown in enriched [CO₂] environments, allowing them to take better advantage of supplemental
418 CO₂, increasing net photosynthetic rates and associated yields (Figure 3), it should also be noted
419 that some reports have suggested that increases in yield in genetically enhanced photosynthetic
420 crops are likely not uniquely down to increases in carbon assimilation but a combination of
421 factors; for example improvements in carbon uptake allow for an increase in N assimilation ¹²⁰.
422 Furthermore, it has also been reported that such increase in yield from enhanced photosynthetic
423 efficiency critically rely on the availability and uptake of water and nutrients (for review see
424 ^{121,122}), therefore, genetic engineering as an approach alone may be limiting if other aspects of
425 crop cultivation, such as irrigation, planting regimes, fertilisation (i.e NUE) and growth media
426 (i.e soil, coir, rockwool), are not taken into account and co-optimised.

427 428 *Non-foliar photosynthesis*

429 Leaves are not the only location within the plant where photosynthesis occurs, with
430 evidence of photosynthesis in petioles and stems ^{123,124}, and fruit ¹²⁴ that may provide significant
431 and alternative sources of photo-assimilates essential for optimal yield. Assimilation of
432 atmospheric CO₂ is dependent on the number and behaviour of stomata, and the stems of many
433 plants have stomata distributed along the epidermis ^{125,126} and an evaluation of the
434 photosynthetic activity in stems of various plants accounted for up to 4% of the total
435 photosynthetic activity ¹²⁷. Furthermore, Hu et al. demonstrated the importance of stem
436 photosynthesis to yield in cotton; maintaining the stem in darkness reduced seed weight by 16
437 % ¹²⁸ showing the stem provides photoassimilates for plant development and growth.

438 As previously noted, many fruiting crops produce green fruit containing all the
439 necessary proteins and enzymes to carry out photosynthesis ^{127,129,130} that may provide
440 significant and alternative sources of photoassimilates essential for optimal yield and quality
441 ¹²⁴. Tomato fruit photosynthesis contributes to net sugar accumulation and growth and previous
442 work concluded that tomato fruit photosynthesis contributes between 10% and 15% of the total
443 fixed carbon of the fruit, ^{127,131 132}. It should be noted that, unlike many crops, cucumber fruit
444 remain green through to maturity, have stomata (suggesting they perform gas exchange to drive
445 photosynthesis), and have a similar surface area to an expanded leaf ¹³⁰. It has previously been
446 reported that cucumber fruit had high photosynthetic and respiratory rates ¹³³ and contribute
447 approximately 9.4 % of their own carbon requirements ¹³⁰. It should be noted that in fruit with
448 stomata, such as cucumber, there are two potential major sources of CO₂. Firstly, Rubisco
449 assimilates atmospheric [CO₂] through the stomatal pores, leading to the production of sugars
450 via the CBC and secondly, CO₂ released by mitochondrial respiration is re-fixed (recycling
451 photosynthesis) ^{125,134}. Whilst this confirms that photosynthesis occurs in fruits, the extent and
452 importance is not clear. In $e[CO_2]$, it seems plausible that cucumber fruit photosynthesis may
453 contribute directly to fruit size (and therefore yield by weight) and quality through their ability
454 to directly access carbon in an enriched atmosphere via their stomata (for a review fruit
455 photosynthesis, see ^{124,135}. Therefore, increasing carbon capture by non-foliar tissues has the
456 potential to significantly impact yield and combined with an increase N uptake (i.e. slow release
457 fertilizers ¹³⁶) to balance the increased carbon uptake, and optimised irrigation regimes has the
458 potential to maximise such yield gains.

