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Climate change increases net CO₂ 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 CO₂ in the atmosphere and an increase in temperature. This review examined photosynthesis in strawberry. The mean photosynthetic photon flux (PPF) for the saturation of CO₂ 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 CO₂ for the saturation of assimilation was 869 ± 306 ppm, the median was 900 ppm, and the range was from 410 to 1,750 ppm ($N = 32$). The optimum temperature range for CO₂ 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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Introduction

Climate change has increased the temperature and the concentration of CO₂ 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 CO₂ 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 CO₂ and temperature have increased photosynthesis in many plants. However, the increase in carbon assimilation under higher CO₂ 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 CO₂. 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 CO₂, 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 CO₂ 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.

Grež 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 CO₂ 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 CO₂), plant physiology (leaf nitrogen, leaf expansion and fruit development) and genotype on net CO₂ 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; Fávares et al., 2022; Figueiredo et al., 2013).

About 98% of CO₂ 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 mm². Klamkowski and Treder (2006) showed that leaves of ‘Salut’ had 203 stomata per mm², 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 mm² in plants in a greenhouse in Beijing, China and a mean stomatal conductance (g_s) of 306 ± 13 mmol per m² per s. The conductance of water vapour out of the leaves varies across cultivars. Grant et al. (2012) demonstrated that g_s in well-watered plants ranged from 200 to 600 mmol per m² 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_v/F_m 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 µm², 13 ± 2 µm² for a starch grain, 0.57 ± 0.07 µm² for a mitochondrion and 0.50 ± 0.03 µm² 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 ²	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 (μm)	Height of adaxial epidermis (μm)	Height of abaxial epidermis (μm)	Height of vascular tissue (μm)	Height of hypodermis (μm)
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

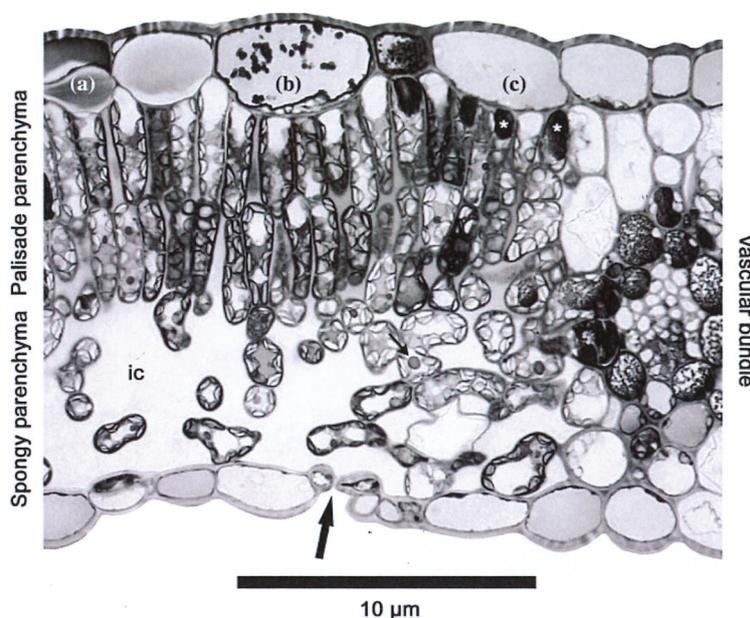


Figure 1. Cross-section of a strawberry leaflet using a light microscope (400 \times magnification) showing palisade and spongy parenchyma, vascular bundle, and adaxial (upper cell layer) and abaxial epidermis (lower cell layer). Different types of epidermal cells are shown: (a) two-layered zone with 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).

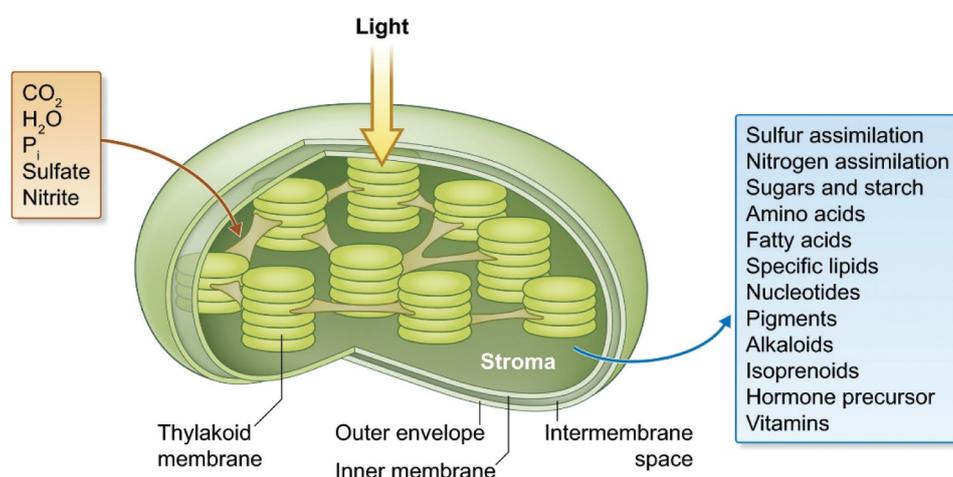


Figure 2. Structure of a higher plant chloroplast and overview about its metabolic competence. The chloroplast takes low-energy components (orange box) and converts them into high-energy metabolites (blue box) using sunlight. Drawn from Kirchhoff (2019).

environment such as light (Gjindali & Johnson, 2023; Li et al., 2020b). The ultrastructure of the chloroplast also changes with variations in CO₂. Li et al. (2020a) demonstrated that exposure of

wheat plants to elevated CO₂ (800 ppm) increased the number of grana lamellae and the concentration of chlorophyll in the leaves compared with those under ambient CO₂ (400 ppm).

Photosynthesis varies across strawberry species, hybrids and cultivars

Net CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ assimilation was 12.7 ± 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 α) was 0.034 ± 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 CO₂ 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 CO₂ 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 ± 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 ± 0.003 $\mu\text{mol per } \mu\text{mol}$ across C₃ 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 CO₂ 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,

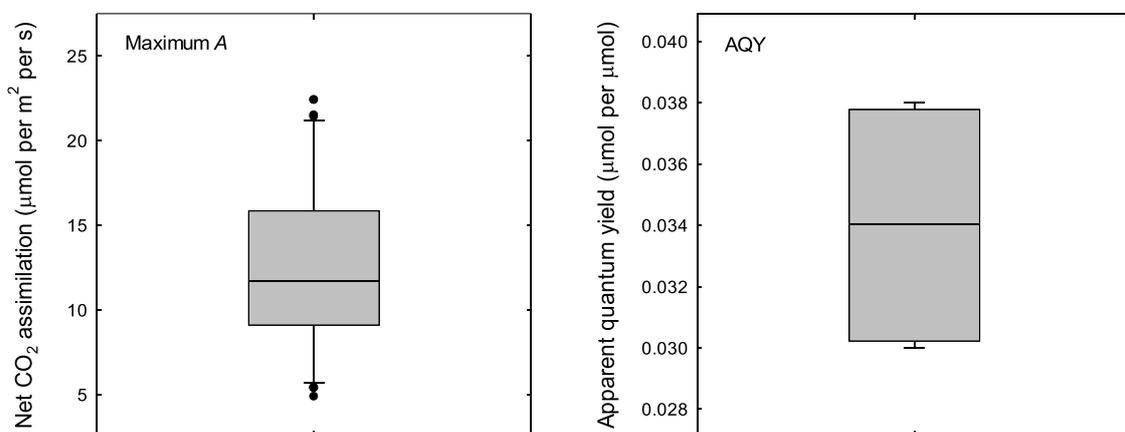


Figure 3. Box plots showing the distribution of maximum net CO₂ assimilation (A) and apparent quantum yield (AQY or α) in species, hybrids and cultivars of strawberry ($N = 41$ or 6). Data are from the various authors shown in Table S1.

suggesting that polyploidy was associated with low gas exchange. Hancock et al. (1989) indicated that there were moderate correlations between net CO₂ 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 μm versus 169 μm), mainly due to a thicker palisade (84 μm versus 62 μm) and spongy mesophyll (146 μm versus 120 μm). The leaves of *F. chiloensis* had higher mesophyll conductance ($g_m = 87.5$ mmol CO₂ per m² per s versus 62.1 mmol CO₂ per m² per s). Kanno et al. (2022) investigated gas exchange in seven cultivars in Japan. Net CO₂ 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 CO₂ 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 & Tworokoski, 1999). The first set of plants comprising 186 individuals was developed from an F₂ population from 'Benihoppe' \times '105 (14-9)'. The second set comprising 158 individuals was developed from an F₂ 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 C₃ species, net CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ assimilation nearly doubled from 8 February to 9 March (10.5 µmol per m² per s to 18.0 µmol per m² 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 CO₂ from the atmosphere to the sugars needed for growth. Photosynthesis can be limited by external factors such as light, the concentration of CO₂ 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 CO₂ assimilation per leaf area is higher under moderate or high radiation than under low radiation. For most C₃ and C₄ plants, a photosynthetic light-response curve describes the relationship between net CO₂ assimilation and photosynthetic photon flux or PPF (Coe & Lin, 2018; Stirling et al., 1994). Maximum values of PPF are about 2,500 µmol per m² 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 CO₂ assimilation, derived from the slope of the initial linear response of CO₂ 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 CO₂ 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 CO₂ 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 m² during the experiment. Photosynthesis was measured after six weeks, with a PPF of 1,000 µmol per m² per s, CO₂ of 400 ppm and a temperature of 25°C. Net CO₂ assimilation was 29, 42 or 62% higher in the control (18.0 µmol per m² per s) than after 3, 5 or 7 hours of shading. Higher photosynthesis in the controls was associated with higher stomatal conductance (*g_s*, *r* = 1.00) and lower leaf chlorophyll a and b (*r* = -0.56 and -0.56). Estimates of CO₂ 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 CO₂ 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 CO₂ assimilation in strawberry (Table S2). The mean maximum net CO₂ assimilation from the light-response curves was 13.9 ± 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 (α) was 0.043 ± 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 CO₂.

Chen et al. (2022c) examined the effect of light, CO₂ and temperature on gas exchange in ‘Hong yan’ in a greenhouse in Hefei, Anhui Province, China. Net CO₂ 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, CO₂ 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 CO₂ and temperature. Maximum (\pm s.e.) net CO₂ assimilation was higher at high CO₂ (800 ppm) than at low CO₂ (400 ppm) (14.5 ± 0.4 $\mu\text{mol per m}^2$ per s versus 6.0 ± 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 CO₂ and with a PPF of 1,150 $\mu\text{mol per m}^2$ per s at low CO₂. Maximum net CO₂ assimilation was higher at 29°C than at 18°C (6.0 ± 0.4 $\mu\text{mol per m}^2$ per s versus 3.3 ± 0.01 $\mu\text{mol per m}^2$ per s) (Figure 5; CO₂ 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 CO₂

The leaves of plants absorb CO₂ 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 CO₂ is converted to sugars through

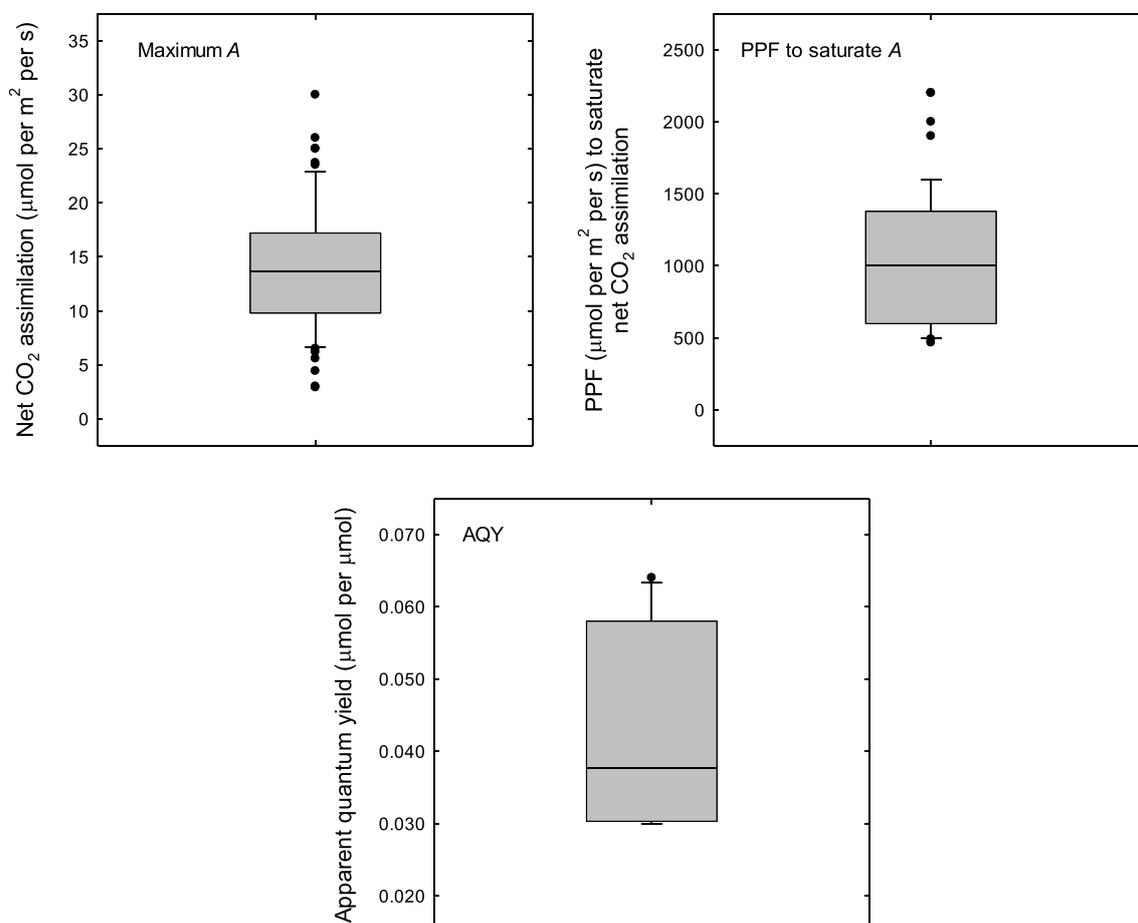


Figure 4. Box plots showing the distribution of maximum net CO₂ assimilation (A), the photosynthetic photon flux (PPF) associated with the saturation of assimilation and apparent quantum yield (AQY or α) in strawberry ($N = 43, 49$ or 11). Data are from the various authors shown in Table S2.

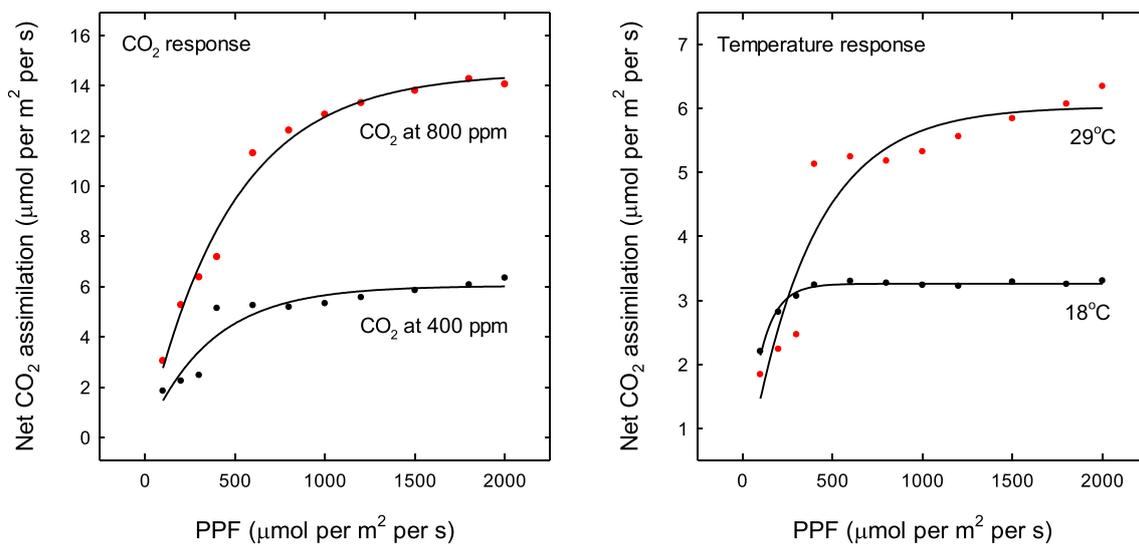


Figure 5. Relationship between net CO₂ assimilation (A_{Net}) and photosynthetic photon flux (PPF) in strawberry in China. The response to light was examined at low or high CO₂ and at low or high temperatures. Standard conditions were a CO₂ of 400 ppm and a temperature of 29°C. The responses to PPF followed 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 CO₂, with net CO₂ assimilation increasing with increasing CO₂ and then stabilising. The concentration of CO₂ can be measured in the intercellular spaces (C_i), surface of the photosynthetic mesophyll cells (C_w) or chloroplasts (C_c) in C₃ plants (Kirschbaum, 1994; Manter & Kerrigan, 2004; Márquez et al., 2023; Sharkey et al., 2007).

The relationship between net CO₂ assimilation and CO₂ 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 CO₂ 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 C₃ plants to CO₂ across 630 experiments. Average values of net CO₂ assimilation more than doubled over CO₂ from 200 to 1,200 ppm and was saturated at 1,500 ppm. Trees showed the greatest response to CO₂, followed by fertilised C₃ crops and grasses (Ainsworth & Long, 2005). Shrubs, legumes and forbs were less responsive. Zheng and Peng (2001) examined the effect of CO₂ on the physiology of plants across 84 studies. Net CO₂ assimilation increased by 40.4% in C₃ plants when the concentration of CO₂ 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 CO₂ above the plants (Allen et al., 2020).

Information was collected on the relationship between photosynthesis and the concentration of CO₂ in strawberry (Table S3). The mean maximum

net CO₂ assimilation was 25.3 ± 10.1 µmol per m² per s, the median was 27.4 µmol per m² per s, and the range was from 4.8 to 40.0 µmol per m² per s (Figure 6; $N = 28$). Photosynthesis was saturated with a mean CO₂ of 869 ± 306 ppm, a median of 900 ppm, and the range was from 410 to 1,750 ppm (Figure 6; $N = 26$). The concentration of CO₂ 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 m² per s, CO₂ ranged from 200 to 1,500 ppm and the temperature ranged from 18° to 32°C. The effect of CO₂ on photosynthesis followed a typical CO₂-response curve and was dependent on the PPF and the temperature. Maximum (\pm s.e.) net CO₂ assimilation was higher at high PPF (1,500 µmol per m² per s) than at low PPF (600 µmol per m² per s) (15.3 ± 3.0 µmol per m² per s versus 12.2 ± 3.2 µmol per m² per s) (Figure 7; Temperature of 29°C). Gas exchange was saturated at a CO₂ of 800 ppm at both light levels. Maximum net CO₂ assimilation was higher at 29°C than at 18°C (16.3 ± 3.0 µmol per m² per s versus 5.2 ± 0.3 µmol per m² per s) (Figure 7; PPF of 1,500 µmol per m² per s). Gas exchange was saturated at a CO₂ of 800 ppm at 29°C and at 600 ppm at 18°C.

Plants adapt to higher CO₂, 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

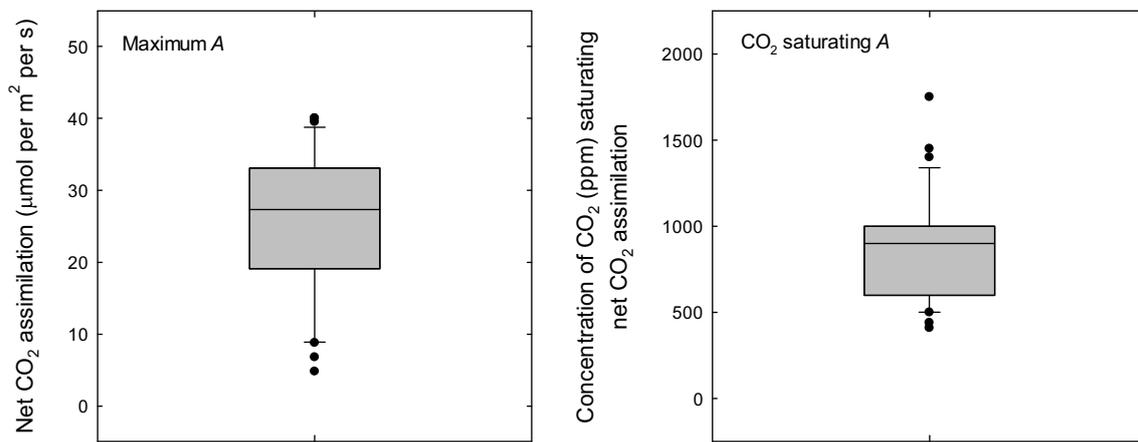


Figure 6. Box plots showing the distribution of maximum net CO₂ assimilation (A) and the concentration of CO₂ associated with the saturation of assimilation in strawberry ($N = 23$ or 22). Data are from the various authors shown in Table S3.

