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# Climate change increases net CO<sub>2</sub> assimilation in the leaves of strawberry, but not yield

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## ABSTRACT

Fruit growth in strawberry is dependent on photosynthesis in the leaves. The main scenarios for climate change include an increase in the concentration of CO<sub>2</sub> in the atmosphere and an increase in temperature. This review examined photosynthesis in strawberry. The mean photosynthetic photon flux (PPF) for the saturation of CO<sub>2</sub> assimilation was  $1,031 \pm 447$   $\mu\text{mol per m}^2$  per s, the median was  $1,000$   $\mu\text{mol per m}^2$  per s, and the range was from 467 to  $2,200$   $\mu\text{mol per m}^2$  per s ( $N = 59$ ). The mean concentration of CO<sub>2</sub> for the saturation of assimilation was  $869 \pm 306$  ppm, the median was 900 ppm, and the range was from 410 to 1,750 ppm ( $N = 32$ ). The optimum temperature range for CO<sub>2</sub> assimilation was 20° to 30°C, with lower photosynthesis at lower or higher temperatures. The optimum temperatures for photosynthesis are higher than those for flowering and fruit growth. The impact of climate change on production varies across growing areas. In warm locations, higher temperatures increase photosynthesis, but not yield. In cool locations, higher temperatures increase plant growth and the length of the production season, but this comes at the expense of flower initiation.

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climate change; concentration of CO<sub>2</sub>; global warming; temperature; yield

## Introduction

Climate change has increased the temperature and the concentration of CO<sub>2</sub> in the atmosphere in the last 100 years compared with earlier periods (Båki Iz, 2022; Meinshausen et al., 2022; Solomon et al., 2009; Wang et al., 2023a). For instance, the concentration of CO<sub>2</sub> in the atmosphere near Mauna Loa in Hawaii increased from 320 ppm in 1960 to 420 ppm in 2020 (Båki Iz, 2022). Additionally, the global surface temperature increased by nearly 1°C from 2001 to 2020 compared with 1850 to 1900 (Wang et al., 2023a). These changes in CO<sub>2</sub> and temperature have increased photosynthesis in many plants. However, the increase in carbon assimilation under higher CO<sub>2</sub> and temperature is often accompanied by a decrease in flower and fruit development (Lee et al., 2017; Pereira et al., 2017; Srinivasan et al., 2017).

Elevated temperatures have a greater effect on productivity than elevated CO<sub>2</sub>. The impact of temperature on yield can be due to higher average temperatures or short-term increases in temperatures above the optimum range (Campoy et al., 2019; Chavan et al., 2019). The effect of global warming on the changes in temperature varies across regions and ecosystems and between days and nights (Cox et al., 2020; Hou et al., 2018; Shi et al., 2023; Sun et al., 2014; Zheng et al., 2021). There can also be differences between the temperature of the canopy ( $T_c$ ) and that of the air ( $T_a$ ) (Guo et al., 2023). These authors

demonstrated that the differences between  $T_c$  and  $T_a$  ranged from 0° to 6°C across the globe.

Some models predict higher yields in the short-term with climate change and lower yields in the long-term, while others predict lower yields across both periods or under current conditions (Amani-Male et al., 2024; Benlloch-González et al., 2019; Challinor et al., 2014; Hammer et al., 2020; Heide & Sønsteby, 2020; Lollato et al., 2020; Ma et al., 2021; Minoli et al., 2022; Mistry et al., 2017; Petersen, 2019; Ray et al., 2019; Schlenker & Roberts, 2009; Vogel et al., 2019; Wang et al., 2022a, 2020b; Yin & Leng, 2022; Zhang et al., 2017). Warming is also expected to decrease net cropping frequency (the number of cropping cycles per year at a given location) across the globe by  $4.2 \pm 2.5\%$  by 2050 (Zhu et al., 2022).

A study across the globe indicated that the impact of climate change on maize varied across regions (Ocwa et al., 2023). An increase in temperature of 1° to 4°C decreased yield by 5 to 14% in warm areas and increased yield by less than 5% in cold areas. In non-crop species, changes in temperature affect the persistence or expansion of plants across ecosystems (Anderson et al., 2020). Grüter et al. (2022) demonstrated that coffee was vulnerable to climate change, with a negative impact in all the main producing regions. The areas suitable for avocado and cashew are expected to expand globally, while in the main

producing countries, the areas of highest suitability will decrease.

Productivity is difficult to estimate because the changes in CO<sub>2</sub>, temperature and water supply vary across regions (Mohammadi et al., 2023). There are also uncertainties in how species respond to environmental conditions. Keeping warming to within 1.5°C is less problematic than to within 2.0°C (Leng, 2018; Schleussner et al., 2018; Wang et al. 2023a). The development of adapted cultivars and other mitigating strategies can reduce the impact of climate change on productivity (Abramoff et al., 2023; Zhang et al., 2022).

Strawberry is one of the most popular fruit crops, and the most important of the berry fruit in the family Rosaceae (Borrero & Borrero-Domínguez, 2023; Hancock, 2020; Hancock et al., 2000; Mezzetti et al., 2018; Porter et al., 2023). Total production is 14 million tonnes each year, with major production in China, California and Europe (Lei et al., 2021; Samtani et al., 2019).

The plants are adapted to a wide range in ecological conditions, in terms of light levels, rainfall, daylength and temperature (Bird et al., 2021; Hancock, 2020; Jiang et al., 2023; Makaraci & Flore, 2009; Sammarco et al., 2022; Zareei et al., 2021). In the northern hemisphere in the Americas, production occurs from the high latitudes of Canada to the low latitudes of Mexico. In the southern hemisphere in the Asia-Pacific region, production occurs from the high latitudes of New Zealand to the low latitudes of Indonesia. There are numerous cultivars developed for specific locations and a range in production systems, including open field and protected cropping (Gomes et al., 2023; Kirschbaum et al., 2023; Lustosa da Silva et al., 2023; Mezzetti et al., 2018; Still et al., 2023; Weber, 2021a, 2021b; Zhou et al., 2023).

Research has indicated that elevated CO<sub>2</sub> and temperatures affect the development of strawberry (Bethere et al., 2016; Dale, 2009; Dara et al., 2019; Deschenes & Kolstad, 2011; Døving, 2009; Elias et al., 2015; Esitken et al., 2009; Hong et al., 2020; Husaini & Xu, 2016; Kerr et al., 2018; Krüger, 2009; Lobell & Field, 2011; Lobell et al., 2007; Maskey et al., 2019; Morton et al., 2017; Neri et al., 2012; Palencia et al., 2009; Pathak et al., 2018; Qiu et al., 2023; Sammarco et al., 2022; Łysiak and Szot, 2023). Two analyses in California demonstrated that yields might decrease by 10% by 2050 and by 43% from 2070 to 2099 (Deschenes & Kolstad, 2011; Lobell et al., 2007). High temperatures and low rainfall in November were associated with low yields in California from 1980 to 2003 (Lobell et al., 2007). In Florida, yields will decrease by 11% by the middle of the century in Hillsborough County (Environmental Defence Fund, 2023). It was proposed that production should be shifted further north to Marion County where temperatures in 2050 would be similar to those currently in Hillsborough.

Grez et al. (2020) indicated that global warming will decrease the yields of *F. chiloensis* in its native habit in

Chile. Another report found that the distribution of tetraploid species of *Fragaria* will shrink under climate change in Yunnan Province in China (Yang et al., 2020). In contrast, the habitat for diploid species will expand. Gamboa-Mendoza et al. (2019) showed that plants of *F. mexicana* at 5.1°C above ambient in Mexico had 41% fewer flowers and 38% fewer fruit than those at ambient (a mean temperature of 19.6°C). Sun et al. (2012) demonstrated that elevated temperatures overrode the benefits of elevated CO<sub>2</sub> on productivity.

This paper reviews photosynthesis in strawberry. The main objective of the study was to assess the effect of environment (light, temperature and the concentration of CO<sub>2</sub>), plant physiology (leaf nitrogen, leaf expansion and fruit development) and genotype on net CO<sub>2</sub> assimilation in the leaves. The optimum temperatures for leaf expansion and yield were compared with those for photosynthesis to determine the impact of climate change on productivity.

### Ultrastructure of the leaves

Most of the photosynthesis in a strawberry plant occurs in the leaves (Blanke, 1991, 2002). Several authors have provided information on the anatomy of the leaves, with the reports agreeing with each other (Abu Zeid et al., 2023; Allan-Wojtas et al., 2010; Arroyo et al., 2005; Avestan et al., 2021; Converse & Schaper, 1988; Fabbri et al., 1986; Kielkiewicz, 1985; Kitajima et al., 1973; Liu et al., 2020a; Mackerron, 1976; Ontivero et al., 2000; Papp et al., 2000, 2005; Pardo et al., 2012; Park et al., 1992; Sances et al., 1979; Yang et al., 2022).

A study in the United Kingdom with ‘Cambridge Favourite’ indicated that the leaves had a mostly uniform epidermis with two to three rows of oblong mesophyll palisade cells (containing numerous chloroplast) next to the adaxial or upper leaf surface (Watkins et al., 1992). There was a layer of spongy mesophyll cells below the palisade cells, with large spaces between the individual cells. The cytoplasm contained well-defined chloroplasts, mitochondria, golgi apparatus (golgi complex or golgi), an endoplasmic reticulum and a nuclei. The nuclei had a well-defined nucleolus, with the nuclear chromatin condensed into clumps. The chloroplasts were smooth and contained starch grains. They were closely associated with each other, interrupted only by the presence of the nucleus. The chloroplasts were arranged more closely together in the palisade cells than in the spongy cells.

The adaxial and abaxial (or lower) leaf surfaces have a complex epicuticular layer of wax to protect the leaf from injury and to reduce the loss of water (Blanke, 1991; Kim et al., 2009). The surfaces of the leaves typically have glandular and non-glandular trichomes or hairs, which can help prevent infestation of pests such as spider mites (de Resende et al., 2020; Fávoro et al., 2022; Figueiredo et al., 2013).

About 98% of CO<sub>2</sub> uptake and water loss from most plants occurs through the stomatal apertures (Pathoumthong et al., 2023). The stomata are found only on the abaxial leaf surface, indicating that strawberry is a hypostomatous plant (Barbosa et al., 2013; Mackerron, 1976). The alternative arrangement of having stomata on both surfaces or amphistomaty occurs predominantly in fast-growing herbaceous annuals and in slow-growing perennial shrubs and trees (Drake et al., 2019).

Blanke and Cooke (2004) indicated that the leaves of 'Cambridge Favourite' and 'Florika' had 320 to 360 stomata per mm<sup>2</sup>. Klamkowski and Treder (2006) showed that leaves of 'Salut' had 203 stomata per mm<sup>2</sup>, and that the stomata were 28 µm × 23 µm. Xu et al. (2022) found that there was a mean (± s.e.) of 189 ± 10 stomata per mm<sup>2</sup> in plants in a greenhouse in Beijing, China and a mean stomatal conductance (g<sub>s</sub>) of 306 ± 13 mmol per m<sup>2</sup> per s. The conductance of water vapour out of the leaves varies across cultivars. Grant et al. (2012) demonstrated that g<sub>s</sub> in well-watered plants ranged from 200 to 600 mmol per m<sup>2</sup> per s in ten cultivars in the United Kingdom.

Avestan et al. (2021) provided details on the size of the tissues within the leaves of 'Camarosa' in Iran. The average leaf was 230 µm thick, with 2.67 layers of palisade (107 µm thick) and a 68.9 µm thick layer of spongy parenchyma. The adaxial epidermis was 36.1 µm thick and the abaxial one was 18.1 µm thick. Abu Zeid et al. (2023) provided similar data for the same cultivar in Saudi Arabia. The leaves were 165.0 µm thick, with 52.8 µm of palisade, 36.3 µm of spongy tissue, a 29.7 µm adaxial epidermis and a 39.6 µm abaxial epidermis.

A study in Finland indicated that there are differences in the anatomy of leaves of *F. vesca* initiated in summer or winter (Aström et al., 2015). Leaves in summer had fewer layers of palisade than those in winter (Table 1). The first layer of the palisade tissues was thicker in the summer leaves. They also had more air spaces in the mesophyll and fewer stomata. The leaves initiated in winter were more adapted to cold than those initiated in summer. They had higher SPAD values (30.5 versus 7.5) and higher chlorophyll fluorescence (F<sub>v</sub>/F<sub>m</sub> of 0.66 versus 0.18).

Kasiamdari et al. (2017) provided similar data on the ultrastructure of commercial strawberry in Indonesia (Table 2). Overall, the leaves were thicker than those of the woodland strawberry. There was a variation in the thickness of the various tissues, which varied by a factor of 1.4 to 2.2 across the nine cultivars. These authors included information on the hypodermis, which forms a prominent layer under the epidermis in some plants. Takeda and Glenn (1989) described hydathodes in the leaves of commercial strawberry, which are responsible for guttation in vascular plants. The hydathodes were below the epidermis and opened into pores on the leaf surface, but had no guard cells.

Heijari et al. (2006) provided information on the organelles within the cells. The mean (± s.d. or standard deviation) area for a chloroplast was 21 ± 2 µm<sup>2</sup>, 13 ± 2 µm<sup>2</sup> for a starch grain, 0.57 ± 0.07 µm<sup>2</sup> for a mitochondrion and 0.50 ± 0.03 µm<sup>2</sup> for a peroxisome (Figure 1).