460 CONCLUSIONS

461 These data show that the yield of fruiting crops benefit from growth in supplemented
462 atmospheres, although, some data suggests that increase in yield can come at the expense of

463 quality traits. It is therefore essential to determine the optimal $[\text{CO}_2]$ concentrations on a crop-
464 by-crop basis, to maximise productivity. An evaluation of fruit quality under these conditions
465 has also been shown to be highly variable between treatments and difference are observed
466 between cultivars with the same treatment suggesting that much more research is required to
467 identify the specific mechanisms behind changes in fruit quality. In the case of soft fruit
468 production in greenhouse environments, it will be important to determine if the quality of fruit
469 harvested early in the season differs from that of fruit harvested later in the season when plants
470 have spent a more significant period of time exposed to $e[\text{CO}_2]$ growth conditions. Cherry for
471 instance, when grown under prolonged periods of $e[\text{CO}_2]$, acclimates to prolonged exposure
472 and initial significant gains in yield observed after two months are less detectable after ten
473 months and are not significantly different to control plants grown at $a[\text{CO}_2]$ ⁷². This may in one
474 respect account for differences in nutritional quality observed in fruit grown in similar
475 conditions in different studies (i.e. fruit harvested at different times in the study) where
476 additional fertilizer treatments aren't provided.

477 Increases in yield associated with $e[\text{CO}_2]$ controlled environments may be about more
478 than additional carbon. Controlled environments also allow the regulation of transpiration (e.g.
479 by controlling vapour pressure deficit) and therefore water uptake and the inclusion of
480 additional fertilisation (specifically N). Breeding new varieties adapted to these growth
481 conditions may also be more amenable given the hostility towards genetically modified crops.
482 A recent review noted that new phenomics, genomics, and bioinformatics tools make it possible
483 to harness the untapped potential of crop genetic resources (including wild relatives) to create
484 combinations of traits to enhance yield in high $[\text{CO}_2]$ controlled environments ¹³⁷.

485 Breeding alone may not be sufficient to adapt all varieties, or all crops, to high $[\text{CO}_2]$
486 growing environments traditionally used in greenhouses. However, over the last several
487 decades, agricultural research has adopted technologies such as genetic engineering and

488 'genome editing' to improve traits in key crops that could be useful in these circumstances ^{85,138-}
489 ¹⁴⁰. These include advances in the tools available to carry out this work, including vectors for
490 multiple gene insertion ¹⁴¹⁻¹⁴⁵ and tissue specific promoters ¹⁴⁶⁻¹⁵⁰. If the promise of these
491 biotechnology programs is to be realized, it will be necessary to address the public perception
492 of genetic modification and genome editing technologies to gain greater acceptance.

493 Genetic manipulation, may need to go beyond the direct manipulation of carbon
494 assimilation in leaves ⁸⁴, but focus on the manipulating and control of stomatal function ^{151,152},
495 the manipulation of pigments complexes in ripening fruit ¹⁵³, enhancement of light capture by
496 the leaves through the manipulation of chlorophyll distribution and form ¹⁵⁴ and importantly
497 look a methodologies for increasing N uptake via transgenic ⁹⁶ or traditional means (improved
498 fertilization regimes).

499 It should also be noted that the introduction of new growing, hydroponics, aquaponics
500 and aeroponics may require further study, to breed and adapt or engineer plants root architecture
501 for these new growth media. In conclusion, greenhouse cultivation offers the opportunity to
502 manipulate growing atmosphere, lights and VPD for improved yields and we can now look at
503 the opportunities to breed and engineer plants specifically optimise for these conditions.

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Contributions

N.H.D and A.J.S drafted and wrote the manuscript with input from T.L, C.A.R and C.W who also edited the final version.

Data availability statement

Conflict of interests

The authors declare no competing interests

Figure 1. Schematic representation of elevated [CO₂] on carbon assimilation. Created with BioRender.com

Figure 2. Effects of elevated [CO₂] on yield and quality of fruiting crops. Created with BioRender.com

Figure 3. Effects of elevated [CO₂] on yield of fruiting crops and a representation of the potential for the manipulation of plant material for further yield increases. Created with BioRender.com

Table 1. Impact of elevated atmospheric [CO₂] on yield and nutritional quality of tomato