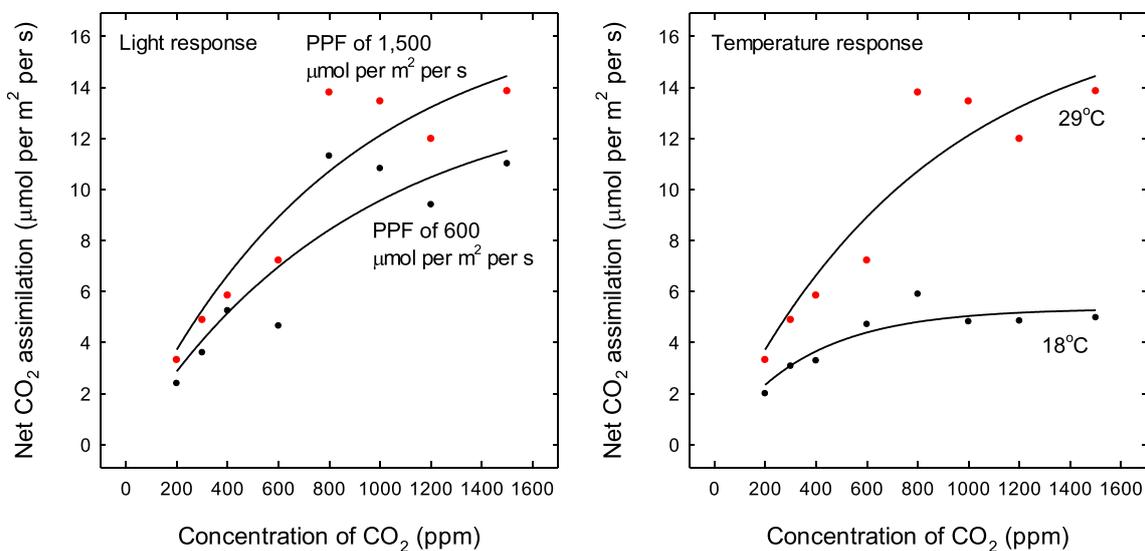


Figure 7. Relationship between net CO₂ assimilation (A_{Net}) and CO₂ (ppm) in strawberry in China. The response to CO₂ was examined at low or high light and at low or high temperatures. Standard conditions were a photosynthetic photon flux (PPF) of 1,500 $\mu\text{mol per m}^2 \text{ per s}$ and a temperature of 29°C. The responses to CO₂ 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 CO₂ 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 CO₂ and temperature. They showed that elevated CO₂ decreased stomatal aperture in the short term and stomatal density and size in the long term.

Bunce (2001) investigated the effect of elevated CO₂ on the performance of strawberry over 300 days in growth chambers in Maryland, United States. Average net CO₂ assimilation for plants at 600 ppm CO₂ 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 CO₂ (353

ppm during the day). Acclimation to elevated CO₂ was evident on two-thirds of the days when gas exchange was measured.

Keutgen et al. (1997) indicated that plants exposed to high CO₂ (750 or 900 ppm) for two months had lower gas exchange than those exposed to moderate CO₂ (600 ppm). Elevated CO₂ 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 CO₂ of 670 ppm for three and half-years had higher net CO₂ 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 CO₂ had lower concentrations of leaf nitrogen ($362 \pm 9 \text{ mg per m}^2$) than those under ambient CO₂ ($402 \pm 20 \text{ mg per m}^2$).

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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 C₄ species than in C₃ 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 CO₂ (Dusenge et al., 2019; Morison & Lawlor, 1999). Photosynthesis is higher under high PPFs and high CO₂. 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 CO₂ 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 CO₂ assimilation varied across the studies, reflecting differences in cultivars, leaf age, light and CO₂. 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 CO₂ 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 CO₂ 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 CO₂ (400 or 1,000 ppm). Maximum net CO₂ assimilation was higher under high CO₂ (39.9 µmol per m² per s) than under low CO₂ (21.4 µmol per m² per s). The optimum range for photosynthesis was 20° to 25°C at low CO₂ and 25° to 30°C at high CO₂. 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 CO₂ (360 or 1,350 ppm). Maximum net CO₂ assimilation was higher under high CO₂ (8.1 µmol per m² per s) than under low CO₂ (3.7 µmol per m² per s). The optimum range for photosynthesis was 13° to 23°C at low CO₂ and 23° to 33°C at high CO₂.

Photosynthesis is affected by extreme and average conditions. Fu et al. (2023) examined the effect of environmental stress (PPF of 1,800 µmol per m² 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 m² per s and a temperature of 23°C. Net CO₂ assimilation ranged from 10 to 13 µmol per m² per s in the controls. In contrast, net CO₂ assimilation decreased to 5 µmol per m² per s after eight hours of stress. Poor gas exchange after stress was associated with low stomatal conductance (g_s).

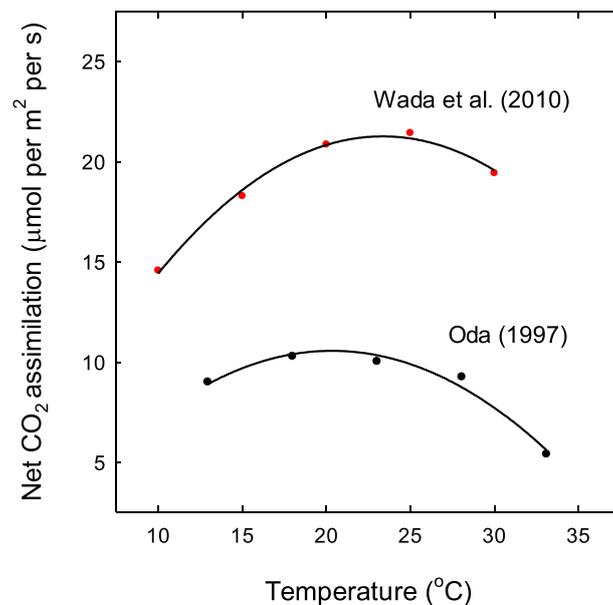


Figure 8. Relationship between net CO₂ assimilation (A_{Net}) and temperature (T , °C) in strawberry in Japan. The response to temperature was examined at low or high CO₂. For Wada et al. (2010), standard conditions were a photosynthetic photon flux (PPF) of 2,000 µmol per m² per s. For Oda (1997), standard conditions were a PPF of 552 µmol per m² per s. For Wada et al. (2010): A_{Net} (µmol per m² per s) at 400 ppm CO₂ = Intercept + 1.79 × T - 0.038 × T^2 ($P = 0.007$, $R^2 = 0.99$). For Oda (1997): A_{Net} (µmol per m² per s) at 360 ppm CO₂ = Intercept + 1.24 × T - 0.030 × 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ from the atmosphere to the chloroplasts and decrease the efficiency of CO₂ 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 CO₂ assimilation and total nitrogen per leaf area recorded as mmol per m² (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 CO₂ 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 CO₂.

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

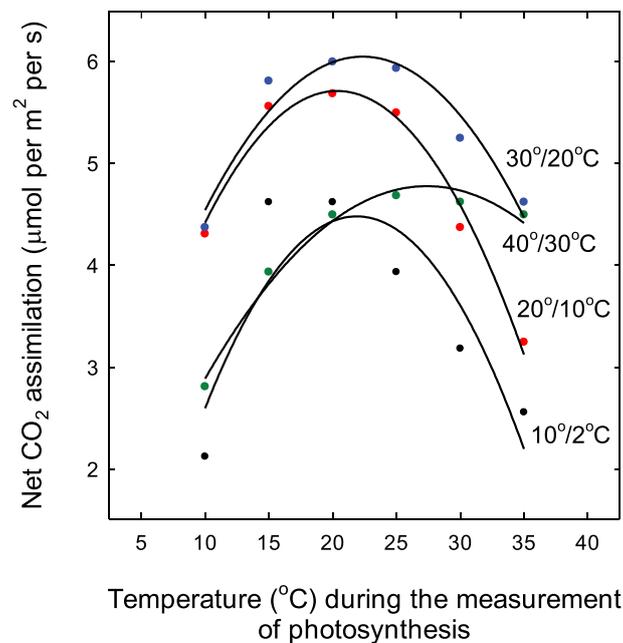


Figure 9. Relationship between net CO₂ assimilation (A_{Net}) and temperature (T , °C) in *F. vesca* in New York, United States. The plants were grown at 10°/2°, 20°/10°, 30°/20° or 40°/30°C and photosynthesis measured after five weeks. The temperature in the leaf chamber ranged from 10° to 35°C and 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 NH₄-N and 60% from NO₃-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 CO₂ 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 m² and net CO₂ 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 m², and net CO₂ 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 CO₂ 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

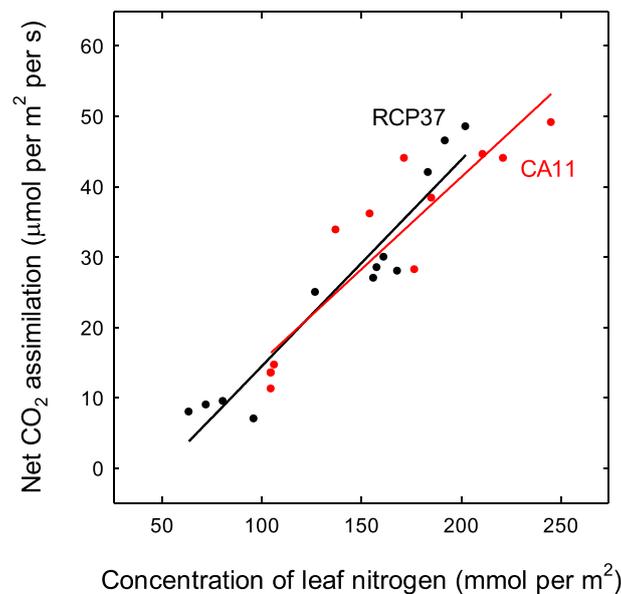


Figure 10. Relationship between net CO₂ assimilation (A_{Net}) and the concentration of nitrogen per leaf area (N_a) in two cultivars of *F. chiloensis* in Arizona, United States. Standard conditions were a photosynthetic photon flux (PPF) of 1,400 to 1,600 $\mu\text{mol per m}^2$ per s and a temperature 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 ± 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 CO₂ 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 CO₂ 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 CO₂ assimilation increased with crop load up to a maximum of 12 fruit per m² of leaf area ($R^2 = 0.85$).

The relationship between photosynthesis and fruit development was examined in strawberry (Table S7). The authors measured net CO₂ assimilation in various tissues, including the young or old leaves or the whole canopy. A two-sided *t*-test was used to determine if CO₂ 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 CO₂ assimilation in the non-fruiting plants compared with fruiting plants was 0.90 ± 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 CO₂ 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 CO₂ 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 CO₂ assimilation in the canopy does not reflect CO₂ 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 m² over six weeks, and net CO₂ assimilation ranged from 11.0 to 16.5 μmol per m² per s. Average leaf area was 0.050 ± 0.002 m² and average net CO₂ assimilation was 14.2 ± 0.8 μmol per m² per s. Schaffer et al. (1986) conducted a similar experiment in Florida using 'Tribute'. Leaf area (0.012 to 0.082 m² per plant) and net CO₂ assimilation per plant increased over six weeks. In contrast, net CO₂ assimilation per leaf area decreased from 12.0 to 6.7 μmol per m² per s. There was a strong negative linear relationship between CO₂ 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 CO₂ assimilation was related to the area of the ground covered by the canopy (m²) 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

CO₂ assimilation was saturated at a PPF of 1,150 μmol per m² per s with a CO₂ of 400 to 500 ppm. Net CO₂ assimilation was saturated with a CO₂ of 1,000 ppm with a PPF of 460 μmol per m² per s. The responses to light and CO₂ 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 CO₂ assimilation was similar in the two groups under high light and CO₂ (Table 3). In contrast, net CO₂ assimilation was higher in the leaves than in the canopy under low light and CO₂. 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 m² per s with a CO₂ 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 CO₂ in the atmosphere and an increase in average temperatures. The effect of climate change on yield depends on the effect of CO₂ and temperature on photosynthesis and the effect of temperature on leaf area expansion and fruit growth.

Net CO₂ assimilation increases with increasing CO₂ 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 CO₂ 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 CO₂. It is not clear if models based on leaves predict photosynthesis by the canopy. Research in Japan suggests that there is close agreement between CO₂ assimilation in leaves and the canopy only under high light and high CO₂ (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 CO₂ assimilation is affected by changes in CO₂ 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 CO₂. 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 ² /s and CO ₂ of 400 ppm			PPF of 1,000 μmol/m ² /s and CO ₂ of 1,000 ppm		
	Net CO ₂ assimilation (μmol/m ² /s)	Stomatal conductance (mmol/m ² /s)	Transpiration (mmol/m ² /s)	Net CO ₂ assimilation (μmol/m ² /s)	Stomatal conductance (mmol/m ² /s)	Transpiration (mmol/m ² /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

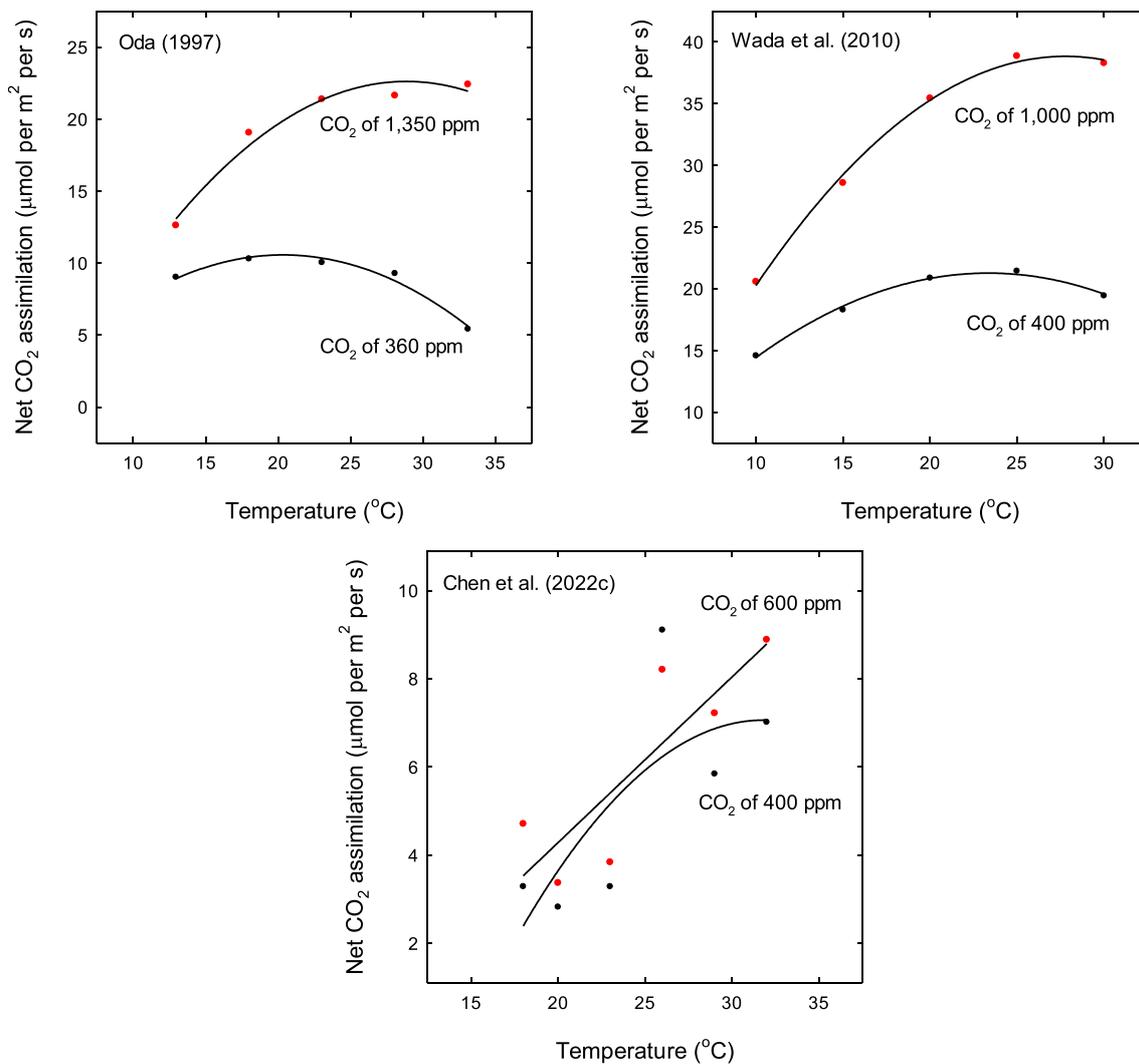


Figure 11. Relationship between net CO₂ assimilation (A_{Net}) and temperature (T , °C) under low or high CO₂ in strawberry. For Oda (1997): A_{Net} (μmol per m² per s) at 360 ppm CO₂ = Intercept + $1.24 \times T - 0.030 \times T^2$ ($P = 0.027$, $R^2 = 0.94$) and A_{Net} (μmol per m² per s) at 1,350 ppm CO₂ = Intercept + $2.18 \times T - 0.038 \times T^2$ ($P = 0.034$, $R^2 = 0.93$). For Wada et al. (2010): A_{Net} (μmol per m² per s) at 400 ppm CO₂ = Intercept + $1.79 \times T - 0.038 \times T^2$ ($P = 0.007$, $R^2 = 0.99$) and A_{Net} (μmol per m² per s) at 1,000 ppm CO₂ = Intercept + $3.26 \times T - 0.059 \times T^2$ ($P = 0.004$, $R^2 = 0.99$). For Chen et al. (2022c): A_{Net} (μmol per m² per s) at 400 ppm CO₂ = Intercept + $1.79 \times T - 0.038 \times T^2$ ($P = 0.300$, $R^2 = 0.24$) and A_{Net} (μmol per m² per s) at 600 ppm CO₂ = 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 μmol per m² per s.

under elevated CO₂ than under ambient CO₂ and the optimum temperatures are higher (Figure 11). Chen et al. (2022c) demonstrated that maximum net CO₂ assimilation was higher under CO₂ of 600 ppm than under 400 ppm (8.0 versus 6.2 μmol per m² per s; PPF = 1,500 μmol per m² per s). The optimum temperature range for gas exchange was 29° to 32°C at ambient CO₂. In contrast, gas exchange was increasing at the highest temperature at elevated CO₂.

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 CO₂ assimilation per leaf area when combined with elevated CO₂. 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 CO₂ and temperature on yield in growth chambers in China. Control plants under ambient CO₂ of 360 ppm and temperatures of 20°/15°C had low and similar yields as those under ambient CO₂ and elevated temperatures of

25°/20°C or under elevated CO₂ of 720 ppm and elevated temperatures (10.5 to 12.0 g dry weight per plant; $P > 0.05$). The plants at elevated CO₂ 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 CO₂ assimilation was higher at a CO₂ of 650 or 900 ppm than at 400 ppm. In contrast, temperature had only a small effect on CO₂ assimilation. Yields were higher at intermediate CO₂ and lower at 30°C than at 25°C. The highest yields were obtained at 25°C with a CO₂ of 400 or 650 ppm. These results suggest that the best yields occur with moderate to high CO₂ and low to moderate temperatures.

Redondo-Gómez et al. (2022) studied the effect of CO₂ and temperature on the performance of 'Fortuna' in growth chambers in Spain. The plants were grown at 25°/14°C and 400 ppm CO₂ or at 29°/18°C and 700 ppm CO₂. Plant dry weight (3.95 g versus 4.05 g) and net CO₂ assimilation (11.8 μmol per m² per s versus 10.0 μmol per m² per s) were similar in the two groups. The benefits of high CO₂ were negated by the impacts of high temperature on growth and gas exchange. Zhang et al. (2021) assessed the effect of elevated CO₂ and temperatures on gas exchange in plants across 337 studies. They found that elevated CO₂ increased net CO₂ assimilation by 28.6%, while elevated temperatures decreased net CO₂ assimilation by 23.2%.

There is controversy about the methods used to assess whether higher CO₂ 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 CO₂ 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 CO₂ (Meng et al., 2023).