The anatomy of the leaves varies with the genotype and environment (Jurik et al., 1982; Salamone et al., 2013). Catling and Porebski (1998) studied the morphology of 87 plants of *F. chiloensis* and *F. virginiana* from the Pacific coast of Canada. The leaves were rated from thin (index of one) to thick (index of three). The mean (± s.d.) scores for leaf thickness ranged from 2.51 ± 0.50 to 3.00 ± 0.00. Genotypes of *F. chiloensis* generally have thicker leaves than other species of *Fragaria*. Razmi et al. (2022) indicated that artificial tetraploids of commercial strawberry had fewer stomata than a standard octoploid, although the stomata were larger. The tetraploids also had larger chloroplasts. Jurik et al. (1982) demonstrated that leaves of *F. virginiana* under high light were thicker (188 ± 11 µm) (mean ± s.e.) than those under low light (149 ± 22 µm).

The chloroplasts in the cells of the leaf harvest light from the sun and use the energy to produce sugars and other substance needed for growth (Häder, 2022; Oliver et al., 2023; Sierra et al., 2023). The basic structure of the chloroplast is similar across species of higher plants (Figure 2; Kang et al., 2022; Kirchhoff, 2019).

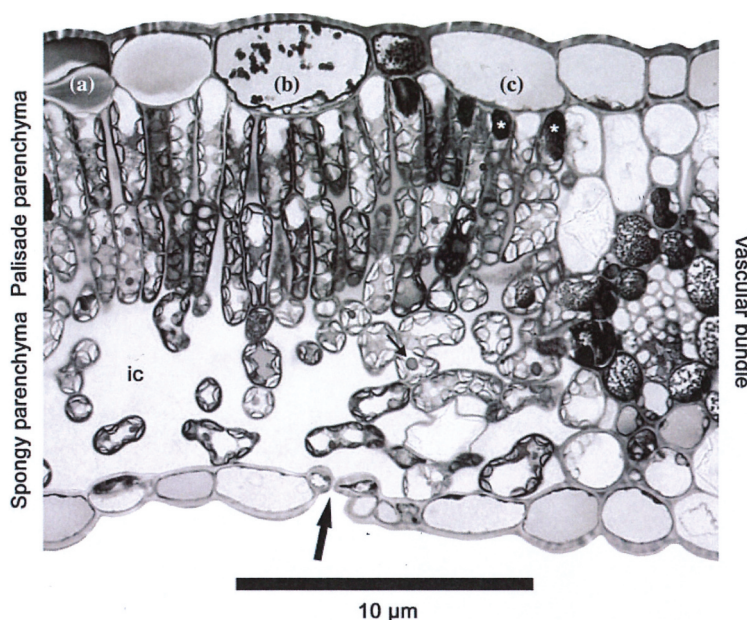
The important part of the chloroplast is the thylakoid, which is one of the most complex, highly organised membranes in biology (Kirchhoff, 2018; Svoboda et al., 2023). The thylakoid in the inner part of the chloroplast consists of appressed grana stacks and unstacked stroma lamellae (Gu et al., 2022; Koochak et al., 2019; Kratsch & Wise, 2000; Mazur et al., 2021; Zenkteler & Borkowska, 2002). Photosystem II (PSII) is mainly located in the grana stacks, whereas Photosystem I (PSI) and ATP synthase are mainly located in the stroma lamellae. The outer part of the chloroplast is comprised of an inner and outer membrane separated by an intermembrane space. The structure of stacked grana area changes in response to the

**Table 1.** Anatomy of summer and winter leaves of *F. vesca* in Helsinki, Finland. Data show means with standard errors (s.e.). Means in a row followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Data are from Aström et al. (2015).

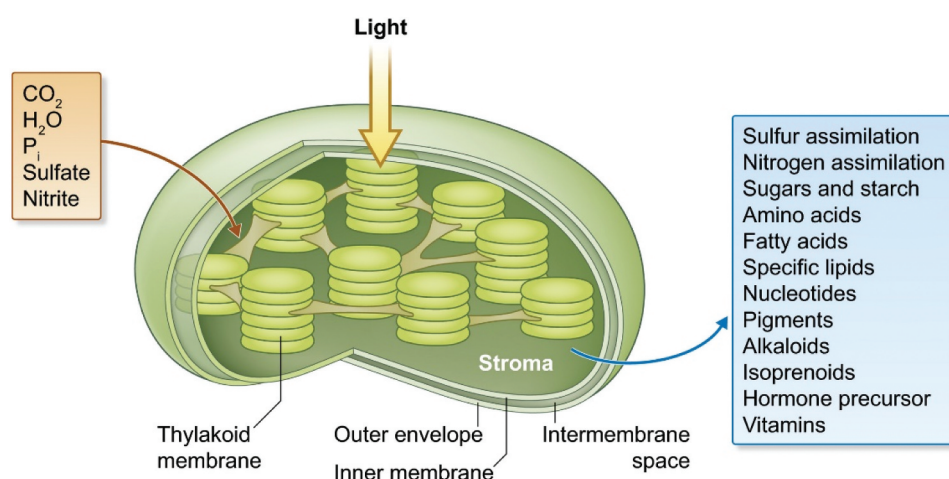
Parameter	Summer leaves	Winter leaves
Leaf thickness (µm)	97.4 ± 2.1 a	100.0 ± 2.8 a
Height of adaxial epidermis (µm)	20.7 ± 0.6 a	21.7 ± 0.6 a
Height of abaxial epidermis (µm)	14.5 ± 0.3 a	14.8 ± 0.3 a
Number of palisade layers	1.7 ± 0.1 a	2.2 ± 0.1 b
Height of first palisade layer (µm)	22.9 ± 0.4 a	20.4 ± 0.3 b
Height of second palisade layer (µm)	16.6 ± 0.5 a	15.9 ± 0.6 a
Percentage of mesophyll air space	24.6 ± 1.8 a	14.2 ± 1.4 b
Number of stomata/mm <sup>2</sup>	205 ± 11 a	269 ± 18 b
Length of stomata (µm)	20.2 ± 0.2 b	17.4 ± 0.4 a

**Table 2.** Anatomy of leaves of commercial strawberry in Indonesia. Data show the means of nine cultivars with standard errors (s. e.) along with the range in values. Data are from Kasiamdari et al. (2017).

	Height of mesophyll ( $\mu\text{m}$ )	Height of adaxial epidermis ( $\mu\text{m}$ )	Height of abaxial epidermis ( $\mu\text{m}$ )	Height of vascular tissue ( $\mu\text{m}$ )	Height of hypodermis ( $\mu\text{m}$ )
Mean ( $\pm$ s.e.)	278 $\pm$ 13	14.7 $\pm$ 1.0	34.7 $\pm$ 2.3	179 $\pm$ 9.0	22.8 $\pm$ 1.8
Minimum	242	10.4	23.6	127	14.8
Maximum	357	21.4	48.1	236	33.0



**Figure 1.** Cross-section of a strawberry leaflet using a light microscope (400 $\times$  magnification) showing palisade and spongy parenchyma, vascular bundle, and adaxial (upper cell layer) and abaxial epidermis (lower cell layer). Different types of epidermal cells are shown: (a) two-layered zone with mucilaginous lower layer and tannin containing upper layer; (b) tannin containing cells; and (c) empty cells. Note the presence of tannin in the vacuoles of palisade parenchyma cells (asterisk) and lipids in the spongy parenchyma cells (small arrow). A stoma is marked with a large arrow. ic = intercellular space. Drawn from Heijari et al. (2006).



**Figure 2.** Structure of a higher plant chloroplast and overview about its metabolic competence. The chloroplast takes low-energy components (orange box) and converts them into high-energy metabolites (blue box) using sunlight. Drawn from Kirchhoff (2019).

environment such as light (Gjindali & Johnson, 2023; Li et al., 2020b). The ultrastructure of the chloroplast also changes with variations in CO<sub>2</sub>. Li et al. (2020a) demonstrated that exposure of

wheat plants to elevated CO<sub>2</sub> (800 ppm) increased the number of grana lamellae and the concentration of chlorophyll in the leaves compared with those under ambient CO<sub>2</sub> (400 ppm).

## Photosynthesis varies across strawberry species, hybrids and cultivars

Net CO<sub>2</sub> assimilation per leaf area varies across crop plants and ecosystems (Cruz & Avenson, 2021; Faralli & Lawson, 2020; Hiker et al., 2008; Hikosaka & Tsujimoto, 2021; Liu et al., 2023b; Ryu et al., 2019; Siebers et al., 2021; Taylor et al., 2023). These variations in gas exchange are due to differences in the biochemistry of photosynthesis, electron transport in the chloroplasts and in the diffusion of CO<sub>2</sub> from the atmosphere to the chloroplasts (Álvarez-Iglesias et al., 2022; Joubert et al., 2023; Matuszyńska et al., 2019; Prado & De Moraes, 1997; Yan et al., 2023).

The efficiency of photosynthesis is related to the morphology of the leaf and the concentrations of the photosynthetic pigments, including chlorophyll and carotenoids (Cutolo et al., 2023). Luo et al. (2019) demonstrated that the inclusion of leaf chlorophyll content improved models of photosynthesis in deciduous forests, croplands, grasslands, savannas and wetlands, but had mixed impacts in shrublands and evergreen forests, and negative impacts in evergreen needleleaf forests.

Kulberg et al. (2023) found that photosynthesis in six subtropical trees in Florida was limited mainly by the conductance of CO<sub>2</sub> through the stomata, with leaf biochemistry less important. In contrast, photosynthesis in rose in China was limited more by biochemistry (60%) than by the diffusion of CO<sub>2</sub> through the leaf (Wang et al., 2023b). Cultivars of rice with high gas exchange had larger mesophyll cells and more chloroplasts than those with low exchange (Mathan et al., 2021). The better cultivars had fewer mesophyll cells, and a larger surface area exposed to the intercellular spaces.

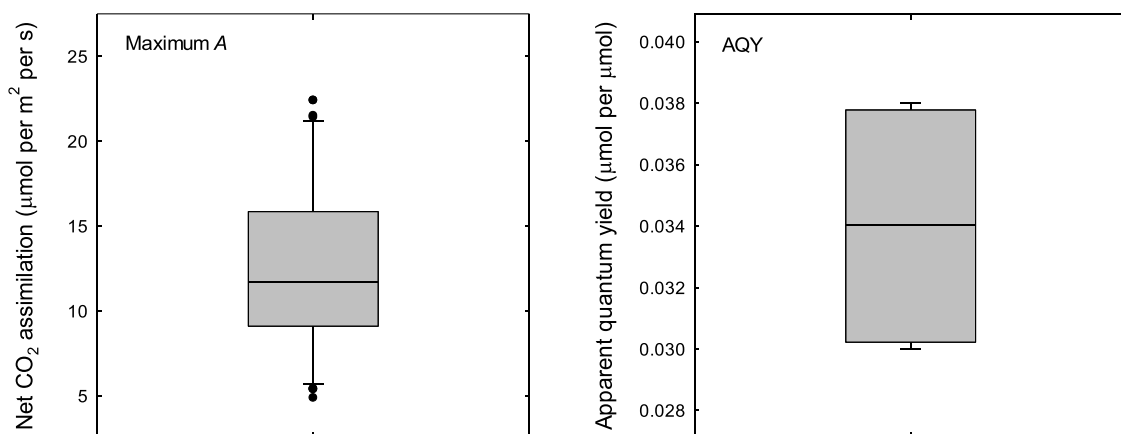
Photosynthesis varies with different species, hybrids and cultivars of strawberry (Table S1). The mean ( $\pm$  s.d.) net CO<sub>2</sub> assimilation was  $12.7 \pm 5.0$   $\mu\text{mol per m}^2$  per s, the median was  $11.7$   $\mu\text{mol per m}^2$  per s, and the range was from 5.0 to 22.4  $\mu\text{mol per m}^2$  per s (Figure 3;  $N = 41$ ). There is less information on the

efficiency of photosynthesis per unit light interception. The mean apparent quantum yield (AQY or  $\alpha$ ) was  $0.034 \pm 0.024$   $\mu\text{mol per } \mu\text{mol}$ , the median was  $0.034$   $\mu\text{mol per } \mu\text{mol}$ , and the range was from 0.030 to 0.038  $\mu\text{mol per } \mu\text{mol}$  (Figure 3;  $N = 6$ ).

It is difficult to compare the results across studies because of variations in environmental conditions during the measurements. There were also differences in the growing conditions and both short- and long-term studies. Reekie et al. (2005) demonstrated that net CO<sub>2</sub> assimilation was 34 to 41% higher in the field than in growth chambers. Light levels were three to five times higher in the field.

Apparent quantum yield indicates the efficiency of photosynthesis as the ratio of oxygen consumption to light absorption (Lei et al., 2023; Singaas et al., 2001; Timm et al., 2002; Zhang et al., 2006). Lin et al. (2022) demonstrated that there was a strong relationship between net CO<sub>2</sub> assimilation and AQY across nine arid and semi-arid sites in China ( $P < 0.01$ ,  $R^2 = 0.84$ ). Fu et al. (2015) reported that an increase in the mean temperature of 1°C under global warming increased AQY by 11.1% across plant communities on the Tibetan Plateau. Hdider and Desjardins (1994) indicated that mean ( $\pm$  s.e.) AQY was  $0.053 \pm 0.003$   $\mu\text{mol per } \mu\text{mol}$  for strawberry in growth cabinets. Apparent quantum yield ranged from 0.037 to 0.077  $\mu\text{mol per } \mu\text{mol}$ . Skillman (2008) found that mean AQY was  $0.052 \pm 0.003$   $\mu\text{mol per } \mu\text{mol}$  across C<sub>3</sub> plants ( $N = 127$ ). Estimates of AQY in wheat in China varied from 0.060 to 0.103  $\mu\text{mol per } \mu\text{mol}$  depending on the model used to describe the relationship between photosynthesis and light (Ye & Yu, 2008).