CO ₂ Treatment	Additional Treatment(s)	Fruit Yield	Fruit Quality	Ref
510 ppm	N/A	9.9 % increase in fruit yield.	N/A	45
590 ppm	root drying	Fruit dry weight not significantly affected by [CO ₂] across all irrigation treatments.	N/A	155
375 ppm – 675 ppm	Ozone treatment 80 nmol mol ⁻¹	24% increase in fruit yield. 31 % decrease in fruit yield when exposed to ozone. Ozone and CO ₂ treated fruit yields were not significantly different to plants grown in ambient conditions.	N/A	156
550 ppm 700 ppm	N/A	54 % increase in fruit yield at 550 ppm and 125 % increase in fruit yield at 700 ppm.	1.4 % – 11.4 % decrease in total soluble solids, 27.3 % – 31.8 % decrease in total acids and 16.1 % – 29.0 % increase in vitamin C.	19
	+2 °C increase in temperature	18.4 % – 21.4 % increase in fruit yield due to increased [CO ₂].	10% increase in total sugars, 44 % increase in vitamin C, 32 % increase in lycopene at e[CO ₂] in absence of other treatments. e[CO ₂] rescues reduction in quality from increased temperature.	25
650 ppm 1000 ppm	N/A	17 % increase in fruit yield at 650 ppm and 48 % increase in fruit yield at 1000 ppm.	N/A	3
700 ppm	Doubled N fertilisation	N/A	13 % – 25 % decrease in fruit lycopene content across harvests with e[CO ₂]. 9 % increase in fruit lycopene content with increased N fertilisation.	157
	UV-B exposure up to 1.744 kJ m ⁻²	38 % increase in fruit yield in absence of additional UV-B treatment, up to 46 % increase in fruit yield with UV-B treatment.	Up to ~22 % increase in soluble sugars, ~24 % increase in organic acids, ~40 increase in vitamin C and ~47 % increase in lycopene content of fruits grown under e[CO ₂] and UV-B treatment.	15
700 ppm 900 ppm	N/A	~30 % increase in individual fruit weight.	~18 % increase in vitamin C. ~Up to 20 % reduction in major acids (citric, malic, oxalic). ~45 % increase in sugars (glucose, fructose).	16
700 ppm 1000 ppm	N/A	32 % increase in marketable fruit yield.	N/A	158
800 ppm	0 – 0.5 g N kg ⁻¹ soil. Soil water content 25 % – 35 %	Across all treatments, -3.3 % – 28 % increase in total fruit yield.	-17.9 % – 11.9 % increase in total fruit sugars and -18.9 % – 12.7 % increase in total fruit acids across all treatments.	159
	Salinity treatments at 5 – 7 dS m ⁻¹	13 % increase in yield in carbon-enriched atmosphere and 31 % reduction in marketable fruit yield in increased salinity.	7% increase in total soluble solids. No significant change in citric acid content. Organoleptic qualities of tomatoes grown under increased salinity and CO ₂ found preferable in sensory trials.	14
	100 or 200 mg N kg ⁻¹ soil, 70 % irrigation of control and root drying	8 % increase in fresh fruit yield with increased [CO ₂].	No significant difference in total sugars, organic acid or fruit firmness for fruits grown in e[CO ₂].	160
800 ppm – 900 ppm	N/A	N/A	~28 % increase in vitamin C at ripe stage, ~8 % increase in total soluble solids and no difference in total acids. Marked preference in sensory trials for fruits grown under enriched [CO ₂].	13
900 ppm	N/A	30 % increase in marketable fruit yield.	N/A	161
	100 μmol s ⁻¹ m ⁻² supp lighting	12 % – 15 % increase in yield under supp lighting, 7 % increase in yield in absence of additional treatment.	N/A	162
	N/A	22 % increase in total fruit yield for plants grown in e[CO ₂].	N/A	163
1000 ppm	N/A	30 % increase in total fresh fruit yield per plant.	N/A	164
		43 % increase in total fruit yield.	No significant effect on fruit quality parameters.	165
		74.3 % – 83.6 % increase in tomato fresh weight per plant.	16.1 % – 20.9 % increase in total sugars. 20.0 % – 24.7 % decrease in vitamin C. 4.79 % – 6.8 % decrease in total acids.	17
		15.6 % increase in fruit yield across 8 different cultivars.	N/A	166
1200 ppm	Salinity up to 4.58 x control	> 40 % loss in dry fruit yield at highest salinity treatment completely offset by increased [CO ₂].	Increased salinity and [CO ₂] combined increases total sugar and acid content by up to ~30%.	167

