Feeding the world: impacts of elevated [CO_2] on nutrient content of greenhouse grown fruit crops and options for future yield gains

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Abstract

Several long-term studies have provided strong support demonstrating that growing crops under elevated [CO_2] can increase photosynthesis and result in an increase in yield, flavour and nutritional content (including but not limited to Vitamins C, E and pro-vitamin A). In the case of tomato, increases in yield by as much as 80 % are observed when plants are cultivated at 1000ppm [CO_2], which is consistent with current commercial greenhouse production methods in the tomato fruit industry. These results provide a clear demonstration of the potential for elevating [CO_2] for improving yield and quality in greenhouse crops. The major focus of this review is to bring together 50 years of observations evaluating the impact of elevated [CO_2] on fruit yield and fruit nutritional quality. In the final section, we consider the need to engineer improvements to photosynthesis and nitrogen assimilation to allow plants to take greater advantage of elevated CO_2 growth conditions.

Keywords: Photosynthesis, fruit, quality, climate, nutrition

INTRODUCTION

Elevated [CO_2] (e[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[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[CO_2], and focus almost exclusively on soft fruit such as strawberry, tomato and cucumber. Early work in the 1980's suggested that e[CO_2] increased the average yield of all plants tested by approximately 30%, with optional [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 cops, much of the work has been carried out in controlled environments, in which elevated [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 [CO_2] concentration [7]. A meta-analysis of 107 selected articles showed that e[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[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[CO_2] (see

Myers et al [10]). In 2018, Zhu et al [11] confirmed these results, and moreover demonstrated that rice grown under *e*[CO_2] showed consistent declines in the quantities of vitamins B1, B2, B5, and B9 and, an increase in vitamin E. Finally, studies have shown that grains (wheat, rice, and barley), legumes, and maize-have a 4-10% reduction in iron concentrations of when grown under *e*[CO_2] (~550 ppm)[12]. These results shown that *e*[CO_2] can positively and negatively impact on legumes, grain and vegetables on a crop-by-crop basis and simultaneously alter quality attributes in the same harvestable material.

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

IMPACT OF ELEVATED [CO_2] ON YIELD AND QUALITY OF GREENHOSUE GROWN CROPS

Impact of elevated [CO_2] on solanaceous crops

Commercially, tomato crops are grown in greenhouses with *e*[CO_2], in some cases as high as 2000 ppm. The effects of *e*[CO_2] of fruit yield and quality has been extensively studied (Figure 2). Under *e*[CO_2], tomato fruit yield increases ranged from 7 % – 125 % with [CO_2] ranged from 450 ppm – 1200 ppm compared with plants grown under *a*[CO_2]. An increase in the quantity of non-reducing sugars (glucose and fructose) has been reported [13-17] and fully ripe tomatoes grown in an *e*[CO_2] were found to be preferable for consumption in sensory panels

[13]. As liking sweetness has been shown to be a universal trait [18], it is possible that this increase in sugar is responsible for preference of the carbon enriched tomato fruits. An increase in vitamin C was also found between most studies [13,15,16,19], potentially improving the health benefit gains from consumption of carbon-enriched grown tomatoes (Table 1). Vitamin C is an important dietary requirement and at high concentrations it has been used as a treatment for cancer, arteriosclerosis, and cardiovascular diseases [20-22]. These results suggest that increasing environmental [CO_2] could contribute to an increase in Vitamin C improving their nutritional value for the consumer. However, growth at *e*[CO_2] does not have the same impact on all species, as another studies in barley reported a significant decrease in Vitamin C content [23] highlighting the species–species response differences to *e*[CO_2] and suggesting that high carbon growth environments may not always provide the best outcome for the consumer even though increases in yield maybe the producers primary concern (see Fenech et al. [24] and references therein).

Similarly, tomato fruit concentration of lycopene and β-carotene (pro-vitamin A) were found to increase in response to *e*[CO_2] by as much as 30 % and 70 % respectively [13]. Rangaswamy et al. [25] reported an increase in carotenoid (+20 %) and lycopene (+31 %) in the fruits of tomato plants grown at 550 ppm [CO_2], however carotenoid content decreased (- 12%) when the concentration was increased to 700 ppm, suggesting that the level of CO_2 enrichment impacts fruit quality and careful consideration is needed to ensure an appropriate balance between levels of *e*[CO_2] and final yield. Lycopene is an important phytonutrient, is sold commercially as a dietary supplement, and has been reported to possess anti-cancer properties and can improve cardiovascular health [26,27].

β-carotene is the precursor for Vitamin A, also known as retinol. Vitamin A is an essential micronutrient playing important roles in growth and development, vision [28] and the immune system [29]. More than a third of all pre-school children and a significant number of pregnant women around the world are affected by Vitamin A deficiency, increasing the risk of night blindness and miscarriage [30,31]. Importantly, most people suffering from a deficiency in Vitamin A show no clinical symptoms resulting in a phenomenon termed 'Hidden Hunger' [32]. Production of crops with increased Vitamin A is therefore an important target for improving the diet and health of these at-risk groups; enhanced uptake of carbon may be a useful approach to achieve this. Increases in the Vitamin A precursor β-carotene has been observed in tomato fruit grown under *e*[CO_2] of 800-900ppm, in addition to a 28 % increase in vitamin C at ripe stage and an ~8 % increase in total soluble solids (Table 1) (Zhang et al. [13], suggesting the under these growth conditions, improved vitamin A and C and increased carotenoid content may be attainable.

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

Similar results have also been found in pepper crops with yield increase of 12.9 % – 370.2 % was reported when grown at *e*[CO_2] between 450 ppm – 1000 ppm (Table 2) with most other studies reporting yield increases in the range of 12.9 % – 47.4 % in the absence of other parameters [41-47]. However, it should be noted that growth at ~800ppm $e[CO_2]$ was found to reduce sweet pepper total amino acid content by up to 29 %, including reductions in the sweet tasting amino acids alanine and glycine, which could be detrimental to the perceived fruit flavour [42]. Yield was also found to vary with different irrigation programmes [41,48], nitrogen sources [48], substrate salinity [42,44] and pruning regimens [46]. Given that previous work in tomato has shown an increase in potential phytonutrients in fruit grown at 550 ppm and a decrease in those grown at 700 ppm, further research is needed to better identify the specific quantity of CO_2 fertilisation necessary for maximally improved yield in solanaceous crops, especially when considering that CO_2 uplift is often accompanied by additional treatments, such as increased nutrient and nitrogen (N) fertilisation (Figure 2).

In chili pepper, yield increases of 43.8 % – 142 % were reported for $e[CO_2]$ (in the range of 500 ppm – 1140 ppm). These yield increases were in part attributed to an increase in the size of fruits [49]. However, in controlled environments a 4°C increase in temperature decreased yield, even at $e[CO_2]$ (750 ppm), [50,51], indicating that carbon enrichment is not sufficient to rescue yield where glasshouse facilities or growth tunnels experience periods of elevated temperature in an extreme climate change scenario. Carbon-enriched growth was found to increase the capsaicinoid content of fruits, resulting in an increase in Scoville Heat Units (SHU) [49,52]. This approach therefore has potential for producing hotter varieties of chili, a growing and competitive market. However, at the same time Vitamin C concentration decrease by up to 15.84 % [53], reducing potential health benefits gained from growing chilli plants under $e[CO_2]$. (Table 2).

These reports suggest that the effects of growing crops in $e[CO_2]$ can have both a positive influence on yield and nutritional quality, however, growth at $[CO_2]$ levels above what is optimum can negatively impact some quality traits.

Impact of elevated [CO_2] 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 CO_2 in strawberry leaves at optimal *e*[CO_2] of 600 ppm [55-60]. 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 genes [60], 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 acids [62]. These increases in sugar-acid ratio is highly favourable for a more pleasant perception of strawberry flavour by the consumer [18] and an increase in key volatile organic compounds, including furaneol, linalool and major esters, was also reported, further enhancing the "strawberry" aroma [62]. Growth in a carbon-enriched atmosphere therefore strongly enhances strawberry flavour and increases vitamin C (an important nutritional compound) by up to 13.3 % alongside other antioxidant compounds [64,65]. Growth in carbon-enriched atmospheres therefore simultaneously improves yield, flavour and health benefits of strawberry fruits, creating enormous potential for strategies involving enhanced photosynthesis of strawberry plants, including genetic manipulation. The greatest reported increase in fresh fruit yield where obtained when [CO_2] was kept between 600 ppm – 1000 ppm [58], linking greater carbon assimilation to increased fresh fruit yield in strawberry and demonstrating an optimal degree of CO_2 fertilisation for strawberries (Table 3).

Impact of elevated [CO_2] on cucurbitaceous crops

Cucumber is the most studied fruit crop of the cucurbitaceae in relation to growth in carbon-enriched atmospheres (Figure 2; Table 4). Improved carbon assimilation rates of up to 99 % and 112 % have been reported for cucumber and melon respectively when grown in *e*[CO_2] [66,67], demonstrating that growth in *e*[CO_2] improves photosynthesis of cucurbitaceous crops.

In cucumber (*Cucumis sativus*), fruit yield increases for plants grown in enriched-carbon atmospheres ([CO_2] = 450 ppm – 3000 ppm) ranged between 16.2 % and 41 % in the absence of other parameters that could alter fruit yield. In high nitrogen supplemented fertilisation, fruit yield was as high as 106 % when grown under *e*[CO_2] of 800 ppm [68], indicating the potential of increased nitrogen fertilisation alongside [CO_2] enrichment to unlock the greatest yield increases in cucumber. Interestingly, when grown under *e*[CO_2] of 1200 ppm with the addition of high nitrogen fertilisation treatment, studies found a yield increase between 71 % – 73 % [66,68], which was lower than the 106% for plants grown at *e*[CO_2] of 800 ppm. Concentrations of [CO_2] above optimal reduced stomatal density, stomatal conductance (*gs*), the maximum carboxylation rate (*Vc*max) and the maximum photosynthetic electron transport rate (*J*max) [69]. This suggests that an optimal concentration of atmospheric [CO2] exists for maximum yield returns and deserves further investigation. There is large variation between studies on how cucumber fruit quality is impacted by carbon-enriched growth. Fructose and glucose were reported to increase by 6 % and 12 % in one study [68] and by 75 % and 73 % respectively in another [70]. The inorganic nutrient content of fruits was also reported to decrease in fruits grown in *e*[CO_2], however only phosphorus showed a significant reduction in multiple cycles [71]. These data do suggest that *e*[CO_2] may enhance fruit flavour and fruit yield at the expense of nutritional value.