Wild species of strawberry, including *F. chiloensis*, *F. virginiana*, *F. moschata*, *F. nilgerrensis* and *F. vesca* have higher net CO<sub>2</sub> assimilation than commercial strawberry (Cameron & Hartley, 1990; Fallahi et al., 2000; Hancock et al., 1989; Harbut et al., 2010, 2012). Gao et al. (2017) found that the diploid *F. pentaphylla* had higher gas exchange than the tetraploid *F. moupinensis* in China,



**Figure 3.** Box plots showing the distribution of maximum net CO<sub>2</sub> assimilation (A) and apparent quantum yield (AQY or  $\alpha$ ) in species, hybrids and cultivars of strawberry ( $N = 41$  or 6). Data are from the various authors shown in Table S1.

suggesting that polyploidy was associated with low gas exchange. Hancock et al. (1989) indicated that there were moderate correlations between net CO<sub>2</sub> assimilation and the proportion of *F. chiloensis*-derived genes in 20 cultivars and breeding lines in Michigan in the United States ( $r = 0.58$  in the field and  $r = 0.85$  in a glasshouse).

Fallahi et al. (2000) suggested that the differences in gas exchange between *F. chiloensis* and commercial strawberry were associated with changes in leaf anatomy. *F. chiloensis* had thicker leaves than commercial strawberry (188  $\mu\text{m}$  versus 169  $\mu\text{m}$ ), mainly due to a thicker palisade (84  $\mu\text{m}$  versus 62  $\mu\text{m}$ ) and spongy mesophyll (146  $\mu\text{m}$  versus 120  $\mu\text{m}$ ). The leaves of *F. chiloensis* had higher mesophyll conductance ( $g_m = 87.5$  mmol CO<sub>2</sub> per m<sup>2</sup> per s versus 62.1 mmol CO<sub>2</sub> per m<sup>2</sup> per s). Kanno et al. (2022) investigated gas exchange in seven cultivars in Japan. Net CO<sub>2</sub> assimilation was correlated with stomatal conductance ( $g_s$ ) ( $P < 0.01$ ,  $r = 0.89$  or  $0.88$ ). However, their analysis does not mean that higher photosynthesis was due to higher CO<sub>2</sub> diffusion.

There is limited information on the genetics of photosynthesis in strawberry. Gas exchange is controlled by genes in the chloroplasts as well as those in the nucleus (Chen et al., 2023; Theeuwens et al., 2022). During evolution, many genes of ancestral chloroplasts have been transferred from the chloroplast into the nucleus (Dobrogojski et al., 2020). However, the genes which are essential for photosynthesis have been retained in the chloroplast.

The genome of chloroplasts has been determined for several cultivated and wild species (Bai et al., 2017; Cheng et al., 2017; Harrison et al., 1997; Honjo et al., 2009; Huang et al., 2019a; Li et al., 2021a; Song et al., 2023; Sun et al., 2021). Different types of photosynthesis-related genes respond differently to hybridisation and chromosome doubling within *Fragaria* (Wang et al., 2018). In China, the species were divided into two groups based on variations in the genomics of the chloroplast (Li et al., 2021a). Species in the first group were mainly from western China, while species from the second were mainly from Europe and the Americas. Commercial strawberry has the smallest chloroplast genome within *Fragaria*. The genome encodes 112 unique genes, comprising 78 protein-coding genes, 30 tRNA genes and 4 rRNA genes.

Siddique et al. (2021) examined the genetics of chlorophyll content in Korea. In many crops, there is a strong relationship between photosynthesis and the concentration of chlorophyll (Fleischer, 1935; Li et al., 2018). Siddique and colleagues used SPAD values to estimate chlorophyll levels in the leaves (Himelrick et al., 1992; Takeda & Tworokski, 1999). The first set of plants comprising 186 individuals was developed from an F<sub>2</sub> population from 'Benihoppe'  $\times$  '105 (14-9)'. The second set comprising 158 individuals was developed from an F<sub>2</sub> population from '26 (8-9)'.

The SPAD values from the first population ranged from 34.0 to 57.9, while those from the second ranged from 20.0 to 62.9. Broad-sense heritability ( $H^2$ ) ranged from 0.44 to 0.55, indicating moderate heritability. A total of seven QTL, including major and minor effects, common and specific to populations explained 1.4 to 26.4% of the phenotypic variation in SPAD values. SPAD values reflect the concentration of nitrogen in the leaves of plants, with photosynthesis promoted with high nitrogen levels (Güler et al., 2006).

## Diurnal changes in photosynthesis

Carbon assimilation in the leaves of plants varies over the day. In C<sub>3</sub> species, net CO<sub>2</sub> assimilation peaks in the late morning or at midday and declines in the afternoon or peaks in the morning and afternoon, with lower values at midday or a midday depression (Bunce, 2021; Gómez et al., 2005; Koester et al., 2016; Kumudini, 2004; Miao et al., 2021). Under some conditions, there is a short rise in gas exchange before the sun sets. The changes in net CO<sub>2</sub> assimilation are due to changes in environmental conditions influencing gas exchange and changes in leaf physiology.

The increase in photosynthesis in the morning reflects increasing light levels, while the decrease in the afternoon reflects increasing evaporative demand and closing of the stomata (Maxwell, 2002; Singaas et al., 2000). Zhang et al. (2023b) demonstrated that net CO<sub>2</sub> assimilation in trees in the Amazonian forests responded positively to vapour pressure deficit (VPD) in the morning, but negatively in the afternoon. Gas exchange in the afternoon was  $6.7 \pm 2.4\%$  (s.e.) lower than in the morning. Variations in leaf physiology affect gas exchange. Nomura et al. (2022) indicated that lower net CO<sub>2</sub> assimilation in eggplant reflected the accumulation of non-structural carbohydrates in the leaves.

Gas exchange in strawberry increases in the early morning to peak between late morning and early afternoon (Iwao et al., 2021; Kimura et al., 2020, 2023; Li & Gao, 2015; Nakai et al., 2022; Yokoyama et al., 2023). For instance, Yokoyama et al. (2023) found that net CO<sub>2</sub> assimilation on a sunny day in May in Japan increased from 11.8  $\mu\text{mol per m}^2$  per s at 0700 h to 15.0  $\mu\text{mol per m}^2$  per s between 0900 and 1300 h and then decreased to 11.0  $\mu\text{mol per m}^2$  per s at 1700 h. The changes in photosynthesis reflected changes in light levels, temperature and the opening and closing of the stomata.

In growth chambers, photosynthesis was stable under artificial light (Le et al., 2021; Wu et al., 2012). Garcia and Kubota (2017) noted a different response, with gas exchange in a greenhouse in Arizona, United States decreasing from 0900 to 1500 h. Light levels were maintained during the measurements, with a PPF of 1,000  $\mu\text{mol per m}^2$  per s. The concentration of CO<sub>2</sub> was 400 ppm. The authors indicated that gas

exchange was not related to differences in light or VPD and suggested that changes in leaf physiology (accumulation of leaf carbohydrates) were important.

### Seasonal changes in photosynthesis

Net CO<sub>2</sub> assimilation varies over the season in plants (Araque et al., 2012; Bunce, 1982; Chang et al., 2016; Prado et al., 2001; Reich et al., 1991b), although there are exceptions where gas exchange is stable (e.g. Greer, 2019 for apple in New South Wales, Australia). The pattern of carbon assimilation varies across species and ecosystems. In some plants, key drivers of the response include changes in water supply, temperature or snow-fall (Bosiö et al., 2014; Guan et al., 2018; Zhou et al., 2018).

Gas exchange in strawberry varies over days or weeks (Bunce, 2001; Garcia & Kubota, 2017; Kerkhoff et al., 1988; Sung & Chen, 1991; Yokoyama et al., 2023), although there are exceptions (Calderón-Zavala et al., 2022 in a glasshouse in Mexico). In Taiwan, gas exchange peaked 70 days after planting and then decreased (Sung & Chen, 1991). A study in Korea demonstrated that net CO<sub>2</sub> assimilation nearly doubled from 8 February to 9 March (10.5 µmol per m<sup>2</sup> per s to 18.0 µmol per m<sup>2</sup> per s), reflecting higher light levels in the greenhouse (Choi, 2021b). Differences in carbon assimilation over the season also reflect changes in temperature (Kimura et al., 2023).

### Relationship between photosynthesis and light

Solar radiation drives photosynthesis, cell metabolism and growth in plants (Coe & Lin, 2018; Lazár et al., 2022; Li et al., 2023a; Stirbet et al., 2020; Tcherkez & Limami, 2019). The chloroplasts absorb the radiation and use the energy to convert CO<sub>2</sub> from the atmosphere to the sugars needed for growth. Photosynthesis can be limited by external factors such as light, the concentration of CO<sub>2</sub> and temperature. Gas exchange is also affected by the arrangement of cells in the leaves, the arrangement of the chloroplasts within the cells and by the density of the stomata per leaf area (Leister, 2023; Sharkey, 1985). Leaves respond to average and instantaneous light conditions (Li et al., 2023b).

Wright and Sandrang (1995) calculated that strawberry produces 1.34 g of shoot dry matter for each megajoule of solar radiation intercepted by the leaves. Global estimates of light use efficiency (LUE) across numerous ecosystems ranged from 0.73 ± 0.22 g per MJ to 1.30 ± 0.55 g per MJ in two studies (He et al., 2022a; Tang et al., 2020).

The interception of light through a plant canopy can be described by a non-linear function using a light extinction co-efficient or *k* (Lacasa et al.,

2021). A low value of *k* indicates that much of the radiation reaches the leaves in the bottom of the canopy (Zhang et al., 2014). These authors reported that the average value of *k* was 0.56 across 88 terrestrial ecosystems. Croplands had the highest values of *k* (0.62), while needleleaf forests had the lowest (0.45). Savé et al. (1993) collected data on the distribution of leaf area in the canopy of 'Chandler' strawberry in Spain after seven months. The bulk of the leaf area was found from 20 to 30 cm above the soil level (63% of total), with less from 10 to 20 cm (28%) or from 0 to 10 cm (9%).

Net CO<sub>2</sub> assimilation per leaf area is higher under moderate or high radiation than under low radiation. For most C<sub>3</sub> and C<sub>4</sub> plants, a photosynthetic light-response curve describes the relationship between net CO<sub>2</sub> assimilation and photosynthetic photon flux or PPF (Coe & Lin, 2018; Stirling et al., 1994). Maximum values of PPF are about 2,500 µmol per m<sup>2</sup> per s and reflect radiation at noon in summer in many locations. The light-response curve is defined by three parameters. These are the maximum quantum yield of CO<sub>2</sub> assimilation, derived from the slope of the initial linear response of CO<sub>2</sub> uptake to PPF, the upper asymptote, representing the light-saturated rate of assimilation and the convexity coefficient, describing the curvature between the end of the linear phase and the asymptote.

The relationship between net CO<sub>2</sub> assimilation and PPF varies over the short and long term. The leaves of plants adapt to variations in the light environment, with changes in leaf anatomy and biochemistry (Poorter et al., 2019). Leaves of strawberry under shade moved to full sun had higher CO<sub>2</sub> exchange than those maintained in the full sun for the whole time (Jurik et al., 1979). In contrast, leaves in the full sun moved to shade had lower exchange than those maintained under the shade for the whole time.

Choi (2021a) obtained different results for commercial strawberry in Korea. The plants were grown with 0, 3, 5 or 7 hours of shade each day (no light), providing 1,285, 1,139, 770 or 364 mol of photosynthetic active radiation (PAR) per m<sup>2</sup> during the experiment. Photosynthesis was measured after six weeks, with a PPF of 1,000 µmol per m<sup>2</sup> per s, CO<sub>2</sub> of 400 ppm and a temperature of 25°C. Net CO<sub>2</sub> assimilation was 29, 42 or 62% higher in the control (18.0 µmol per m<sup>2</sup> per s) than after 3, 5 or 7 hours of shading. Higher photosynthesis in the controls was associated with higher stomatal conductance (*g<sub>s</sub>*, *r* = 1.00) and lower leaf chlorophyll a and b (*r* = -0.56 and -0.56). Estimates of CO<sub>2</sub> uptake based on long-term conditions are better than those based on instantaneous measurements.

The light-response curve is dependent on other environmental conditions. The light-saturated rate of assimilation is greater under high than under low CO<sub>2</sub> and greater under moderate than under low temperatures



(Chen et al., 2022c). The relationship between gas exchange and radiation also depends on the ratio of direct and diffuse light. There is a greater proportion of diffuse light under cloud cover or fog (Baguskas et al., 2021; Durand et al., 2021; Yan et al., 2020). Net gas exchange is greater under fog than under clear skies for the equivalent incoming radiation (Baguskas et al., 2021).