Rakhmankulova et al. (2023) reported on the effects of short-term elevated temperatures and CO₂ (400 or 800 ppm) on gas exchange in a C₃ (*Chenopodium quinoa* or quinoa) and C₄ plant (*Amaranthus retroflexus* or amaranth) in Russia. The plants were grown at 25° or 35°C (for four days) at low or high CO₂ (400 or 800 ppm). Net CO₂ assimilation in quinoa decreased by 28 and 18% under elevated temperatures at both normal and elevated CO₂ compared with the control. Net CO₂ assimilation in amaranth decreased an average of 33% compared with the control. Zheng et al. (2022) conducted similar work with *Glycine max* or soybean (C₃) and *Amaranthus tricolor* (C₄) in China. There were four combinations of temperature (28° or 35°C) and CO₂ (400 or 800 ppm) with a PPF of 600 μmol per m² per s. In *Glycine max*, high temperatures increased gas exchange under both low and high CO₂ 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

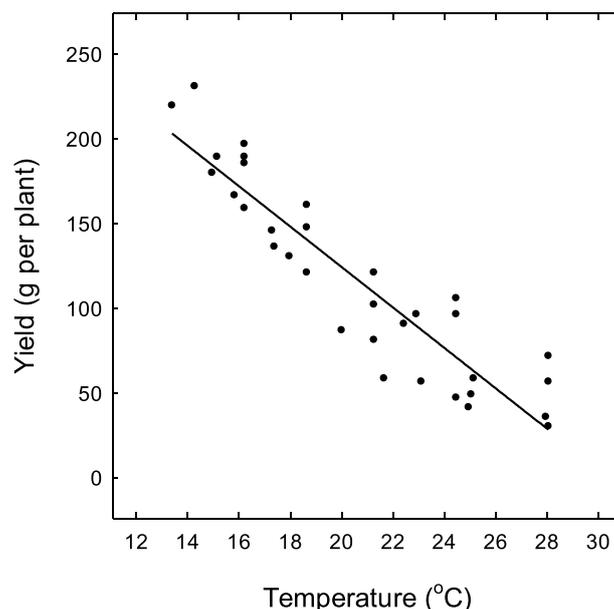


Figure 12. Relationship between yield and temperature (T, °C) in strawberry in the United Kingdom. Yield (g per plant) = Intercept - 11.92 × T ($P < 0.001$, $R^2 = 0.84$). Data are from Le Mière et al. (1998).

will decline, especially in the second half of the century (Gardi et al., 2022; Hasegawa et al., 2022). The benefits of higher CO₂ 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 CO₂ was lower than 395 ppm. The effect of CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 & Sønsteby, 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 CO₂ and temperatures increase photosynthesis in strawberry, at least in the short-term. However, the optimum temperatures for yield are lower than those for CO₂ 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 CO₂ 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 CO₂ and temperature on gas exchange. Maximum net CO₂ assimilation is 23% higher at a CO₂ of 600 ppm than at 400 ppm. Gas exchange keeps increasing at 32°C at elevated CO₂, whereas it is saturated at this temperature at low CO₂. 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 CO₂ 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.

References

- Abramoff, R. Z., Ciais, P., Zhu, P., Hasegawa, T., Wakatsuki, H., & Makowski, D. (2023). Adaptation strategies strongly reduce the future impacts of climate change on simulated crop yields. *Earth's Future*, 11, e2022EF003190. <https://doi.org/10.1029/2022EF003190>
- Abu Zeid, I. M., Mohamed, F. H., & Metwali, E. M. R. (2023). Responses of two strawberry cultivars to NaCl-induced salt stress under the influence of ZnO nanoparticles. *Saudi Journal of Biological Sciences*, 30(4), 103623. <https://doi.org/10.1016/j.sjbs.2023.103623>
- Ainsworth, E. A., Davey, P. A., Hymus, G. J., Drake, B. G., & Long, S. P. (2002). Long-term response of photosynthesis to elevated carbon dioxide in a Florida scrub-oak ecosystem. *Ecological Applications*, 12(5), 1267–1275. [https://doi.org/10.1890/1051-0761\(2002\)012\[1267:LTROPT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1267:LTROPT]2.0.CO;2)
- Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist*, 165(2), 351–372. <https://doi.org/10.1111/j.1469-8137.2004.01224.x>
- Allan-Wojtas, P., Hilderbrand, P. D., Braun, P. G., Smith-King, H. L., Carbyn, S., & Renderos, W. E. (2010). Low temperature and anhydrous electron microscopy techniques to observe the infection process of the bacterial pathogen *Xanthomonas fragariae* on strawberry leaves. *Journal of Microscopy*, 239(3), 249–258. <https://doi.org/10.1111/j.1365-2818.2010.03373.x>
- Allen, L. H., Kimball, B. A., Bunce, J. A., Yoshimoto, M., Harazono, Y., Baker, J. T., Boote, K. J., & White, J. W. (2020). Fluctuations of CO₂ in free-air CO₂ enrichment (FACE) depress plant photosynthesis, growth and yield. *Agricultural and Forest Meteorology*, 284, 107899. <https://doi.org/10.1016/j.agrformet.2020.107899>
- Al-Salman, Y., Cano, F. J., Pan, L., Koller, F., Piñeiro, J., Jordan, D., & Ghannoum, O. (2023). Anatomical drivers of stomatal conductance in sorghum lines with different leaf widths grown under different temperatures. *Plant, Cell & Environment*, 46(7), 2142–2158. <https://doi.org/10.1111/pce.14592>
- Álvarez-Iglesias, L., Vales, M. I., De Ron, A. M., Rodiño, A. P., Tejada-Hinojoza, J. L., Taboada, A., & Revilla, P. (2022). Variability of photosynthetic and related traits in maize and other summer crops in a temperate humid area. *Plant Physiology Reports*, 27(4), 596–602. <https://doi.org/10.1007/s40502-022-00693-6>
- Amani-Male, O., Feizabadi, Y., & Norouzi, G. (2024). A model-based evaluation of farmers' income variability under climate change (case study: Autumn crops in Iran). *Brazilian Journal of Biology*, 84, e261997. <https://doi.org/10.1590/1519-6984.261997>
- Anderson, J. T., Wadgyamar, S. M., & Angert, A. (2020). Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters*, 23(1), 181–192. <https://doi.org/10.1111/ele.13427>
- Araque, O., Jaimez, R. E., Tezars, W., Coronel, I., Ulrich, R., & Espinoza, W. (2012). Comparative photosynthesis, water relations, growth and survival rates in juvenile criollo cacao cultivars (*Theobroma cacao*) during dry and wet seasons. *Experimental Agriculture*, 48(4), 513–522. <https://doi.org/10.1017/S0014479712000427>
- Arief, M. A. A., Kim, H., Kurniawan, H., Nugroho, A. P., Kim, T., & Cho, B.-K. (2023). Chlorophyll fluorescence imaging for early detection of drought and heat stress in strawberry plants. *Plants*, 12(6), 1387. <https://doi.org/10.3390/plants12061387>
- Arney, S. E. (1947). The respiration of strawberry leaves attached to the plant. *New Phytologist*, 46(1), 68–96. <https://doi.org/10.1111/j.1469-8137.1947.tb05072.x>
- Arney, S. E. (1953a). The initiation, growth, and emergence of leaf primordia in *Fragaria*. *Annals of Botany*, 17(3), 477–492. <https://doi.org/10.1093/oxfordjournals.aob.a083364>
- Arney, S. E. (1953b). Studies in growth and development in the genus *Fragaria* I. Factors affecting the rate of leaf production in Royal Sovereign strawberry. *Journal of Horticultural Science*, 28(2), 73–84. <https://doi.org/10.1080/00221589.1953.11513771>
- Arney, S. E. (1954). Studies of growth and development in the genus *Fragaria*: III. The growth of leaves and shoots. *Annals of Botany*, 18(3), 349–365. <https://doi.org/10.1093/oxfordjournals.aob.a083400>
- Arroyo, F. T., Moreno, J., García-Herdugo, G., De Los Santos, B., Barrau, C., Porras, M., Blanco, C., & Romero, F. (2005). Ultrastructure of the early stages of *Colletotrichum acutatum* infection of strawberry tissues. *Canadian Journal of Botany*, 83(5), 491–500. <https://doi.org/10.1139/b05-022>
- Aström, H., Metsovuori, E., Saarinen, T., Lundell, R., & Hänninen, H. (2015). Morphological characteristics and photosynthetic capacity of *Fragaria vesca* L. winter and summer leaves. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 215, 33–39. <https://doi.org/10.1016/j.flora.2015.07.001>
- Avestan, S., Ghasemnezhad, M., Esfahani, M., & Barker, A. V. (2021). Effects of nanosilicon dioxide on leaf anatomy, chlorophyll fluorescence, and mineral element composition of strawberry under salinity stress. *Journal of Plant Nutrition*, 44(20), 3005–3019. <https://doi.org/10.1080/01904167.2021.1936036>
- Bagley, J., Rosenthal, D. M., Ruiz-Vera, U. M., Siebers, M. H., Kumar, P., Ort, D. R., & Bernacchi, C. J. (2015). The influence of photosynthetic acclimation to rising CO₂ and warmer temperatures on leaf and canopy photosynthesis models. *Global Biogeochemical Cycles*, 29(2), 194–206. <https://doi.org/10.1002/2014GB004848>
- Baguskas, S. A., Oliphant, A. J., Clemesha, R. E. S., & Loik, M. E. (2021). Water and light-use efficiency are enhanced under Summer coastal fog in a California Agricultural System. *Journal of Geophysical Research: Biogeosciences*, 126(5), e2020JG006193. <https://doi.org/10.1029/2020JG006193>
- Bahar, N. H. A., Hayes, L., Scafaro, A. P., Atkin, O. K., & Evans, J. R. (2018). Mesophyll conductance does not contribute to greater photosynthetic rate per unit nitrogen in temperate compared with tropical evergreen wet-forest tree leaves. *New Phytologist*, 218(2), 492–505. <https://doi.org/10.1111/nph.15031>
- Bai, L.-J., Ye, Y.-T., Chen, Q., & Tang, H.-R. (2017). The complete chloroplast genome sequence of the white strawberry *Fragaria pentaphylla*. *Conservation Genetics Resources*, 9(4), 659–661. <https://doi.org/10.1007/s12686-017-0713-5>

- Báki Iz, H. (2022). The evolution of large-scale variations in globally averaged atmospheric CO₂ concentrations since 1830. *All Earth*, 34(1), 16–26. <https://doi.org/10.1080/27669645.2022.2058688>
- Balasoorya, H. N., Dassanayake, K. B., Seneweera, S., & Ajlouni, S. (2018). Interaction of elevated carbon dioxide and temperature on strawberry (*Fragaria* × *ananassa*) growth and fruit yield. *International Journal of Science, Engineering and Technology*, 12(9), 279–287. <https://doi.org/10.5281/zenodo.1474461>
- Barbosa, L. M. P., de Paiva Neto, V. B., Dias, L. L. C., Festucci-Buselli, R. A., Alexandre, R. S., Iarema, L., Finger, F. L., & Otoni, W. C. (2013). Biochemical and morpho-anatomical analyses of strawberry vitroplants hyperhydric tissues affected by BA and gelling agents. *Revista Ceres*, 60(2), 152–160. <https://doi.org/10.1590/S0034-737X2013000200002>
- Baruah, U., Das, S., Kalita, P., Saikia, M., Bhogal, S., Pal, S., & Das, R. (2023). High-night temperature-induced changes in chlorophyll fluorescence, gas exchange, and leaf anatomy determine grain yield in rice varieties. *Journal of Plant Growth Regulation*, 42(9), 5538–5557. <https://doi.org/10.1007/s00344-023-10934-z>
- Benlloch-González, M., Sánchez-Lucas, R., Bejaoui, M. A., Benlloch, M., & Fernández-Escobar, R. (2019). Global warming effects on yield and fruit maturation of olive trees growing under field conditions. *Scientia Horticulturae*, 249, 162–167. <https://doi.org/10.1016/j.scienta.2019.01.046>
- Ben Mariem, S., Soba, D., Zhou, B., Loladze, I., Morales, F., & Aranjuelo, I. (2021). Climate change, crop yields, and grain quality of C₃ cereals: A meta-analysis of [CO₂], temperature, and drought effects. *Plants*, 10(6), 1052. <https://doi.org/10.3390/plants10061052>
- Bethere, L., Sile, T., Seņņikovs, J., & Bethers, U. (2016). Impact of climate change on the timing of strawberry phenological processes in the Baltic States. *Estonian Journal of Earth Sciences*, 65(1), 48–58. <https://doi.org/10.3176/earth.2016.04>
- Bird, K. A., Hardigan, M. A., Ragsdale, A. P., Knapp, S. J., VanBuren, R., & Edger, P. P. (2021). Diversification, spread, and admixture of octoploid strawberry in the Western hemisphere. *American Journal of Botany*, 108(11), 2269–2281. <https://doi.org/10.1002/ajb2.1776>
- Blanke, M. (1991). Surface morphology of strawberry leaves. *Erwerbsobstbau*, 33(1), 79–81.
- Blanke, M. (2002). Photosynthesis of strawberry fruit. *Acta Horticulturae*, 567, 373–376. <https://doi.org/10.17660/ActaHortic.2002.567.81>
- Blanke, M. M., & Cooke, D. T. (2004). Effects of flooding and drought on stomatal activity, transpiration, photosynthesis, water potential and water channel activity in strawberry stolons and leaves. *Plant Growth Regulation*, 42(2), 153–160. <https://doi.org/10.1023/B:GROW.0000017489.21970.d4>
- Borrero, J. D., & Borrero-Domínguez, J.-D. (2023). Enhancing short-term berry yield prediction for small growers using a novel hybrid machine learning model. *Horticulturae*, 9(5), 549. <https://doi.org/10.3390/horticulturae9050549>
- Bosiö, J., Stiegler, C., Johansson, M., Mbufong, H. N., & Christensen, T. R. (2014). Increased photosynthesis compensates for shorter growing season in subarctic tundra—8 years of snow accumulation manipulations. *Climatic Change*, 127(2), 321–334. <https://doi.org/10.1007/s10584-014-1247-4>
- Bunce, J. (2021). Carboxylation capacity can limit C₃ photosynthesis at elevated CO₂ throughout diurnal cycles. *Plants*, 10(12), 2603. <https://doi.org/10.3390/plants10122603>
- Bunce, J. A. (1982). Photosynthesis at ambient and elevated humidity over a growing season in soybean. *Photosynthesis Research*, 3(4), 307–311. <https://doi.org/10.1007/BF00034111>
- Bunce, J. A. (2001). Seasonal patterns of photosynthetic response and acclimation to elevated carbon dioxide in field-grown strawberry. *Photosynthesis Research*, 68(3), 237–245. <https://doi.org/10.1023/A:1012928928355>
- Calderón-Zavala, G., López-García, R., Alvarado-Raya, H. E., Jaen-Contreras, D., & Vaquera-Huerta, H. (2022). Photosynthesis, growth, and yield in strawberry with sheep manure compost and peat. *Current Topics in Agronomic Science*. <https://doi.org/10.5154/r.ctas.2022.0602a>
- Cameron, J. S., & Hartley, C. A. (1990). Gas exchange characteristics of *Fragaria chiloensis* genotypes. *HortScience*, 25(3), 327–329. <https://doi.org/10.21273/HORTSCI.25.3.327>
- Campoy, J. A., Darbyshire, R., Dirlwanger, E., Quero-García, J., & Wenden, B. (2019). Yield potential definition of the chilling requirement reveals likely underestimation of the risk of climate change on winter chill accumulation. *International Journal of Biometeorology*, 63(2), 183–192. <https://doi.org/10.1007/s00484-018-1649-5>
- Cannell, M. G. R., & Thornley, J. H. M. (1998). Temperature and CO₂ responses of leaf and canopy photosynthesis: A clarification using the non-rectangular hyperbola model of photosynthesis. *Annals of Botany*, 82(6), 883–892. <https://doi.org/10.1006/anbo.1998.0777>
- Catling, P. M., & Porebski, S. (1998). An ecoregional analysis of morphological variation in British Columbia coastal strawberries (*Fragaria*) for germplasm protection. *Canadian Journal of Plant Science*, 78(1), 117–124. <https://doi.org/10.4141/P97-050>
- Chabot, B. F. (1978). Environmental influences on photosynthesis and growth in *Fragaria vesca*. *New Phytologist*, 80(1), 87–98. <https://doi.org/10.1111/j.1469-8137.1978.tb02267.x>
- Chabot, B. F., & Chabot, J. F. (1977). Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. *Oecologia*, 26(4), 363–377. <https://doi.org/10.1007/BF00345535>
- Chabot, B. F., & Hicks, D. J. (1982). The ecology of leaf life spans. *Annual Review of Ecology and Systematics*, 13, 229–259. <https://doi.org/10.1146/annurev.es.13.110182.001305>
- Challinor, A. J., Watson, J., Lobell, D. B., Howden, S. M., Smith, D. R., & Chhetri, N. (2014). A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, 4(4), 287–291. <https://doi.org/10.1038/nclimate2153>
- Chang, C. Y., Fréchette, E., Unda, F., Mansfield, S. D., & Ensminger, I. (2016). Elevated temperature and CO₂ stimulate late season photosynthesis but impair cold hardening in pine. *Plant Physiology*, 172, 802–818. <https://doi.org/10.1104/pp.16.00753>
- Chang, Q., Xiao, X., Doughty, R., Wu, X., Jiao, W., & Qin, Y. (2021). Assessing variability of optimum air temperature for photosynthesis across site-years, sites and biomes and their effects on photosynthesis estimation. *Agricultural and Forest Meteorology*, 298/299, 108277. <https://doi.org/10.1016/j.agrformet.2020.108277>
- Chavan, S. G., Duursma, R. A., Tausz, M., Ghannoum, O., & Hancock, R. (2019). Elevated CO₂ alleviates the negative