Table 2 Impact of elevated atmospheric [CO₂] on yield and nutritional quality of other Solanaceous crops

Crop	CO ₂ Treatment	Additional Treatment(s)	Fruit Yield	Fruit Quality	Ref
Sweet Pepper	350 ppm – 450 ppm	N/A	12.9 % increase in fruit yield 350 ppm and 47.4 % increase in fruit yield 450 ppm.	N/A	45
	400 ppm – 800 ppm	20 mmol L ⁻¹ NaCl, foliar calcium treatment	18.9 % to 26.6 % increase in yield at 400 and 800 ppm respectively. Foliar calcium treatment had no impact on yield. e[CO ₂] rescued total yield loss from high salinity.	Little significant effect of increased [CO ₂] on fruit inorganic nutrients or colour.	42
	700 ppm	High/low irrigation and N treatments	Fruit yield for e[CO ₂] increased with irrigation with no significant difference in fruit yield at lowest irrigation.	N/A	48
	700 ppm – 750 ppm	N/A	18 % – 22 % increase in total fruit yield.	N/A	46
	800 ppm	Nitrogen source and saline treatment (8 and 25 mM NaCl)	8 % and 22 % increase in marketable fruit yield under salinity stress and unstressed respectively. 23 % and 29 % maximum increase in daily fruit harvest yield for 2 different nitrogen sources at low salinity.	N/A	43,44,168
	900 ppm	N/A	7 % increase in early yielding fruits, no change in total fruit yield.	N/A	162
	367 ppm – 1000 ppm	Range of irrigation regimens	Yield increased with irrigation and carbon dioxide with a maximum yield increase with both treatments of 264 %.	N/A	41
	1000 ppm	N/A	51 % – 370 % increase in fruit weight per plant.	N/A	169
	10,000 ppm	N/A	20 % increase in fruit yield.	N/A	61
	Chili pepper	380 ppm – 750 ppm	+2 °C and +4 °C temperature elevation	Up to 41.9 % increase in fruit diameter under both increased carbon dioxide and increased temperature.	27 % – 44 % increase in capsaicin across all treatments for 2 cultivars across 2 growth years.
380 ppm – 750 ppm		+2 °C and +4 °C temperature elevation	53.8 % increase in fruit number at [CO ₂] = 550 ppm and ambient + 2°C temperature, 12.3 % decrease in fruit number per plant for [CO ₂] = 750 ppm and ambient + 4°C temperature. Up to ~140 % increase in fruit yield per plant for [CO ₂] = 550 ppm and ambient + 2°C temperature, up to ~36 % reduction in fruit yield per plant for [CO ₂] = 750 ppm and ambient + 4°C temperature.	N/A	50,51
380 ppm – 1140 ppm		N/A	Up to 88.5 % increase in number of fruits per plant, up to 13.0 % increase in fruit length, up to 15.0 % increase in fruit width and up to 14.3 % increase in pericarp thickness. Up to 142 % increase in fruit yield.	No change in colour of ripe fruits. Up to 28.6 % increase in capsaicinoids in ripe fruit.	49,170
400 ppm – 900 ppm		Natural light (233 μmol m ⁻² s ⁻¹) and supplementary light (463 μmol m ⁻² s ⁻¹)	92 % – 113 % increase in total fruit yield per plant across all CO ₂ treatments with supplementary lighting relative to ambient control at 400 ppm. 47 % – 113 % increase in total fruit yield per plant across all CO ₂ treatments with natural lighting relative to ambient control at 400 ppm.	2 % – 10 % decrease in soluble sugars. 13 % – 34 % decrease in vitamin C in e[CO ₂]. 61 % increase in capsaicin at [CO ₂] = 550 ppm, 49 % – 61 % decrease in capsaicin for [CO ₂] > 550 ppm.	171
1000 ppm		N/A	43.80 % – 59.55 % increase in fruit fresh weight per plant across 5 cultivars.	Up to ~15 % increase in total fruit sugars. 11.84 % – 15.84 % decrease in fruit vitamin C, non-significant decrease in fruit titratable acids. Variable effects on inorganic nutrient concentrations. Fruit amino acids and fatty acids mostly reduced.	53
Eggplant	200 ppm – 3000 ppm	N/A	209 % increase in fruit fresh weight and 134 % increase in fruit dry weight.	N/A	172
	1000 ppm	N/A	31 % increase in fruit yield across a full year of harvests.	N/A	169
	663 ppm	N/A	23.6 % increase in fruit yield.	N/A	45