Information was collected on the effect of solar radiation on net CO<sub>2</sub> assimilation in strawberry (Table S2). The mean maximum net CO<sub>2</sub> assimilation from the light-response curves was  $13.9 \pm 5.8$   $\mu\text{mol per m}^2$  per s, the median was  $13.7$   $\mu\text{mol per m}^2$  per s, and the range was from 2.9 to 30.0  $\mu\text{mol per m}^2$  per s (Figure 4;  $N = 62$ ). Gas exchange was saturated with a mean PPF of  $1,031 \pm 447$   $\mu\text{mol per m}^2$  per s, a median of 1,000  $\mu\text{mol per m}^2$  per s, and the range was from 467 to 2,200  $\mu\text{mol per m}^2$  per s (Figure 4;  $N = 59$ ). The mean apparent quantum yield ( $\alpha$ ) was  $0.043 \pm 0.014$   $\mu\text{mol per } \mu\text{mol}$ , the median was 0.038  $\mu\text{mol per } \mu\text{mol}$ , and the range was from 0.030 to 0.064  $\mu\text{mol per } \mu\text{mol}$  (Figure 4;  $N = 11$ ). Variations in the response reflect different cultivars, temperatures and concentrations of CO<sub>2</sub>.

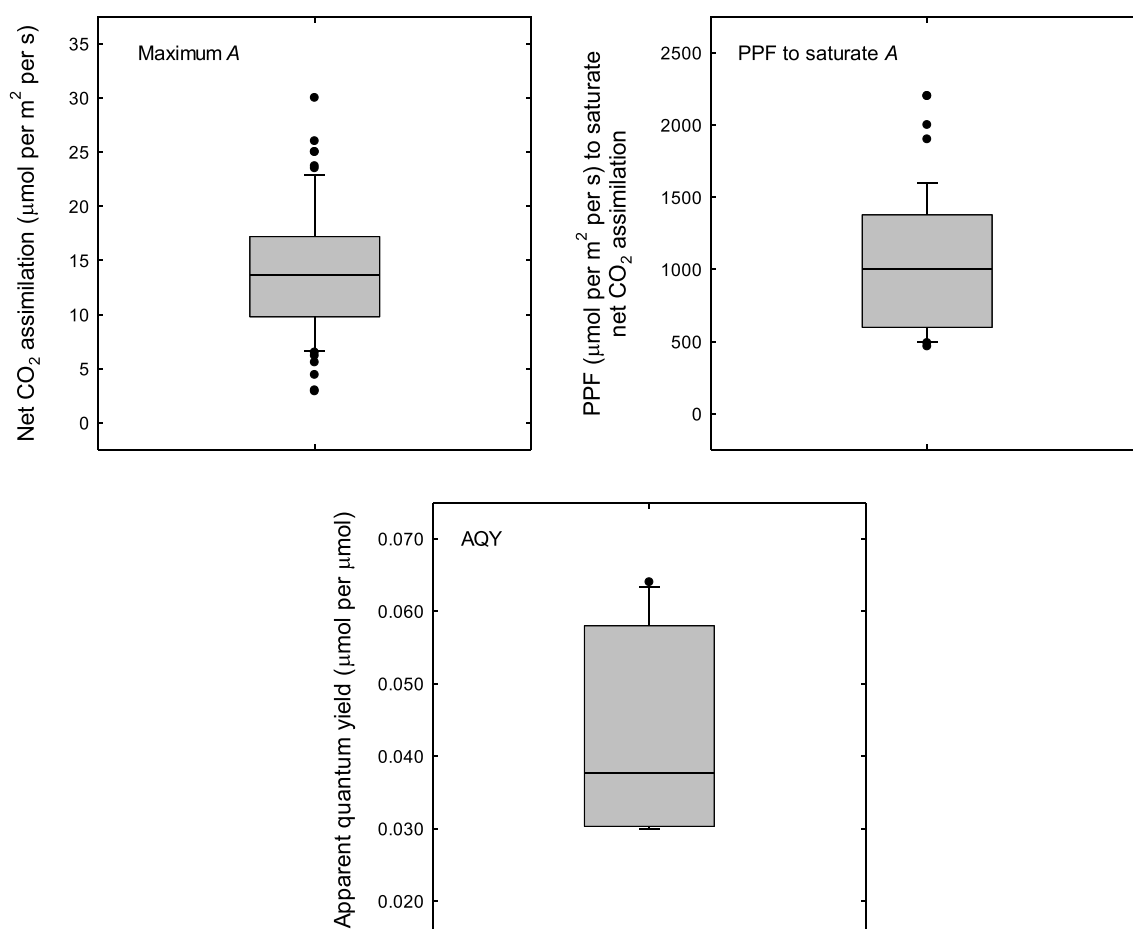
Chen et al. (2022c) examined the effect of light, CO<sub>2</sub> and temperature on gas exchange in ‘Hong yan’ in a greenhouse in Hefei, Anhui Province, China. Net CO<sub>2</sub> assimilation was measured using a Li-6800

portable photosynthesis system, using PPFs from 100 to 2,000  $\mu\text{mol per m}^2$  per s, CO<sub>2</sub> from 200 to 1,500 ppm and temperatures from 18° to 32°C.

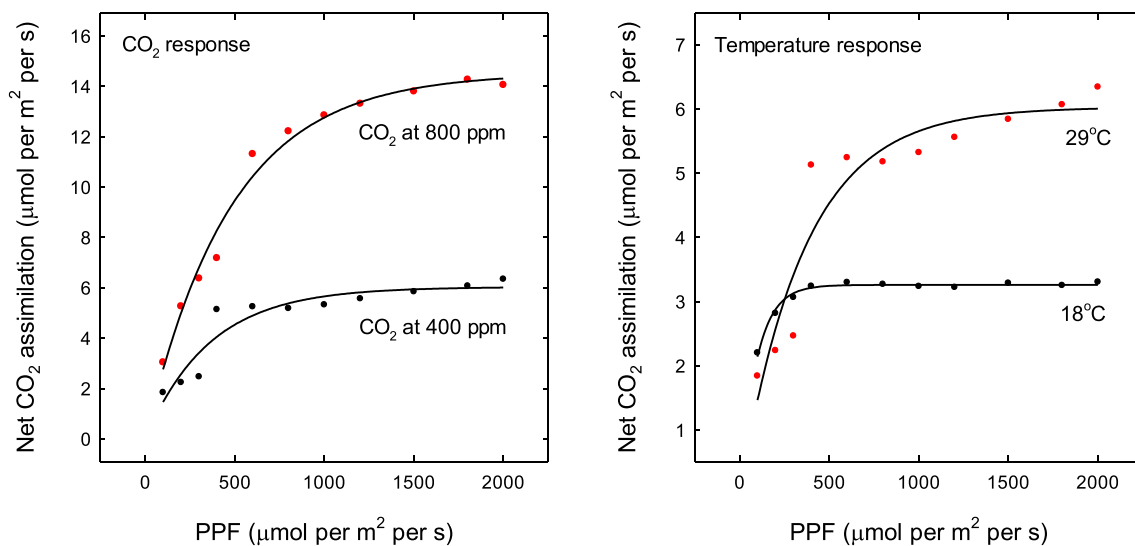
The effect of radiation on photosynthesis followed a typical light-response curve and was depended on CO<sub>2</sub> and temperature. Maximum ( $\pm$  s.e.) net CO<sub>2</sub> assimilation was higher at high CO<sub>2</sub> (800 ppm) than at low CO<sub>2</sub> (400 ppm) ( $14.5 \pm 0.4$   $\mu\text{mol per m}^2$  per s versus  $6.0 \pm 0.4$   $\mu\text{mol per m}^2$  per s) (Figure 5; Temperature of 29°C). Gas exchange was saturated with a PPF of 1,500  $\mu\text{mol per m}^2$  per s at high CO<sub>2</sub> and with a PPF of 1,150  $\mu\text{mol per m}^2$  per s at low CO<sub>2</sub>. Maximum net CO<sub>2</sub> assimilation was higher at 29°C than at 18°C ( $6.0 \pm 0.4$   $\mu\text{mol per m}^2$  per s versus  $3.3 \pm 0.01$   $\mu\text{mol per m}^2$  per s) (Figure 5; CO<sub>2</sub> of 400 ppm). Gas exchange was saturated with a PPF of 1,250  $\mu\text{mol per m}^2$  per s at 29°C and with a PPF of 350  $\mu\text{mol per m}^2$  per s at 18°C.

### Relationship between photosynthesis and CO<sub>2</sub>

The leaves of plants absorb CO<sub>2</sub> from the atmosphere when the stomata are open, with the gas reaching the thylakoids in the chloroplast (Gardner et al., 2023; Pang et al., 2023; Potkay & Feng, 2023). At the same time, water vapour from inside the leaves is lost to the atmosphere. The CO<sub>2</sub> is converted to sugars through



**Figure 4.** Box plots showing the distribution of maximum net CO<sub>2</sub> assimilation (A), the photosynthetic photon flux (PPF) associated with the saturation of assimilation and apparent quantum yield (AQY or  $\alpha$ ) in strawberry ( $N = 43, 49$  or 11). Data are from the various authors shown in Table S2.



**Figure 5.** Relationship between net CO<sub>2</sub> assimilation ( $A_{\text{Net}}$ ) and photosynthetic photon flux (PPF) in strawberry in China. The response to light was examined at low or high CO<sub>2</sub> and at low or high temperatures. Standard conditions were a CO<sub>2</sub> of 400 ppm and a temperature of 29°C. The responses to PPF followed exponential regressions, where  $A_{\text{Net}} = a \times (1 - \exp. (-b \times \text{PPF}))$  ( $P < 0.001$ ,  $R^2$ 's = 0.88 to 0.98). Data are from Chen et al. (2022c).

the process of photosynthesis. There is a strong relationship between photosynthesis and the concentration of CO<sub>2</sub>, with net CO<sub>2</sub> assimilation increasing with increasing CO<sub>2</sub> and then stabilising. The concentration of CO<sub>2</sub> can be measured in the intercellular spaces ( $C_i$ ), surface of the photosynthetic mesophyll cells ( $C_w$ ) or chloroplasts ( $C_c$ ) in C<sub>3</sub> plants (Kirschbaum, 1994; Manter & Kerrigan, 2004; Márquez et al., 2023; Sharkey et al., 2007).

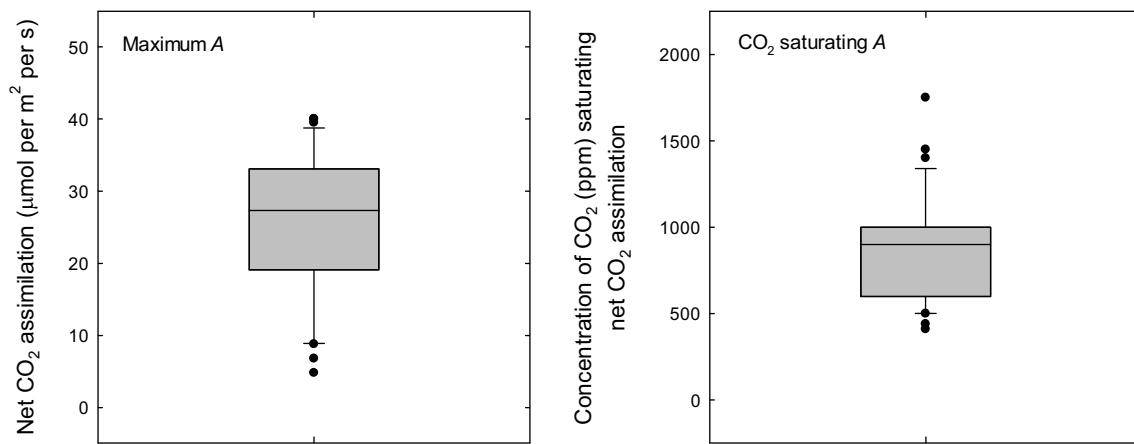
The relationship between net CO<sub>2</sub> assimilation and CO<sub>2</sub> is described by  $A/C_i$  or  $A/C_c$  curves (Coursolle et al., 2019; Moualeu-Ngangue et al., 2016; Zeng et al., 2010; Zhou et al., 2019). The response to high CO<sub>2</sub> varies across species and ecosystems and with light and temperature (Hu et al., 2022; Kabir et al., 2023; Liu et al., 2022; Mndela et al., 2022; Wullschleger, 1993). Poorter et al. (2022) conducted a meta-analysis of the response of C<sub>3</sub> plants to CO<sub>2</sub> across 630 experiments. Average values of net CO<sub>2</sub> assimilation more than doubled over CO<sub>2</sub> from 200 to 1,200 ppm and was saturated at 1,500 ppm. Trees showed the greatest response to CO<sub>2</sub>, followed by fertilised C<sub>3</sub> crops and grasses (Ainsworth & Long, 2005). Shrubs, legumes and forbs were less responsive. Zheng and Peng (2001) examined the effect of CO<sub>2</sub> on the physiology of plants across 84 studies. Net CO<sub>2</sub> assimilation increased by 40.4% in C<sub>3</sub> plants when the concentration of CO<sub>2</sub> was increased by a factor of 1.7 to 2.3 compared with ambient conditions (340 to 400 ppm). Experiments conducted in growth chambers are more reliable than those in the open field where there are variations in the concentration of CO<sub>2</sub> above the plants (Allen et al., 2020).