- impact of heat stress on wheat physiology but not on grain yield. *Journal of Experimental Botany*, 70(21), 6447–6459. <https://doi.org/10.1093/jxb/erz386>
- Chen, B., Ke, Y., Ciais, P., Zeng, Z., Black, A., Lv, H., Huang, M., Yuan, W., Xiao, X., Fang, J., Hou, K., Wang, Y.-P., & Luo, Y. (2022a). Inhibitive effects of recent exceeding air temperature optima of vegetation productivity and increasing water limitation on photosynthesis reversed global greening. *Earth's Future*, 10(11), e2022EF002788. <https://doi.org/10.1029/2022EF002788>
- Chen, C., Riley, W.J., Prentice, I.C., & Keenan, T.F. (2022b). CO₂ fertilization of terrestrial photosynthesis inferred from site to global scales. *Proceedings of the National Academy of Science of the United States of America*, 119(10), e2115627119. <https://doi.org/10.1073/pnas.2115627119>
- Chen, L., Yang, Y., Zhao, Z., Lu, S., Lu, Q., Cui, C., Parry, M. A. J., & Hu, Y.-G. (2023). Genome-wide identification and comparative analyses of key genes involved in C₄ photosynthesis in five main gramineous crops. *Frontiers in Plant Science*, 14, 1134170. <https://doi.org/10.3389/fpls.2023.1134170>
- Chen, X., Jiang, Z., Tai, Q., Shen, C., Rao, Y., & Zhang, W. (2022c). Construction of a photosynthetic rate prediction model for greenhouse strawberries with distributed regulation of light environment. *Mathematical Biosciences and Engineering*, 19(12), 12774–12791. <https://doi.org/10.3934/mbe.2022596>
- Cheng, H., Li, J., Zhang, H., Cai, B., Gao, Z., Qiao, Y., & Mi, L. (2017). The complete chloroplast genome sequence of strawberry (*Fragaria × ananassa* Duch.) and comparison with related species of Rosaceae. *PeerJ*, 5, e3919. <https://doi.org/10.7717/peerj.3919>
- Choi, H. G. (2021a). Correlation among phenotypic parameters related to the growth and photosynthesis of strawberry (*Fragaria × ananassa* Duch.) grown under various light intensity conditions. *Frontiers in Plant Science*, 12, 647585. <https://doi.org/10.3389/fpls.2021.647585>
- Choi, H. G. (2021b). Influence of TiO₂ foliar spray application on photosynthesis and chlorophyll fluorescence of strawberry during low light intensity season in a greenhouse. *Acta Horticulturae*, 1309, 247–252. <https://doi.org/10.17660/ActaHortic.2021.1309.36>
- Choma, M. E., Garner, J. L., Marini, R. P., & Barden, J. A. (1982). Effects of fruiting on net photosynthesis and dark respiration of 'Hecker' strawberries. *HortScience*, 17(2), 212–213. <https://doi.org/10.21273/HORTSCI.17.2.212>
- Coast, O., Posch, B. C., Rognoni, B. G., Bramley, H., Gaju, O., Mackenzie, J., Pickles, C., Kelly, A. M., Lu, M., Ruan, Y.-L., Trethowan, R., & Atkin, O. K. (2022). Wheat photosystem II heat tolerance: Evidence for genotype-by-environment interactions. *Plant Journal*, 111(5), 1368–1382. <https://doi.org/10.1111/tbj.15894>
- Coe, R. A., & Lin, S.-C. (2018). Light-response curves in land plants. In S. Covshoff (Ed.), *Photosynthesis: Methods and Protocols, Methods in Biology, Volume 1771* (pp. 83–94). Springer Nature. https://doi.org/10.1007/978-1-4939-7786-4_5
- Converse, R. H., & Schaper, U. (1988). Irregular occurrence of Rhabdoviruslike particles in tissues of *Fragaria vesca* plants infected with strawberry crinkle virus. *Journal of Phytopathology*, 123(4), 289–296. <https://doi.org/10.1111/j.1439-0434.1988.tb04480.x>
- Coursolle, C., Prud'homme, G. O., Lamothe, M., & Isabel, N. (2019). Measuring rapid A-C_i curves in boreal conifers: Black spruce and balsam fir. *Frontiers in Plant Science*, 10, 1276. <https://doi.org/10.3389/fpls.2019.01276>
- Cox, A. J. F., Hartley, I. P., Meir, P., Sitch, S., Dusenage, M. E., Restrepo, Z., González-Caro, S., Villegas, J. C., Uddling, J., & Mercado, L. M. (2023). Acclimation of photosynthetic capacity and foliar respiration in Andean tree species to temperature change. *New Phytologist*, 238(6), 2329–2344. <https://doi.org/10.1111/nph.18900>
- Cox, D. T. C., Maclean, I. M. D., Gardner, A. S., & Gaston, K. J. (2020). Global variation in diurnal asymmetry in temperature, cloud cover, specific humidity and precipitation and its association with leaf area index. *Global Change Biology*, 26(12), 7099–7111. <https://doi.org/10.1111/gcb.15336>
- Crous, K. Y., Uddling, J., & De Kauwe, M. G. (2022). Temperature responses of photosynthesis and respiration in evergreen trees from boreal to tropical latitudes. *New Phytologist*, 234(2), 353–374. <https://doi.org/10.1111/nph.17951>
- Cruz, J. A., & Avenson, T. J. (2021). Photosynthesis: A multiscope view. *Journal of Plant Research*, 134(4), 665–682. <https://doi.org/10.1007/s10265-021-01321-4>
- Cutolo, E. A., Guardini, Z., Dall'osto, L., & Bassi, R. (2023). A paler shade of green: Engineering cellular chlorophyll content to enhance photosynthesis in crowded environments. *New Phytologist*, 239(5), 1567–1583. <https://doi.org/10.1111/nph.19064>
- Dale, A. (2009). How climate change could influence breeding and modern production systems in berry crops. *Acta Horticulturae*, 838, 161–168. <https://doi.org/10.17660/ActaHortic.2009.838.27>
- Dara, S., Gupta, H., & Poursheikhani, B. (2019). Developing resilience to climate extremes for strawberries. *Vegetables West*, 23(9), 23.
- DeJong, T. M. (1986). Fruit effects on photosynthesis in *Prunus persica*. *Physiologia Plantarum*, 66(1), 149–153. <https://doi.org/10.1111/j.1399-3054.1986.tb01248.x>
- de Resende, J. T. V., Filho, R. B. L., Ribeiro, L. K., Corrêa, J. V. W., Maciel, C. D. G., & Youssef, K. (2020). Strawberry genotypes with resistance to *Tetranychus urticae* mediated by leaf trichomes. *Ciência e Agrotecnologia*, 44, e006920. <https://doi.org/10.1590/1413-7054202044006920>
- Deschenes, O., & Kolstad, C. (2011). Economic impacts of climate change on California agriculture. *Climatic Change*, 109(S1), 365–386. <https://doi.org/10.1007/s10584-011-0322-3>
- Dobrogojski, J., Adamiec, M., & Luciński, R. (2020). The chloroplast genome: A review. *Acta Physiologica Plantarum*, 42(6), 98. <https://doi.org/10.1007/s11738-020-03089-x>
- Døvåg, A. (2009). Climate change and strawberry season in Norway. *Acta Horticulturae*, 842, 753–756. <https://doi.org/10.17660/ActaHortic.2009.842.164>
- Drake, P. L., de Boer, H. J., Schymanski, S. J., & Veneklaas, E. J. (2019). Two sides to every leaf: Water and CO₂ transport in hypostomatous and amphistomatous leaves. *New Phytologist*, 222(3), 1179–1187. <https://doi.org/10.1111/nph.15652>
- Durand, M., Murchie, E. H., Lindfors, A. V., Urban, O., Aphalo, P. J., & Robson, T. M. (2021). Diffuse solar radiation and canopy photosynthesis in a changing environment. *Agricultural and Forest Meteorology*, 311, 108684. <https://doi.org/10.1016/j.agrformet.2021.108684>
- Dusenage, M. E., Duarte, A. G., & Way, D. A. (2019). Plant carbon metabolism and climate change: Elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist*, 221(1), 32–49. <https://doi.org/10.1111/nph.15283>
- Edwards, E. J., Chatelet, D. S., Sack, L., Donoghue, M. J., & Cornwell, W. (2014). Leaf life span and the leaf economic

- spectrum in the context of whole plant architecture. *Journal of Ecology*, 102(2), 328–336. <https://doi.org/10.1111/1365-2745.12209>
- Elias, E., Steele, C., Havstad, K., Steenwerth, K., Chambers, J., Deswood, H., Kerr, A., Rango, A., Schwartz, M., Stine, P., & Steele, R. (2015). *Southwest regional climate hub and California subsidiary hub assessment of climate change vulnerability and adaptation and mitigation strategies*. United States Department of Agriculture.
- Environmental Defence Fund. (2023). *Understanding climate change impacts on Florida strawberries*. Environmental Defence Fund.
- Esitken, A., Ercisli, S., Yildiz, H., & Orhan, E. (2009). Does climate change have an effect on strawberry yield in colder growing areas? *Acta Horticulturae*, 838, 59–62. <https://doi.org/10.17660/ActaHortic.2009.838.8>
- Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia*, 78(1), 9–19. <https://doi.org/10.1007/BF00377192>
- Evans, J. R., & Clarke, V. C. (2019). The nitrogen cost of photosynthesis. *Journal of Experimental Botany*, 70(1), 7–15. <https://doi.org/10.1093/jxb/ery366>
- Fabbri, A., Sutter, E., & Dunston, S. K. (1986). Anatomical changes in persistent leaves of tissue-cultured strawberry plants after removal from culture. *Scientia Horticulturae*, 28(4), 331–337. [https://doi.org/10.1016/0304-4238\(86\)90107-X](https://doi.org/10.1016/0304-4238(86)90107-X)
- Fallahi, E., Moon, J. W., Jr., Huang, Y., & Jensen, R. (2000). Effects of ribulose 1,5 biphosphate carboxylase/oxygenase content, leaf nitrogen and leaf morphology on CO₂ assimilation in strawberry genotypes. *Acta Horticulturae*, 527, 177–184. <https://doi.org/10.17660/ActaHortic.2000.527.21>
- Faralli, M., & Lawson, T. (2020). Natural genetic variation in photosynthesis: An untapped resource to increase crop yield potential? *Plant Journal*, 101(3), 518–528. <https://doi.org/10.1111/tpj.14568>
- Fávoro, R., de Resende, J. T. V., Zeist, A. R., Cordeiro, E. C. N., Youssef, K., Zeffa, D. M., de Oliveira, J. N. M., & Leal, M. H. S. (2022). Morpho-physiological alterations and resistance to *Tetranychus urticae* in strawberries plants treated with salicylic acid. *Phytoparasitica*, 50(4), 921–932. <https://doi.org/10.1007/s12600-022-01010-5>
- Figueiredo, A. S. T., Resende, J. T. V., Morales, R. G. F., Gonçalves, A. P. S., & da Silva, P. R. (2013). The role of glandular and non-glandular trichomes in the negative interactions between strawberry cultivars and spider mite. *Arthropod-Plant Interactions*, 7(1), 53–58. <https://doi.org/10.1007/s11829-012-9218-z>
- Finzi, A., Giasson, M.-A., Baker Plotkin, A. A., Aber, J. D., Boose, E. R., Davidson, E. A., Dietze, M. C., Ellison, A. M., Frey, S. D., Goldman, E., Keenan, T. F., Melillo, J. M., Munger, J. W., Nadelhoffer, K. J., Ollinger, S. V., Orwig, D. A., Pederson, N., Richardson, A. D. . . . Zhou, Z. (2020). Carbon budget of Harvard Forest long-term ecological research site: Pattern, process, and response to global change. *Ecological Monographs*, 90(4), e01423. <https://doi.org/10.1002/ecm.1423>
- Fleischer, W. E. (1935). The relation between chlorophyll content and rate of photosynthesis. *Journal of General Physiology*, 18(4), 573–597. <https://doi.org/10.1085/jgp.18.4.573>
- Fu, E., Zhang, Y., Li, H., Wang, X., Zhang, H., Xiao, W., Chen, X., & Li, L. (2023). Chitosan reduces damages of strawberry seedlings under high-temperature and high-light stress. *Agronomy*, 13(2), 517. <https://doi.org/10.3390/agronomy13020517>
- Fu, G., Shen, Z.-X., Sun, W., Zong, Z.-M., Zhang, X.-Z., & Zhou, Y.-T. (2015). A meta-analysis of the effects of experimental warming on plant physiology and growth on the Tibetan Plateau. *Journal of Plant Growth Regulation*, 34(1), 57–65. <https://doi.org/10.1007/s00344-014-9442-0>
- Fujii, J. A., & Kennedy, R. A. (1985). Seasonal changes in the photosynthetic rate in apple trees. *Plant Physiology*, 78(3), 519–524. <https://doi.org/10.1104/pp.78.3.519>
- Gamboa-Mendoza, A. P., Delgadillo-Martínez, J., Almaraz-Suárez, J. J., Robledo-Paz, A., & Alarcón, A. (2019). Respuesta de *Fragaria mexicana* y comunidades microbianas rizosféricas al aumento de temperatura. *Revista de Biología Tropical*, 67(1), 94–106. <https://doi.org/10.15517/rbt.v67i1.33040>
- Gao, S., Yan, Q., Chen, L., Song, Y., Li, J., Fu, C., Dong, M., & Yang, J. (2017). Effects of ploidy level and haplotype on variation of photosynthetic traits: Novel evidence from two *Fragaria* species. *PLoS One*, 12(6), e0179899. <https://doi.org/10.1371/journal.pone.0179899>
- Gao, Z., Li, J., Liu, S., & Chen, Y. (2023). Within-leaf chloroplasts and nitrogen allocation to thylakoids in relation to photosynthesis during grain filling in maize. *Plant Physiology and Biochemistry*, 196, 830–840. <https://doi.org/10.1016/j.plaphy.2023.02.034>
- Gara, T. W., Skidmore, A. K., Darvishzadeh, R., & Wang, T. (2019). Leaf to canopy upscaling approach affects the estimation of canopy traits. *GIScience & Remote Sensing*, 56(4), 554–575. <https://doi.org/10.1080/15481603.2018.1540170>
- Garcia, K., & Kubota, C. (2017). Physiology of strawberry plants under controlled environment: Diurnal change in leaf net photosynthetic rate. *Acta Horticulturae*, 1156, 445–452. <https://doi.org/10.17660/ActaHortic.2017.1156.66>
- Gardner, A., Jiang, M., Ellsworth, D. S., MacKenzie, A. R., Pritchard, J., Bader, M. K. F., Barton, C. V. M., Bernacchi, C., Calfapietra, C., Crous, K. Y., Dusenge, M. E., Gimeno, T. E., Hall, M., Lamba, S., Leuzinger, S., Uddling, J., Warren, J., Wallin, G., & Medlyn, B. E. (2023). Optimal stomatal theory predicts CO₂ responses of stomatal conductance in both gymnosperm and angiosperm trees. *New Phytologist*, 237(4), 1229–1241. <https://doi.org/10.1111/nph.18618>
- Gardi, M. W., Haussmann, B. I. G., Malik, W. A., & Högy, P. (2022). Effects of elevated atmospheric CO₂ and its interaction with temperature and nitrogen on yield of barley (*Hordeum vulgare* L.): A meta-analysis. *Plant and Soil*, 475(1–2), 535–550. <https://doi.org/10.1007/s11104-022-05386-5>
- Gjindali, A., & Johnson, G. N. (2023). Photosynthetic acclimation to changing environments. *Biochemical Society Transactions*, 51(2), 473–486. <https://doi.org/10.1042/BST20211245>
- Gomes, G. C., Nascimento, D. A., de Oliveira, L. V. B., de Paula Gomes, G. F., Ivamoto-Suzuki, S. T., Ziest, A. R., Marigule, K. H., Roberto, S. R., & de Resende, J. T. V. (2023). Adaptability and stability analyses of improved strawberry genotypes for tropical climate. *Horticulturae*, 9(6), 643. <https://doi.org/10.3390/horticulturae9060643>
- Gómez, L. F., López, J. C., Riaño, N. M., López, Y., & Montoya, E. C. (2005). Diurnal changes in leaf gas exchange and validation of a mathematical model for coffee (*Coffea arabica* L.) canopy photosynthesis. *Photosynthetica*, 43(4), 575–582. <https://doi.org/10.1007/s11099-005-0090-2>
- Grant, O., Davies, M. J., James, C. M., Johnson, A. W., Leinonen, I., & Simpson, D. W. (2012). Thermal imaging and carbon isotope composition indicate variation amongst strawberry (*Fragaria×ananassa*) cultivars in

- stomatal conductance and water use efficiency. *Environmental and Experimental Botany*, 76, 7–15. <https://doi.org/10.1016/j.envexpbot.2011.09.013>
- Greer, D. H. (2019). Limitations to photosynthesis of leaves of apple (*Malus domestica*) trees across the growing season prior to and after harvest. *Photosynthetica*, 57(2), 483–490. <https://doi.org/10.32615/ps.2019.063>
- Grez, J., Contreras, E., Sánchez, S., Alcalde, J. A., & Gambardella, M. (2020). Floral induction and dormancy behaviour in ‘Chilean white strawberry’ (*Fragaria chiloensis* (L.) Mill. subsp. *chiloensis* f. *chiloensis*). *Scientia Horticulturae*, 274, 109648. <https://doi.org/10.1016/j.scienta.2020.109648>
- Grüter, R., Trachs el, T., Laube, P., Jaisli, I., & Chemura, A. (2022). Expected global suitability of coffee, cashew and avocado due to climate change. *PLoS One*, 17(1), e0261976. <https://doi.org/10.1371/journal.pone.0261976>
- Gu, L., Grodzinski, B., Han, J., Marie, T., Zhang, Y.-J., Song, Y. C., & Sun, Y. (2022). Granal thylakoid structure and function: Explaining an enduring mystery of higher plants. *New Phytologist*, 236(2), 319–329. <https://doi.org/10.1111/nph.18371>
- Guan, K., Good, S. P., Caylor, K. K., Medvigy, D., Pan, M., Wood, E. F., Sato, H., Biasutti, M., Chen, M., Ahlström, A., & Xu, X. (2018). Simulated sensitivity of African terrestrial ecosystem photosynthesis to rainfall frequency, intensity, and rainy season length. *Environmental Research Letters*, 13(2), 025013. <https://doi.org/10.1088/1748-9326/aa9f30>
- Güler, S., Macit, İ., Koç, A., & İbriki, H. (2006). Estimating leaf nitrogen status of strawberry by using chlorophyll meter reading. *Journal of Biological Sciences*, 6(6), 1011–1016. <https://doi.org/10.3923/jbs.2006.1011.1016>
- Guo, Z., Still, C. J., Lee, C. K. F., Ryu, Y., Blonder, B., Wang, J., Bonebrake, T. C., Hughes, A., Li, Y., Yeung, H. C. H., Zhang, K., Law, Y. K., Lin, Z., & Wu, J. (2023). Does plant ecosystem thermoregulation occur? An extratropical assessment at different spatial and temporal scales. *New Phytologist*, 238(3), 1004–1018. <https://doi.org/10.1111/nph.18632>
- Gutteridge, S., & Gutteridge, S. (2018). The impact of a changing atmosphere on chloroplast function, photosynthesis, yield, and food security. *Essays in Biochemistry*, 62(1), 1–11. <https://doi.org/10.1042/EBC20180023>
- Häder, D.-P. (2022). Photosynthesis in plants and algae. *Anticancer Research*, 42(10), 5035–5041. <https://doi.org/10.21873/anticancer.16012>
- Hammer, G. L., McLean, G., van Oosterom, E., Chapman, S., Zheng, B., Wu, A., Doherty, A., & Jordan, D. (2020). Designing crops for adaptation to the drought and high-temperature risks anticipated in future climates. *Crop Science*, 60(2), 605–621. <https://doi.org/10.1002/csc2.20110>
- Han, M., Ji, C., Zuo, W., & He, J. (2007). Interactive effects of elevated CO₂ and temperature on the anatomical characteristics of leaves in eleven species. *Frontiers of Biology in China*, 2(3), 333–339. <https://doi.org/10.1007/s11515-007-0049-8>
- Hancock, J. F. (2020). *Strawberries*. CABI.
- Hancock, J. F., Flore, J. A., & Galletta, G. J. (1989). Gas exchange properties of strawberry species and their hybrids. *Scientia Horticulturae*, 40(2), 139–144. [https://doi.org/10.1016/0304-4238\(89\)90096-4](https://doi.org/10.1016/0304-4238(89)90096-4)
- Hancock, J. F., Sjulín, T. M., & Lobos, G. A. (2000). Strawberries. In A. Erez (Ed.), *Temperate Fruit Crops in Warm Climates* (pp. 445–455). Springer. https://doi.org/10.1007/978-94-017-3215-4_17
- Harbut, R. M., Sullivan, J. A., Proctor, J. T. A., & Swartz, H. J. (2010). Temperature affects dry matter production and net carbon exchange rate of lower-ploidy *Fragaria* species and species hybrids. *Canadian Journal of Plant Science*, 90(6), 885–892. <https://doi.org/10.4141/cjps09144>
- Harbut, R. M., Sullivan, J. A., Proctor, J. T. A., & Swartz, H. J. (2012). Net carbon exchange rate of *Fragaria* species, synthetic octoploids, and derived germplasm. *Journal of the American Society for Horticultural Science*, 137(3), 202–209. <https://doi.org/10.21273/JASHS.137.3.202>
- Harrison, R. E., Luby, J. J., & Furnier, G. R. (1997). Chloroplast DNA restriction fragment variation among strawberry (*Fragaria* spp.) taxa. *Journal of the American Society for Horticultural Science*, 122(1), 63–68. <https://doi.org/10.21273/JASHS.122.1.63>
- Hasegawa, T., Wakatsuki, H., Ju, H., Vyas, S., Nelson, G. C., Farrell, A., Deryng, D., Meza, F., & Makowski, D. (2022). A global dataset for the projected impacts of climate change on four major crops. *Scientific Data*, 9(1), 58. <https://doi.org/10.1038/s41597-022-01150-7>
- Hassan, M. R., & Ito, D. (2023). Down-regulation of photosynthesis in apple leaves under elevated CO₂ concentration: A long-term field study with different fruit load. *Journal of Agricultural Meteorology*, 79(1), 49–57. <https://doi.org/10.2480/agrmet.D-22-00021>
- Hdider, C., & Desjardins, Y. (1994). Effects of sucrose on photosynthesis and phosphoenolpyruvate carboxylase activity of in vitro cultured strawberry plantlets. *Plant Cell, Tissue and Organ Culture*, 36(1), 27–33. <https://doi.org/10.1007/BF00048312>
- He, M., Chen, S., Lian, X., Wang, X., Peñuelas, J., & Piao, S. (2022a). Global spectrum of vegetation light-use efficiency. *Geophysical Research Letters*, 49(16), e2022GL099550. <https://doi.org/10.1029/2022GL099550>
- He, M., Piao, S., Huntingford, C., Xu, H., Wang, X., Bastos, A., Cui, J., & Gasser, T. (2022b). Amplified warming from physiological responses to carbon dioxide reduces the potential of vegetation for climate change mitigation. *Communications Earth & Environment*, 3(1), 160. <https://doi.org/10.1038/s43247-022-00489-4>
- He, Y., Liu, Y., Lei, L., Terrer, C., Huntingford, C., Peñuelas, J., Xu, H., & Piao, S. (2023). CO₂ fertilization contributed more than half of the observed forest biomass increase in northern extra-tropical land. *Global Change Biology*, 29(15), 4313–4326. <https://doi.org/10.1111/gcb.16806>
- Heerema, R. J., VanLeeuwen, D., St. Hilaire, R., Gutschick, V. P., & Cook, B. (2014). Leaf photosynthesis in nitrogen-starved ‘Western’ pecan is lower on fruiting shoots than non-fruiting shoots during kernel fill. *Journal of the American Society for Horticultural Science*, 139(3), 267–274. <https://doi.org/10.21273/JASHS.139.3.267>
- Heide, O. M., & Sønsteby, A. (2020). Climate-photothermographs, a tool for ecophysiological assessment of effects of climate warming in crop plants: Examples with three berry crops. *Journal of Berry Research*, 10(3), 411–418. <https://doi.org/10.3233/JBR-190490>
- Heijari, J., Kivimäenpää, M., Hartikainen, H., Julkunen-Titto, R., & Wulff, A. (2006). Responses of strawberry (*Fragaria × ananassa*) to supplemental UV-B radiation and selenium under field conditions. *Plant and Soil*, 282(1–2), 27–39. <https://doi.org/10.1007/s11104-005-5168-x>
- Helman, D., & Bonfil, D. J. (2022). Six decades of warming and drought in the world’s top wheat-producing countries offset the benefits of rising CO₂ to yield. *Scientific Reports*, 12(1), 7921. <https://doi.org/10.1038/s41598-022-11423-1>