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

Sweet clonal cherry (*Prunus avium* L.) plants were grown for 19 months in climate-controlled greenhouses at ambient (1994-358 ppm; 1995-360 ppm) or *e*[CO_2] (700 ppm). Elevated [CO_2] treatment increased photosynthesis and dry matter production, leaf (55%) and stem (61%), after two months at 700 ppm, however, this initial stimulation is not sustained. Photosynthetic rates were less after 10 months of growth than after 2 months of growth, and only small increases in dry mass are still evident after 10-months, suggesting that sweet cherry acclimates to *e*[CO_2] due to long-term exposure [72]. Due to the young nature of plants studied compared with fully grown mature trees (deciduous tree 15-32 m in height and with a trunk up to 1.5 m in circumference [73,74], no information is available to determine the impacts of *e*[CO_2] on fruit yield or quality. In Nashi pear, a CO_2-enriched atmosphere of 700 ppm increased fruit weight, diameter and length along with a 22.5 % increase in Brix, (a key measure of sweetness for marketable fruit [75]). However, this also resulted in a reduction in fruit firmness demonstrating that improvements in yield can be nullified by negative impacts on fruit quality (Table 3).

While these studies are limited in, they do indicate the potential of CO_2-enriched growth for improving photosynthesis, increasing yield and quality of tree crops. However, they also suggest that some crops, especially perennial crops, may become acclimated to higher [CO_2] and any gains may be lost over time.

DOES INCREASING CARBON ASSIMILATION INCREASE ENVIRONMENTAL TOLERANCES?

The work presented above also suggest that increasing CO_2 uptake could have other benefits. It is notable that growth of fruit crops in carbon enriched atmospheres has a similar effect of protecting against environmental stresses, such as drought and elevated temperature, that may become increasingly common due to climate change as plants genetically engineered to increase carbon assimilation. For example, in melon (*Cucumis melo*), growing plants in *e*[CO_2] has been shown to mitigate yield losses from increased salinity [67], and in sweet pepper, *e*[CO_2] of 800 ppm was sufficient to rescue any significant yield loss of total and marketable fruits from salinity stress (20 mmol L^{-1} NaCl) [42]. It could be hypothesised that increasing CO_2 assimilation increases sugar and chlorophyll content triggering salt tolerance. However, it should be noted that these results are not universally translatable. Gray et al. [76] demonstrated in soybean that *e*[CO_2] was insufficient to protect yields from drought conditions triggered by higher temperatures demonstrating that benefits in some crops may not be translatable across all crops of agronomical importance. Furthermore, in tomato plant Zhou et al. [77] showed that plants grown in *e*[CO_2] were more sensitive to combined drought and heat stress; *e*[CO_2] drives *gs* and transpiration reducing net photosynthesis and therefore productivity, which is concerning given that greenhouses tend to have elevated temperatures compared to the external environment due to the nature of their construction, glass and metal, and therefore *e*[CO_2] in 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 [CO_2] 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 [CO_2] and temperature increase simultaneously, yields were maintained compared with data where temperature is increased in the absence of *e*[CO_2] 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 [CO_2] 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 CO_2 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 [CO_2] for photosynthesis or increasing the plants' ability to assimilate [CO_2] 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.

[83] concluded that the manipulation of CO_2 uptake could mitigate against the effects of global increases in temperature under *e*[CO_2]. This may be deemed especially important given the expected impact of global climate change. This suggests that increasing carbon assimilation through manipulation of photosynthesis [84,85] can have similar outputs to improved photosynthesis through growth in an enriched carbon atmosphere and further demonstrates the viability of this approach for improvement of yield and quality in fruiting crops. This must be studied considering the recent work showing that improved carbon assimilation also results in improved nutrient uptake and an increase in NUE [86].

FUTURE OPPORTUNITIES

As [CO_2] surpasses 550 ppm, A_{sat} will be limited by the rate of RuBP regeneration rather than Rubisco activity suggesting there is scope to improve plant photosynthesis to increase yield in greenhouse environments where CO_2 is routinely increased to 1000 ppm or more for short periods of time. These short time-periods are furthermore unpredictable and chaotic given that greenhouses must be vented, due to external environmental conditions, to maintain, as close as possible, optimal growing conditions i.e temperature and humidity inside the growth facility. Furthermore, the [CO_2] dosing capacity must be economically beneficial, especially given the chaotic nature of CO_2 loss to the environment during periods of venting. As dosing increases, costs go up accordingly determined by the cost of CO_2. Moreover, at some point, there is a price limit where the supplemental cost of CO_2 increases to a point where costs cannot be recovered by the selling price of the product. In the last year, CO_2 costs have increased for £100 per tonne to as much as £3000 per tonne [87,88]. Therefore, future options that maximize the ability of the crop to take full benefit of the *e*[CO_2], or maintaining higher yields when CO_2 costs are unmanageable become more important.

Araus et al [89], noted that canopy photosynthesis holds a crucial place in a context of yield gains through photosynthetic improvement, which requires additional factors including the availability and uptake of nutrients, such as nitrogen, irrigation, the transport of photoassimilates and sink-source balance. As such, in addition to improving photosynthetic rates via CO_2 supplementation, the improvement of other plant processes such as N uptake, non-foliar photosynthesis, stomatal function, and rubisco(activase) thermotolerance so that crops are better adapted for growth in [CO_2] enriched environments such as greenhouses are discussed below (Figure 3). These works will also need to account for changes to the landscape of greenhouse crop cultivation, such as a move to vertical farming, changes in growth medium from soil to substrates such as coir (derived from coconut husks) or rockwool [90]. It is estimated that more than 50 % of strawberry production occurs in substrate rather than soil [91]. Coir is often used as it has been shown to retains water more efficiently than soil, so strawberry plants require less frequent watering improving water use efficiency. Coir also has a high level of aeration, which is ideal for strawberries' whose root systems require a lot of oxygen. More recent developments in hydroponics [92] and aeroponics [93], will impact on irrigation, fertiliser regimes and N uptake.

Nitrogen use efficiency (NUE)

With regards to fruit quality, this is a complex trait that may not be simply attributed to enhanced carbon assimilation. More research is needed to link increased assimilate, with assimilate distribution and transport, NUE to better understand the sink-source relationship in any given crop, which can vary significantly across varieties and crop types. NUE is determined by yield per unit of available N in the growth medium (i.e often coir in greenhouse grown crops). Plants with higher NUE may allocate N toward both the photosynthetic complexes (i.e N is major component of chlorophyll; total N allocated to Rubisco $18.2 \pm 6.2\%$; [94]) and/or toward the development of additional sinks. The second definition of NUE could be described as the efficiency with which N is applied to soils, (through artificial means in greenhouse crops), is taken up by plants and converted to usable products (i.e. biomass, grain yield). This can be manipulated through breeding to identify new varieties with high NUE uptake from selected growing mediums or through engineering nitrogen symbiosis (Figure 3). Recently, scientists reported the engineering nitrogen-fixation into non-legume cereal crops by enabling them to interact with soil bacteria to convert N from the air into ammonia fertiliser [95]. These works could firstly reduce the reliance on commercial synthetic fertilisers and secondly provide alternate sources of N that along with improvements to carbon assimilation, foliar or non-foliar, co-contribute to improving photosynthesis and yields in crops (Figure 3).

A recent review has identified a number of targets in the literature to improve N uptake, assimilation and remobilisation through genetic manipulation (see [96] for review). One of these, the over-expression of the nitrate transporter (NRT2.3) was shown to increase nitrate concentrations in tomato increasing biomass and fruit weight [97]. More recently, the transcription factor DREB1C has been identified as a regulator of NUE by controlling the expression of several important growth-related genes including the rubisco small subunit 3 (RBCS3), nitrate transporters (NRT1.1B, NRT2.4), nitrate reductase (NR2) and the flowering regulator (FTL3). Once over-expressed (OE), OsDREB1C increased the abundance of photosynthetic pigments, plants were shown to have about one-third more chloroplasts, 38% more rubisco and improved photosynthesis and N uptake. The OE of OsDREB1C resulted in a >40% increase in grain yield in elite rice varieties and an ~20% increase in wheat yields, while in Arabidopsis, a significant increase in biomass [98]. Many of these identified genes have potential for improving NUE in fruiting crops grown in *e*[CO_2]. A recent report of a large grain rice cultivar, Akita 63, having a high yield due to an enlarged sink capacity without and photosynthesis improvement. However, this work demonstrated that source capacity was strongly limiting the yield potential under high N fertilization. These authors suggested that enhancing photosynthesis is an important step to further increase yield of current high-yielding cultivars [99]. This work can be extrapolated that engineering NUE and photosynthesis in plants grown at $e[CO_2]$ could provide a step-change in yields in greenhouse cultivated crops.

Genetic variation in photosynthetic traits in crops and wild relatives

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

In transgenic rice, overproducing Rubisco, increases the biomass production and yield under high N fertilization in paddy fields suggesting that the development of new rice varieties with both high photosynthesis and large sink capacity is essential [99]. Furthermore, genes encoding thermostable variants of Rubisco activase (thermos-Rca) have been identified in wild rice relatives. When over-expressed in domesticated rice, thermos-Rca was sufficient to enhance carbohydrate accumulation and improve yields after periodic exposure to elevated temperatures (+45°C) throughout the vegetative phase [112,113]. Thermostable Rca have been identified in Thermophilic cyanobacteria, bacteria that thrive in high-temperature environments, making them a potential source of novel genes for engineering crops for growth at higher temperatures [114]. Improving the thermal tolerance of rubisco activase, either through breeding with wild populations or genetic engineering, could aid greenhouse grown crops better tolerate the elevated temperatures that often occur during the growing season (Figure 3).