Information was collected on the relationship between photosynthesis and the concentration of CO<sub>2</sub> in strawberry (Table S3). The mean maximum

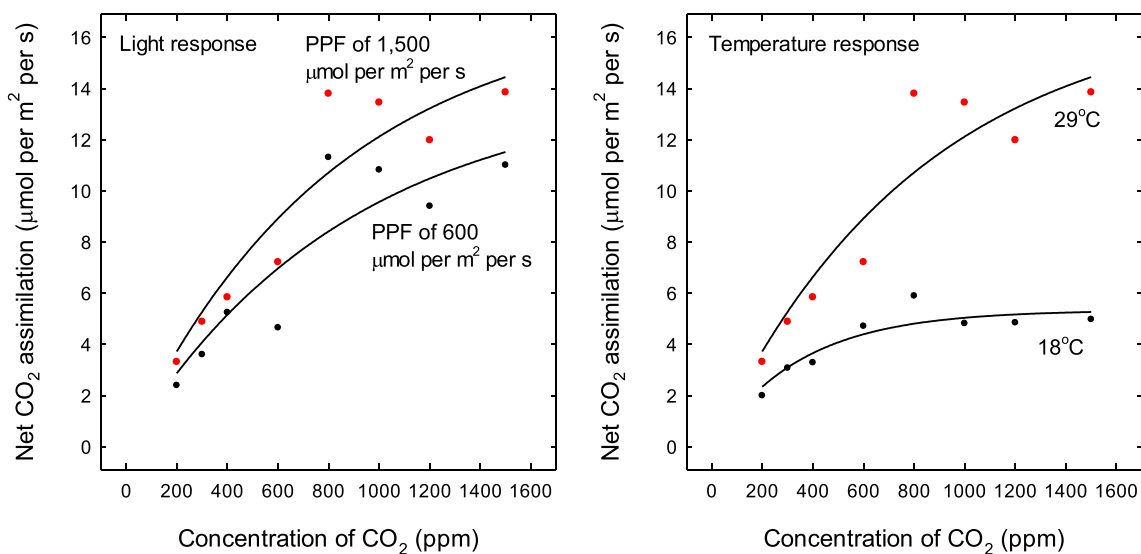
net CO<sub>2</sub> assimilation was  $25.3 \pm 10.1$  µmol per m<sup>2</sup> per s, the median was  $27.4$  µmol per m<sup>2</sup> per s, and the range was from  $4.8$  to  $40.0$  µmol per m<sup>2</sup> per s (Figure 6;  $N = 28$ ). Photosynthesis was saturated with a mean CO<sub>2</sub> of  $869 \pm 306$  ppm, a median of 900 ppm, and the range was from 410 to 1,750 ppm (Figure 6;  $N = 26$ ). The concentration of CO<sub>2</sub> used in the analyses was measured in the atmosphere ( $C_a$ ), and occasionally in the air spaces between the cells in the leaf ( $C_i$ ) or in the chloroplasts ( $C_c$ ). There were also variations in light and temperature conditions (Table S3).

Chen et al. (2022c) examined carbon assimilation in 'Hong yan' in China. The photosynthetic photon flux (PPF) ranged from 100 to 2,000 µmol per m<sup>2</sup> per s, CO<sub>2</sub> ranged from 200 to 1,500 ppm and the temperature ranged from 18° to 32°C. The effect of CO<sub>2</sub> on photosynthesis followed a typical CO<sub>2</sub>-response curve and was dependent on the PPF and the temperature. Maximum ( $\pm$  s.e.) net CO<sub>2</sub> assimilation was higher at high PPF (1,500 µmol per m<sup>2</sup> per s) than at low PPF (600 µmol per m<sup>2</sup> per s) ( $15.3 \pm 3.0$  µmol per m<sup>2</sup> per s versus  $12.2 \pm 3.2$  µmol per m<sup>2</sup> per s) (Figure 7; Temperature of 29°C). Gas exchange was saturated at a CO<sub>2</sub> of 800 ppm at both light levels. Maximum net CO<sub>2</sub> assimilation was higher at 29°C than at 18°C ( $16.3 \pm 3.0$  µmol per m<sup>2</sup> per s versus  $5.2 \pm 0.3$  µmol per m<sup>2</sup> per s) (Figure 7; PPF of 1,500 µmol per m<sup>2</sup> per s). Gas exchange was saturated at a CO<sub>2</sub> of 800 ppm at 29°C and at 600 ppm at 18°C.

Plants adapt to higher CO<sub>2</sub>, with maximum rates of photosynthesis decreasing after long-term exposure (Ainsworth et al., 2002; Hassan & Ito, 2023; Shin et al., 2022; Smith & Dukes, 2013; Thompson et al., 2017; Wang et al., 2020a; Zheng et al., 2019). This response



**Figure 6.** Box plots showing the distribution of maximum net CO<sub>2</sub> assimilation (A) and the concentration of CO<sub>2</sub> associated with the saturation of assimilation in strawberry ( $N = 23$  or  $22$ ). Data are from the various authors shown in Table S3.



**Figure 7.** Relationship between net CO<sub>2</sub> assimilation ( $A_{\text{Net}}$ ) and CO<sub>2</sub> (ppm) in strawberry in China. The response to CO<sub>2</sub> was examined at low or high light and at low or high temperatures. Standard conditions were a photosynthetic photon flux (PPF) of 1,500  $\mu\text{mol per m}^2 \text{ per s}$  and a temperature of 29°C. The responses to CO<sub>2</sub> followed exponential regressions, where  $A_{\text{Net}} = a \times (1 - \exp. (-b \times \text{CO}_2))$  ( $P < 0.001$ ,  $R^2$ s = 0.79 to 0.85). Data are from Chen et al. (2022c).

is associated with changes in leaf anatomy, biochemistry and nutrient concentrations. For instance, Wang et al. (2020a) indicated that effect of elevated CO<sub>2</sub> on photosynthesis declined across most terrestrial regions of the globe from 1982 to 2015. These changes were correlated with lower nutrient concentrations and levels of soil water. Liang et al. (2023) surveyed gas exchange in 444 species under elevated CO<sub>2</sub> and temperature. They showed that elevated CO<sub>2</sub> decreased stomatal aperture in the short term and stomatal density and size in the long term.

Bunce (2001) investigated the effect of elevated CO<sub>2</sub> on the performance of strawberry over 300 days in growth chambers in Maryland, United States. Average net CO<sub>2</sub> assimilation for plants at 600 ppm CO<sub>2</sub> was 35.1  $\mu\text{mol per m}^2 \text{ per s}$  when measured at 950 ppm compared with 42  $\mu\text{mol per m}^2 \text{ per s}$  for those without supplemented CO<sub>2</sub> (353

ppm during the day). Acclimation to elevated CO<sub>2</sub> was evident on two-thirds of the days when gas exchange was measured.

Keutgen et al. (1997) indicated that plants exposed to high CO<sub>2</sub> (750 or 900 ppm) for two months had lower gas exchange than those exposed to moderate CO<sub>2</sub> (600 ppm). Elevated CO<sub>2</sub> induced nutrient deficiencies in the plants growing in sand culture. Osborne et al. (1997) reported different results for the related Indiana strawberry, *Duchesnea indica*, which is an understory plant in the forests of Maryland. Plants exposed to CO<sub>2</sub> of 670 ppm for three and half-years had higher net CO<sub>2</sub> assimilation ( $4.7 \pm 0.1 \mu\text{mol per m}^2 \text{ per s}$ ) than those exposed to 380 ppm ( $3.3 \pm 0.6 \mu\text{mol per m}^2 \text{ per s}$ ). The plants under elevated CO<sub>2</sub> had lower concentrations of leaf nitrogen ( $362 \pm 9 \text{ mg per m}^2$ ) than those under ambient CO<sub>2</sub> ( $402 \pm 20 \text{ mg per m}^2$ ).

## Relationship between photosynthesis and temperature

Temperature is a key factor driving photosynthesis (Chen et al., 2022a; Moore et al., 2021; Yamaguchi et al., 2019). Temperature affects the conductance of CO<sub>2</sub> from the outside of the leaves to the chloroplasts and controls the chemistry of carbon fixation (Bahar et al., 2018; Leister, 2020; Leister et al., 2023). Short- and long-term temperatures affect leaf anatomy and physiology (Baruah et al., 2023; Han et al., 2007; Huang et al., 2022; Venzhik et al., 2023; Wu et al., 2023).

Most plants have a broad optimum for net CO<sub>2</sub> assimilation, with gas exchange only decreasing at extreme temperatures, usually above 30° or 35°C (Matsuda & Takaragawa, 2023). Some plants have high rates of gas exchange at temperatures above 30° C (e.g. Al-Salman et al., 2023 with sorghum). Huang et al. (2019b) demonstrated that the optimum temperature for growth across ecosystems was lower than that for photosynthesis. The average optimum for growth was 23.6° ± 6.0°C, while the average optimum for gas exchange was higher than 30°C.

The optimum temperatures for photosynthesis vary across species and ecosystems (Chang et al., 2021; Liu, 2020; McGowan et al., 2020; Medlyn et al., 2002; Phillips et al., 2022; Reich et al., 2015; Scafaro et al., 2017; Tan et al., 2017). Crous et al. (2022) indicated that the optimum for CO<sub>2</sub> assimilation in 101 evergreen species increased by 0.34°C for every 1°C increase in the local temperature. Photosynthesis is affected by conditions during the time of measurement and with those during growth (Coast et al., 2022; Cox et al., 2023). The optimum range for CO<sub>2</sub> assimilation is higher for plants under moderate temperatures than those under low temperatures (Hikosaka et al., 2006; Sage & Kubien, 2007; Zaka et al., 2016).

A meta-analysis of productivity of forest trees across 52 studies and 522 observations noted that net CO<sub>2</sub> assimilation increased by 9.9% when the temperature increased from 0.3° to 10°C (Yuan et al., 2018). The data were collected from sites between 30° to 60°S latitude, indicating cool to cold locations. Wang and Wang (2022) investigated the effect of temperature on gas exchange across 107 studies. Temperatures of 1° to 17°C above ambient decreased net CO<sub>2</sub> assimilation by 18.4%. The study explored the response of plants across a range of ecosystems, including crops, wild herbaceous plants and forest species.

Wang et al. (2019) demonstrated that the negative effect of elevated temperatures on gas exchange was greater in C<sub>4</sub> species than in C<sub>3</sub> species, and greater if applied for more than a year. Scafaro et al. (2023) indicated that the rates of both Rubisco carboxylation and electron transport within the chloroplast were limited at high temperatures. The optimum temperature

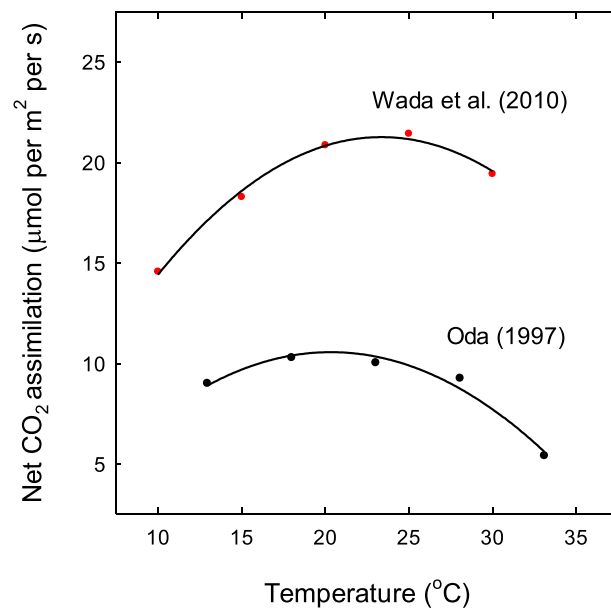
for electron transport was 28.1°C for cool-season species and 31.9°C for warm-season species.

The response to temperature is dependent on light and CO<sub>2</sub> (Dusenge et al., 2019; Morison & Lawlor, 1999). Photosynthesis is higher under high PPFs and high CO<sub>2</sub>. Temperatures during the day are correlated with solar radiation in temperate and subtropical regions, whereas warm weather can be associated with cloud cover in wet tropical regions. Climate change is associated with increases in CO<sub>2</sub> in the atmosphere and increases in average temperatures (Bagley et al., 2015).

The relationship between photosynthesis and temperature was explored in strawberry (Table S4). The optimum temperatures for net CO<sub>2</sub> assimilation varied across the studies, reflecting differences in cultivars, leaf age, light and CO<sub>2</sub>. The optimum ranged from 20° to 30°C, with lower photosynthesis at lower or higher temperatures. There was a broad range in temperature where photosynthesis was satisfactory, with CO<sub>2</sub> assimilation only decreasing sharply at extremes. Kimura et al. (2020) demonstrated that the optimum for maximum carboxylation ( $V_{cmax}$ ) was higher than that for the rate of light-saturated electron transport ( $J_{high}$ ). The first process was increasing at 35°C, whereas the second started to decrease at 35°C. Leaf temperature during the experiment ranged from 15° to 35°C.