- Hiker, T., Coops, N. C., Wulder, M. A., Black, T. A., & Guy, R. D. (2008). The use of remote sensing in light use efficiency based models of gross primary production: A review of current status and future requirements. *Science of the Total Environment*, 404(2–3), 411–423. <https://doi.org/10.1016/j.scitotenv.2007.11.007>
- Hikosaka, K. (2004). Interspecific difference in the photosynthesis-nitrogen relationship: Patterns, physiological causes, and ecological importance. *Journal of Plant Research*, 117(6), 481–494. <https://doi.org/10.1007/s10265-004-0174-2>
- Hikosaka, K., Ishikawa, K., Borjigidai, A., Muller, O., & Onoda, Y. (2006). Temperature acclimation of photosynthesis: Mechanisms involved in the changes in temperature dependence of photosynthetic rate. *Journal of Experimental Botany*, 57(2), 291–302. <https://doi.org/10.1093/jxb/erj049>
- Hikosaka, K., Nagamatsu, D., Ishii, H. S., & Hirose, T. (2002). Photosynthesis-nitrogen relationships in species at different altitudes on Mount Kinabalu, Malaysia. *Ecological Research*, 17(3), 305–313. <https://doi.org/10.1046/j.1440-1703.2002.00490.x>
- Hikosaka, K., & Tsujimoto, K. (2021). Linking remote sensing parameters to CO₂ assimilation rates at a leaf scale. *Journal of Plant Research*, 134(4), 695–711. <https://doi.org/10.1007/s10265-021-01313-4>
- Himelrick, D. G., Wood, C. W., & Dozier, W. A., Jr. (1992). Relationship between SPAD-502 meter values and extractable chlorophyll in strawberry. *Advances in Strawberry Research*, 11, 59–61.
- Hong, C., Mueeler, N. D., Burney, J. A., Zhang, Y., AghaKouchak, A., Moore, F. C., Qin, Y., Tong, D., & Davis, S. J. (2020). Impacts of ozone and climate change on yields of perennial crops in California. *Nature Food*, 1(3), 166–172. <https://doi.org/10.1038/s43016-020-0043-8>
- Honjo, M., Kataoka, S., Yui, S., Morishita, M., Kunihisa, M., Yano, T., Hamano, M., & Yamazaki, H. (2009). Maternal lineages of the cultivated strawberry, *Fragaria × ananassa*, revealed by chloroplast DNA variation. *HortScience*, 44(6), 1562–1565. <https://doi.org/10.21273/HORTSCI.44.6.1562>
- Hopf, A., Boote, K. J., Oh, J., Guan, Z., Agehara, S., Shelia, V., Whitaker, V. M., Asseng, S., Zhao, X., & Hoogenboom, G. (2022). Development and improvement of the CROPGRO-Strawberry model. *Scientia Horticulturae*, 291, 110538. <https://doi.org/10.1016/j.scienta.2021.110538>
- Hou, X., Gao, S., Sui, X., Liang, S., & Wang, M. (2018). Changes in day and night temperatures and their asymmetric effects on vegetation phenology for the period of 2001–2016 in Northeast China. *Canadian Journal of Remote Sensing*, 44(6), 629–642. <https://doi.org/10.1080/07038992.2019.1578204>
- Hu, S., Chen, W., Tong, K., Wang, Y., Jing, L., Wang, Y., & Yang, L. (2022). Response of rice growth and leaf physiology to elevated CO₂ concentrations: A meta-analysis of 20-year FACE studies. *Science of the Total Environment*, 807, 151017. <https://doi.org/10.1016/j.scitotenv.2021.151017>
- Huang, G., Zhang, Q., Yang, Y., Shu, Y., Ren, X., Peng, S., & Li, Y. (2022). Interspecific variation in the temperature response of mesophyll conductance is related to leaf anatomy. *Plant Journal*, 112(1), 221–234. <https://doi.org/10.1111/tpj.15942>
- Huang, J., Zhao, X., Lin, S., Wang, X., Zhou, F., & Huang, J. (2019a). Phylogenetic relationships and characterization of the complete chloroplast genome of strawberry, *Fragaria × ananassa* (Rosaceae: *Fragaria*). *Mitochondrial DNA Part B*, 4(1), 916–918. <https://doi.org/10.1080/23802359.2019.1624210>
- Huang, M., Piao, S., Ciais, P., Peñuelas, J., Wang, X., Keenan, T. F., Peng, S., Berry, J. A., Wang, K., Mao, J., Alkama, R., Cescatti, A., Cuntz, M., De Deurwaerder, H., Gao, M., He, Y., Liu, Y., Luo, Y., and Wu, J. (2019b). Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution*, 3(5), 772–779. <https://doi.org/10.1038/s41559-019-0838-x>
- Husaini, A. M., & Xu, Y. W. (2016). Challenges of climate change to strawberry cultivation: Uncertainty and beyond. In A. M. Husaini & D. Neri (Eds.), *Strawberry: Growth, Development and Diseases* (pp. 262–287). CABI. <https://doi.org/10.1079/9781780646633.0262>
- Iwao, T., Murakami, T., Akaboshi, O., Cho, H. Y., Yamada, M., Takahashi, S., Kato, M., Horiuchi, N., & Ogiwara, I. (2021). Possibility of harvesting June-bearing strawberries in a plant factory with artificial light during summer and autumn by re-using plants cultivated by forcing culture. *Environmental Control in Biology*, 59(2), 99–105. <https://doi.org/10.2525/ecb.59.99>
- Jahn, O. L., & Dana, M. N. (1970). Effects of cultivar and plant age on vegetative growth of the strawberry, *Fragaria ananassa*. *American Journal of Botany*, 57(8), 993–999. <https://doi.org/10.1002/j.1537-2197.1970.tb09899.x>
- Jiang, N., Yang, Z., Zhang, H., Xu, J., & Li, C. (2023). Effect of low temperature on photosynthetic physiological activity of different photoperiod types of strawberry seedlings and stress diagnosis. *Agronomy*, 13(5), 1321. <https://doi.org/10.3390/agronomy13051321>
- Joubert, D., Zhang, N., Berman, S. R., Kaiser, E., Molenaar, J., & Stiger, J. D. (2023). A small dynamic leaf-level model predicting photosynthesis in greenhouse tomatoes. *PLoS One*, 18(3), e0275047. <https://doi.org/10.1371/journal.pone.0275047>
- Jurik, T. W., & Chabot, B. F. (1986). Leaf dynamics and profitability in wild strawberries. *Oecologia*, 69(2), 296–304. <https://doi.org/10.1007/BF00377637>
- Jurik, T. W., Chabot, J. F., & Chabot, B. F. (1979). Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. *Plant Physiology*, 63(3), 542–547. <https://doi.org/10.1104/pp.63.3.542>
- Jurik, T. W., Chabot, J. F., & Chabot, B. F. (1982). Effects of light and nutrients on leaf size, CO₂ exchange, and anatomy in wild strawberry (*Fragaria virginiana*). *Plant Physiology*, 70(4), 1044–1048. <https://doi.org/10.1104/pp.70.4.1044>
- Kabir, M. Y., Nambeesan, S. U., & Díaz-Pérez, J. C. (2023). Carbon dioxide and light curves and leaf gas exchange responses to shade levels in bell pepper (*Capsicum annuum* L.). *Plant Science*, 326, 111532. <https://doi.org/10.1016/j.plantsci.2022.111532>
- Kadir, S., Sidhu, G., & Al-Khatib, K. (2006). Strawberry (*Fragaria × ananassa* Duch.) growth and productivity as affected by temperature. *HortScience*, 41(6), 1423–1430. <https://doi.org/10.21273/HORTSCI.41.6.1423>
- Kang, B.-H., Anderson, C. T., Arimura, S.-I., Bayer, E., Bezanilla, M., Botella, M. A., Brandizzi, F., Burch-Smith, T. M., Chapman, K. D., Dünser, K., Gu, Y., Jaillais, Y., Kirchhoff, H., Otegui, M. S., Rosado, A., Tang, Y., Kleine-Vehn, J., Wang, P., & Zolman, B. K. (2022). A glossary of plant cell structures: Current insights and future questions. *The Plant Cell*, 34(1), 10–52. <https://doi.org/10.1093/plcell/koab247>
- Kanno, K., Sugiyama, T., Eguchi, M., Iwasaki, Y., & Higashide, T. (2022). Leaf photosynthesis characteristics

- of seven Japanese strawberry cultivars grown in a greenhouse. *The Horticulture Journal*, 91(1), 8–15. <https://doi.org/10.2503/hortj.UTD-237>
- Kasiamdari, R. S., Aristya, G. R., & Inayati, E. (2017). Phylogenetic relationships of nine cultivars of strawberries (*Fragaria* spp.) based on anatomical and morphological characters. *Planta Tropika: Journal of Agro Science*, 5(2), 116–126. <https://doi.org/10.18196/pt.2017.072.116-126>
- Kattge, J., Knorr, W., Raddatz, T., & Wirth, C. (2009). Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, 15(4), 976–991. <https://doi.org/10.1111/j.1365-2486.2008.01744.x>
- Keenan, T. F., Luo, X., De Kauwe, M. G., Medlyn, B. E., Prentice, I. C., Stocker, B. D., Smith, N. G., Terrer, C., Wang, H., Zhang, Y., & Zhou, S. (2021). A constraint on historic growth in global photosynthesis due to increasing CO₂. *Nature*, 600(7888), 253–258. <https://doi.org/10.1038/s41586-021-04096-9>
- Keenan, T. F., Luo, X., De Kauwe, M. G., Medlyn, B. E., Prentice, I. C., Stocker, B. D., Smith, N. G., Terrer, C., Wang, H., Zhang, Y., & Zhou, S. (2022). Retraction note: A constraint on historic growth in global photosynthesis due to increasing CO₂. *Nature*, 606(7913), 420. <https://doi.org/10.1038/s41586-022-04869-w>
- Keenan, T. F., Prentice, I. C., Canadell, J. G., Williams, C. A., Wang, H., Raupach, M., & Collatz, G. J. (2016). Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake. *Nature Communications*, 7(1), 13428. <https://doi.org/10.1038/ncomms13428>
- Keenan, T. F., & Williams, C. A. (2018). The terrestrial carbon sink. *Annual Review of Environment and Resources*, 43, 219–243. <https://doi.org/10.1146/annurev-environ-102017-030204>
- Kerkhoff, K. L., Williams, J. M., & Barden, J. A. (1988). Net photosynthetic rates and growth of strawberry after partial defoliation. *HortScience*, 23(6), 1086. <https://doi.org/10.21273/HORTSCI.23.6.1086>
- Kerr, A., Dialesandro, J., Steenwerth, K., Lopez-Brody, N., & Elias, E. (2018). Vulnerability of California specialty crops to projected mid-century temperature changes. *Climatic Change*, 148(3), 419–436. <https://doi.org/10.1007/s10584-017-2011-3>
- Keutgen, N., Chen, K., & Lenz, F. (1997). Responses of strawberry leaf photosynthesis, chlorophyll fluorescence and macronutrient contents to elevated CO₂. *Journal of Plant Physiology*, 150(4), 395–400. [https://doi.org/10.1016/S0176-1617\(97\)80088-0](https://doi.org/10.1016/S0176-1617(97)80088-0)
- Khan, A., Yan, L., Hasan, M. M., Wang, W., Xu, K., Zou, G., Liu, X.-D., & Fang, X.-W. (2022). Leaf traits and leaf nitrogen shift photosynthesis adaptive strategies among functional groups and diverse biomes. *Ecological Indicators*, 141, 109098. <https://doi.org/10.1016/j.ecoind.2022.109098>
- Kielkiewicz, M. (1985). Ultrastructural changes in strawberry leaves infested by two-spotted spider mites. *Entomologia Experimentalis et Applicata*, 37(1), 49–54. <https://doi.org/10.1111/j.1570-7458.1985.tb03451.x>
- Kim, J., & Verma, S. B. (1991). Modeling canopy photosynthesis: Scaling up from a leaf to canopy in a temperate grassland ecosystem. *Agricultural and Forest Meteorology*, 57(1–3), 187–208. [https://doi.org/10.1016/0168-1923\(91\)90086-6](https://doi.org/10.1016/0168-1923(91)90086-6)
- Kim, K. W., Ahn, J. J., & Lee, J.-H. (2009). Micromorphology of epicuticular wax structures of the garden strawberry leaves by electron microscopy: Syntopism and polymorphism. *Micron*, 40(3), 327–334. <https://doi.org/10.1016/j.micron.2008.11.002>
- Kimura, K., Yasutake, D., Koikawa, K., & Kitano, M. (2020). Spatiotemporal variability of leaf photosynthesis and its linkage with microclimates across an environment-controlled greenhouse. *Biosystems Engineering*, 195, 97–115. <https://doi.org/10.1016/j.bioystemseng.2020.05.003>
- Kimura, K., Yasutake, D., Koikawa, K., & Kitano, M. (2023). Spatiotemporally variable incident light, leaf photosynthesis, and yield across a greenhouse: Fine-scale hemispherical photography and a photosynthesis model. *Precision Agriculture*, 24(1), 114–138. <https://doi.org/10.1007/s11119-022-09933-z>
- Kirchhoff, H. (2018). Structure-function relationships in photosynthetic membranes: Challenges and emerging fields. *Plant Science*, 266, 76–82. <https://doi.org/10.1016/j.plantsci.2017.09.021>
- Kirchhoff, H. (2019). Chloroplast ultrastructure in plants. *New Phytologist*, 223(2), 565–574. <https://doi.org/10.1111/nph.15730>
- Kirschbaum, D. S., Quiroga, R. J., Funes, C. F., & Villagra, E. L. (2023). Strawberry cultivars performance in contrasting cropping conditions in Tucumán (Argentina). *Revista Agronómica del Noroeste Argentino*, 43(1), 26–34.
- Kirschbaum, M. U. F. (1994). The sensitivity of C₃ photosynthesis to increasing CO₂ concentration: A theoretical analysis of its dependence on temperature and background CO₂ concentration. *Plant, Cell & Environment*, 17(6), 747–754. <https://doi.org/10.1111/j.1365-3040.1994.tb00167.x>
- Kitajima, E. W., Betti, J. A., & Costa, A. S. (1973). Strawberry vein-banding virus, a member of the cauliflower mosaic virus group. *Journal of General Virology*, 20(1), 117–119. <https://doi.org/10.1099/0022-1317-20-1-117>
- Klamkowski, K., & Treder, W. (2006). Morphological and physiological responses of strawberry plants to water stress. *Agriculturae Conspectus Scientificus*, 71(4), 159–165.
- Koester, R. P., Nohl, B. M., Diers, B. W., & Ainsworth, E. A. (2016). Has photosynthetic capacity increased with 80 years of soybean breeding? An examination of historical soybean cultivars. *Plant, Cell & Environment*, 39(5), 1058–1067. <https://doi.org/10.1111/pce.12675>
- Koochak, H., Puthiyaveetil, S., Mullendore, D. L., Li, M., & Kirchhoff, H. (2019). The structural and functional domains of plant thylakoid membranes. *Plant Journal*, 97(3), 412–429. <https://doi.org/10.1111/tpj.14127>
- Kratsch, H. A., & Wise, R. R. (2000). The ultrastructure of chilling stress. *Plant, Cell & Environment*, 23(4), 337–350. <https://doi.org/10.1046/j.1365-3040.2000.00560.x>
- Krüger, E. (2009). Temperature conditions as a result of changes in climate and their relevance to the cultivation of straw- and raspberries. *Erwerbs-Obstbau*, 51(3), 121–128. <https://doi.org/10.1007/s10341-009-0090-7>
- Kulberg, A. T., Slot, M., & Feeley, K. J. (2023). Thermal optimum of photosynthesis is controlled by stomatal conductance and does not acclimate across an urban thermal gradient in six subtropical trees. *Plant, Cell & Environment*, 46(3), 831–849. <https://doi.org/10.1111/pce.14533>
- Kumudini, S. (2004). Effect of radiation and temperature on cranberry photosynthesis and characterization of diurnal change in photosynthesis. *Journal of the American Society for Horticultural Science*, 129(1), 106–111. <https://doi.org/10.21273/JASHS.129.1.0106>
- Lacasa, J., Hefley, T. J., Otegui, M. E., & Ciampitti, I. A. (2021). A practical guide to estimating the light extinction

- coefficient with nonlinear models—a case study on maize. *Plant Methods*, 17(1), 60. <https://doi.org/10.1186/s13007-021-00753-2>
- Lauarn, G., Frak, E., Zaka, S., Prieto, J., & Lebon, E. (2015). An empirical model that uses light attenuation and plant nitrogen status to predict within-canopy nitrogen distribution and upscale photosynthesis from leaf to whole canopy. *Aob Plants*, 7, lv116. <https://doi.org/10.1093/aobpla/plv116>
- Lazár, D., Stirbet, A., Björn, L. O., & Govindjee, G. (2022). Light quality, oxygenic photosynthesis and more. *Photosynthetica*, 60(Special Issue), 25–58. <https://doi.org/10.32615/ps.2021.055>
- Le, L. T., Dinh, H. T., Takaragawa, H., Watanabe, K., & Kawamitsu, Y. (2021). Whole-plant and single-leaf photosynthesis of strawberry under various environmental conditions. *Environmental Control in Biology*, 59(4), 173–180. <https://doi.org/10.2525/ecb.59.173>
- Lee, S. G., Kim, S. K., Lee, H. J., Lee, H. S., & Lee, J. H. (2017). Impact of moderate and extreme climate change scenarios on growth, morphological features, photosynthesis, and fruit production of hot pepper. *Ecology and Evolution*, 8, 197–206.
- Lei, J. J., Jiang, S., Ma, R. Y., Xue, L., Zhao, J., & Dai, H. P. (2021). Current status of strawberry industry in China. *Acta Horticulturae*, 1309, 349–352. <https://doi.org/10.17660/ActaHortic.2021.1309.50>
- Lei, Z., Han, J., Chen, Y., Zhang, W., Cai, X., Liu, F., & Zhang, Y. (2023). The effect of shift in physiological and anatomical traits on light use efficiency under cotton domestication. *Physiologia Plantarum*, 175(2), e13884. <https://doi.org/10.1111/ppl.13884>
- Leister, D. (2020). Alternative electron pathways in photosynthesis: Strength in numbers. *New Phytologist*, 228(4), 1166–1168. <https://doi.org/10.1111/nph.16911>
- Leister, D. (2023). Enhancing the light reactions of photosynthesis: Strategies, controversies, and perspectives. *Molecular Plant*, 16(1), 4–22. <https://doi.org/10.1016/j.molp.2022.08.005>
- Leister, D., Sharma, A., Kerber, N., Nägele, T., Reiter, B., Paschi, V., Beeh, S., Jahns, P., Barbato, R., Pribil, M., & Ruhle, T. (2023). An ancient metabolite damage-repair system sustains photosynthesis in plants. *Nature Communications*, 14(1), 3023. <https://doi.org/10.1038/s41467-023-38804-y>
- Le Mière, P., Hadley, P., Darby, J., & Battey, N. H. (1998). The effect of thermal environment, planting date and crown size on growth, development and yield of *Fragaria* × *ananassa* Duch. cv. Elsanta. *Journal of Horticultural Science and Biotechnology*, 73(6), 786–795. <https://doi.org/10.1080/14620316.1998.11511049>
- Leng, G. (2018). Keeping global warming within 1.5 °C reduces future risk of yield loss in the United States: A probabilistic modeling approach. *Science of the Total Environment*, 644, 52–59. <https://doi.org/10.1016/j.scitotenv.2018.06.344>
- Li, C., Cai, C., Tao, Y., Sun, Z., Jiang, M., Chen, L., & Li, J. (2021a). Variation and evolution of the whole chloroplast genomes of *Fragaria* spp. (Rosaceae). *Frontiers in Plant Science*, 12, 754209. <https://doi.org/10.3389/fpls.2021.754209>
- Li, H., Liu, S., Guo, J., Liu, F., Song, F., & Li, X. (2020a). Effect of the transgenerational exposure to elevated CO₂ on low temperature tolerance of winter wheat: Chloroplast ultrastructure and carbohydrate metabolism. *Journal of Agronomy and Crop Science*, 206(6), 773–783. <https://doi.org/10.1111/jac.12443>
- Li, M., Mukhopadhyay, R., Svoboda, V., Oung, H. M. O., Mullendore, D. L., & Kirchoff, H. (2020b). Measuring the dynamic response of the thylakoid architecture in plant leaves by electron microscopy. *Plant Direct*, 4(11), e00280. <https://doi.org/10.1002/pld3.280>
- Li, N., Yao, N., Li, J., Chen, J., Liu, D., Biswas, A., Li, L., Wang, T., & Chen, X. (2021b). A meta-analysis of the possible impact of climate change on global cotton yield based on crop simulation approaches. *Agricultural Systems*, 193, 103221. <https://doi.org/10.1016/j.agry.2021.103221>
- Li, R., He, Y., Chen, J., Zheng, S., & Zhuang, C. (2023a). Research progress in improving photosynthetic efficiency. *International Journal of Molecular Sciences*, 24(11), 9286. <https://doi.org/10.3390/ijms24119286>
- Li, R., Yu, D., Zhang, Y., Han, J., Zhang, W., Yang, Q., Gessler, A., Li, M.-H., Xu, M., Guan, X., Chen, L., Wang, Q., & Wang, S. (2022). Investment of needle nitrogen to photosynthesis controls the nonlinear productivity response of young Chinese fir trees to nitrogen deposition. *Science of the Total Environment*, 840, 156537. <https://doi.org/10.1016/j.scitotenv.2022.156537>
- Li, Y., He, N., Hou, J., Xu, L., Liu, C., Zhang, J., Wang, Q., Zhang, X., & Wu, X. (2018). Factors influencing leaf chlorophyll content in natural forests at the biome scale. *Frontiers in Ecology and Evolution*, 6, 64. <https://doi.org/10.3389/fevo.2018.00064>
- Li, Y.-T., Gao, H.-Y., and Zhang, Z.-S. (2023b). Effects of environmental and non-environmental factors on dynamic photosynthetic carbon assimilation in leaves under changing light. *Plants*, 12(10), 2015. <https://doi.org/10.3390/plants12102015>
- Li, Z., & Gao, Z. (2015). Simulation of photosynthetic capacity of strawberry plants at different leaf ages. *Advance Journal of Food Science & Technology*, 9(9), 735–740. <https://doi.org/10.19026/ajfst.9.1770>
- Liang, X., Wang, D., Ye, Q., Zhang, J., Liu, M., Liu, H., Yu, K., Wang, Y., Hou, E., Zhong, B., Xu, L., Lv, T., Peng, S., Lu, H., Sicard, P., Anav, A., & Ellsworth, D. S. (2023). Stomatal responses of terrestrial plants to global change. *Nature Communications*, 14(1), 2188. <https://doi.org/10.1038/s41467-023-37934-7>
- Lin, Y., Chen, Z., Yang, M., Chen, S.-O., Gao, Y.-H., Liu, R., Hao, Y.-B., Xin, X.-P., Zhou, X.-P., & Yu, G.-R. (2022). Temporal and spatial variations of ecosystem photosynthetic parameters in arid and semi-arid areas of China and its influencing factors. *Chinese Journal of Ecology*, 46(12), 1461–1472. <https://doi.org/10.17521/cjpe.2021.0426>
- Liu, B., Song, L., Deng, X., Lu, Y., Lieberman-Lazarovich, M., Shabala, S., & Ouyang, B. (2023a). Tomato heat tolerance: Progress and prospects. *Scientia Horticulturae*, 322, 112435. <https://doi.org/10.1016/j.scienta.2023.112435>
- Liu, L., Hao, L., Zhang, Y., Zhou, H., Ma, B., Cheng, Y., Tian, Y., Chang, Z., & Zheng, Y. (2022). The CO₂ fertilization effect on leaf photosynthesis of maize (*Zea mays* L.) depends on growth temperatures with changes in leaf anatomy and soluble sugars. *Frontiers in Plant Science*, 13, 890928. <https://doi.org/10.3389/fpls.2022.890928>
- Liu, L., Shi, H., Li, S., Sun, M., Zhang, R., Wang, Y., & Ren, F. (2020a). Integrated analysis of molybdenum nutrition and nitrate metabolism in strawberry. *Frontiers in Plant Science*, 11, 1117. <https://doi.org/10.3389/fpls.2020.01117>
- Liu, S., Yan, Z., Wang, Z., Serbin, S., Visser, M., Zeng, Y., Ryu, Y., Su, Y., Guo, Z., Song, G., Wu, Q., Zhang, H., Cheng, K. H., Dong, J., Hau, B. C. H., Zhao, P., Yang, X., Liu, L., Rogers, A., & Wu, J. (2023b). Mapping foliar