Genetic engineering of photosynthetic traits in crops

Increasing the expression of enzymes and/or proteins involved in the regeneration of RuBP, CO_2 transport or chloroplast electron transport have previously been shown to enhance photosynthetic efficiency and increases in yield [84,85,115-117]. However, once again, it cannot be ignored that much of this work has focused on non-fruiting crops, such as Arabidopsis, tobacco, wheat and rice, (see Simkin et al. [84] for review), grown in controlled conditions, performed in pots, in soil or in the field with controlled irrigation, which is not typical of global agriculture. Furthermore, work carried out in tomato, over-expression of sedoheptulose-1,7-bisphosphatase, involved in RuBP regeneration, did not report on fruit yield [82]. These data indicating that more work is required to understand how these manipulations would impact fruiting crops grown in tightly controlled environments.

One potential target for genetic manipulation is the starch synthesis enzyme adenosine diphosphate glucose pyrophosphorylase (AGPase); increasing AGPase activity has potential to increase starch accumulation for growth. Increased accumulation of starch has been shown to have little negative feedback on photosynthesis [118] and increased AGPase activity in the chloroplast would increase the strength of the transient starch pool, which acts as a sink in the chloroplast. Reduced sink capacity does induce negative feedback on photosynthesis and can limit photosynthesis even in favourable conditions (e.g. elevated [CO_2]) [119], suggesting that increasing the sink may allow for greater CO_2 assimilation in supplemented [CO_2] growth environments.

Although genetic manipulation has the potential to further increase yields in crops grown in enriched [CO_2] environments, allowing them to take better advantage of supplemental CO_2, increasing net photosynthetic rates and associated yields (Figure 3), it should also be noted that some reports have suggested that increases in yield in genetically enhanced photosynthetic crops are likely not uniquely down to increases in carbon assimilation but a combination of factors; for example improvements in carbon uptake allow for an increase in N assimilation [120]. Furthermore, it has also been reported that such increase in yield from enhanced photosynthetic efficiency critically rely on the availability and uptake of water and nutrients (for review see [121,122]), therefore, genetic engineering as an approach alone may be limiting if other aspects of crop cultivation, such as irrigation, planting regimes, fertilisation (i.e NUE) and growth media (i.e soil, coir, rockwool), are not taken into account and co-optimised.

Non-foliar photosynthesis

Leaves are not the only location within the plant where photosynthesis occurs, with evidence of photosynthesis in petioles and stems [123,124], and fruit [124] that may provide significant and alternative sources of photo-assimilates essential for optimal yield. Assimilation of atmospheric CO_2 is dependent on the number and behaviour of stomata, and the stems of many plants have stomata distributed along the epidermis [125,126] and an evaluation of the photosynthetic activity in stems of various plants accounted for up to 4% of the total photosynthetic activity [127]. Furthermore, Hu et al. demonstrated the importance of stem photosynthesis to yield in cotton; maintaining the stem in darkness reduced seed weight by 16 % [128] showing the stem provides photoassimilates for plant development and growth.

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

CONCLUSIONS

These data show that the yield of fruiting crops benefit from growth in supplemented atmospheres, although, some data suggests that increase in yield can come at the expense of quality traits. It is therefore essential to determine the optimal [CO_2] concentrations on a crop-by-crop basis, to maximise productivity. An evaluation of fruit quality under these conditions has also been shown to be highly variable between treatments and difference are observed between cultivars with the same treatment suggesting that much more research is required to identify the specific mechanisms behind changes in fruit quality. In the case of soft fruit production in greenhouse environments, it will be important to determine if the quality of fruit harvested early in the season differs from that of fruit harvested later in the season when plants have spent a more significant period of time exposed to *e*[CO_2] growth conditions. Cherry for instance, when grown under prolonged periods of *e*[CO_2], acclimates to prolonged exposure and initial significant gains in yield observed after two months are less detectable after ten months and are not significantly different to control plants grown at *a*[CO_2] [72]. This may in one respect account for differences in nutritional quality observed in fruit grown in similar conditions in different studies (i.e. fruit harvested at different times in the study) where additional fertilizer treatments aren't provided.

Increases in yield associated with *e*[CO_2] controlled environments may be about more than additional carbon. Controlled environments also allow the regulation of transpiration (e.g. by controlling vapour pressure deficit) and therefore water uptake and the inclusion of additional fertilisation (specifically N). Breeding new varieties adapted to these growth conditions may also be more amenable given the hostility towards genetically modified crops. A recent review noted that new phenomics, genomics, and bioinformatics tools make it possible to harness the untapped potential of crop genetic resources (including wild relatives) to create combinations of traits to enhance yield in high [CO_2] controlled environments [137].

Breeding alone may not be sufficient to adapt all varieties, or all crops, to high [CO_2] growing environments traditionally used in greenhouses. However, over the last several decades, agricultural research has adopted technologies such as genetic engineering and ‘genome editing’ to improve traits in key crops that could be useful in these circumstances [85,138-140]. These include advances in the tools available to carry out this work, including vectors for multiple gene insertion [141-145] and tissue specific promoters [146-150]. If the promise of these biotechnology programs is to be realized, it will be necessary to address the public perception of genetic modification and genome editing technologies to gain greater acceptance.

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

It should also be noted that the introduction of new growing, hydroponics, aquaponics and aeroponics may require further study, to breed and adapt or engineer plants root architecture for these new growth media. In conclusion, greenhouse cultivation offers the opportunity to manipulate growing atmosphere, lights and VPD for improved yields and we can now look at 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 [CO_2] on carbon assimilation. Created with BioRender.com

Figure 2. Effects of elevated [CO_2] on yield and quality of fruiting crops. Created with BioRender.com

Figure 3. Effects of elevated [CO_2] 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 [CO_2] 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 [CO_2] 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.	52
	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

Table 3 Impact of elevated atmospheric [CO_2] 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^{-2-0} 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_4NO_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

Table 4. Impact of elevated atmospheric [CO_2] 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. *e*[CO_2] reduced dietary fibre by 13 % – 18 % across all fertilisation treatments. Up to 84 % reduction in fruit nitrogenous compounds in *e*[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 *e*[CO_2]	No significant change in fruit dry matter content	45
	400 – 500 ppm	N/A	19 % increase in fresh fruit yield at *e*[CO_2]	N/A	175
	600 – 700 ppm	N/A	20 % increase in fresh fruit yield at *e*[CO_2]	N/A	176
	700 ppm	N/A	14.2 % – 18.4 % increase in fresh fruit yield at *e*[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 *e*[CO_2] conditions	N/A	178
	1000 ppm	N/A	8.9 % increase in fruit weight but no significant change in fruit number at *e*[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 *e*[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 *e*[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

References

1. Ainsworth, E.A. & Rogers, A. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant Cell Environ* **30**, 258-270 http://dx.doi.org/10.1111/j.1365-3040.2007.01641.x (2007).
2. Kimball, B.A. Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature. *Curr Opin Plant Biol* **31**, 36-43 http://dx.doi.org/10.1016/j.pbi.2016.03.006 (2016).
3. Kimball, B.A. & Mitchell, S.T. CO_2 enrichment of tomatoes in unventilated greenhouses in an arid climate. *ActaHortic.* **87**, 131-138 http://dx.doi.org/10.17660/ActaHortic.1978.87.12 (1978).
4. Mortensen, L.M. Review: CO2 enrichment in greenhouses. Crop responses. *Scientia Horticulturae* **33**, 1-25 http://dx.doi.org/https://doi.org/10.1016/0304-4238(87)90028-8 (1987).
5. Idso, S.B. Three phases of plant response to atmospheric CO_2 enrichment. *Plant Physiology* **87**, 5-7 http://dx.doi.org/10.1104/pp.87.1.5 (1988).
6. Prior, S.A., Rogers, H.H., Runion, G.B. & Mauney, J.R. Effects of free-air CO_2 enrichment on cotton root growth *Agricultural and Forest Meteorology* **70**, 69-86 (1994).
7. Mortensen, L.M. Effects of elevated CO_2 concentrations on growth and yield of eight vegetable species in a cool climate. *Scientia Horticulturae* **58**, 177-185 http://dx.doi.org/https://doi.org/10.1016/0304-4238(94)90149-X (1994).
8. Dong, J. *et al.* Sustainable vegetable production under changing climate: The impact of elevated CO_2 on yield of vegetables and the interactions with environments-A review. *Journal of Cleaner Production* **253**, 119920 http://dx.doi.org/https://doi.org/10.1016/j.jclepro.2019.119920 (2020).
9. Dong, J., Gruda, N., Lam, S.K., Li, X. & Duan, Z. Effects of elevated CO_2 on nutritional quality of vegetables: A review. *Frontiers in Plant Science* (Review) **9**, http://dx.doi.org/10.3389/fpls.2018.00924 (2018).
10. Myers, S.S. *et al.* Increasing CO_2 threatens human nutrition. *Nature* **510**, 139 http://dx.doi.org/10.1038/nature13179 (2014).
11. Zhu, C. *et al.* Carbon dioxide (CO_2) levels this century will alter the protein, micronutrients, and vitamin content of rice grains with potential health consequences for the poorest rice-dependent countries. *Science Advances* **4**, eaaq1012 http://dx.doi.org/10.1126/sciadv.aaq1012 (2018).
12. Smith, M.R., Golden, C.D. & Myers, S.S. Potential rise in iron deficiency due to future anthropogenic carbon dioxide emissions. *Geohealth* **1**, 248-257 http://dx.doi.org/10.1002/2016gh000018 (2017).
13. Zhang, Z., Liu, L., Zhang, M., Zhang, Y. & Wang, Q. Effect of carbon dioxide enrichment on health-promoting compounds and organoleptic properties of tomato fruits grown in greenhouse. *Food Chemistry* **153**, 157-163 http://dx.doi.org/https://doi.org/10.1016/j.foodchem.2013.12.052 (2014).
14. Sánchez-González, M.J. *et al.* Carbon dioxide enrichment: a technique to mitigate the negative effects of salinity on the productivity of high value tomatoes. *Spanish Journal of Agricultural Research* **14**, e0903 http://dx.doi.org/10.5424/sjar/2016142-8392 (2016).
15. Li, F. *et al.* Combined effects of enhanced ultraviolet-B radiation and doubled CO_2 concentration on growth, fruit quality and yield of tomato in winter plastic greenhouse. *Frontiers of Biology in China* **2**, 414-418 http://dx.doi.org/10.1007/s11515-007-0063-x (2007).
16. Shahidul Islam, M., Matsui, T. & Yoshida, Y. Effect of carbon dioxide enrichment on physico-chemical and enzymatic changes in tomato fruits at various stages of maturity. *Scientia Horticulturae* **65**, 137-149 http://dx.doi.org/https://doi.org/10.1016/0304-4238(95)00867-5 (1996).
17. Khan, I., Azam, A. & Mahmood, A. The impact of enhanced atmospheric carbon dioxide on yield, proximate composition, elemental concentration, fatty acid and vitamin C contents of tomato (*Lycopersicon esculentum*). *Environmental Monitoring and Assessment* **185**, 205-214 http://dx.doi.org/10.1007/s10661-012-2544-x (2013).
18. Drewnowski, A., Mennella, J.A., Johnson, S.L. & Bellisle, F. Sweetness and food preference. *The Journal of Nutrition* **142**, 1142S-1148S http://dx.doi.org/10.3945/jn.111.149575 (2012).
19. Mamatha, H. *et al.* Impact of elevated CO_2 on growth, physiology, yield, and quality of tomato (*Lycopersicon esculentum* Mill) cv. Arka Ashish. *Photosynthetica* **52**, 519-528 http://dx.doi.org/10.1007/s11099-014-0059-0 (2014).