There is an interaction between temperature and CO<sub>2</sub> on photosynthesis. Wada et al. (2010) examined the relationship between photosynthesis and temperature under controlled-environment conditions in Japan (Figure 8). The plants were exposed to temperatures from 10° to 30°C and to low or high CO<sub>2</sub> (400 or 1,000 ppm). Maximum net CO<sub>2</sub> assimilation was higher under high CO<sub>2</sub> (39.9 µmol per m<sup>2</sup> per s) than under low CO<sub>2</sub> (21.4 µmol per m<sup>2</sup> per s). The optimum range for photosynthesis was 20° to 25°C at low CO<sub>2</sub> and 25° to 30°C at high CO<sub>2</sub>. Oda (1997) conducted similar work in the same area (Figure 8). The plants were grown at temperatures from 10° to 35°C at low or high CO<sub>2</sub> (360 or 1,350 ppm). Maximum net CO<sub>2</sub> assimilation was higher under high CO<sub>2</sub> (8.1 µmol per m<sup>2</sup> per s) than under low CO<sub>2</sub> (3.7 µmol per m<sup>2</sup> per s). The optimum range for photosynthesis was 13° to 23°C at low CO<sub>2</sub> and 23° to 33°C at high CO<sub>2</sub>.

Photosynthesis is affected by extreme and average conditions. Fu et al. (2023) examined the effect of environmental stress (PPF of 1,800 µmol per m<sup>2</sup> per s and a temperature of 38°C) on gas exchange in 'Xuelixiang' strawberry in China. Control plants were exposed to a PPF of 400 µmol per m<sup>2</sup> per s and a temperature of 23°C. Net CO<sub>2</sub> assimilation ranged from 10 to 13 µmol per m<sup>2</sup> per s in the controls. In contrast, net CO<sub>2</sub> assimilation decreased to 5 µmol per m<sup>2</sup> per s after eight hours of stress. Poor gas exchange after stress was associated with low stomatal conductance ( $g_s$ ).



**Figure 8.** Relationship between net CO<sub>2</sub> assimilation ( $A_{Net}$ ) and temperature ( $T$ , °C) in strawberry in Japan. The response to temperature was examined at low or high CO<sub>2</sub>. For Wada et al. (2010), standard conditions were a photosynthetic photon flux (PPF) of 2,000  $\mu\text{mol per m}^2 \text{ per s}$ . For Oda (1997), standard conditions were a PPF of 552  $\mu\text{mol per m}^2 \text{ per s}$ . For Wada et al. (2010):  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 400 ppm CO<sub>2</sub> = Intercept + 1.79  $\times T$  - 0.038  $\times T^2$  ( $P = 0.007$ ,  $R^2 = 0.99$ ). For Oda (1997):  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 360 ppm CO<sub>2</sub> = Intercept + 1.24  $\times T$  - 0.030  $\times T^2$  ( $P = 0.027$ ,  $R^2 = 0.94$ ).

Leaves can adapt to changes in temperatures. Leaves initiated at high temperatures have higher maximum net CO<sub>2</sub> assimilation than those initiated at low temperatures. There is a shift in the optimum range for photosynthesis, with the range higher when the plants are exposed to warm weather.

Chabot (1978) examined the effect of temperature on gas exchange in *F. vesca* in growth chambers in New York. The plants were grown at 10°/2°, 20°/10°, 30°/20° or 40°/30°C and data collected on photosynthesis after five weeks. The temperature in the leaf chamber ranged from 10° to 35°C. Net CO<sub>2</sub> assimilation was highest under moderate growth temperatures from 20° to 30°C (Figure 9). Maximum carbon fixation occurred from 20° to 25°C during the time of measurement, except at the coldest regime. Each growth regime produced a different response curve. There was a shift in the optimum in the direction of the prevailing growth regime. There was an improvement in gas exchange at higher growth temperatures, except for the leaves at 10°/2°C. Photosynthesis was less sensitive to temperature when the plants were grown at higher temperatures. Low photosynthesis at extremes was associated with closure of the stomata.

Chabot and Chabot (1977) investigated the relationship between photosynthesis, leaf anatomy and temperature in New York. Net CO<sub>2</sub> assimilation adapted to higher temperatures during growth, with gas exchange limited only by extreme conditions. Plants with higher rates of carbon assimilation had thinner leaves than those with lower rates and dense mesophylls.

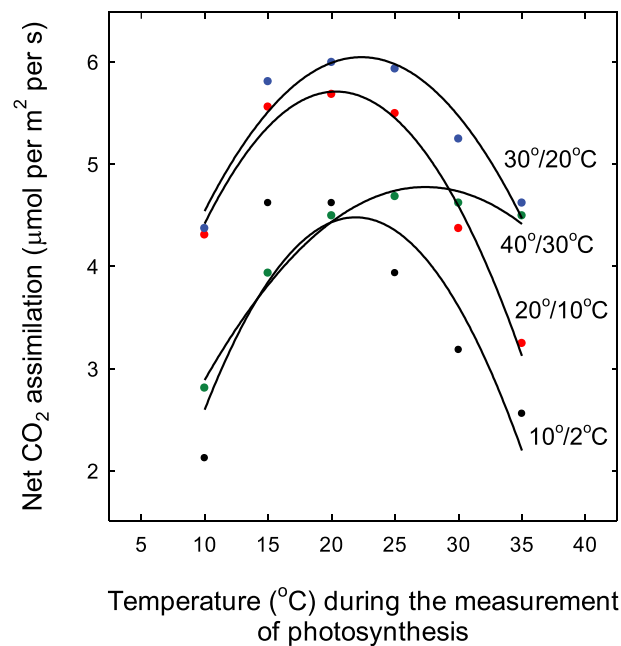
### Relationship between photosynthesis and nitrogen

Most of the nitrogen in the leaves of higher plants is used in the proteins required for photosynthesis (Evans & Clarke, 2019). Low concentrations of nitrogen decrease the diffusion of CO<sub>2</sub> from the atmosphere to the chloroplasts and decrease the efficiency of CO<sub>2</sub> assimilation (Gao et al., 2023; Kattge et al., 2009; Li et al., 2022; Mu & Chen, 2021).

The allocation of nitrogen to the leaves and to the chloroplasts varies across species and ecosystems (Khan et al., 2022; Luo et al., 2021). A study around the globe found that a mean of  $18.2 \pm 6.2\%$  of nitrogen in the leaves was allocated to the photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO). In many wild and crop plants, there is a strong relationship between net CO<sub>2</sub> assimilation and total nitrogen per leaf area recorded as mmol per m<sup>2</sup> (Evans, 1989; Hikosaka, 2004; Hikosaka et al., 2002; Ripullone et al., 2003; Sinclair & Horie, 1989).

The relationship between gas exchange and nitrogen was examined in strawberry (Table S5,  $N = 15$ ). Net CO<sub>2</sub> assimilation or net assimilation rate (NAR) was usually higher with high nitrogen, although there were exceptions. The results were difficult to compare because of different proxies used to measure the amount of nitrogen applied to the plants or the concentration of nitrogen in the leaves. There were variations in cultivar, temperature and CO<sub>2</sub>.

Moon et al. (1990) investigated the effect of nitrogen on carbon assimilation in two genotypes of *F. chiloensis* in Arizona. The plants were grown in a



**Figure 9.** Relationship between net CO<sub>2</sub> assimilation ( $A_{Net}$ ) and temperature ( $T$ , °C) in *F. vesca* in New York, United States. The plants were grown at 10°/2°, 20°/10°, 30°/20° or 40°/30°C and photosynthesis measured after five weeks. The temperature in the leaf chamber ranged from 10° to 35°C and the photosynthetic photon flux (PPF) was 800  $\mu\text{mol per m}^2 \text{ per s}$ . For 10°/2°C:  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) = Intercept +  $0.582 \times T - 0.013 \times T^2$  ( $P = 0.118$ ,  $R^2 = 0.60$ ). For 20°/10°C:  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) = Intercept +  $0.490 \times T - 0.012 \times T^2$  ( $P = 0.004$ ,  $R^2 = 0.95$ ). For 30°/20°C:  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) = Intercept +  $0.441 \times T - 0.001 \times T^2$  ( $P = 0.022$ ,  $R^2 = 0.87$ ). For 40°/30°C:  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) = Intercept +  $0.342 \times T - 0.006 \times T^2$  ( $P = 0.002$ ,  $R^2 = 0.97$ ). Data are from Chabot (1978).

greenhouse under natural, light with a PPF of  $20.2 \pm 3.7 \text{ mol per m}^2 \text{ per day}$ . The day/night temperatures were 22°/17°C. The plants were given 0, 100, 200 or 300 mg N per litre, with 40% coming from NH<sub>4</sub>-N and 60% from NO<sub>3</sub>-N. Higher applications increased leaf nitrogen up to 200 mg N per litre, with greater accumulation in ‘CA11’ than in ‘RCP37’.

There were strong positive linear relationships between net CO<sub>2</sub> assimilation and nitrogen per leaf area or  $N_a$  (Figure 10;  $R^2 = 0.83$  or  $0.91$ ). The slope from the regression or the photosynthetic nitrogen use efficiency (PNUE) was higher in ‘RCP37’ (0.32) than in ‘CA11’ (0.26). The first cultivar was from a high-nutrient inland site, while the second cultivar was from a low-nutrient dune site near the Pacific Ocean. Leaf nitrogen ranged from 50 to 250 mmol per m<sup>2</sup> and net CO<sub>2</sub> assimilation ranged from 10 to 60  $\mu\text{mol per m}^2 \text{ per s}$ . In a study across crops, leaf nitrogen ranged from 10 to 300 mmol per m<sup>2</sup>, and net CO<sub>2</sub> assimilation ranged from 2 to 45  $\mu\text{mol per m}^2 \text{ per s}$  (Evans, 1989).

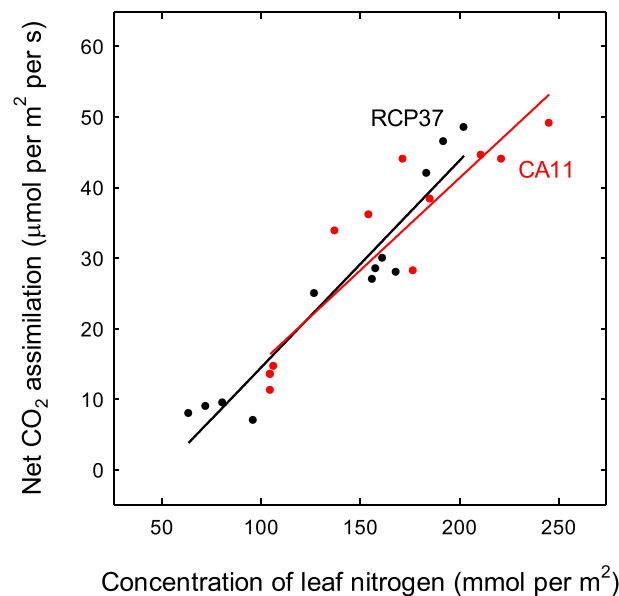
Yousefi et al. (2023) grew plants with different amounts of nitrogen in a greenhouse in Iran. They found that plants given 180 mg N per litre had higher concentrations of nitrogen in the shoots (2.07% DW) than those given 120 mg N per litre (1.32% DW). The plants given high nitrogen had higher concentrations of chlorophyll (1.63 mg per g FW versus 1.35 mg per g FW) and higher photosynthetic efficiency ( $F_v/F_m$  of 0.82 versus 0.78). A study in Korea found a strong correlation ( $r = 0.75$ ) between chlorophyll

fluorescence ( $F_v/F_m$ ) and relative chlorophyll content (SPAD) in a growth chamber (Arief et al., 2023). SPAD values typically reflect the concentration of nitrogen in leaves (Wu et al., 2020).

### Changes in photosynthesis with leaf development

There are changes in the rate of photosynthesis as leaves emerge, unfold, expand and senesce (Niinemets, 2016; Schultz, 2003; Suzuki & Takahashi, 2020; Wujeska-Klaus et al., 2019). Net CO<sub>2</sub> assimilation reaches a maximum after the leaves are fully expanded. This period of gas exchange lasts for a few days to several months, depending on the species and growing conditions. Increases in photosynthesis in young leaves reflect increases in the concentration of chlorophyll, while decreases in old leaves reflect the export of nitrogen and other mobile nutrients to new growth.

Arney (1953a, 1953b, 1954) found that a leaf emerged every eight to ten days in ‘Royal Sovereign’ from June to September in the United Kingdom. Pérez de Camacaro et al. (2002) indicated that leaf production was linear over 64 days in one cultivar and linear over 96 days in two cultivars. A leaf was produced every two to five days during the main period of growth. Le Mière et al. (1998) demonstrated that plants in glasshouses produced 1.1 leaves per week at 12°C and 1.8 leaves per week at 28°C. Leaf production



**Figure 10.** Relationship between net CO<sub>2</sub> assimilation ( $A_{Net}$ ) and the concentration of nitrogen per leaf area ( $N_a$ ) in two cultivars of *F. chiloensis* in Arizona, United States. Standard conditions were a photosynthetic photon flux (PPF) of 1,400 to 1,600  $\mu\text{mol per m}^2$  per s and a temperature of 20°C. For 'RCP37':  $A_{Net}$  ( $\mu\text{mol per m}^2$  per s) = Intercept +  $0.331 \times N_a$  ( $P < 0.001$ ,  $R^2 = 0.91$ ). For 'CA11':  $A_{Net}$  ( $\mu\text{mol per m}^2$  per s) = Intercept +  $0.261 \times N_a$  ( $P < 0.001$ ,  $R^2 = 0.83$ ). Data are from Moon et al. (1990).

was nearly linear over 120 days in Wisconsin, with a leaf produced every six to thirteen days (Jahn & Dana, 1970.).