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Table 3 Impact of elevated atmospheric [CO₂] on yield and nutritional quality of Rosaceous crops

Crop	CO ₂ Treatment	Additional Treatment(s)	Fruit Yield	Fruit Quality	Ref
Strawberry	553 ppm	Nitrate treatment (4 x 10 ⁻² mM)	42 % increase in fresh fruit yield in e[CO ₂] at high N, 17 % increase in fresh fruit yield in e[CO ₂] at low N.	N/A	173
	400 ppm, 650 ppm and 900 ppm	Ambient temperature (25 °C) and elevated (30 °C)	9.9 % – 33.4 % increase in total fruit yield at ambient temperature for cultivar “Albion”, 0.9 % – 31.2 % decrease in total fruit yield at ambient temperature for cultivar “San Andreas”. Elevated [CO ₂] rescues yield loss from elevated temperature.	Total fruit polyphenolic content, flavonoid content, monomeric anthocyanin content and antioxidant content increased in correlation with e[CO ₂] at both temperatures for multiple cultivars (~9 % – ~325 % increase overall increase at [CO ₂] = 900 ppm).	56 65
	720 ppm	5 °C increase in temperature, nitrate treatment (50 mL 0.1 % NH ₄ NO ₃ twice per week)	~120 % increase in total fruit dry weight in e[CO ₂], ~73 % increase in total fruit dry weight in e[CO ₂] with nitrogen treatment. No significant change in fruit yield for all other treatments individually and in combination.	48 %, 21 %, 36 % and 18 % decrease in fruit anthocyanin content, total phenolic content, total flavonoid content and total antioxidant content respectively at e[CO ₂]. 29 % and 35 % increase in fruit fructose and glucose respectively. 43 % increase in total sugars.	63
	600 ppm – 1000 ppm	N/A	62 % increase in total fruit yield in e[CO ₂].	N/A	58
	700 ppm – 1000 ppm	N/A	17.6 % and 38.5 % increase in individual fruit weight at [CO ₂] = ambient + 300 ppm and [CO ₂] = ambient + 600 ppm respectively.	7.0 % – 25.9 % increase in glucose, fructose and sucrose. 5.2 % – 47.4 % decrease in citric, malic and quinic acids. Stepwise increase in concentration of most key volatile esters and up to 115.0 % and 149.6 % increase in fruit furaneol and linalool content.	62
	700 ppm – 1000 ppm		N/A	13.3 % increase in fruit ascorbic acid. Stepwise increase in antioxidant and flavonoid compounds with increasing carbon dioxide.	64
	700 ppm – 1000 ppm		5.4 % and 12.7 % increase in marketable fruit yield for cultivars “Irvine” and “Chandler” respectively.	N/A	158
	1000 ppm	N/A	47 % increase in fruit number per plant, no significant change in individual fruit weight.	N/A	55
	900 ppm, 1500 ppm, 3000 ppm	N/A	31 %, 43 % and 51 % increase in fruit yield at 900 ppm, 1500 ppm and 3000 ppm respectively.	N/A	61
Raspberry	436 ppm	N/A	12 % increase in total berry yield and 5 % increase in average individual berry weight.	N/A	174
Nashi Pear	700 ppm	Ambient + 4 °C temperature	16.6 % increase in fruit weight with e[CO ₂]. Elevated [CO ₂] rescues yield loss from increased temperature.	Up to 15.9 % reduction in fruit firmness with e[CO ₂]. Up to 22.5 % increase in total soluble solids with no significant change in acidity with e[CO ₂].	75