20. Du, J., Cullen, J.J. & Buettner, G.R. Ascorbic acid: Chemistry, biology and the treatment of cancer. *Biochimica et Biophysica Acta (BBA) - Reviews on Cancer* **1826**, 443-457 http://dx.doi.org/https://doi.org/10.1016/j.bbcan.2012.06.003 (2012).
21. Leong, S.Y. & Oey, I. Effects of processing on anthocyanins, carotenoids and vitamin C in summer fruits and vegetables. *Food Chemistry* **133**, 1577-1587 http://dx.doi.org/https://doi.org/10.1016/j.foodchem.2012.02.052 (2012).
22. Da Silva Dias, J.C. Nutritional and Health Benefits of Carrots and Their Seed Extracts. *Food and Nutrition Sciences* **5**, 2147-2156 (2014).
23. Robinson, J.M. & Sicher, R.C. Antioxidant levels decrease in primary leaves of barley during growth at ambient and elevated carbon dioxide levels. *International Journal of Plant Sciences* **165**, 965-972 http://dx.doi.org/10.1086/423867 (2004).
24. Fenech, M., Amaya, I., Valpuesta, V. & Botella, M.A. Vitamin C content in fruits: Biosynthesis and regulation. *Frontiers in Plant Science* (Review) **9**, http://dx.doi.org/10.3389/fpls.2018.02006 (2019).
25. Rangaswamy, T.C. *et al.* Assessing the impact of higher levels of CO_2 and temperature and their interactions on tomato (*Solanum lycopersicum* L.). *Plants* **10**, 256 https://www.mdpi.com/2223-7747/10/2/256 (2021).
26. Simkin, A.J. Carotenoids and apocarotenoids in planta: Their role in plant development, contribution to the flavour and aroma of fruits and flowers, and their nutraceutical benefits. *Plants* **10**, 2321 (2021).
27. Story, E.N., Kopec, R.E., Schwartz, S.J. & Harris, G.K. An update on the health effects of tomato lycopene. *Annual Review of Food Science and Technology* **1**, 189-210 http://dx.doi.org/10.1146/annurev.food.102308.124120 (2010).
28. Rando, R.R. The chemistry of vitamin A and vision. *Angewandte Chemie International Edition* **29**, 461-480 (1990).
29. West, C.E., Rombout, J.H., van der Zijpp, A.J. & Sijtsma, S.R. Vitamin A and immune function. *Proceedings of the Nutrition Society* **50**, 251-262 https://www.ncbi.nlm.nih.gov/pubmed/1749794 (1991).
30. WHO. Global Prevalence of Vitamin A Deficiency in Populations at Risk 1995 - 2005. WHO Global Database on Vitamin A Deficiency. (Geneva: World Health Organisation, 2005).
31. WHO. World Health Organisation : Micronutrient Deficiencies. (2019).
32. Hodge, J. Hidden hunger: Approaches to tackling micronutrient deficiencies in Nourishing millions: Stories of change in nutrition. (eds Gillespie, S., Hodge, J., Yosef, S. & Pandya-Lorch, R.) 35-46 Ch. 4 (International Food Policy Research Institute (IFPRI), 2016).
33. Simkin, A.J. *et al.* Circadian regulation of the PhCCD1 carotenoid cleavage dioxygenase controls emission of beta-ionone, a fragrance volatile of petunia flowers. *Plant Physiology* **136**, 3504-3514 http://dx.doi.org/10.1104/pp.104.049718 (2004).
34. Simkin, A.J., Schwartz, S.H., Auldridge, M., Taylor, M.G. & Klee, H.J. The tomato carotenoid cleavage dioxygenase 1 genes contribute to the formation of the flavor volatiles β-ionone, pseudoionone, and geranylacetone. *The Plant Journal* **40**, 882-892 http://dx.doi.org/10.1111/j.1365-313X.2004.02263.x (2004).
35. Zhang, X. *et al.* Overexpression and characterization of CCD4 from Osmanthus fragrans and β-ionone biosynthesis from β-carotene in vitro. *Journal of Molecular Catalysis B: Enzymatic* **134**, 105-114 http://dx.doi.org/https://doi.org/10.1016/j.molcatb.2016.10.003 (2016).
36. Vogel, J.T., Tan, B.-C., McCarty, D.R. & Klee, H.J. The carotenoid cleavage dioxygenase 1 enzyme has broad substrate specificity, cleaving multiple carotenoids at two different bond positions. *Journal of Biological Chemistry* **283**, 11364-11373 http://dx.doi.org/10.1074/jbc.M710106200 (2008).
37. Ilg, A., Beyer, P. & Al-Babili, S. Characterization of the rice carotenoid cleavage dioxygenase 1 reveals a novel route for geranial biosynthesis. *The FEBS Journal* **276**, 736-747 http://dx.doi.org/10.1111/j.1742-4658.2008.06820.x (2009).

38. Baldwin, E.A., Scott, J.W., Shewmaker, C.K. & Schuch, W. Flavor Trivia and Tomato Aroma: Biochemistry and Possible Mechanisms for Control of Important Aroma Components. *HortScience* **35**, 1013-1022 (2000).

39. Buttery, R.G., Teranishi, R., Ling, L.C. & Turnbaugh, J.G. Quantitative and sensory studies on tomato paste volatiles. *Journal of Agricultural and Food Chemistry* **38**, 336-340 http://dx.doi.org/10.1021/jf00091a074 (1990).

40. Simkin, A.J. *et al.* Fibrillin influence on plastid ultrastructure and pigment content in tomato fruit. *Phytochemistry* **68**, 1545-1556 http://dx.doi.org/10.1016/j.phytochem.2007.03.014 (2007).

41. Rezende, F.C., Frizzone, J.A., Oliveira, R.F.d. & Pereira, A.S. CO_2 and irrigation in relation to yield and water use of the bell pepper crop. *Scientia Agricola* **60**, 7-12 http://dx.doi.org/https://doi.org/10.1590/s0103-90162003000100002 (2003).

42. Piñero, M.C., Pérez-Jiménez, M., López-Marín, J. & del Amor, F.M. Fruit quality of sweet pepper as affected by foliar Ca applications to mitigate the supply of saline water under a climate change scenario. *Journal of the Science of Food and Agriculture* **98**, 1071-1078 http://dx.doi.org/https://doi.org/10.1002/jsfa.8557 (2018).

43. Porras, M.E. *et al.* Photosynthetic acclimation to elevated CO_2 concentration in a sweet pepper (*Capsicum annuum*) crop under Mediterranean greenhouse conditions: influence of the nitrogen source and salinity. *Functional Plant Biology* **44**, 573-586 http://dx.doi.org/https://doi.org/10.1071/FP16362 (2017).

44. Porras, M.E. *et al.* Sweet pepper grown under salinity stress as affected by CO_2 enrichment and nitrogen source. *ActaHortic.* **1170**, 805-812 http://dx.doi.org/10.17660/ActaHortic.2017.1170.103 (2017).

45. Nederhoff, E.M. Effects of CO_2 concentration on photosynthesis, transpiration and production of greenhouse fruit vegetable crops. (1994).

46. Alonso, F.J., Lorenzo, P., Medrano, E. & SÃ¡nchez-Guerrero, M.C. Greenhouse sweet pepper productive response to carbon dioxide enrichment and crop pruning. *ActaHortic.* **927**, 345-351 http://dx.doi.org/10.17660/ActaHortic.2012.927.41 (2012).

47. Aloni, B. & Karni, L. Effects of CO_2 enrichment on yield, carbohydrate accumulation and changes in the activity of antioxidative enzymes in bell pepper (*Capsicum annuum* L.). *The Journal of Horticultural Science and Biotechnology* **77**, 534-540 http://dx.doi.org/10.1080/14620316.2002.11511534 (2002).

48. Penuelas, J., Biel, C. & Estiarte, M. Growth, biomass allocation and phenology responses of pepper to elevated CO_2 concentrations and different water and nitrogen supply. *Photosynthetica* **31**, 91-99 (1995).

49. Garruña-Hernández, R., Monforte-González, M., Canto-Aguilar, A., Vázquez-Flota, F. & Orellana, R. Enrichment of carbon dioxide in the atmosphere increases the capsaicinoids content in Habanero peppers (*Capsicum chinense* Jacq.). *Journal of the Science of Food and Agriculture* **93**, 1385-1388 http://dx.doi.org/https://doi.org/10.1002/jsfa.5904 (2013).

50. Das, S., Das, R., Kalita, P. & Baruah, U. Growth responses of hot chilli (*Capsicum chinense* jacq.) to elevated carbon dioxide and temperature. *Journal of Experimental Biology and Agricultural Sciences* **8**, 434-440 http://dx.doi.org/https://doi.org/10.18006/2020.8(4).434.440 (2020).

51. Das, S., Das, R., Kalita, P. & Bharali, B. Developmental processes in hot chilli (*Capsicum chinense* Jacq.) as affected by elevated carbondioxide and temperature. *Plant Physiology Reports* **25**, 386-394 http://dx.doi.org/10.1007/s40502-020-00522-8 (2020).