Leaf senescence is the final stage of leaf development when the leaves turn from green to yellow (Zhao et al., 2022). These changes are accompanied by a decrease in the contents of chlorophyll and proteins and a decrease in photosynthesis (Song et al., 2014). The life-span of leaves varies across species and growing conditions (Chabot & Hicks, 1982; Edwards et al., 2014; Reich et al., 1991a). In a study conducted across 189 deciduous and 506 evergreen species, the leaves lived for 1.48 to 258 months (Van Ommen Kloeke et al., 2012). Arney (1947) collected data on leaf ageing and senescence in strawberry in Southampton in the United Kingdom. The leaves began to turn yellow after  $87.0 \pm 20.1$  days, the median time was 84.5 days, and the range was from 55.0 to 126.0 days. Jurik and Chabot (1986) demonstrated that the leaves of the wild strawberry, *F. virginiana* lived mostly for 50 to 150 days, depending on the season and habitat in the forest of New York.

The relationship between photosynthesis and leaf development was explored in strawberry (Table S6). The authors measured net CO<sub>2</sub> assimilation per leaf area under controlled-environment conditions. The youngest leaves were 1 to 3 days-old, while the oldest leaves were 60 to 65 days-old. The effect of leaf age on gas exchange was mixed. In some of the studies, photosynthesis was acceptable over a broad range of development. In the others, photosynthesis was optimal in the middle of leaf development, with lower photosynthesis in young or old leaves.

### Effect of fruit growth on photosynthesis

Photosynthesis in plants is affected by the demand for carbohydrates (Kerkhoff et al., 1988; Neales & Incoll, 1968). The effect of fruit growth on gas exchange is mixed. In some studies, leaves on trees or branches without fruit had lower CO<sub>2</sub> assimilation than those with fruit (Fujii & Kennedy, 1985). In the second scenario, differences between the two treatments were limited to a part of the season (DeJong, 1986; Nii, 1993; Roper et al., 1988; Vemmos, 1994; Wang et al., 2010). Finally, in the third, there were no differences in gas exchange between fruiting and non-fruiting plots (Rom & Ferree, 1986) or gas exchange was greater in non-fruiting branches (Heerema et al., 2014).

Palmer et al. (1997) explored the effect of fruit thinning on the physiology of apple trees in New Zealand. There was a strong relationship between photosynthesis and the density of fruit production. Net CO<sub>2</sub> assimilation increased with crop load up to a maximum of 12 fruit per m<sup>2</sup> of leaf area ( $R^2 = 0.85$ ).

The relationship between photosynthesis and fruit development was examined in strawberry (Table S7). The authors measured net CO<sub>2</sub> assimilation in various tissues, including the young or old leaves or the whole canopy. A two-sided *t*-test was used to determine if CO<sub>2</sub> assimilation in non-fruiting plants was lower than that in fruiting plants ( $P < 0.05$ ). The null hypothesis that the mean ratio equals one was then rejected. The mean relative CO<sub>2</sub> assimilation in the non-fruiting plants compared with fruiting plants was  $0.90 \pm 0.15$ , the median was 0.85, and the range was from 0.71 to 1.27 ( $N = 12$ ,  $P = 0.042$ ). The null hypothesis was rejected, indicating that

plants without fruit had slightly lower CO<sub>2</sub> assimilation than those with fruit.

The response across the experiments was variable, reflecting differences in the tissues used to measure photosynthesis and differences in the times when the data were collected. Lower CO<sub>2</sub> assimilation in fruiting plants than in non-fruiting plants is associated with lower concentrations of nitrogen in the leaves (Heerema et al., 2014).

### Photosynthesis by the canopy

Estimates of canopy photosynthesis based on models of individual leaves are problematic (Bagley et al., 2015; Gara et al., 2019; Kim & Verma, 1991; Terashima & Hikosaka, 1995; Zhang et al., 2023a). This is because net CO<sub>2</sub> assimilation in the canopy does not reflect CO<sub>2</sub> assimilation in the leaves at the top of the canopy (Cannell & Thornley, 1998). There are large spatial variations in light interception and leaf nitrogen throughout the canopy (Lauarn et al., 2015). Leaves in the lower canopy also adapt to shade.

There is limited information on canopy photosynthesis in strawberry. Choma et al. (1982) studied the physiology of 'Hecker' in Virginia. The leaf area of the plants ranged from 0.045 to 0.057 m<sup>2</sup> over six weeks, and net CO<sub>2</sub> assimilation ranged from 11.0 to 16.5 μmol per m<sup>2</sup> per s. Average leaf area was 0.050 ± 0.002 m<sup>2</sup> and average net CO<sub>2</sub> assimilation was 14.2 ± 0.8 μmol per m<sup>2</sup> per s. Schaffer et al. (1986) conducted a similar experiment in Florida using 'Tribute'. Leaf area (0.012 to 0.082 m<sup>2</sup> per plant) and net CO<sub>2</sub> assimilation per plant increased over six weeks. In contrast, net CO<sub>2</sub> assimilation per leaf area decreased from 12.0 to 6.7 μmol per m<sup>2</sup> per s. There was a strong negative linear relationship between CO<sub>2</sub> assimilation per leaf area and leaf area per plant ( $P = 0.032$ ,  $R^2 = 0.65$ ). The results of this experiment suggest that the leaves at the bottom of the canopy became shaded as the plants grew.

Yoshida and Morimoto (1997) modelled photosynthesis in 'Nyoho' in Japan. Net CO<sub>2</sub> assimilation was related to the area of the ground covered by the canopy (m<sup>2</sup>) and was 20% higher in December than from February to March. This was because the plants had a higher leaf area index (LAI) in December. Net

CO<sub>2</sub> assimilation was saturated at a PPF of 1,150 μmol per m<sup>2</sup> per s with a CO<sub>2</sub> of 400 to 500 ppm. Net CO<sub>2</sub> assimilation was saturated with a CO<sub>2</sub> of 1,000 ppm with a PPF of 460 μmol per m<sup>2</sup> per s. The responses to light and CO<sub>2</sub> were similar to those for single leaves (Figures 5 and 8).

Le et al. (2021) compared photosynthesis in single leaves and the canopy of 'Sachinoka' in Japan. Mean net CO<sub>2</sub> assimilation was similar in the two groups under high light and CO<sub>2</sub> (Table 3). In contrast, net CO<sub>2</sub> assimilation was higher in the leaves than in the canopy under low light and CO<sub>2</sub>. The lower leaves were too shaded under low light to contribute to carbon fixation. The leaves in the middle and lower canopy were older than those measured at the top of the canopy. Photosynthesis in the canopy was saturated at a PPF of 1,379 μmol per m<sup>2</sup> per s with a CO<sub>2</sub> of 400 ppm.

### Effect of climate change on photosynthesis, leaf area expansion and yield

The main scenarios for climate change include an increase in the concentration of CO<sub>2</sub> in the atmosphere and an increase in average temperatures. The effect of climate change on yield depends on the effect of CO<sub>2</sub> and temperature on photosynthesis and the effect of temperature on leaf area expansion and fruit growth.

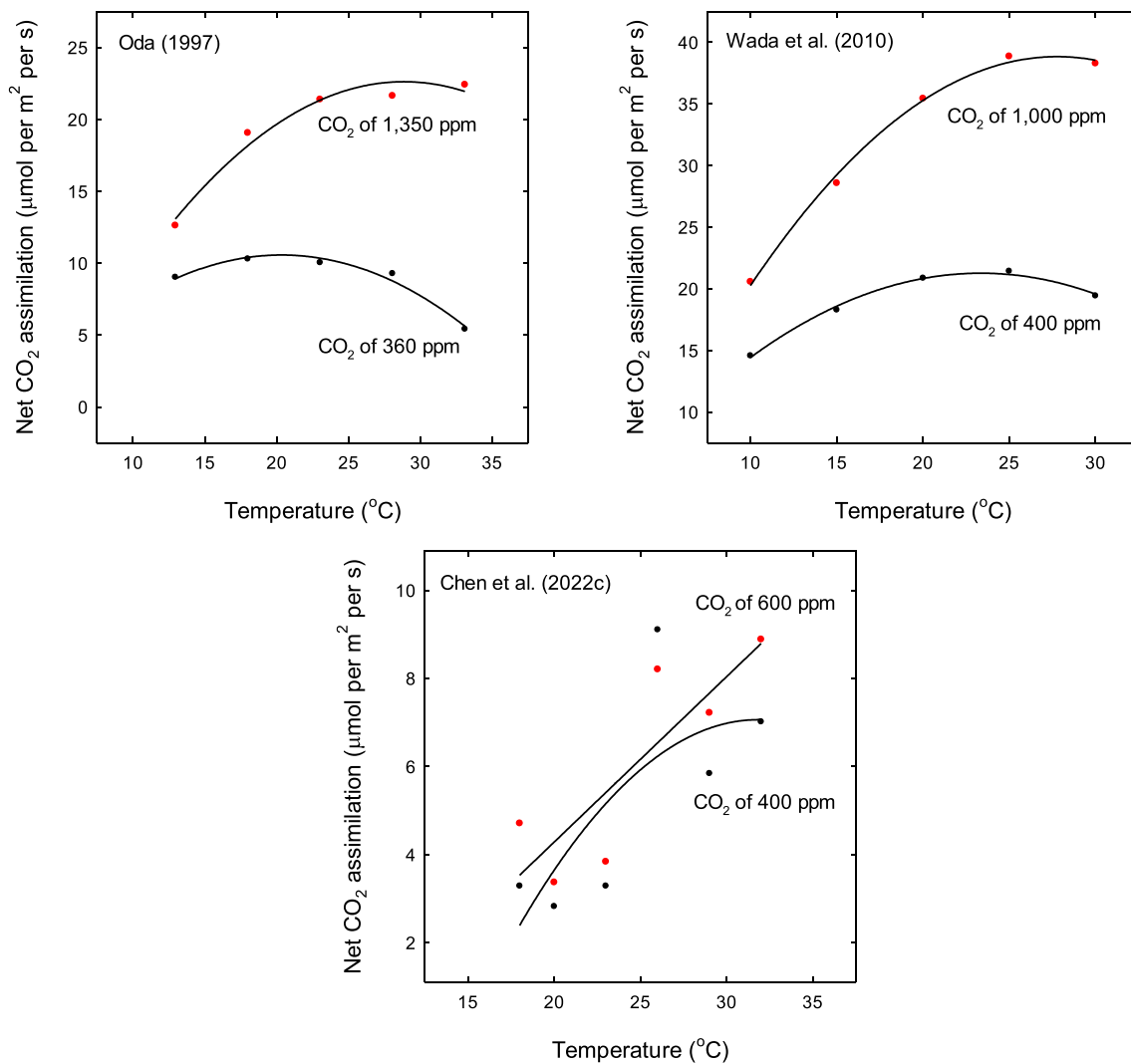
Net CO<sub>2</sub> assimilation increases with increasing CO<sub>2</sub> up to about 1,000 ppm and is satisfactory over a broad range of temperatures from 20° to 30°C (Figures 8 and 9). The leaves adapt to high CO<sub>2</sub> and this dampens the response. There is a shift in the optimum temperatures for photosynthesis, with the optima higher when plants are grown under warm weather and elevated CO<sub>2</sub>. It is not clear if models based on leaves predict photosynthesis by the canopy. Research in Japan suggests that there is close agreement between CO<sub>2</sub> assimilation in leaves and the canopy only under high light and high CO<sub>2</sub> (Le et al., 2021). A recent analysis indicated that yield decreases by 60 g per plant for each 1°C increase in temperature (Menzel, 2023). However, this study did not take into account changes in carbon production under climate change.

Net CO<sub>2</sub> assimilation is affected by changes in CO<sub>2</sub> and temperature. Gas exchange is higher

**Table 3.** Gas exchange in single leaves and the whole canopy of 'Sachinoka' strawberry in Japan. The plants were grown in a greenhouse under artificial light with different concentrations of CO<sub>2</sub>. The temperature was 23°C. Means in a column followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. PPF = photosynthetic photon flux. Data are from Le et al. (2021).