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546**Table 4. Impact of elevated atmospheric [CO₂] on yield and nutritional quality of Cucurbitaceous crops**

Crop	CO ₂ Treatment	Additional Treatment(s)	Fruit Yield	Fruit Quality	Ref
Cucumber	400 ppm, 625 ppm, 1200 ppm	2 mmol L ⁻¹ , 7 mmol L ⁻¹ , 14 mmol L ⁻¹ NO ₃ ⁻	Up to 73 % increase in fresh fruit yield for plants grown at highest [CO ₂] versus plants grown at lowest [CO ₂] at greatest N fertilisation. No significant difference in yield for lower N fertilisation.	75 % increase in fruit fructose, 73 % increase in glucose at 7 mmol L ⁻¹ at highest [CO ₂]. No significant change in fruit titratable acidity. <i>e</i> [CO ₂] reduced dietary fibre by 13 % – 18 % across all fertilisation treatments. Up to 84 % reduction in fruit nitrogenous compounds in <i>e</i> [CO ₂] across all nitrogen treatments.	66 68
	400 ppm, 800 ppm, 1200 ppm	0.06 g N kg ⁻¹ soil (low N), 0.24 g N kg ⁻¹ soil (high N)	31 % – 37 % increase in fresh fruit yield for [CO ₂] = 800 ppm and 1200 ppm at low N. 71 % – 106 % increase in fresh fruit yield for [CO ₂] = 800 ppm and 1200 ppm at high N	Across both nitrogen treatments at [CO ₂] = 1200 ppm, fruit fructose was increased by 5 % – 6 %, fruit glucose was increased by 10 % – 12 % and starch was increased by 29 % – 40 %.	70
	364 ppm, 620 ppm	N/A	Up to 10.2 % increase in individual fruit weight for August production in <i>e</i> [CO ₂]	No significant change in fruit dry matter content	45
	400 – 500 ppm	N/A	19 % increase in fresh fruit yield at <i>e</i> [CO ₂]	N/A	175
	600 – 700 ppm	N/A	20 % increase in fresh fruit yield at <i>e</i> [CO ₂]	N/A	176
	700 ppm	N/A	14.2 % – 18.4 % increase in fresh fruit yield at <i>e</i> [CO ₂] across two crop cycles.	Overall reduction in fruit inorganic nutrients (N, P, K, Ca, Mg).	71
	780 ppm	N/A	35 % increase in fresh fruit yield in greenhouse supplemented with [CO ₂] versus control greenhouse.	N/A	177
	700 ppm – 1000 ppm	N/A	20 % – 30 % increase in marketable fruit yield across two growing seasons.	N/A	158
	900 – 1000 ppm	0.6 °C – 1.8 °C cooling	35.4 % increase in dry fruit mass in cooled and <i>e</i> [CO ₂] conditions	N/A	178
	1000 ppm	N/A	8.9 % increase in fruit weight but no significant change in fruit number at <i>e</i> [CO ₂]	N/A	179
900 ppm, 1500 ppm, 3000 ppm	N/A	18.4 % – 26.3 % increase in fresh fruit yield across all CO ₂ elevations.	N/A	61	
Melon	400 ppm, 800 ppm, 1200 ppm	0, 25, 50 mmol NaCl	Up to 29 % increase in fruit yield in all <i>e</i> [CO ₂] at no additional salinity. Elevated [CO ₂] partially rescues yield loss from salinity (by up to 18 %) but is insufficient to fully mitigate yield loss.	N/A	67
	1000 ppm	N/A	13 % increase in muskmelon fruit number and 8 % increase in muskmelon fruit weight during summer production under <i>e</i> [CO ₂]	N/A	169
Squash	700 – 1000 ppm	N/A	15.5 % – 19.7 % increase in total marketable yield across 2 growing seasons.	N/A	158