52. Das, S., Das, R., Hemendra, C. & Ananta, S. Interactive effect of elevated carbondioxide and high temperature on quality of hot chilli (*Capsicum chinense* Jacq.). *International Journal of Tropical Agriculture* **34**, 1977-1981 (2016).

53. Azam, A., Hameed, A. & Khan, I. Impact of elevated atmospheric carbon dioxide on yield, vitamin c, proximate, fatty acid and amino acid composition of Capsicum (*Capsicum Annuum*). *Environmental Pollution and Protection* **2**, 153-167 http://dx.doi.org/https://doi.org/10.22606/epp.2017.24001 (2017).

54. Gödecke, T., Stein, A.J. & Qaim, M. The global burden of chronic and hidden hunger: Trends and determinants. *Global Food Security* **17**, 21-29 http://dx.doi.org/https://doi.org/10.1016/j.gfs.2018.03.004 (2018).
55. Sung, F.J.M. & Chen, J.J. Gas exchange rate and yield response of strawberry to carbon dioxide enrichment. *Scientia Horticulturae* **48**, 241-251 http://dx.doi.org/https://doi.org/10.1016/0304-4238(91)90132-I (1991).
56. Balasooriya, H.N., Dassanayake, K.B., Seneweera, S. & Ajlouni, S. Interaction of elevated carbon dioxide and temperature on strawberry (*Fragaria × ananassa*) growth and fruit yield. *International Journal of Biological, Life and Agricultural Sciences* **11**, 9 http://dx.doi.org/https://doi.org/https://doi.org/10.5281/zenodo.1474461 (2018).
57. Bunce, J.A. Seasonal patterns of photosynthetic response and acclimation to elevated carbon dioxide in field-grown strawberry. *Photosynthesis Research* **68**, 237-245 http://dx.doi.org/10.1023/A:1012928928355 (2001).
58. Bushway, L.J. & Pritts, M.P. Enhancing early spring microclimate to increase carbon resources and productivity in june-bearing strawberry. *Journal of the American Society for Horticultural Science* **127**, 415-422 http://dx.doi.org/10.21273/jashs.127.3.415 (2002).
59. Keutgen, N., Chen, K. & Lenz, F. Responses of strawberry leaf photosynthesis, chlorophyll fluorescence and macronutrient contents to elevated CO_2. *Journal of plant physiology* **150**, 395-400 http://dx.doi.org/https://doi.org/10.1016/S0176-1617(97)80088-0 (1997).
60. Li, X. *et al.* Physiological and molecular basis of promoting leaf growth in strawberry (*Fragaria ananassa* Duch.) by CO_2 enrichment. *Biotechnology & Biotechnological Equipment* **34**, 905-917 http://dx.doi.org/10.1080/13102818.2020.1811766 (2020).
61. Enoch, H.Z., Rylski, I. & Spigelman, M. CO_2 enrichment of strawberry and cucumber plants grown in unheated greenhouses in Israel. *Scientia Horticulturae* **5**, 33-41 http://dx.doi.org/https://doi.org/10.1016/0304-4238(76)90020-0 (1976).
62. Wang, S. & Bunce, J. Elevated carbon dioxide affects fruit flavor in field-grown strawberries (*Fragaria × ananassa* Duch). *Journal of the Science of Food and Agriculture* **84**, 1464-1468 http://dx.doi.org/https://doi.org/10.1002/jsfa.1824 (2004).
63. Sun, P. *et al.* Effects of elevated CO_2 and temperature on yield and fruit quality of strawberry (*Fragaria × ananassa* Duch.) at two levels of nitrogen application. *PLOS ONE* **7**, e41000 http://dx.doi.org/10.1371/journal.pone.0041000 (2012).
64. Wang, S.Y., Bunce, J.A. & Maas, J.L. Elevated carbon dioxide increases contents of antioxidant compounds in field-grown strawberries. *Journal of Agricultural and Food Chemistry* **51**, 4315-4320 http://dx.doi.org/10.1021/jf021172d (2003).
65. Balasooriya, H.N., Dassanayake, K.B., Seneweera, S. & Ajlouni, S. Impact of elevated carbon dioxide and temperature on strawberry polyphenols. *Journal of the Science of Food and Agriculture* **99**, 4659-4669 http://dx.doi.org/https://doi.org/10.1002/jsfa.9706 (2019).
66. Dong, J., Li, X., Chu, W. & Duan, Z. High nitrate supply promotes nitrate assimilation and alleviates photosynthetic acclimation of cucumber plants under elevated CO_2. *Scientia Horticulturae* **218**, 275-283 http://dx.doi.org/https://doi.org/10.1016/j.scienta.2016.11.026 (2017).
67. Mavrogianopoulos, G.N., Spanakis, J. & Tsikalas, P. Effect of carbon dioxide enrichment and salinity on photosynthesis and yield in melon. *Scientia Horticulturae* **79**, 51-63 http://dx.doi.org/https://doi.org/10.1016/S0304-4238(98)00178-2 (1999).
68. Dong, J. *et al.* Elevated and super-elevated CO_2 differ in their interactive effects with nitrogen availability on fruit yield and quality of cucumber. *Journal of the Science of Food and Agriculture* **98**, 4509-4516 http://dx.doi.org/https://doi.org/10.1002/jsfa.8976 (2018).
69. Xu, M. The optimal atmospheric CO2 concentration for the growth of winter wheat (Triticum aestivum). *Journal of plant physiology* **184**, 89-97 http://dx.doi.org/10.1016/j.jplph.2015.07.003 (2015).

70. Dong, J.-l., Li, X., Nazim, G. & Duan, Z.-q. Interactive effects of elevated carbon dioxide and nitrogen availability on fruit quality of cucumber (*Cucumis sativus* L.). *Journal of Integrative Agriculture* **17**, 2438-2446 http://dx.doi.org/https://doi.org/10.1016/S2095-3119(18)62005-2 (2018).

71. Segura, M.L., Parra, J.F., Lorenzo, P., Sánchez-Guerrero, M.C. & Medrano, E. The effects of CO_2 enrichment on cucumber growth under greenhouse conditions. *ActaHortic.* **559**, 217-222 http://dx.doi.org/10.17660/ActaHortic.2001.559.31 (2001).

72. Atkinson, C.J., Taylor, J.M., Wilkins, D. & Besford, R.T. Effects of elevated CO_2 on chloroplast components, gas exchange and growth of oak and cherry. *Tree Physiology* **17**, 319-325 http://dx.doi.org/10.1093/treephys/17.5.319 (1997).

73. Vignati, E., Lipska, M., Dunwell, J.M., Caccamo, M. & Simkin, A.J. Fruit development in sweet cherry. *Plants* **11**, 1531 http://dx.doi.org/10.3390/plants11121531 (2022).

74. Vignati, E., Lipska, M., Dunwell, J.M., Caccamo, M. & Simkin, A.J. Options for the generation of seedless cherry, the ultimate snacking product. *Planta* **256**, 90 http://dx.doi.org/10.1007/s00425-022-04005-y (2022).

75. Han, J.-H. *et al.* Effects of elevated carbon dioxide and temperature on photosynthesis and fruit characteristics of 'Niitaka' pear *(Pyrus pyrifolia* Nakai). *Horticulture, Environment, and Biotechnology* **53**, 357-361 http://dx.doi.org/10.1007/s13580-012-0047-x (2012).

76. Gray, S.B. *et al.* Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. *Nature Plants* **2**, 16132 http://dx.doi.org/10.1038/nplants.2016.132 (2016).

77. Zhou, R. *et al.* Interactive effects of elevated CO_2 concentration and combined heat and drought stress on tomato photosynthesis. *BMC Plant Biology* **20**, 260 http://dx.doi.org/10.1186/s12870-020-02457-6 (2020).

78. Stips, A., Macias, D., Coughlan, C., Garcia-Gorriz, E. & Liang, X.S. On the causal structure between CO_2 and global temperature. *Scientific Reports* **6**, 21691 http://dx.doi.org/10.1038/srep21691 (2016).

79. Koutsoyiannis, D. & Kundzewicz, Z.W. Atmospheric temperature and CO_2: Hen-Or-Egg Causality? *Sci* **2**, 83 https://www.mdpi.com/2413-4155/2/4/83 (2020).

80. Simkin, A.J. *et al.* Simultaneous stimulation of sedoheptulose 1,7-bisphosphatase, fructose 1,6-bisphophate aldolase and the photorespiratory glycine decarboxylase H-protein increases CO_2 assimilation, vegetative biomass and seed yield in Arabidopsis. *Plant Biotechnology Journal* **15**, 805-816 http://dx.doi.org/10.1111/pbi.12676 (2017).

81. Chen, Y. *et al.* Uncovering candidate genes responsive to salt stress in *Salix matsudana* (Koidz) by transcriptomic analysis. *PLOS ONE* **15**, e0236129 http://dx.doi.org/10.1371/journal.pone.0236129 (2020).

82. Ding, F., Wang, M., Zhang, S. & Ai, X. Changes in SBPase activity influence photosynthetic capacity, growth, and tolerance to chilling stress in transgenic tomato plants. *Scientific Reports* **6**, 32741 http://dx.doi.org/10.1038/srep32741 (2016).

83. Kohler, I.H. *et al.* Expression of cyanobacterial FBP/SBPase in soybean prevents yield depression under future climate conditions. *Journal of Experimental Botany* **68**, 715-726 http://dx.doi.org/10.1093/jxb/erw435 (2017).

84. Simkin, A.J., Lopez-Calcagno, P.E. & Raines, C.A. Feeding the world: improving photosynthetic efficiency for sustainable crop production. *Journal of Experimantal Botany* **70**, 1119-1140 http://dx.doi.org/10.1093/jxb/ery445 (2019).

85. Simkin, A.J. Genetic engineering for global food security: photosynthesis and biofortification. *Plants* **8**, 586 https://www.mdpi.com/2223-7747/8/12/586 (2019).

86. Sekhar, K.M., Kota, V.R., Reddy, T.P., Rao, K.V. & Reddy, A.R. Amelioration of plant responses to drought under elevated CO_2 by rejuvenating photosynthesis and nitrogen use efficiency: implications for future climate-resilient crops. *Photosynth Res* **150**, 21-40 http://dx.doi.org/10.1007/s11120-020-00772-5 (2021).