Tissue	PPF of 200 μmol/m <sup>2</sup> /s and CO <sub>2</sub> of 400 ppm			PPF of 1,000 μmol/m <sup>2</sup> /s and CO <sub>2</sub> of 1,000 ppm		
	Net CO <sub>2</sub> assimilation (μmol/m <sup>2</sup> /s)	Stomatal conductance (mmol/m <sup>2</sup> /s)	Transpiration (mmol/m <sup>2</sup> /s)	Net CO <sub>2</sub> assimilation (μmol/m <sup>2</sup> /s)	Stomatal conductance (mmol/m <sup>2</sup> /s)	Transpiration (mmol/m <sup>2</sup> /s)
Single leaf	7.5 b	215 a	2.4 b	26.1 a	314 a	3.4 b
Whole plant	5.0 a	347 b	1.0 a	26.4 a	351 a	1.7 a





**Figure 11.** Relationship between net CO<sub>2</sub> assimilation ( $A_{Net}$ ) and temperature ( $T$ , °C) under low or high CO<sub>2</sub> in strawberry. For Oda (1997):  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 360 ppm CO<sub>2</sub> = Intercept +  $1.24 \times T - 0.030 \times T^2$  ( $P = 0.027$ ,  $R^2 = 0.94$ ) and  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 1,350 ppm CO<sub>2</sub> = Intercept +  $2.18 \times T - 0.038 \times T^2$  ( $P = 0.034$ ,  $R^2 = 0.93$ ). For Wada et al. (2010):  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 400 ppm CO<sub>2</sub> = Intercept +  $1.79 \times T - 0.038 \times T^2$  ( $P = 0.007$ ,  $R^2 = 0.99$ ) and  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 1,000 ppm CO<sub>2</sub> = Intercept +  $3.26 \times T - 0.059 \times T^2$  ( $P = 0.004$ ,  $R^2 = 0.99$ ). For Chen et al. (2022c):  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 400 ppm CO<sub>2</sub> = Intercept +  $1.79 \times T - 0.038 \times T^2$  ( $P = 0.300$ ,  $R^2 = 0.24$ ) and  $A_{Net}$  ( $\mu\text{mol per m}^2 \text{ per s}$ ) at 600 ppm CO<sub>2</sub> = Intercept +  $0.376 \times T$  ( $P = 0.031$ ,  $R^2 = 0.65$ ). The photosynthetic photon flux (PPF) in the three studies was 828, 2,000 and 1,500  $\mu\text{mol per m}^2 \text{ per s}$ .

under elevated CO<sub>2</sub> than under ambient CO<sub>2</sub> and the optimum temperatures are higher (Figure 11). Chen et al. (2022c) demonstrated that maximum net CO<sub>2</sub> assimilation was higher under CO<sub>2</sub> of 600 ppm than under 400 ppm (8.0 versus 6.2  $\mu\text{mol per m}^2 \text{ per s}$ ; PPF = 1,500  $\mu\text{mol per m}^2 \text{ per s}$ ). The optimum temperature range for gas exchange was 29° to 32°C at ambient CO<sub>2</sub>. In contrast, gas exchange was increasing at the highest temperature at elevated CO<sub>2</sub>.

There are mixed effects of temperature on leaf growth in strawberry, although most researchers indicate that leaf growth is lower above 30°C than below 30°C. The results from some studies indicate that leaf growth was best from 18° to 24°C (Wang & Camp, 2000), 22° to 30°C (Kadir et al., 2006) or 20° to 24°C (Hopf et al., 2022). In contrast, other experiments, leaf growth decreased as the temperature increased from

12° to 28°C (Le Mièrè et al., 1998) or from 27° to 36°C (Xu et al., 2021). Le Mièrè et al. (1998) also showed that there was a strong negative linear relationship between yield and temperature (Figure 12). Low yields at high temperatures were associated with poor leaf area expansion and fewer berries.

High temperatures increase CO<sub>2</sub> assimilation per leaf area when combined with elevated CO<sub>2</sub>. The optimum temperature for photosynthesis is higher than that for leaf area expansion and fruit production. High temperatures also have an indirect effect on photosynthesis by reducing the area of the leaves available for carbon capture.

Sun et al. (2012) examined the effect of CO<sub>2</sub> and temperature on yield in growth chambers in China. Control plants under ambient CO<sub>2</sub> of 360 ppm and temperatures of 20°/15°C had low and similar yields as those under ambient CO<sub>2</sub> and elevated temperatures of

25°/20°C or under elevated CO<sub>2</sub> of 720 ppm and elevated temperatures (10.5 to 12.0 g dry weight per plant;  $P > 0.05$ ). The plants at elevated CO<sub>2</sub> and ambient temperatures had the best yields (25 g dry weight per plant;  $P < 0.05$ ). Balasooriya et al. (2018) conducted similar work in Australia. Net CO<sub>2</sub> assimilation was higher at a CO<sub>2</sub> of 650 or 900 ppm than at 400 ppm. In contrast, temperature had only a small effect on CO<sub>2</sub> assimilation. Yields were higher at intermediate CO<sub>2</sub> and lower at 30°C than at 25°C. The highest yields were obtained at 25°C with a CO<sub>2</sub> of 400 or 650 ppm. These results suggest that the best yields occur with moderate to high CO<sub>2</sub> and low to moderate temperatures.

Redondo-Gómez et al. (2022) studied the effect of CO<sub>2</sub> and temperature on the performance of 'Fortuna' in growth chambers in Spain. The plants were grown at 25°/14°C and 400 ppm CO<sub>2</sub> or at 29°/18°C and 700 ppm CO<sub>2</sub>. Plant dry weight (3.95 g versus 4.05 g) and net CO<sub>2</sub> assimilation (11.8 μmol per m<sup>2</sup> per s versus 10.0 μmol per m<sup>2</sup> per s) were similar in the two groups. The benefits of high CO<sub>2</sub> were negated by the impacts of high temperature on growth and gas exchange. Zhang et al. (2021) assessed the effect of elevated CO<sub>2</sub> and temperatures on gas exchange in plants across 337 studies. They found that elevated CO<sub>2</sub> increased net CO<sub>2</sub> assimilation by 28.6%, while elevated temperatures decreased net CO<sub>2</sub> assimilation by 23.2%.

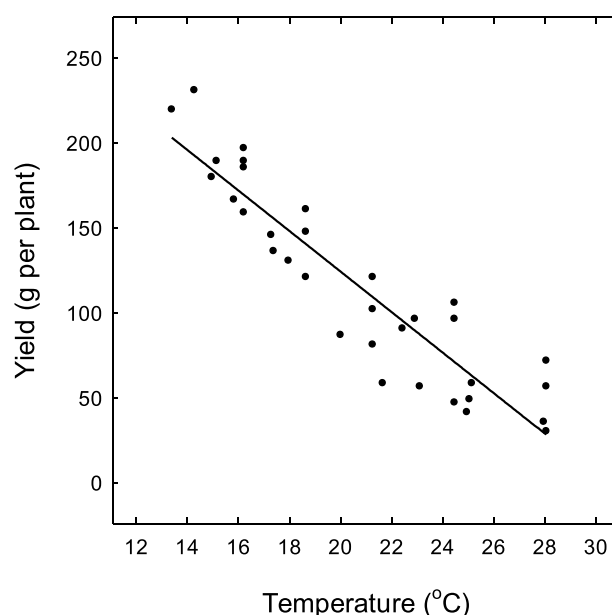
There is controversy about the methods used to assess whether higher CO<sub>2</sub> under climate change has contributed to higher photosynthesis around the globe (Sang et al., 2021; Wang et al., 2021; Keenan et al., 2021, 2022; Walker et al., 2021; Wang et al., 2022b).

Some studies suggest that photosynthesis has increased in the past 20 years (Chen et al., 2022b; He et al., 2022b; He et al., 2023; Keenan & Williams, 2018),

while others suggest that the effect of higher CO<sub>2</sub> has declined (Keenan et al., 2016, 2021, 2022; Wang et al., 2021; Zhu et al., 2019). Chen et al. (2022a) investigated photosynthesis in plant communities under climate change. Temperatures were too high for best gas exchange in most of the tropics and low latitudes, whereas exchange was affected by water deficits in northern high latitudes greater than 45°N. In some areas, higher photosynthesis under climate change was associated with higher mean temperatures and a longer growing season (Finzi et al., 2020). Photosynthesis is dependent on canopy cover in some communities complicating the relationship between carbon fixation and rising CO<sub>2</sub> (Meng et al., 2023).

Rakhmankulova et al. (2023) reported on the effects of short-term elevated temperatures and CO<sub>2</sub> (400 or 800 ppm) on gas exchange in a C<sub>3</sub> (*Chenopodium quinoa* or quinoa) and C<sub>4</sub> plant (*Amaranthus retroflexus* or amaranth) in Russia. The plants were grown at 25° or 35°C (for four days) at low or high CO<sub>2</sub> (400 or 800 ppm). Net CO<sub>2</sub> assimilation in quinoa decreased by 28 and 18% under elevated temperatures at both normal and elevated CO<sub>2</sub> compared with the control. Net CO<sub>2</sub> assimilation in amaranth decreased an average of 33% compared with the control. Zheng et al. (2022) conducted similar work with *Glycine max* or soybean (C<sub>3</sub>) and *Amaranthus tricolor* (C<sub>4</sub>) in China. There were four combinations of temperature (28° or 35°C) and CO<sub>2</sub> (400 or 800 ppm) with a PPF of 600 μmol per m<sup>2</sup> per s. In *Glycine max*, high temperatures increased gas exchange under both low and high CO<sub>2</sub> compared with the other regimes. In *Amaranthus tricolor*, gas exchange was similar across the four regimes.

The effect of climate change on the yields of crops is mixed, although several reports suggest that productivity



**Figure 12.** Relationship between yield and temperature (T, °C) in strawberry in the United Kingdom. Yield (g per plant) = Intercept - 11.92 × T ( $P < 0.001$ ,  $R^2 = 0.84$ ). Data are from Le Mière et al. (1998).

will decline, especially in the second half of the century (Gardi et al., 2022; Hasegawa et al., 2022). The benefits of higher CO<sub>2</sub> are often overridden by higher temperatures or prolonged droughts (Ben Mariem et al., 2021; Zhou et al., 2021). The response to climate change varies with the crop and region, with the results variable across studies (eg. Li et al., 2021b for cotton across the globe; and Liu et al., 2020b for rice, wheat and maize in China). The degree to which productivity declines depends on whether better cultivars or growing technologies are adopted (Challinor et al., 2014; Hasegawa et al., 2022). Wilcox and Makowski (2014) modelled the responses in wheat. More than half of the simulations resulted in losses of yield when the mean temperature increased by more than 2.3°C or when CO<sub>2</sub> was lower than 395 ppm. The effect of CO<sub>2</sub> greater than 640 ppm outweighed the impact of temperatures up to + 2°C on yields.

Gutteridge and Gutteridge (2018) analysed the effect of climate change on photosynthesis and yield in crops. Losses of yield had less to do with photosynthesis and more to do with the sensitivity of flowering and fruit development to heat stress. They concluded that increasing atmospheric CO<sub>2</sub> enhances the yields of major crops. However, these effects on carbon output are more than offset by the rise in temperatures. A study in the United States indicated that the yields of major species such as soybean and corn will decrease by 17% for every 1°C increase in temperature (Lobell & Asner, 2003). Helman and Bonfil (2022) analysed the productivity of wheat in the major producing countries over six decades where the concentration of CO<sub>2</sub> increased by 98 ppm. They demonstrated that in two of the three top countries (China and the former Soviet Union), yields were 5.5% lower than expected, due to warming and drought.

The impact of climate change on strawberry production will vary across growing areas. In warm locations such as California, Florida and Spain, increases in photosynthesis under higher CO<sub>2</sub> are offset by decreases in flowering and fruiting under higher temperatures (Environmental Defence Fund, 2023; Maskey et al., 2019; Palencia et al., 2009; Pathak et al., 2018). Overall yields are lower. In contrast, the impact of climate change in cool locations in Europe is mixed. Higher temperatures increase growth and the length of the production season, but decrease flower initiation (Døving, 2009; Bethere et al., 2016; Esitken et al., 2009; Heide & Sønstebj, 2020).

Neri et al. (2012) reviewed strawberry cultivation in Europe under climate change. They divided production into three zones with different weather conditions. Northern Europe had severe winters, often characterised by snow cover. Central Europe had occasional severe winters and relatively mild autumns and springs. Southern Europe had mild winters, where the temperature was almost never lower than 0°C. The impact of climate change on production is more severe in Southern Europe than in the other areas.

## Challenges and future prospects

Climate change affects crop production around the world. Elevated CO<sub>2</sub> and temperatures increase photosynthesis in strawberry, at least in the short-term. However, the optimum temperatures for yield are lower than those for CO<sub>2</sub> assimilation in the leaves. Climate change decreases yields in warm location, but may be beneficial in cool locations. The long-term solution to climate change is to develop heat-tolerant cultivars that grow and fruit under the warmer conditions. Genome-wide association (GWA) and genomic prediction (GP) will accelerate the identification of adapted populations and individuals under global warming. These studies should examine the genes associated with acceptable CO<sub>2</sub> assimilation in the leaves at high temperatures, and acceptable leaf, flower and fruit growth under the same conditions. Liu et al. (2023a) indicated that traditional breeding is not efficient in developing cultivars adapted to warm weather. Genotypes with high photosynthesis will not be more productive under climate change, unless the better gas exchange is associated with better growth and fruiting.

## Conclusions

Photosynthesis in strawberry is sensitive to environmental conditions and leaf physiology. There is an interaction between CO<sub>2</sub> and temperature on gas exchange. Maximum net CO<sub>2</sub> assimilation is 23% higher at a CO<sub>2</sub> of 600 ppm than at 400 ppm. Gas exchange keeps increasing at 32°C at elevated CO<sub>2</sub>, whereas it is saturated at this temperature at low CO<sub>2</sub>. Leaf area expansion and yield decrease when the temperature is above 30°C, indicating that the optimum temperatures for these processes are lower than those for gas exchange. The impact of climate change on production varies across growing areas. In warm-locations, elevated CO<sub>2</sub> and temperatures increase gas exchange in the leaves, but not yield. In some cool locations, elevated temperatures increase plant growth and the length of the production season. However, the higher temperatures in cool areas decrease flower initiation.

## Disclosure statement

No potential conflict of interest was reported by the author.

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## Data availability statement

The author confirms that the data supporting the findings of this study are available within the supplementary materials published online with this paper or available from the author on reasonable request.

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