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Figure 1

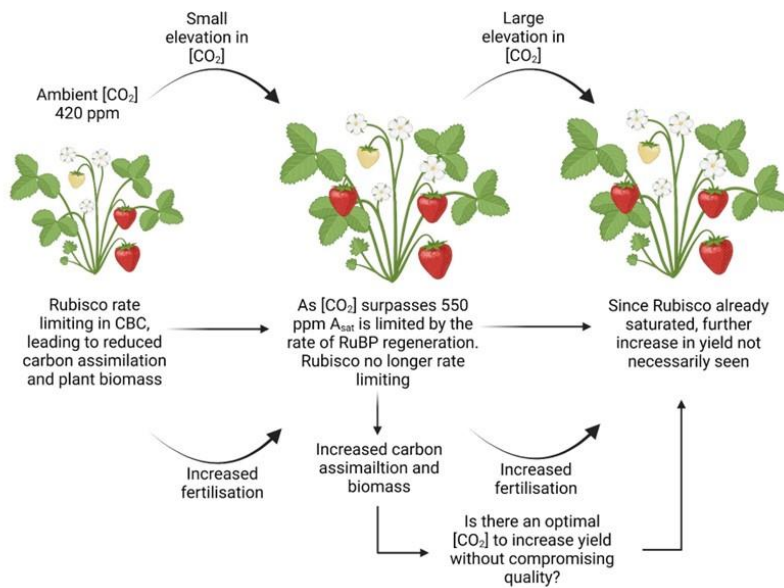


Fig. 1. Schematic representation of elevated [CO₂] on carbon assimilation. Created with BioRender.com