- photosynthetic capacity in sub-tropical and tropical forests with UAS-based imaging spectroscopy: Scaling from leaf to canopy. *Remote Sensing of Environment*, 293, 113612. <https://doi.org/10.1016/j.rse.2023.113612>
- Liu, Y. (2020). Optimum temperature for photosynthesis: From leaf to ecosystem-scale. *Science Bulletin*, 65(8), 601–604. <https://doi.org/10.1016/j.scib.2020.01.006>
- Liu, Y., Li, N., Zhang, Z., Huang, C., Chen, X., & Wang, F. (2020b). The central trend in crop yields under climate change in China: A systematic review. *Science of the Total Environment*, 704, 135355. <https://doi.org/10.1016/j.scitotenv.2019.135355>
- Lobell, D., Cahill, K. N., & Field, C. B. (2007). Historical effects of temperature and precipitation on California crop yields. *Climatic Change*, 81(2), 187–203. <https://doi.org/10.1007/s10584-006-9141-3>
- Lobell, D., & Field, C. (2011). California perennial crops in a changing climate. *Climatic Change*, 109(S1), 317–333. <https://doi.org/10.1007/s10584-011-0303-6>
- Lobell, D. B., & Asner, G. P. (2003). Climate and management contributions to recent trends in U.S. agricultural yields. *Science*, 299(5609), 1032. <https://doi.org/10.1126/science.1078475>
- Lollato, R. P., Bavia, G. P., Perin, V., Knapp, M., Santos, E. A., Patrignani, A., & DeWolf, E. D. (2020). Climate-risk assessment for winter wheat using long-term weather data. *Agronomy Journal*, 112(3), 2132–2151. <https://doi.org/10.1002/agj2.20168>
- Luo, X., Croft, H., Chen, J. M., He, L., & Keenan, T. F. (2019). Improved estimates of global terrestrial photosynthesis using information on leaf chlorophyll content. *Global Change Biology*, 25(7), 2499–2514. <https://doi.org/10.1111/gcb.14624>
- Luo, X., Keenan, T. F., Chen, J. M., Croft, H., Prentice, I. C., Smith, N. G., Walker, A. P., Wang, H., Wang, R., Xu, C., & Zhang, Y. (2021). Global variation in the fraction of leaf nitrogen allocated to photosynthesis. *Nature Communications*, 12(1), 4866. <https://doi.org/10.1038/s41467-021-25163-9>
- Lustosa da Silva, I. F., Shimizu, G. D., dos Santos, E. L., Erpen-Dalla Corte, L., Zeist, A. R., Roberto, S. R., & de Resende, J. T. V. (2023). Breeding short-day strawberry genotypes for cultivation in tropical and subtropical regions. *Horticulturae*, 9(6), 614. <https://doi.org/10.3390/horticulturae9060614>
- Łysiak, G. P., & Szot, I. (2023). The use of temperature based indices for estimation of fruit production conditions and risks in temperate climates. *Agriculture*, 13(5), 960. <https://doi.org/10.3390/agriculture13050960>
- Ma, L., Fang, Q. X., Sima, M. W., Burkey, K. O., & Harmel, R. D. (2021). Simulated climate change effects on soybean production using two crop modules in RZWQM2. *Agronomy Journal*, 113(2), 1349–1365. <https://doi.org/10.1002/agj2.20548>
- McGowan, H. A., Lowry, A. L., & Gray, M. A. (2020). Identification of optimum temperatures for photosynthetic production in subtropical coastal ecosystems: Implications for CO₂ sequestration in a warming world. *Journal of Geophysical Research: Biogeosciences*, 125(8), e2020JG005678. <https://doi.org/10.1029/2020JG005678>
- Mackerron, D. K. L. (1976). Wind damage to the surface of strawberry leaves. *Annals of Botany*, 40(2), 351–354. <https://doi.org/10.1093/oxfordjournals.aob.a085137>
- Makaraci, A. Z., & Flore, J. A. (2009). The use of chlorophyll fluorescence to determine the effects of different acclimation temperatures on strawberry leaves exposed to mild frost damage. *Acta Horticulturae*, 842, 813–816. <https://doi.org/10.17660/ActaHortic.2009.842.179>
- Manter, D. K., & Kerrigan, J. (2004). A/C_i curve analysis across a range of woody plant species: Influence of regression analysis parameters and mesophyll conductance. *Journal of Experimental Botany*, 55(408), 2581–2588. <https://doi.org/10.1093/jxb/erh260>
- Márquez, D. A., Stuart-Williams, H., Cernusak, L. A., & Farquhar, G. D. (2023). Assessing the CO₂ concentration at the surface of photosynthetic mesophyll cells. *New Phytologist*, 238(4), 1446–1460. <https://doi.org/10.1111/nph.18784>
- Maskey, M. L., Pathak, T. B., & Dara, S. K. (2019). Weather based strawberry yield forecasts at field scale using statistical and machine learning models. *Atmosphere*, 10(7), 378. <https://doi.org/10.3390/atmos10070378>
- Mathan, J., Singh, A., Jathar, V., Ranjan, A., & Sharwood, R. (2021). High photosynthesis rate in two wild rice species is driven by leaf anatomy mediating high Rubisco activity and electron transport rate. *Journal of Experimental Botany*, 72(20), 7119–7135. <https://doi.org/10.1093/jxb/erab313>
- Matsuda, H., & Takaragawa, H. (2023). Leaf photosynthetic reduction at high temperatures in various genotypes of passion fruit (*Passiflora* spp.). *The Horticulture Journal*. <https://doi.org/10.2503/hortj.QH-060>
- Matuszyńska, A., Saadat, N. P., & Ebenhöf, O. (2019). Balancing energy supply during photosynthesis – a theoretical perspective. *Physiologia Plantarum*, 166(1), 392–402. <https://doi.org/10.1111/ppl.12962>
- Maxwell, K. (2002). Resistance is useful: Diurnal patterns of photosynthesis in C₃ and crassulacean acid metabolism epiphytic bromeliads. *Functional Plant Biology*, 29(6), 679–687. <https://doi.org/10.1071/PP01193>
- Mazur, R., Mostowska, A., & Kowalewska, L. (2021). How to measure grana – ultrastructural features of thylakoid membranes of plant chloroplasts. *Frontiers in Plant Science*, 12, 756009. <https://doi.org/10.3389/fpls.2021.756009>
- Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X., Montpied, P., Strassmeyer, J., Walcroft, A., Wang, K., & Loustau, D. (2002). Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment*, 25(9), 1167–1179. <https://doi.org/10.1046/j.1365-3040.2002.00891.x>
- Meng, F., Liu, D., Wang, Y., Wang, S., & Wang, T. (2023). Negative relationship between photosynthesis and late-stage canopy development and senescence over Tibetan Plateau. *Global Change Biology*, 29(11), 3147–3158. <https://doi.org/10.1111/gcb.16668>
- Meinshausen, M., Lewis, J., McGlade, C., Gütschow, J., Nicholls, Z., Burdon, R., Cozzi, L., & Hackmann, B. (2022). Realization of Paris agreement pledges may limit warming just below 2 °C. *Nature*, 604(7905), 304–309. <https://doi.org/10.1038/s41586-022-04553-z>
- Menzel, C. M. (2023). Effect of global warming on the yields of strawberry in Queensland: A mini-review. *Horticulturae*, 9(2), 142. <https://doi.org/10.3390/horticulturae9020142>
- Mezzetti, B., Giampieri, F., Zhang, Y.-T., & Zhong, C.-F. (2018). Status of strawberry breeding programs and cultivation systems in Europe and the rest of the world. *Journal of Berry Research*, 8(3), 205–221. <https://doi.org/10.3233/JBR-180314>
- Miao, Y., Cai, Y., Wu, H., & Wang, D. (2021). Diurnal and seasonal variations in the photosynthetic characteristics and

- the gas exchange simulations of two rice cultivars grown at ambient and elevated CO₂. *Frontiers in Plant Science*, 12, 651606. <https://doi.org/10.3389/fpls.2021.651606>
- Minoli, S., Jägermeyr, J., Asseng, S., Urfels, A., & Müller, C. (2022). Global crop yields can be lifted by timely adaptation of growing periods to climate change. *Nature Communications*, 13(1), 7079. <https://doi.org/10.1038/s41467-022-34411-5>
- Mistry, M. N., Wing, I. S., & de Cian, E. (2017). Simulated vs. empirical weather responsiveness of crop yields: US evidence and implications for the agricultural impacts of climate change. *Environmental Research Letters*, 12(7), 075007. <https://doi.org/10.1088/1748-9326/aa788c>
- Mndela, M., Tjelele, J. T., Madakadze, I. C., Mangwane, M., Samuels, I. M., Muller, F., & Pule, H. T. (2022). A global meta-analysis of woody plant responses to elevated CO₂: Implications on biomass, growth, leaf N content, photosynthesis and water relations. *Ecological Processes*, 11(1), 52. <https://doi.org/10.1186/s13717-022-00397-7>
- Mohammadi, S., Rydgren, K., Bakkestuen, V., & Gillespie, M. A. K. (2023). Impacts of recent climate change on crop yield can depend on local conditions in climatically diverse regions of Norway. *Scientific Reports*, 13(1), 3633. <https://doi.org/10.1038/s41598-023-30813-7>
- Moon, J. W., Jr., Bailey, D. A., Fallahi, E., Jensen, R. G., & Zhu, G. (1990). Effect of nitrogen application on growth and photosynthetic nitrogen use efficiency in two ecotypes of wild strawberry, *Fragaria chiloensis*. *Physiologia Plantarum*, 80(4), 612–618. <https://doi.org/10.1111/j.1399-3054.1990.tb05686.x>
- Moore, C. E., Meacham-Hensold, K., Lemonnier, P., Slattery, R. A., Benjamin, C., Bernacchi, C. J., Lawson, T., Cavanagh, A. P., & Hancock, R. (2021). The effect of increasing temperature on crop photosynthesis: From enzymes to ecosystems. *Journal of Experimental Botany*, 72(8), 2822–2844. <https://doi.org/10.1093/jxb/erab090>
- Morison, J. I. L., & Lawlor, D. W. (1999). Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell & Environment*, 22(6), 659–682. <https://doi.org/10.1046/j.1365-3040.1999.00443.x>
- Morton, L. W., Peres, N., Fraisse, C., & Gleason, M. (2017). Climate, weather and strawberries. Sociology and Technical Report, Department of Sociology, Iowa State University 1047, 16 pp.
- Moualeu-Ngangue, D. P., Chen, T.-W., & Stützel, H. (2016). A new method to estimate photosynthetic parameters through net assimilation rate–intercellular space CO₂ concentration (A–C_i) curve and chlorophyll fluorescence measurements. *New Phytologist*, 213(3), 1543–1554. <https://doi.org/10.1111/nph.14260>
- Mu, X., & Chen, Y. (2021). The physiological response of photosynthesis to nitrogen deficiency. *Plant Physiology and Biochemistry*, 158, 76–82. <https://doi.org/10.1016/j.plaphy.2020.11.019>
- Nakai, H., Yasutake, D., Kimura, K., Kengo, I., Hidaka, K., Eguchi, T., Hirota, T., Okayasu, T., Ozaki, Y., & Kitano, M. (2022). Dynamics of carbon export from leaves as translocation affected by the coordination of carbohydrate availability in field strawberry. *Environmental and Experimental Botany*, 196, 104806. <https://doi.org/10.1016/j.envexpbot.2022.104806>
- Neales, T. F., & Incoll, L. D. (1968). The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. *The Botanical Review*, 34(2), 107–125. <https://doi.org/10.1007/BF02872604>
- Neri, D., Baruzzi, G., Massetani, F., & Faedi, W. (2012). Strawberry production in forced and protected culture in Europe as a response to climate change. *Canadian Journal of Plant Science*, 92(6), 1021–1036. <https://doi.org/10.4141/cjps2011-276>
- Nii, N. (1993). Fruiting effects on leaf characteristics, photosynthesis, and root growth in peach trees. *Journal of the Japanese Society for Horticultural Science*, 62(3), 519–526. <https://doi.org/10.2503/jjshs.62.519>
- Niinemets, Ü. (2016). Leaf-age dependent changes in within-canopy variation in leaf functional traits: A meta-analysis. *Journal of Plant Research*, 129, 313–338. <https://doi.org/10.1007/s10265-016-0815-2>
- Nomura, K., Saito, M., Ito, M., Yamane, S., Iwao, T., Tada, I., Yamazaki, T., Ono, S., Yasutake, D., & Kitano, M. (2022). Diurnal decline in the photosynthetic capacity of uppermost leaves in an eggplant canopy grown in a horticultural greenhouse. *Photosynthetica*, 60(3), 457–464. <https://doi.org/10.32615/ps.2022.040>
- Ocwa, A., Harsanyi, E., Széles, A., Holb, I. J., Szabó, S., Rátonyi, T., & Mohammed, S. (2023). A bibliographic review of climate change and fertilization as the main drivers of maize yield: Implications for food security. *Agriculture & Food Security*, 12(1), 14. <https://doi.org/10.1186/s40066-023-00419-3>
- Oda, Y. (1997). Effects of light intensity, CO₂ concentration and leaf temperature on gas exchange of strawberry plants – feasibility studies on CO₂ enrichment in Japanese conditions. *Acta Horticulturae*, 439, 563–574. <https://doi.org/10.17660/ActaHortic.1997.439.95>
- Oliver, T., Kim, T. D., Trinugroho, J. P., Cerdón-Preciado, V., Wijayatilake, N., Bhatia, A., Rutherford, A. W., & Cardona, T. (2023). The evolution and evolvability of photosystem II. *Annual Review of Plant Biology*, 74, 225–257. <https://doi.org/10.1146/annurev-arplant-070522-062509>
- Ontivero, M., Arias, M., Ricci, J. D., Babot, J., Albornoz, P., & Castagnaro, A. (2000). Analysis of genetic similarities among species of *Fragaria*, *Potentilla*, and *Duchesnea* found in northwest Argentina by using morphological, anatomical, and molecular characters. *Canadian Journal of Botany*, 78(4), 547–556. <https://doi.org/10.1139/b00-026>
- Osborne, C. P., Drake, B. G., LaRoche, J., & Long, S. P. (1997). Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? (Indiana strawberry in a Maryland forest). *Plant Physiology*, 114(1), 337–344. <https://doi.org/10.1104/pp.114.1.337>
- Palencia, P., Martínez, F., Medina, J. J., Vázquez, E., Flores, F., & López-Medina, J. (2009). Effects of climate change on strawberry production. *Acta Horticulturae*, 838, 51–54. <https://doi.org/10.17660/ActaHortic.2009.838.6>
- Palmer, J. W., Giuliani, R., & Adams, H. M. (1997). Effect of crop load on fruiting and leaf photosynthesis of 'Braeburn'/M.26 apple trees. *Tree Physiology*, 17(11), 741–746. <https://doi.org/10.1093/treephys/17.11.741>
- Pang, Y., Liao, Q., Peng, H., Qian, C., & Wang, F. (2023). CO₂ mesophyll conductance regulated by light: A review. *Planta*, 258(1), 11. <https://doi.org/10.1007/s00425-023-04157-5>
- Papp, J., Gracza, P., Szenthe, A., Sárdi, E., & Simon, G. (2005). Anatomical relations of the leaves in strawberry. *International Journal of Horticultural Science*, 11(1), 81–84. <https://doi.org/10.31421/IJHS/11/1/563>
- Papp, J., Lenkefi, I., Gara, M., & Gracza, P. (2000). The tissue structure of the vegetative organs of strawberry (*Fragaria moschata* Duch.). *International Journal of Horticultural Science*, 6(1), 28–31. <https://doi.org/10.31421/IJHS/6/1/61>