87. ECIU. Gas prices adding £1.7 billion to cost of beer and bangers. in *Informed debate on energy and climate change* (ed. Smeeton, G.) (Energy and climate intelligence unit, 2022).

88. ECIU. Farming, Fertilisers and Fossil Fuels. How the gas crisis is squeezing Britain's farmers. 1-22 (Energy and climate intelligence unit, 2022).
89. Araus, J.L., Sanchez-Bragado, R. & Vicente, R. Improving crop yield and resilience through optimization of photosynthesis: panacea or pipe dream? *Journal of Experimental Botany* **72**, 3936-3955 http://dx.doi.org/10.1093/jxb/erab097 (2021).
90. Xiong, J., Tian, Y., Wang, J., Liu, W. & Chen, Q. Comparison of coconut coir, rockwool, and peat cultivations for tomato production: Nutrient balance, plant growth and fruit quality. *Frontiers in Plant Science* **8**, 1327 http://dx.doi.org/10.3389/fpls.2017.01327 (2017).
91. Robinson Boyer, L. *et al.* The use of arbuscular mycorrhizal fungi to improve strawberry production in coir substrate. *Frontiers in Plant Science* (Original Research) **7**, 1237 http://dx.doi.org/10.3389/fpls.2016.01237 (2016).
92. Nguyen, N.T., McInturf, S.A. & Mendoza-Cózatl, D.G. Hydroponics: A versatile system to study nutrient allocation and plant responses to nutrient availability and exposure to toxic elements. *Journal of Visualized Experiments* 54317 http://dx.doi.org/10.3791/54317 (2016).
93. Eldridge, B.M. *et al.* Getting to the roots of aeroponic indoor farming. *New Phytologist* **228**, 1183-1192 http://dx.doi.org/10.1111/nph.16780 (2020).
94. Luo, X. *et al.* Global variation in the fraction of leaf nitrogen allocated to photosynthesis. *Nature Communications* **12**, 4866 http://dx.doi.org/10.1038/s41467-021-25163-9 (2021).
95. Haskett, T.L. *et al.* Engineered plant control of associative nitrogen fixation. *Proc Natl Acad Sci U S A* **119**, e2117465119 http://dx.doi.org/10.1073/pnas.2117465119 (2022).
96. Lebedev, V.G., Popova, A.A. & Shestibratov, K.A. Genetic engineering and genome editing for improving nitrogen use efficiency in plants. *Cells* **10**, 3303 http://dx.doi.org/10.3390/cells10123303 (2021).
97. Fu, Y., Yi, H., Bao, J. & Gong, J. LeNRT2.3 functions in nitrate acquisition and long-distance transport in tomato. *FEBS Lett* **589**, 1072-9 http://dx.doi.org/10.1016/j.febslet.2015.03.016 (2015).
98. Wei, S. *et al.* A transcriptional regulator that boosts grain yields and shortens the growth duration of rice. *Science* **377**, eabi8455 http://dx.doi.org/doi:10.1126/science.abi8455 (2022).
99. Makino, A., Suzuki, Y. & Ishiyama, K. Enhancing photosynthesis and yield in rice with improved N use efficiency. *Plant Science* 111475 http://dx.doi.org/https://doi.org/10.1016/j.plantsci.2022.111475 (2022).
100. Aflitos, S. *et al.* Exploring genetic variation in the tomato (*Solanum section Lycopersicon*) clade by whole-genome sequencing. *The Plant journal : for cell and molecular biology* **80**, 136-148 http://dx.doi.org/10.1111/tpj.12616 (2014).
101. Sahu, K.K. & Chattopadhyay, D. Genome-wide sequence variations between wild and cultivated tomato species revisited by whole genome sequence mapping. *BMC Genomics* **18**, 430 http://dx.doi.org/10.1186/s12864-017-3822-3 (2017).
102. Blanca, J. *et al.* Genomic variation in tomato, from wild ancestors to contemporary breeding accessions. *BMC Genomics* **16**, 257 http://dx.doi.org/10.1186/s12864-015-1444-1 (2015).
103. Cockerton, H.M. *et al.* Genomic informed breeding strategies for strawberry yield and fruit quality traits. *Frontiers in Plant Science* **12**, 724847 http://dx.doi.org/10.3389/fpls.2021.724847 (2021).
104. Driever, S.M., Lawson, T., Andralojc, P.J., Raines, C.A. & Parry, M.A. Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. *Journal of Experimental Botany* **65**, 4959-73 http://www.ncbi.nlm.nih.gov/pubmed/24963002 (2014).
105. Silva-Pérez, V. *et al.* Genetic variation for photosynthetic capacity and efficiency in spring wheat. *Journal of Experimental Botany* **71**, 2299-2311 http://dx.doi.org/10.1093/jxb/erz439 (2019).
106. Sales, C.R.G. *et al.* Phenotypic variation in photosynthetic traits in wheat grown under field versus glasshouse conditions. *Journal of Experimental Botany* **73**, 3221-3237 http://dx.doi.org/10.1093/jxb/erac096 (2022).
107. Adachi, S. *et al.* Genetic architecture of leaf photosynthesis in rice revealed by different types of reciprocal mapping populations. *Journal of Experimental Botany* **70**, 5131-5144 http://dx.doi.org/10.1093/jxb/erz303 (2019).

108. Adachi, S. *et al.* Fine mapping of carbon assimilation rate 8, a quantitative trait locus for flag leaf nitrogen content, stomatal conductance and photosynthesis in rice. *Frontiers in Plant Science* (Original Research) **8**, 60 http://dx.doi.org/10.3389/fpls.2017.00060 (2017).
109. de Oliveira Silva, F.M. *et al.* The genetic architecture of photosynthesis and plant growth-related traits in tomato. *Plant Cell Environ* **41**, 327-341 http://dx.doi.org/10.1111/pce.13084 (2018).
110. Lana-Costa, J. *et al.* High photosynthetic rates in a *Solanum pennellii* chromosome 2 qtl is explained by biochemical and photochemical changes. *Frontiers in Plant Science* (Original Research) **11**, http://dx.doi.org/10.3389/fpls.2020.00794 (2020).
111. Sharwood, R.E. *et al.* Mining for allelic gold: finding genetic variation in photosynthetic traits in crops and wild relatives. *Journal of Experimental Botany* **73**, 3085-3108 http://dx.doi.org/10.1093/jxb/erac081 (2022).
112. Scafaro, A.P. *et al.* A thermotolerant variant of rubisco activase from a wild relative improves growth and seed yield in rice under heat stress. *Frontiers in Plant Science* (Original Research) **9**, 1663 http://dx.doi.org/10.3389/fpls.2018.01663 (2018).
113. Scafaro, A.P. *et al.* Heat tolerance in a wild Oryza species is attributed to maintenance of Rubisco activation by a thermally stable Rubisco activase ortholog. *New Phytologist* **211**, 899-911 http://dx.doi.org/10.1111/nph.13963 (2016).
114. Ogbaga, C.C., Stepien, P., Athar, H.-U.-R. & Ashraf, M. Engineering Rubisco activase from thermophilic cyanobacteria into high-temperature sensitive plants. *Critical Reviews in Biotechnology* **38**, 559-572 http://dx.doi.org/10.1080/07388551.2017.1378998 (2018).
115. López-Calcagno, P.E. *et al.* Stimulating photosynthetic processes increases productivity and water-use efficiency in the field. *Nature Plants* **6**, 1054-1063 http://dx.doi.org/10.1038/s41477-020-0740-1 (2020).
116. Driever, S.M. *et al.* Increased SBPase activity improves photosynthesis and grain yield in wheat grown in greenhouse conditions. *Philosophical Transactions of the Royal Society B* **372**, 1730 (2017).
117. Raines, C.A., Cavanagh, A.P. & Simkin, A.J. Chapter 9. Improving carbon fixation in Photosynthesis in Action 1 edn, (eds Ruban, A., Murchie, E. & Foyer, C.) (Academic Press, 2022).
118. Petreikov, M. *et al.* Carbohydrate balance and accumulation during development of near-isogenic tomato lines differing in the AGPase-L1 allele. *Journal of the American Society for Horticultural Science* **134**, 134-140 http://dx.doi.org/10.21273/jashs.134.1.134 (2009).
119. Ainsworth, E.A. & Bush, D.R. Carbohydrate export from the leaf: A highly regulated process and target to enhance photosynthesis and productivity. *Plant Physiology* **155**, 64-69 http://dx.doi.org/10.1104/pp.110.167684 (2011).
120. Yoon, D.-K. *et al.* Transgenic rice overproducing Rubisco exhibits increased yields with improved nitrogen-use efficiency in an experimental paddy field. *Nature Food* **1**, 134-139 http://dx.doi.org/10.1038/s43016-020-0033-x (2020).
121. Sinclair, T.R., Rufty, T.W. & Lewis, R.S. Increasing photosynthesis: Unlikely solution for world food problem. *Trends in Plant Science* **24**, 1032-1039 http://dx.doi.org/https://doi.org/10.1016/j.tplants.2019.07.008 (2019).
122. Wu, A., Hammer, G.L., Doherty, A., von Caemmerer, S. & Farquhar, G.D. Quantifying impacts of enhancing photosynthesis on crop yield. *Nature Plants* **5**, 380-388 http://dx.doi.org/10.1038/s41477-019-0398-8 (2019).
123. Hibberd, J.M. & Quick, W.P. Characteristics of C4 photosynthesis in stems and petioles of C3 flowering plants. *Nature* **415**, 451-454 http://dx.doi.org/10.1038/415451a (2002).
124. Simkin, A.J., Faralli, M., Ramamoorthy, S. & Lawson, T. Photosynthesis in non-foliar tissues: Implications for yield. *The Plant Journal* **101**, 1001-1015 (2020).
125. Aschan, G. & Pfanz, H. Non-foliar photosynthesis – a strategy of additional carbon acquisition. *Flora* **198**, 81-97 (2003).
126. Ávila, E., Herrera, A. & Tezara, W. Contribution of stem CO2 fixation to whole-plant carbon balance in nonsucculent species. *Photosynthetica* (journal article) **52**, 3-15 http://dx.doi.org/10.1007/s11099-014-0004-2 (2014).