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Figure 2






Fruit	Effects of elevated [CO ₂] on fruit yield and quality
	<ul style="list-style-type: none"> - 7% to 125% increase in fruit yield across all treatments (e[CO₂] = 450ppm – 1200ppm) - Greater organoleptic preference. - 16 to 44 % increase in vitamin C (e[CO₂] = 900 ppm), 20 to 25% decrease in vitamin C (e[CO₂] = 1000 ppm). - 10 to 22% increase in total major sugars (glucose, sucrose, fructose) given sufficient N fertilisation and irrigation across and range of CO₂ treatments (e[CO₂] = 550-1000 ppm). - Large variation in reported total organic acid content between studies with no detectable trend related to degree of CO₂ fertilisation. - 32% increase in lycopene at e[CO₂] = 550 ppm, however 3.7 to 25% decrease in lycopene at e[CO₂] = 700 ppm. <p>Overall, e[CO₂] of 550 ppm seems optimal for simultaneous increases in yield and quality parameters in tomato</p>
	<ul style="list-style-type: none"> - 12.9 % increase in fruit yield 350 ppm and 47.4 % increase in fruit yield 450 ppm. - 18.9 % to 26.6 % increase in yield at 400 and 800 ppm respectively in absence of other treatment. - Yield with irrigation with no significant difference in fruit yield at lowest irrigation. - Little significant effect of increased [CO₂] on fruit inorganic nutrients or colour increased with irrigation and carbon dioxide with a maximum yield increase with both treatments of 264 %. - Fruit yield for e[CO₂] increased <p>Overall, e[CO₂] increases yield, however little work has been carried out on the impacts of e[CO₂] of quality. Increases in yield variable and not observed to be dose dependent.</p>
	<ul style="list-style-type: none"> - 53.8 % increase in fruit number per plant at 550ppm e[CO₂]. - Up to 142% increase in fruit yield, 47% – 113% increase in total fruit yield per plant across all CO₂ treatments with natural lighting. - Up to ~15% increase in total fruit sugars. - 28% to 61% increase in capsaicin with 2% – 10% decrease in soluble sugars and 13% – 34% decrease in vitamin C in same plants <p>Overall, e[CO₂] increases fruit yield and fruit weight and size. However, increases in yield was variable and accompanied by changes in secondary metabolites (i.e increases in capsaicinoids and decrease in soluble sugars and vitamins).</p>
	<ul style="list-style-type: none"> - 1 to 62 % increase in fruit yields across all CO₂ treatments (450 ppm – 3000 ppm) - 7 to 35% increase in major sugars (glucose, fructose, sucrose) for e[CO₂] = 650 - 950 ppm. - Large variation in effects on total anthocyanin, phenolic, flavonoid and antioxidant content between studies, however 10.2 % increase vitamin C reported at e[CO₂] 650 ppm, 13.3% increase reported at e[CO₂] = 950 ppm. - Total acid content was reduced with increasing [CO₂], reducing by ~10% for every 300 ppm increase in e[CO₂]. - Key aroma constituents (esters, furaneol, linalool), increases stepwise with increasing [CO₂] for the conc. tested (350, 650, 950ppm). <p>No specific degree of CO₂ fertilisation can be determined as being optimal since the effects of e[CO₂] > 950 ppm on fruit quality have not been tested. Greater CO₂ fertilisation appears to enhance both yield and quality</p>
	<ul style="list-style-type: none"> - CO₂ fertilisation (400 ppm – 3000 ppm) sufficient to elevate fresh yields by 14 to 37% with little correlation between yield and degree of fertilisation. - In high nitrogen soil, fresh fruit yield increases of 73% were reported for e[CO₂] = 1200 ppm, with greater fruit biomass also reported. This indicates that nitrogen may be a limiting factor on how well cucumber can utilise CO₂ fertilisation. - For e[CO₂] = 1200 ppm and moderate nitrogen fertilisation, a 73 to 75% increase in fruit fructose and glucose was observed. This was not observed at lower e[CO₂] or at higher N. <p>Optimal concentrations of e[CO₂] and N fertilisation required for optimal cucumber yield and quality</p>

Fig. 2. Effects of elevated [CO₂] on yield and quality of fruiting crops. Created with BioRender.com

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Figure 3

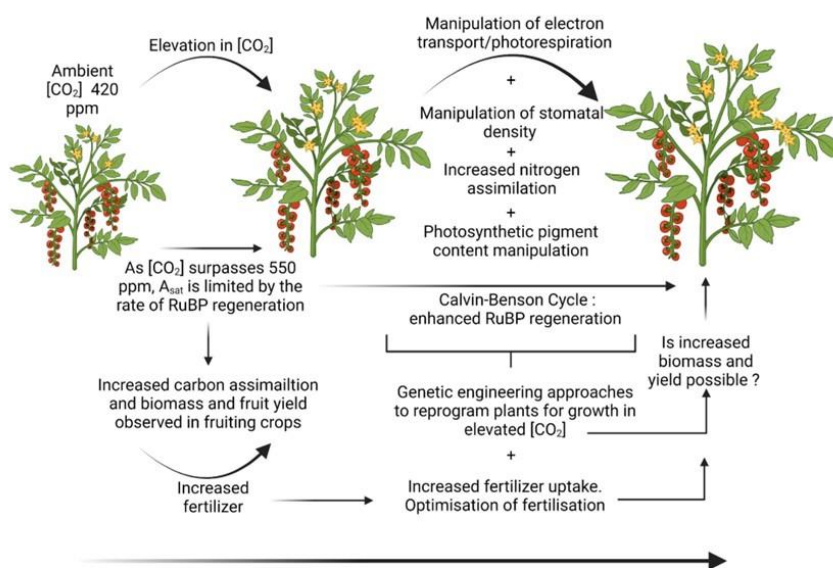


Fig. 3. Effects of elevated [CO₂] on yield of fruiting crops and a representation of the potential for the manipulation of plant material for further yield increases. Created with BioRender.com

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