- Pardo, E. M., Grellet, C. F., Salazar, S. M., Castagnaro, A. P., Díaz Ricci, J. C., & Arias, M. E. (2012). Histopathology of the resistance to *Colletotrichum gloeosporioides* of wild strawberries and species related to commercial strawberry. *Australian Journal of Crop Science*, 6(7), 1147–1153.
- Park, P., Lee, S.-S., Ohno, T., Tsuge, T., & Nishimura, L. S. (1992). Slightly damaged type of plasma membrane modification in strawberry leaves treated with AF-Toxin I produced by *Alternaria alternata* strawberry pathotype. *Annals of the Phytopathological Society of Japan*, 58(3), 431–445. <https://doi.org/10.3186/jjphytopath.58.431>
- Pathak, T. B., Maskey, M. L., Dahlberg, J. A., Kearns, F., Bali, K. M., & Zaccaria, D. (2018). Climate change trends and impacts on California agriculture: A detailed review. *Agronomy*, 8(3), 25. <https://doi.org/10.3390/agronomy8030025>
- Pathoumthong, P., Zhang, Z., Roy, S. J., & El Habti, A. (2023). Rapid non-destructive method to phenotype stomatal traits. *BMC Plant Methods*, 19(1), 36. <https://doi.org/10.1186/s13007-023-01016-y>
- Pereira, F. F. S., Sánchez-Román, R. M., & González, A. M. G. O. (2017). Simulation model of the growth of sweet orange (*Citrus sinensis* L. Osbeck) cv. Natal in response to climate change. *Climatic Change*, 143(1–2), 101–113. <https://doi.org/10.1007/s10584-017-1986-0>
- Pérez de Camacaro, M. E., Camacaro, G. J., Hadley, P., Battey, N. H., & Carew, J. G. (2002). Pattern of growth and development of the strawberry cultivars Elsanta, Bolero, and Everest. *Journal of the American Society for Horticultural Science*, 127(6), 901–907. <https://doi.org/10.21273/JASHS.127.6.901>
- Petersen, L. K. (2019). Impact of climate change on twenty-first century crop yields in the U.S. *Climate*, 7(3), 40. <https://doi.org/10.3390/cli7030040>
- Phillips, A. L., Scafaro, A. P., & Atwell, B. J. (2022). Photosynthetic traits of Australian wild rice (*Oryza australiensis*) confer tolerance to extreme daytime temperatures. *Plant Molecular Biology*, 110(4–5), 347–363. <https://doi.org/10.1007/s11103-021-01210-3>
- Poorter, H., Knopf, O., Wright, I. J., Temme, A. A., Hogewoning, S. W., Graf, A., Cernusak, L. A., & Pons, T. L. (2022). A meta-analysis of responses of C₃ plants to atmospheric CO₂: Dose–response curves for 85 traits ranging from the molecular to the whole-plant level. *New Phytologist*, 233(4), 1560–1596. <https://doi.org/10.1111/nph.17802>
- Poorter, H., Niimets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S., & Pons, T. L. (2019). A meta-analysis of plant response to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist*, 223(3), 1073–1105. <https://doi.org/10.1111/nph.15754>
- Porter, M., Fan, Z., Lee, S., & Whitaker, V. M. (2023). Strawberry breeding for improved flavor. *Crop Science*, 63(4), 1949–1963. <https://doi.org/10.1002/csc2.21012>
- Potkay, A., & Feng, X. (2023). Do stomata optimize turgor-driven growth? A new framework for integrating stomata response with whole-plant hydraulics and carbon balance. *New Phytologist*, 238(2), 506–528. <https://doi.org/10.1111/nph.18620>
- Prado, C. H. B. A., & De Moraes, J. A. P. V. (1997). Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field conditions. *Photosynthetica*, 33(1), 103–112. <https://doi.org/10.1023/A:1022183423630>
- Prado, C. H. B. A., Passos, E. E. M., & De Moraes, J. A. P. V. (2001). Photosynthesis and water relations of six tall genotypes of *Cocos nucifera* in wet and dry seasons. *South African Journal of Botany*, 67(2), 169–176. [https://doi.org/10.1016/S0254-6299\(15\)31116-9](https://doi.org/10.1016/S0254-6299(15)31116-9)
- Qiu, J., Cai, C., Shen, M., Gu, X., Zheng, L., Sun, L., Teng, Y., Yu, H., & Zou, L. (2023). Responses of growth, yield and fruit quality of strawberry to elevated CO₂, LED supplemental light, and their combination in autumn through spring greenhouse production. *Plant Growth Regulation*. <https://doi.org/10.1007/s10725-023-01065-2>
- Rakhmankulova, Z. F., Shuyskaya, E. V., Prokofieva, M. Y., Saidova, L. T., & Voronin, P. Y. (2023). Effect of elevated CO₂ and temperature on plants with different type of photosynthesis: Quinoa (C₃) and amaranth (C₄). *Russian Journal of Plant Physiology*, 70(6), 117. <https://doi.org/10.1134/S1021443723601349>
- Ray, D. K., West, P. C., Clark, M., Gerber, J. S., Prishchepov, A. V., Chatterjee, S., & Jung, Y. H. (2019). Climate change has likely already affected global food production. *PLoS One*, 14(5), e0217148. <https://doi.org/10.1371/journal.pone.0217148>
- Razmi, H., Amiri Fahliani, R., Kavooosi, B., & Masoumias, A. (2022). Cytological and morphological responses of strawberry (*Fragaria* spp.) to polyploidization. *Journal of Agricultural Science and Technology*, 24(4), 939–949.
- Redondo-Gómez, S., García-López, J. V., Mesa-Marín, J., Pajuelo, E., Rodríguez-Llorente, I. D., & Mateos-Naranjo, E. (2022). Synergistic effect of plant-growth-promoting rhizobacteria improves strawberry growth and flowering with soil salinization and increased atmospheric CO₂ levels and temperature conditions. *Agronomy*, 12(9), 2082. <https://doi.org/10.3390/agronomy12092082>
- Reekie, J. Y., Hicklenton, P. R., & Struik, P. C. (2005). Prohexadione-calcium modifies growth and increases photosynthesis in strawberry nursery plants. *Canadian Journal of Plant Science*, 85(3), 671–677. <https://doi.org/10.4141/P04-113>
- Reich, P. B., Sendall, K. M., Rice, K., Rich, R. L., Stefanski, A., Hobbie, S. E., & Montgomery, R. A. (2015). Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nature Climate Change*, 5(2), 148–152. <https://doi.org/10.1038/nclimate2497>
- Reich, P. B., Uhl, C., Walters, M. B., & Ellsworth, D. S. (1991a). Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia*, 86(1), 16–24. <https://doi.org/10.1007/BF00317383>
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1991b). Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. *Plant, Cell & Environment*, 14(3), 251–259. <https://doi.org/10.1111/j.1365-3040.1991.tb01499.x>
- Ripullone, F., Grassi, G., Lauteri, M., & Borghetti, M. (2003). Photosynthesis-nitrogen relationships: Interpretation of different patterns between *Pseudotsuga menziesii* and *Populus x euroamericana* in a mini-stand experiment. *Tree Physiology*, 23(2), 137–144. <https://doi.org/10.1093/treephys/23.2.137>
- Rom, C. R., & Ferree, D. C. (1986). Influence of fruit on spur leaf photosynthesis and transpiration of ‘Golden Delicious’ apple. *HortScience*, 21(4), 1026–1029. <https://doi.org/10.21273/HORTSCI.21.4.1026>
- Roper, T. R., Keller, J. D., Loescher, W. H., & Rom, C. R. (1988). Photosynthesis and carbohydrate partitioning in sweet cherry: Fruiting effects. *Physiologia Plantarum*, 72

- (1), 42–47. <https://doi.org/10.1111/j.1399-3054.1988.tb06620.x>
- Ryu, Y., Berry, J. A., & Baldocchi, D. D. (2019). What is global photosynthesis? History, uncertainties and opportunities. *Remote Sensing of Environment*, 223, 95–114. <https://doi.org/10.1016/j.rse.2019.01.016>
- Sage, R. F., & Kubien, D. S. (2007). The temperature response of C_3 and C_4 photosynthesis. *Plant, Cell & Environment*, 30(9), 1086–1106. <https://doi.org/10.1111/j.1365-3040.2007.01682.x>
- Salamone, I., Govindarajulu, R., Falk, S., Parks, M., Liston, A., & Ashman, T.-L. (2013). Bioclimatic, ecological, and phenotypic intermediacy and high genetic admixture in a natural hybrid of octoploid strawberries. *American Journal of Botany*, 100(5), 939–950. <https://doi.org/10.3732/ajb.1200624>
- Sammarco, I., Münzbergová, Z., & Latzel, V. (2022). DNA methylation can mediate local adaptation and response to climate change in the clonal plant *Fragaria vesca*: Evidence from a European-scale reciprocal transplant experiment. *Frontiers in Plant Science*, 13, 827166. <https://doi.org/10.3389/fpls.2022.827166>
- Samtani, J. B., Rom, C. R., Friedrich, H., Fennimore, S. A., Finn, C. E., Petran, A., Wallace, R. W., Pritts, M. P., Fernandez, G., Chase, C. A., Kubota, C., & Bergfeld, B. (2019). The status and future of the strawberry industry in the United States. *HortTechnology*, 29(1), 11–24. <https://doi.org/10.21273/HORTTECH04135-18>
- Sances, F. V., Wyman, J. A., & Ting, I. P. (1979). Morphological responses of strawberry leaves to infestations of two-spotted spider mite. *Journal of Economic Entomology*, 72(5), 710–713. <https://doi.org/10.1093/jee/72.5.710>
- Sang, Y., Huang, L., Keenan, T. F., He, C., Wang, Y., & He, Y. (2021). Comment on “Recent global decline of CO_2 fertilization effects on vegetation photosynthesis”. *Science*, 373(6562), eabg4420. <https://doi.org/10.1126/science.abg4420>
- Savé, R., Peñuelas, J., Marfà, O., & Serrano, L. (1993). Changes in leaf osmotic and elastic properties and canopy structure of strawberries under mild water stress. *HortScience*, 28(9), 925–927. <https://doi.org/10.21273/HORTSCI.28.9.925>
- Scafaro, A. P., Posch, B. C., Evans, J. R., Farquhar, G. D., & Atkin, O. K. (2023). Rubisco deactivation and chloroplast electron transport rates co-limit photosynthesis above optimal leaf temperature in terrestrial plants. *Nature Communications*, 14(1), 2820. <https://doi.org/10.1038/s41467-023-38496-4>
- Scafaro, A. P., Xiang, S., Long, B. M., Bahar, N. H. A., Weerasinghe, L. K., Creek, D., Evans, J. R., Reich, P. B., & Atkin, O. K. (2017). Strong thermal acclimation of photosynthesis in tropical and temperate wet-forest tree species: The importance of altered Rubisco content. *Global Change Biology*, 23(7), 2783–2800. <https://doi.org/10.1111/gcb.13566>
- Schaffer, B., Barden, J. A., & Williams, J. M. (1986). Whole plant photosynthesis and dry matter partitioning in fruiting and deblossomed day-neutral strawberry plants. *Journal of the American Society for Horticultural Science*, 111(3), 430–433. <https://doi.org/10.21273/JASHS.111.3.430>
- Schlenker, W., & Roberts, M. J. (2009). Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 106(37), 15594–15598. <https://doi.org/10.1073/pnas.0906865106>
- Schleussner, C.-F., Deryng, D., Müller, C., Elliott, J., Saeed, F., Folberth, C., Liu, W., Wang, X., Pugh, T. A. M., Thiery, W., Seneviratne, S. I., & Rogelj, J. (2018). Crop productivity changes in 1.5 °C and 2 °C worlds under climate sensitivity uncertainty. *Environmental Research Letters*, 13(6), 064007. <https://doi.org/10.1088/1748-9326/aab63b>
- Schultz, H. R. (2003). Extension of a Farquhar model for limitations of leaf photosynthesis induced by light environment, phenology and leaf age in grapevines (*Vitis vinifera* L. cvv. White Riesling and Zinfandel). *Functional Plant Biology*, 30(6), 673–687. <https://doi.org/10.1071/FP02146>
- Sharkey, T. D. (1985). Photosynthesis in intact leaves of C_3 plants: Physics, physiology and rate limitations. *The Botanical Review*, 51(1), 53–105. <https://doi.org/10.1007/BF02861058>
- Sharkey, T. D., Bernacchi, C. J., Farquhar, G. D., & Singaas, E. L. (2007). Fitting photosynthetic carbon dioxide response curves for C_3 leaves. *Plant, Cell & Environment*, 30(9), 1035–1040. <https://doi.org/10.1111/j.1365-3040.2007.01710.x>
- Shi, H., Zhou, Q., He, R., Zhang, Q., & Dang, H. (2023). Asymmetric effects of daytime and nighttime warming on alpine treeline recruitment. *Global Change Biology*, 29(12), 3463–3475. <https://doi.org/10.1111/gcb.16675>
- Shin, J., Hwang, I., Kim, D., Kim, J., Kim, J. H., & Son, J. E. (2022). Waning advantages of CO_2 enrichment on photosynthesis and productivity due to accelerated phase transition and source-sink imbalance in sweet pepper. *Scientia Horticulturae*, 301, 111130. <https://doi.org/10.1016/j.scienta.2022.111130>
- Siddique, M. I., Han, K., Lee, J., Lee, E. S., Lee, Y.-R., Lee, S. Y., Kim, D.-S., & Kim, D.-S. (2021). QTL analysis for chlorophyll content in strawberry (*Fragaria × ananassa* Duch.) leaves. *Agriculture*, 11(11), 1163. <https://doi.org/10.3390/agriculture11111163>
- Siebers, M. H., Gomez-Casanovas, N., Fu, P., Meacham-Hensold, K., Moore, C. E., Bernacchi, C. J., Jez, J. M., & Topp, C. N. (2021). Emerging approaches to measure photosynthesis from the leaf to the ecosystem. *Emerging Topics in Life Sciences*, 5(2), 261–274. <https://doi.org/10.1042/ETLS20200292>
- Sierra, J., Escobar-Tovar, L., & Leon, P. (2023). Plastids: Diving into their diversity, their functions, and their role in plant development. *Journal of Experimental Botany*, 74(8), 2508–2526. <https://doi.org/10.1093/jxb/erad044>
- Sinclair, T. R., & Horie, T. (1989). Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. *Crop Science*, 29(1), 90–98. <https://doi.org/10.2135/cropsci1989.0011183X002900010023x>
- Singaas, E. L., Ort, D. R., & DeLucia, E. H. (2000). Diurnal regulation of photosynthesis in understory saplings. *New Phytologist*, 145(1), 39–49. <https://doi.org/10.1046/j.1469-8137.2000.00556.x>
- Singaas, E. L., Ort, D. R., & DeLucia, E. H. (2001). Variation in measured values of photosynthetic quantum yield in ecophysiological studies. *Oecologia*, 128(1), 15–23. <https://doi.org/10.1007/s004420000624>
- Skillman, J. B. (2008). Quantum yield variation across the three pathways of photosynthesis: Not yet out of the dark. *Journal of Experimental Botany*, 59(7), 1647–1661. <https://doi.org/10.1093/jxb/ern029>
- Smith, N. G., & Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO_2 . *Global Change Biology*, 19(1), 45–63. <https://doi.org/10.1111/j.1365-2486.2012.02797.x>

- Solomon, S., Plattner, G.-K., Knutti, R., & Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 106(6), 1704–1709. <https://doi.org/10.1073/pnas.0812721106>
- Song, Y., Li, C., Liu, L., Hu, P., Li, G., Zhao, X., & Zhou, H. (2023). The population genomic analyses of chloroplast genomes shed new insights on the complicated ploidy and evolutionary history in *Fragaria*. *Frontiers in Plant Science*, 13, 1065218. <https://doi.org/10.3389/fpls.2022.1065218>
- Song, Y., Yang, C., Gao, S., Zhang, W., Li, L., & Kuai, B. (2014). Age-triggered and dark-induced leaf senescence require the bHLH transcription factors PIF3, 4, and 5. *Molecular Plant*, 7(12), 1776–1787. <https://doi.org/10.1093/mp/ssu109>
- Srinivasan, V., Kumar, P., & Long, S. P. (2017). Decreasing, not increasing, leaf area will raise crop yields under global atmospheric change. *Global Change Biology*, 23(4), 1626–1635. <https://doi.org/10.1111/gcb.13526>
- Still, S., Hytönen, T., Saarinen, T., & Åström, H. (2023). Latitudinal origins of *Fragaria vesca* show adaptive variation in phenological, morphological and ecophysiological leaf traits associated with winter climate. *Flora*, 305, 152316. <https://doi.org/10.1016/j.flora.2023.152316>
- Stirbet, A., Lazar, D., Guo, Y., & Govindjee, G. (2020). Photosynthesis: Basics, history and modelling. *Annals of Botany*, 126(4), 511–537. <https://doi.org/10.1093/aob/mcz171>
- Stirling, C. M., Aguilera, C., Baker, N. R., & Long, S. P. (1994). Changes in the photosynthetic light response curve during leaf development of field grown maize with implications for modelling canopy photosynthesis. *Photosynthesis Research*, 42(3), 217–225. <https://doi.org/10.1007/BF00018264>
- Sun, H., Chen, Y., Gong, A., Zhao, X., Zhan, W., & Wang, M. (2014). Estimating mean air temperature using MODIS day and night land surface temperatures. *Theoretical and Applied Climatology*, 118(1–2), 81–92. <https://doi.org/10.1007/s00704-013-1033-7>
- Sun, J., Sun, R., Liu, H., Chang, L., Li, S., Zhao, M., Shennan, C., Lei, J., Dong, J., Zhong, C., Xue, L., Gao, Y., Wang, G., & Zhang, Y. (2021). Complete chloroplast genome sequencing of ten wild *Fragaria* species in China provides evidence for phylogenetic evolution of *Fragaria*. *Genomics*, 113(3), 1170–1179. <https://doi.org/10.1016/j.ygeno.2021.01.027>
- Sun, P., Mantri, N., Lou, H., Hu, Y., Sun, D., Zhu, Y., Dong, T., Lu, H., & Bernacchi, C. J. (2012). Effects of elevated CO₂ and temperature on yield and fruit quality of strawberry (*Fragaria × ananassa* Duch.) at two levels of nitrogen application. *PLoS One*, 7(7), e41000. <https://doi.org/10.1371/journal.pone.0041000>
- Sung, F. J. M., & Chen, J. J. (1991). Gas exchange rate and yield response of strawberry to carbon dioxide enrichment. *Scientia Horticulturae*, 48(3–4), 241–251. [https://doi.org/10.1016/0304-4238\(91\)90132-I](https://doi.org/10.1016/0304-4238(91)90132-I)
- Suzuki, R., & Takahashi, K. (2020). Effects of leaf age, elevation and light conditions on photosynthesis and leaf traits in saplings of two evergreen conifers, *Abies veitchii* and *A. mariesii*. *Journal of Plant Ecology*, 13(4), 460–469. <https://doi.org/10.1093/jpe/rtaa034>
- Svoboda, V., Oung, H. M. O., Koochak, H., Yarbrough, R., McKenzie, S. D., Puthiyaveetil, S., & Kirchhoff, H. (2023). Quantification of energy-converting protein complexes in plant thylakoid membranes. *Biochimica et Biophysica Acta – Bioenergetics*, 1864(2), 148945. <https://doi.org/10.1016/j.bbabi.2022.148945>
- Takeda, F., & Glenn, D. M. (1989). Hydathode anatomy and the relationship between guttation and plant water status in strawberry (*Fragaria × ananassa* Duch.). *Acta Horticulturae*, 265, 387–392. <https://doi.org/10.17660/ActaHortic.1989.265.58>
- Takeda, F., & Tworkoski, T. (1999). Effect of leaf age on photosynthesis, chlorophyll content, and SPAD-502 leaf greenness measurements in ‘Jewel’ strawberry. *Advances in Strawberry Research*, 18, 41–46.
- Tan, Z.-H., Zeng, J., Zhang, Y.-J., Slot, M., Gamo, M., Hirano, T., Kosugi, Y., da Rocha, H. R., Saleska, S. R., Goulden, M. L., Wofsy, S. C., Miller, S. D., Manzi, A. O., Nobre, A. D., de Camargo, P. B., & Restrepo-Coupe, N. (2017). Optimum air temperature for tropical forest photosynthesis: Mechanisms involved and implications for climate warming. *Environmental Research Letters*, 12(5), 054022. <https://doi.org/10.1088/1748-9326/aa6f97>
- Tang, S., Wang, X., He, M., Huang, L., Zhang, Y., Yang, H., & Piao, S. (2020). Global patterns and climate controls of terrestrial ecosystem light use efficiency. *Journal of Geophysical Research: Biogeosciences*, 125(12), e2020JG005908. <https://doi.org/10.1029/2020JG005908>
- Taylor, G., Garassino, F., Aarts, M. G. M., & Harbinson, J. (2023). Improving C₃ photosynthesis by exploiting natural genetic variation: *Hirschfeldia incana* as a model species. *Food and Energy Security*, 12(1), e420. <https://doi.org/10.1002/fes3.420>
- Tcherkez, G., & Limami, A. M. (2019). Net photosynthetic CO₂ assimilation: More than just CO₂ and O₂ reduction cycles. *New Phytologist*, 223(2), 520–529. <https://doi.org/10.1111/nph.15828>
- Terashima, I., & Hikosaka, K. (1995). Comparative ecophysiology of leaf and canopy photosynthesis. *Plant, Cell & Environment*, 18(10), 1111–1128. <https://doi.org/10.1111/j.1365-3040.1995.tb00623.x>
- Theeuwens, T. P. J. M., Logie, L. L., Harbinson, J., Aarts, M. G. M., & Kromdijk, J. (2022). Genetics as a key to improving crop photosynthesis. *Journal of Experimental Botany*, 73(10), 3122–3137. <https://doi.org/10.1093/jxb/erac076>
- Thompson, M., Gamage, D., Hirotsu, N., Martin, A., & Seneweera, S. (2017). Effects of elevated carbon dioxide on photosynthesis and carbon partitioning: A perspective on root sugar sensing and hormonal crosstalk. *Frontiers in Physiology*, 8, 578. <https://doi.org/10.3389/fphys.2017.00578>
- Timm, H. C., Stegemann, J., & Küppers, M. (2002). Photosynthetic induction strongly affects the light compensation point of net photosynthesis and coincidentally the apparent quantum yield. *Trees*, 16(1), 47–62. <https://doi.org/10.1007/s004680100123>
- Van Ommen Kloeke, A. E. E., Douma, J. C., Ordoñez, J. C., Reich, P. B., & Van Bodegom, P. M. (2012). Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. *Global Ecology and Biogeography*, 21(2), 224–235. <https://doi.org/10.1111/j.1466-8238.2011.00667.x>
- Vemmos, S. N. (1994). Net photosynthesis, stomatal conductance, chlorophyll content and specific leaf weight of pistachio trees (cv. Aegenes) as influenced by fruiting. *Journal of Horticultural Science*, 69(5), 775–782. <https://doi.org/10.1080/14620316.1994.11516512>
- Venzhik, Y., Deryabin, A., & Moshkov, I. (2023). Adaptive strategy of plant cells during chilling: Aspect of ultrastructural reorganization. *Plant Science*, 332, 111722. <https://doi.org/10.1016/j.plantsci.2023.111722>