127. Hetherington, S.E., Smillie, R.M. & Davies, W.J. Photosynthetic activities of vegetative and fruiting tissues of tomato. *Journal of Experimental Botany* **49**, 1173-1181 http://dx.doi.org/10.1093/jxb/49.324.1173 (1998).
128. Hu, Y.-Y. *et al.* Important photosynthetic contribution from the non-foliar green organs in cotton at the late growth stage. *Planta* **235**, 325-336 http://www.jstor.org/stable/43564330 (2012).
129. Carrara, S., Pardossi, A., Soldatini, G.F., Tognoni, F. & Guidi, L. Photosynthetic Activity of Ripening Tomato Fruit. *Photosynthetica* (journal article) **39**, 75-78 http://dx.doi.org/10.1023/a:1012495903093 (2001).
130. Sui, X. *et al.* The complex character of photosynthesis in cucumber fruit. *Journal of Experimental Botany* **68**, 1625-1637 http://dx.doi.org/10.1093/jxb/erx034 (2017).
131. Obiadalla-Ali, H., Fernie, A.R., Lytovchenko, A., Kossmann, J. & Lloyd, J.R. Inhibition of chloroplastic fructose 1,6-bisphosphatase in tomato fruits leads to decreased fruit size, but only small changes in carbohydrate metabolism. *Planta* **219**, 533-40 http://dx.doi.org/10.1007/s00425-004-1257-y (2004).
132. Tanaka, A., Fujita, K. & Kikuchi, K. Nutrio-physiological studies on the tomato plant. *Soil Science and Plant Nutrition* **20**, 57-68 http://dx.doi.org/10.1080/00380768.1974.10433228 (1974).
133. Todd, G.W., Bean, R.C. & Propst, B. Photosynthesis & respiration in developing fruits II. Comparative rates at various stages of development. *Plant Physiology* **36**, 69-73 http://dx.doi.org/10.1104/pp.36.1.69 (1961).
134. Millar, A.H., Whelan, J., Soole, K.L. & Day, D.A. Organization and regulation of mitochondrial respiration in plants. *Annual Review of Plant Biology* **62**, 79-104 http://dx.doi.org/10.1146/annurev-arplant-042110-103857 (2011).
135. Blanke, M.M. Fruit Photosynthesis (Springer, , 1998).
136. Li, T. *et al.* Enhanced-efficiency fertilizers are not a panacea for resolving the nitrogen problem. *Global Change Biology* **24**, e511-e521 http://dx.doi.org/https://doi.org/10.1111/gcb.13918 (2018).
137. Reynolds, M. *et al.* Addressing research bottlenecks to crop productivity. *Trends in Plant Science* **26**, 607-630 http://dx.doi.org/10.1016/j.tplants.2021.03.011 (2021).
138. Wilson, F., Harrison, K., Armitage, A.D., Simkin, A.J. & Harrison, R.J. CRISPR/Cas9-mediated mutagenesis of phytoene desaturase in diploid and octoploid Strawberry. *BMC Plant Methods* **15**, 45 (2019).
139. Aglawe, S.B., Barbadikar, K.M., Mangrauthia, S.K. & Madhav, M.S. New breeding technique "genome editing" for crop improvement: applications, potentials and challenges. *3 Biotech* **8**, 336 http://dx.doi.org/10.1007/s13205-018-1355-3 (2018).
140. Georges, F. & Ray, H. Genome editing of crops: A renewed opportunity for food security. *GM Crops and Food* **8**, 1-12 http://dx.doi.org/10.1080/21645698.2016.1270489 (2017).
141. Exposito-Rodriguez, M. *et al.* Development of pGEMINI, a plant gateway destination vector allowing the simultaneous integration of two cDNA via a single LR-clonase reaction. *Plants (Basel)* **6**, 55 http://dx.doi.org/10.3390/plants6040055 (2017).
142. Engler, C., Gruetzner, R., Kandzia, R. & Marillonnet, S. Golden gate shuffling: a one-pot DNA shuffling method based on type IIs restriction enzymes. *Plos One* **4**, e5553 http://dx.doi.org/10.1371/journal.pone.0005553 (2009).
143. Engler, C., Kandzia, R. & Marillonnet, S. A one pot, one step, precision cloning method with high throughput capability. *Plos One* **3**, e3647 http://dx.doi.org/10.1371/journal.pone.0003647 (2008).
144. Engler, C. *et al.* A golden gate modular cloning toolbox for plants. *ACS Synth Biol* **3**, 839-43 http://dx.doi.org/10.1021/sb4001504 (2014).
145. Marillonnet, S. & Werner, S. Assembly of multigene constructs using golden gate cloning in Glyco-Engineering: Methods and Protocols (ed Castilho, A.) 269-284 (Springer New York, 2015).
146. Kuntz, M. *et al.* Upregulation of two ripening-related genes from a non-climacteric plant (pepper) in a transgenic climacteric plant (tomato). *The Plant Journal* **13**, 351-361 http://dx.doi.org/10.1046/j.1365-313X.1998.00032.x (1998).

147. Simkin, A.J. *et al.* Oleosin gene family of *Coffea canephora:* quantitative expression analysis of five oleosin genes in developing and germinating coffee grain. *Journal of plant physiology* **163**, 691-708 http://dx.doi.org/10.1016/j.jplph.2005.11.008 (2006).
148. Mukherjee, S., Stasolla, C., Brule-Babel, A. & Ayele, B.T. Isolation and characterization of rubisco small subunit gene promoter from common wheat (*Triticum aestivum* L.). *Plant Signaling and Behavior* **10**, e989033 http://dx.doi.org/10.4161/15592324.2014.989033 (2015).
149. Alotaibi, S.S., Sparks, C.A., Parry, M.A.J., Simkin, A.J. & Raines, C.A. Identification of leaf promoters for use in transgenic wheat. *Plants* **7**, 27 http://dx.doi.org/10.3390/plants7020027 (2018).
150. Alotaibi, S.S. *et al.* Functional analysis of SBPase gene promoter in transgenic wheat under different growth conditions. *Biotechnology* **1**, 15-23 (2019).
151. Faralli, M., Matthews, J. & Lawson, T. Exploiting natural variation and genetic manipulation of stomatal conductance for crop improvement. *Current Opinion in Plant Biology* **49**, 1-7 http://dx.doi.org/https://doi.org/10.1016/j.pbi.2019.01.003 (2019).
152. Lawson, T. & Blatt, M.R. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiology* **164**, 1556-1570 http://dx.doi.org/10.1104/pp.114.237107 (2014).
153. Kapoor, L., Simkin, A.J., George Priya Doss, C. & Siva, R. Fruit ripening: dynamics and integrated analysis of carotenoids and anthocyanins. *BMC Plant Biology* **22**, 27 http://dx.doi.org/10.1186/s12870-021-03411-w (2022).
154. Simkin, A.J. *et al.* The role of photosynthesis related pigments in light harvesting, photoprotection and enhancement of photosynthetic yield in planta. *Photosynthesis Research* **152**, 23–42 http://dx.doi.org/10.1007/s11120-021-00892-6 (2022).
155. Pazzagli, P.T., Weiner, J. & Liu, F. Effects of CO_2 elevation and irrigation regimes on leaf gas exchange, plant water relations, and water use efficiency of two tomato cultivars. *Agricultural Water Management* **169**, 26-33 http://dx.doi.org/https://doi.org/10.1016/j.agwat.2016.02.015 (2016).
156. Reinert, R.A., Eason, G. & Barton, J. Growth and fruiting of tomato as influenced by elevated carbon dioxide and ozone. *New Phytologist* **137**, 411-420 http://dx.doi.org/https://doi.org/10.1046/j.1469-8137.1997.00846.x (1997).
157. Helyes, L., Lugasi, A., Péli, E. & Pék, Z. Effect of elevated CO_2 on lycopene content of tomato (*Lycopersicon lycopersicum* L. Karsten) fruits. *Acta Alimentaria* **40**, 80-86 http://dx.doi.org/10.1556/aalim.40.2011.1.11 (2011).
158. Hartz, T.K., Baameur, A. & Holt, D.B. Carbon dioxide enrichment of high-value crops under tunnel culture. *Journal of the American Society for Horticultural Science* **116**, 970-973 http://dx.doi.org/10.21273/jashs.116.6.970 (1991).
159. Liu, J. *et al.* Carbon dioxide elevation combined with sufficient irrigation and nitrogen fertilization improves fruit quality of tomato grown in glasshouse. *Archives of Agronomy and Soil Science* **67**, 1134-1149 http://dx.doi.org/10.1080/03650340.2020.1783655 (2021).
160. Wei, Z., Du, T., Li, X., Fang, L. & Liu, F. Interactive effects of elevated CO_2 and N fertilization on yield and quality of tomato grown under reduced irrigation regimes. *Frontiers in Plant Science* (Original Research) **9**, http://dx.doi.org/10.3389/fpls.2018.00328 (2018).
161. Hicklenton, P.R. & Jolliffe, P.A. Effects of greenhouse CO_2 enrichment on the yield and photosynthetic physiology of tomato plants. *Canadian Journal of Plant Science* **58**, 801-817 http://dx.doi.org/10.4141/cjps78-119 (1978).
162. Fierro, A., Gosselin, A. & Tremblay, N. Supplemental carbon dioxide and light improved tomato and pepper seedling growth and yield. *HortScience* **29**, 152-154 http://dx.doi.org/10.21273/hortsci.29.3.152 (1994).
163. Yelle, S., Beeson, R.C., Trudel, M.J. & Gosselin, A. Duration of CO_2 enrichment influences growth, yield, and gas exchange of two tomato species. *Journal of the American Society for Horticultural Science jashs* **115**, 52-57 http://dx.doi.org/10.21273/jashs.115.1.52 (1990).

164. Nilsen, S., Hovland, K., Dons, C. & Sletten, S.P. Effect of CO_2 enrichment on photosynthesis, growth and yield of tomato. *Scientia Horticulturae* **20**, 1-14 http://dx.doi.org/https://doi.org/10.1016/0304-4238(83)90106-1 (1983).

165. Ozcelik, N. & Akilli, M. Effects of CO_2 enrichment on vegetative growth, yield and quality of greenhouse - grown tomatoes in soil and soilless cultures. *ActaHortic.* **491**, 155-160 http://dx.doi.org/10.17660/ActaHortic.1999.491.22 (1999).