- Vogel, E., Donat, M. G., Alexander, L. V., Meinshausen, M., Ray, D. K., Karoly, D., Meinshausen, N., & Frieler, K. (2019). The effects of climate extremes on global agricultural yields. *Environmental Research Letters*, 14(5), 054010. <https://doi.org/10.1088/1748-9326/ab154b>
- Wada, Y., Soeno, T., & Inaba, Y. (2010). Effects of light and temperature on photosynthetic enhancement by high CO₂ concentration of strawberry cultivar Tochiotome leaves under forcing or half-forcing culture. *Japanese Journal of Crop Science*, 79(2), 192–197. <https://doi.org/10.1626/jcs.79.192>
- Walker, A. P., De Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R. F., McMahon, S. M., Medlyn, B. E., Moore, D. J. P., Norby, R. J., Zaehle, S., Anderson-Teixeira, K. J., Battipaglia, G., Brienen, R. J. W., Cabugao, K. G., Cailleret, M., Campbell, E., Canadell, J. G., and Whelan, M. E. (2021). Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂. *New Phytologist*, 229(5), 2413–2445. <https://doi.org/10.1111/nph.16866>
- Wang, D., Wang, H., Wang, P., Ling, T., Tao, W., & Yang, Z. (2019). Warming treatment methodology affected the response of plant ecophysiological traits to temperature increases: A quantitative meta-analysis. *Frontiers in Plant Science*, 10, 957. <https://doi.org/10.3389/fpls.2019.00957>
- Wang, F., Zhan, C., & Zou, L. (2023a). Risk of crop yield reduction in China under 1.5 °C and 2 °C global warming from CMIP6 models. *Foods*, 12(2), 413. <https://doi.org/10.3390/foods12020413>
- Wang, H., Zhao, Y., Zhang, Z., Gao, Y., Zhao, S., & He, F. (2010). Photosynthesis of two walnut cultivars as influenced by fruiting. *Acta Horticulturae*, 861, 297–302. <https://doi.org/10.17660/ActaHortic.2010.861.40>
- Wang, S., Xie, W., & Yan, X. (2022a). Effects of future climate change on citrus quality and yield in China. *Sustainability*, 14(15), 9366. <https://doi.org/10.3390/su14159366>
- Wang, S., Zhang, Y., Ju, W., Chen, J. M., Cescatti, A., Sardans, J., Janssens, I. A., Wu, M., Berry, J. A., Campbell, J. E., Fernández-Martínez, M., Alkama, R., Sitch, S., Smith, W. K., Yuan, W., He, W., Lombardozzi, D., Kautz, M., and Goll, D. S. (2021). Response to comments on “Recent global decline of CO₂ fertilization effects on vegetation photosynthesis”. *Science*, 373(6562), eabg7484. <https://doi.org/10.1126/science.abg7484>
- Wang, S., Zhang, Y., Ju, W., Chen, J. M., Ciaia, P., Cescatti, A., Sardans, J., Janssens, I. A., Wu, M., Berry, J. A., Campbell, E., Fernández-Martínez, M., Alkama, R., Sitch, S., Friedlingstein, P., Smith, W. K., Yuan, W., He, W., and Goll, D. S. (2020a). Recent global decline of CO₂ fertilization effects on vegetation photosynthesis. *Science*, 370(6522), 1295–1300. <https://doi.org/10.1126/science.abb7772>
- Wang, S., Zhang, Y., Ju, W., Wu, M., Liu, L., He, W., & Peñuelas, J. (2022b). Temporally corrected long-term satellite solar-induced fluorescence leads to improved estimation of global trends in vegetation photosynthesis during 1995–2018. *ISPRS Journal of Photogrammetry and Remote Sensing*, 194, 222–234. <https://doi.org/10.1016/j.isprsjprs.2022.10.018>
- Wang, S. Y., & Camp, M. J. (2000). Temperatures after bloom affect plant growth and fruit quality of strawberry. *Scientia Horticulturae*, 85(3), 183–199. [https://doi.org/10.1016/S0304-4238\(99\)00143-0](https://doi.org/10.1016/S0304-4238(99)00143-0)
- Wang, T., Huang, D., Chen, B., Mao, N., Qiao, Y., & Ji, M. (2018). Differential expression of photosynthesis-related genes in pentaploid interspecific hybrid and its decaploid of *Fragaria* spp. *Genes & Genomics*, 40(3), 321–331. <https://doi.org/10.1007/s13258-018-0647-7>
- Wang, X., Zhao, C., Müller, C., Wang, C., Ciaia, P., Janssens, I., Peñuelas, J., Asseng, S., Li, T., Elliott, J., Huang, Y., Li, L., & Piao, S. (2020b). Emergent constraint on crop yield response to warmer temperature from field experiments. *Nature Sustainability*, 3(11), 908–916. <https://doi.org/10.1038/s41893-020-0569-7>
- Wang, X.-Q., Zeng, Z.-L., Shi, Z.-M., Wang, J.-H., & Huang, W. (2023b). Variation in photosynthetic efficiency under fluctuating light between rose cultivars and its potential for improving dynamic photosynthesis. *Plants*, 12(5), 1186. <https://doi.org/10.3390/plants12051186>
- Wang, Z., & Wang, C. (2022). Interactive effects of elevated temperature and drought on plant carbon metabolism: A meta-analysis. *Global Change Biology*, 29(10), 2824–2835. <https://doi.org/10.1111/gcb.16639>
- Watkins, C. A., Roberts, I. M., & Jones, A. T. (1992). Ultrastructural changes associated with June yellows in strawberry and with leaf yellowing symptoms of viral and genetic origin in *Fragaria*, *Rubus* and *Ribes*. *Annals of Applied Biology*, 121(1), 151–160. <https://doi.org/10.1111/j.1744-7348.1992.tb03995.x>
- Weber, C. A. (2021a). Performance of strawberry varieties developed for perennial matted-row production in annual plasticulture in a cold climate region. *Agronomy*, 11(7), 1407. <https://doi.org/10.3390/agronomy11071407>
- Weber, C. A. (2021b). Strawberry crown plugs provide flexibility and improved performance in cold climate plasticulture production. *Agronomy*, 11(8), 1635. <https://doi.org/10.3390/agronomy11081635>
- Wilcox, J., & Makowski, D. (2014). A meta-analysis of the predicted effects of climate change on wheat yields using simulation studies. *Field Crops Research*, 156, 180–190. <https://doi.org/10.1016/j.fcr.2013.11.008>
- Wright, C. J., & Sandrang, A. K. (1995). Efficiency of light utilization in the strawberry (*Fragaria* × *ananassa*) cv *Hapil*. *Journal of Horticultural Science*, 70(5), 705–711. <https://doi.org/10.1080/14620316.1995.11515345>
- Wu, C. C., Yen, Y. H., Chang, M. Y., & Fang, W. (2012). Effects of light quality and CO₂ concentration on diurnal photosynthetic characteristics of strawberry. *Acta Horticulturae*, 956, 247–253. <https://doi.org/10.17660/ActaHortic.2012.956.27>
- Wu, G., Jiang, Q., Bai, Y., Tian, C., Pan, W., Jin, X., & Zhang, B. (2020). Nitrogen status assessment for multiple cultivars of strawberries using portable NIR spectrometers combined with cultivar recognition and multivariate analysis. *International Electrical and Electronic Engineering Access*, 8, 126039–126050. <https://doi.org/10.1109/ACCESS.2020.3007862>
- Wu, J., Abudurehman, R., Zhong, H., Yadav, V., Zhang, C., Ma, Y., Liu, X., Zhang, F., Zha, Q., & Wang, X. (2023). The impact of high temperatures in the field on leaf tissue structure in different grape cultivars. *Horticulturae*, 9(7), 731. <https://doi.org/10.3390/horticulturae9070731>
- Wujeska-Klaue, A., Crous, K. Y., Ghannoum, O., & Ellsworth, D. S. (2019). Leaf age and eCO₂ both influence photosynthesis by increasing light harvesting in mature *Eucalyptus tereticornis* at UucFACE. *Environmental and Experimental Botany*, 167, 103857. <https://doi.org/10.1016/j.envexpbot.2019.103857>
- Wullschleger, S. D. (1993). Biochemical limitations to carbon assimilation in C₃ plants—A retrospective analysis of the A/Ci curves from 109 species. *Journal of Experimental Botany*, 44(5), 907–920. <https://doi.org/10.1093/jxb/44.5.907>

- Xu, C., Shen, M.-Y., Wang, M.-T., Yang, Z.-Q., Han, W., & Zheng, S.-H. (2021). Modification of strawberry dry matter accumulation model under short-term high temperature conditions at seedling stage. *Chinese Journal of Agrometeorology*, 42(7), 572–582. <https://doi.org/10.3969/j.issn.1000-6362.2021.07.00>
- Xu, X., Sun, Y., & Liu, F. (2022). Modulating leaf thickness and calcium content impact on strawberry plant thermo-tolerance and water consumption. *Plant Growth Regulation*, 98(3), 539–556. <https://doi.org/10.1007/s10725-022-00884-z>
- Yamaguchi, D. P., Mishima, D., Nakamura, K., Sano, J., Nakaji, T., Hiura, T., & Hikosaka, K. (2019). Limitation in the photosynthetic acclimation to high temperature in canopy leaves of *Quercus serrata*. *Frontiers in Forests and Global Change*, 2, 19. <https://doi.org/10.3389/ffgc.2019.00019>
- Yan, H., Wang, S. Q., Wang, J. B., & Shugart, H. H. (2020). Changes of light components and impacts on interannual variations of photosynthesis in China over 2000–2017 by using a two-leaf light use efficiency model. *Journal of Geophysical Research: Biogeosciences*, 125(12), e2020JG005735. <https://doi.org/10.1029/2020JG005735>
- Yan, Z., Sardans, J., Peñuelas, J., Detto, M., Smith, N. G., Wang, H., Guo, L., Hughes, A. C., Guo, Z., Lee, C. K. F., Liu, L., & Wu, J. (2023). Global patterns and drivers of leaf photosynthetic capacity: The relative importance of environmental factors and evolutionary history. *Global Ecology and Biogeography*, 32(5), 668–682. <https://doi.org/10.1111/geb.13660>
- Yang, J., Song, J., & Jeong, B. R. (2022). Side lighting enhances morphophysiology and runner formation by upregulating photosynthesis in strawberry grown in controlled environment. *Agronomy*, 12(1), 24. <https://doi.org/10.3390/agronomy12010024>
- Yang, J., Su, D., Wei, S., Chen, S., Lou, Z., Shen, X., Zhang, Z., Jamil, A., Tong, J., & Cui, X. (2020). Current and future potential distribution of wild strawberry species in the biodiversity hotspot of Yunnan Province, China. *Agronomy*, 10(7), 959. <https://doi.org/10.3390/agronomy10070959>
- Ye, Z.-P., & Yu, Q. (2008). Comparison of new and several classical models of photosynthesis in response to irradiance. *Chinese Journal of Plant Ecology*, 32(6), 1356–1361. <https://doi.org/10.3773/j.issn.1005-264x.2008.06.016>
- Yin, X., & Leng, G. (2022). Observational constraint of process crop models suggests higher risks for global maize yield under climate change. *Environmental Research Letters*, 17(7), 074023. <https://doi.org/10.1088/1748-9326/ac7ac7>
- Yokoyama, G., Ono, S., Yasutake, D., Hidaka, K., & Hirota, T. (2023). Diurnal changes in the stomatal, mesophyll, and biochemical limitations of photosynthesis in well-watered greenhouse-grown strawberries. *Photosynthetica*, 61(1), 1–12. <https://doi.org/10.32615/ps.2023.001>
- Yoshida, Y., & Morimoto, Y. (1997). Measurement, modeling and seasonal changes of canopy photosynthesis in 'Nyoho' strawberry. *Acta Horticulturae*, 439, 575–582. <https://doi.org/10.17660/ActaHortic.1997.439.96>
- Yousefi, S., Eshghi, S., & Jamali, B. (2023). Evaluation of yield, biochemical characteristics and nutrient composition of 'Camarosa' strawberry in response to different K/N ratios. *Journal of Berry Research*, 13(2), 95–106. <https://doi.org/10.3233/JBR-220056>
- Yuan, Y., Ge, L., Yang, H., & Ren, W. (2018). A meta-analysis of experimental warming effects on woody plant growth and photosynthesis in forests. *Journal of Forestry Research*, 29(3), 727–733. <https://doi.org/10.1007/s11676-017-0499-z>
- Zaka, S., Frak, E., Julier, B., Gastal, F., & Louarn, G. (2016). Intraspecific variation in thermal acclimation of photosynthesis across a range of temperatures in a perennial crop. *AoB Plants*, 8, lw035. <https://doi.org/10.1093/aob/pla/plw035>
- Zareei, E., Karami, F., Gholami, M., Ershadi, A., Avestan, S., Aryal, R., Gohari, G., & Farooq, M. (2021). Physiological and biochemical responses of strawberry crown and leaf tissues to freezing stress. *BMC Plant Biology*, 21(1), 532. <https://doi.org/10.1186/s12870-021-03300-2>
- Zeng, W., Zhou, G. S., Jia, B. R., Jiang, Y. L., & Wang, Y. (2010). Comparison of parameters estimated from A/C_i and A/C_c curve analysis. *Photosynthetica*, 48(3), 323–331. <https://doi.org/10.1007/s11099-010-0042-3>
- Zenkeler, E., & Borkowska, B. (2002). The photosynthetic status of in vitro strawberry shoots. *Acta Horticulturae*, 567, 309–312. <https://doi.org/10.17660/ActaHortic.2002.567.65>
- Zhang, J., Deng, L., Jiang, H., Peng, C., Huang, C., Zhang, M., & Zhang, X. (2021). The effects of elevated CO₂, elevated O₃, elevated temperature, and drought on plant leaf gas exchanges: A global meta-analysis of experimental studies. *Environmental Science and Pollution Research*, 28(12), 15274–15289. <https://doi.org/10.1007/s11356-020-11728-6>
- Zhang, L., Hu, Z., Fan, J., Zhou, D., & Tang, F. (2014). A meta-analysis of the canopy light extinction coefficient in terrestrial ecosystems. *Frontiers of Earth Science*, 8(4), 599–609. <https://doi.org/10.1007/s11707-014-0446-7>
- Zhang, L.-M., Yu, G.-R., Sun, X.-M., Wen, X.-F., Ren, C.-Y., Fu, Y.-L., Li, Q.-K., Li, Z.-Q., Liu, Y.-F., Guan, D.-X., & Yan, J.-H. (2006). Seasonal variations of ecosystem apparent quantum yield (α) and maximum photosynthesis rate (P_{max}) of different forest ecosystems in China. *Agricultural and Forest Meteorology*, 137(3–4), 176–187. <https://doi.org/10.1016/j.agrformet.2006.02.006>
- Zhang, T., He, Y., DePauw, R., Jin, Z., Garvin, D., Yue, X., Anderson, W., Li, T., Dong, X., Zhang, T., & Yang, X. (2022). Climate change may outpace current wheat breeding yield improvements in North America. *Nature Communications*, 13(1), 5591. <https://doi.org/10.1038/s41467-022-33265-1>
- Zhang, X., Yang, W., Tahir, M. M., Chen, X., Saudreau, M., Zhang, D., & Costes, E. (2023a). Contributions of leaf distribution and leaf functions to photosynthesis and water-use efficiency from leaf to canopy in apple: A comparison of interstocks and cultivars. *Frontiers in Plant Science*, 14, 1117051. <https://doi.org/10.3389/fpls.2023.1117051>
- Zhang, Y., Zhao, Y., Wang, C., & Chen, S. (2017). Using statistical model to simulate the impact of climate change on maize yield with climate and crop uncertainties. *Theoretical and Applied Climatology*, 130(3–4), 1065–1071. <https://doi.org/10.1007/s00704-016-1935-2>
- Zhang, Z., Cescatti, A., Wang, Y.-P., Gentile, P., Xiao, J., Guanter, L., Huete, A. R., Wu, J., Chen, J. M., Ju, W., Peñuelas, J., & Zhang, Y. (2023b). Large diurnal compensatory effects mitigate the response of Amazonian forests to atmospheric warming and drying. *Science Advances*, 9(21), eabq4974. <https://doi.org/10.1126/sciadv.abq4974>
- Zhao, W., Zhao, H., Wang, H., & He, Y. (2022). Research progress on the relationship between leaf senescence and quality, yield and stress resistance in horticultural plants. *Frontiers in Plant Science*, 13, 1044500. <https://doi.org/10.3389/fpls.2022.1044500>
- Zheng, F.-Y., & Peng, S.-L. (2001). Meta-analysis of the response of plant ecophysiological variables to double

- atmospheric CO₂ concentrations. *Acta Botanica Sinica*, 43(11), 1101–1109.
- Zheng, T., Yu, Y., Kang, H., & Chaves, M. (2022). Short-term elevated temperature and CO₂ promote photosynthetic induction in the C₃ plant *Glycine max*, but not in the C₄ plant *Amaranthus tricolor*. *Functional Plant Biology*, 49(11), 995–1007. <https://doi.org/10.1071/FP21363>
- Zheng, Y., Li, F., Hao, L., Yu, J., Guo, L., Zhou, H., Ma, C., Zhang, X., & Xu, M. (2019). Elevated CO₂ concentration induces photosynthetic down-regulation with changes in leaf structure, non-structural carbohydrates and nitrogen content of soybean. *BMC Plant Biology*, 19(1), 255. <https://doi.org/10.1186/s12870-019-1788-9>
- Zheng, Z., Zhang, Y., Zhu, J., & Cong, N. (2021). Daytime temperature contributes more than nighttime temperature to the weakened relationship between climate warming and vegetation growth in the extratropical northern hemisphere. *Ecological Indicators*, 131, 108203. <https://doi.org/10.1016/j.ecolind.2021.108203>
- Zhou, H., Akçay, E., & Helliker, B. R. (2019). Estimating C₄ photosynthesis parameters by fitting A/C_i curves. *Photosynthesis Research*, 141(2), 181–194. <https://doi.org/10.1007/s11120-019-00619-8>
- Zhou, H., Xu, M., Hou, R., Zheng, Y., Chi, Y., & Ouyang, Z. (2018). Thermal acclimation of photosynthesis to experimental warming is season-dependent for winter wheat (*Triticum aestivum* L.). *Environmental and Experimental Botany*, 150, 249–259. <https://doi.org/10.1016/j.envexpbot.2018.04.001>
- Zhou, Y., Xiong, J., Shu, Z., Dong, C., Gu, T., Sun, P., He, S., Jiang, M., Xia, Z., Xue, J., Khan, W. U., Chen, F., & Cheng, Z.-M. (2023). The telomere-to-telomere genome of *Fragaria vesca* reveals the genomic evolution of *Fragaria* and the origin of cultivated octoploid strawberry. *Horticulture Research*, 10(4), uhad027. <https://doi.org/10.1093/hr/uhad027>
- Zhou, Y., Xu, L., Xu, Y., Xi, M., Tu, D., Chen, J., & Wu, W. (2021). A meta-analysis of the effects of global warming on rice and wheat yields in a rice–wheat rotation system. *Food and Energy Security*, 10(4), e316. <https://doi.org/10.1002/fes3.316>
- Zhu, P., Burney, J., Chang, J., Jin, Z., Mueller, N. D., Xin, Q., Xu, J., Yu, L., Makowski, D., & Ciais, P. (2022). Warming reduces global agricultural production by decreasing cropping frequency and yields. *Nature Climate Change*, 12(11), 1016–1023. <https://doi.org/10.1038/s41558-022-01492-5>
- Zhu, P., Zhuang, Q., Welp, L., Ciais, P., Heimann, M., Peng, B., Li, W., Bernacchi, C., Roedenbeck, C., & Keenan, T. F. (2019). Recent warming has resulted in smaller gains in net carbon uptake in northern high latitudes. *Journal of Climate*, 32(18), 5849–5863. <https://doi.org/10.1175/JCLI-D-18-0653.1>