166. Tripp, K.E., Peet, M.M., Pharr, D.M., Willits, D.H. & Nelson, P.V. CO_2-enhanced yield and foliar deformation among tomato genotypes in elevated CO_2 environments. *Plant Physiology* **96**, 713-719 http://dx.doi.org/10.1104/pp.96.3.713 (1991).

167. Li, J.H., Sagi, M., Gale, J., Volokita, M. & Novoplansky, A. Response of tomato plants to saline water as affected by carbon dioxide supplementation. I. Growth, yield and fruit quality. *The Journal of Horticultural Science and Biotechnology* **74**, 232-237 http://dx.doi.org/10.1080/14620316.1999.11511100 (1999).

168. Porras, M.E. *et al.* Sweet pepper acclimation to variable CO_2 supply in a Mediterranean greenhouse. *ActaHortic.* **1170**, 797-804 http://dx.doi.org/10.17660/ActaHortic.2017.1170.102 (2017).

169. Milhet, Y. & Costes, C. Effects of CO_2 nutrition on growth and yield of muskmelon (*Cucumis melo* L.), egg-plant (*Solanum Melongena* L.) and sweet-pepper (*Capsicum annuum* L.). *ActaHortic.* **51**, 201-212 http://dx.doi.org/10.17660/ActaHortic.1975.51.21 (1975).

170. Garruña-Hernández, R. *et al.* Changes in flowering and fruiting of Habanero pepper in response to higher temperature and CO_2. *Journal of Food Agriculture and Environment* **10**, 802-808 (2012).

171. Li, X. *et al.* Light supplement and carbon dioxide enrichment affect yield and quality of off-season pepper. *Agronomy Journal* **109**, 2107-2118 http://dx.doi.org/https://doi.org/10.2134/agronj2017.01.0044 (2017).

172. Imazu, T., Yabuki, K. & Oda, Y. Studies on the carbon dioxide environment for plant growth. II. Effect of carbon dioxide concentration on the growth, flowering and fruit setting of eggplant *(Solanum melongena* L.). *Journal of the Japanese Society for Horticultural Science* **36**, 275-280 http://dx.doi.org/10.2503/jjshs.36.275 (1967).

173. Deng, X. & Woodward, F.I. The growth and yield responses of fragaria ananassa to elevated CO_2 and N supply. *Annals of Botany* **81**, 67-71 http://dx.doi.org/10.1006/anbo.1997.0535 (1998).

174. Mochizuki, M.J., Daugovish, O., Ahumada, M.H., Ashkan, S. & Lovatt, C.J. Carbon dioxide enrichment may increase yield of field-grown red raspberry under high tunnels. *HortTechnology* **20**, 213-219 http://dx.doi.org/10.21273/horttech.20.1.213 (2010).

175. Sánchez-Guerrero, M.C., Lorenzo, P., Medrano, E., Baille, A. & Castilla, N. Effects of EC-based irrigation scheduling and CO_2 enrichment on water use efficiency of a greenhouse cucumber crop. *Agricultural Water Management* **96**, 429-436 http://dx.doi.org/https://doi.org/10.1016/j.agwat.2008.09.001 (2009).

176. Sánchez-Guerrero, M.C. *et al.* Effect of variable CO_2 enrichment on greenhouse production in mild winter climates. *Agricultural and Forest Meteorology* **132**, 244-252 http://dx.doi.org/https://doi.org/10.1016/j.agrformet.2005.07.014 (2005).

177. Kläring, H.P., Hauschild, C., Heißner, A. & Bar-Yosef, B. Model-based control of CO_2 concentration in greenhouses at ambient levels increases cucumber yield. *Agricultural and Forest Meteorology* **143**, 208-216 http://dx.doi.org/https://doi.org/10.1016/j.agrformet.2006.12.002 (2007).

178. Luomala, E.M., SÃ¤rkkÃ¤, L. & Kaukoranta, T. Altered plant structure and greater yield of cucumber grown at elevated CO_2 in a semi-closed greenhouse. *ActaHortic.* **801**, 1339-1346 http://dx.doi.org/10.17660/ActaHortic.2008.801.164 (2008).

179. Peet, M.M. Acclimation to high CO_2 in monoecious cucumbers 1: I. Vegetative and reproductive growth. *Plant Physiology* **80**, 59-62 http://dx.doi.org/10.1104/pp.80.1.59 (1986).

Figure 1

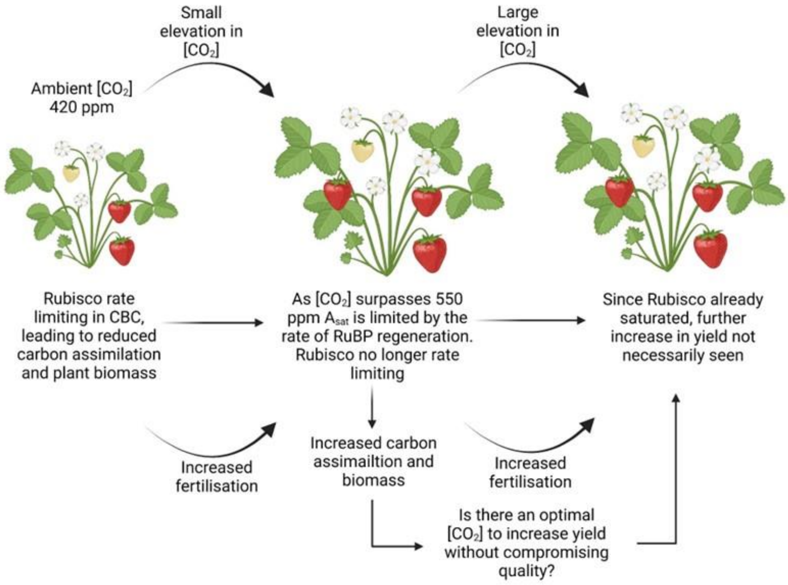

Fig. 1. Schematic representation of elevated $[CO_2]$ on carbon assimilation. Created with BioRender.com

Figure 2

Fruit	Effects of elevated $[CO_2]$ on fruit yield and quality
	- 7% to 125% increase in fruit yield across all treatments ($e[CO_2]$ = 450ppm – 1200ppm) - Greater organoleptic preference. - 16 to 44 % increase in vitamin C ($e[CO_2]$ -<900 ppm), 20 to 25% decrease in vitamin C ($e[CO_2]$ = 1000 ppm. - 10 to 22% increase in total major sugars (glucose, sucrose, fructose) given sufficient N fertilisation and irrigation across and range of CO_2 treatments ($e[CO_2]$ = 550-1000 ppm). - Large variation in reported total organic acid content between studies with no detectable trend related to degree of CO_2 fertilisation. - 32% increase in lycopene at $e[CO_2]$ = 550 ppm, however 3.7 to 25% decrease in lycopene at $e[CO_2]$ = 700 ppm. *Overall, $e[CO_2]$ of 550 ppm seems optimal for simultaneous increases in yield and quality parameters in tomato*
	- 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 $[CO_2]$ 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 $e[CO_2]$ increased *Overall, $e[CO_2]$ increases yield, however little work has been carried out on the impacts of $e[CO_2]$ of quality. Increases in yield variable and not observed to be dose dependent.*
	- 53.8 % increase in fruit number per plant at 550ppm $e[CO_2]$. - 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 *Overall, $e[CO_2]$ 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.*
	- *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 $e[CO_2]$ = 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 $e[CO_2]$ 650 ppm, 13.3% increase reported at $e[CO_2]$ = 950 ppm. - Total acid content was reduced with increasing $[CO_2]$, reducing by ~10% for every 300 ppm increase in $e[CO_2]$. - Key aroma constituents (esters, furaneol, linalool), increases stepwise with increasing $[CO_2]$ for the conc. tested (350, 650, 950ppm). *No specific degree of CO_2 fertilisation can be determined as being optimal since the effects of $e[CO_2]$ > 950 ppm on fruit quality have not been tested. Greater CO_2 fertilisation appears to enhance both yield and quality*
	- CO_2 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 $e[CO_2]$ = 1200 ppm, with greater fruit biomass also reported. This indicates that nitrogen may be a limiting factor on how well cucumber can utilise CO_2 fertilisation. - For $e[CO_2]$ = 1200 ppm and moderate nitrogen fertilisation, a 73 to 75% increase in fruit fructose and glucose was observed. This was not observed at lower $e[CO_2]$ or at higher N. *Optimal concentrations of $e[CO_2]$ and N fertilisation required for optimal cucmber yield and quality*

Fig. 2. Effects of elevated $[CO_2]$ on yield and quality of fruiting crops. Created with BioRender.com

Figure 3

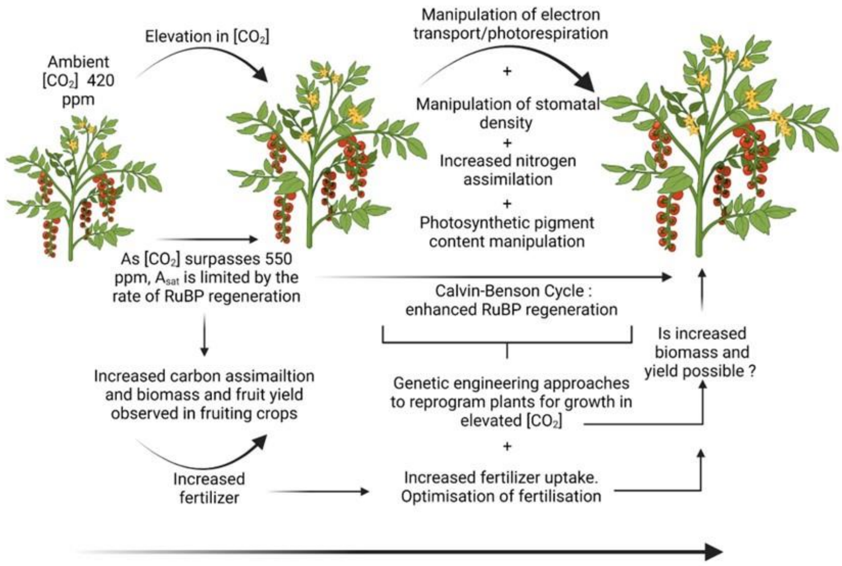

Fig. 3. Effects of elevated $[CO_2]$ on yield of fruiting crops and a representation of the potential for the manipulation of plant material for further yield increases. Created with BioRender.com