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# Temperatures above 30°C decrease leaf growth in strawberry under global warming

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## ABSTRACT

Productivity in strawberry is dependent on carbon assimilation in the leaves. The main scenarios for climate change include an increase in the concentration of CO<sub>2</sub> in the atmosphere and an increase in temperature. This review examined the relationship between leaf growth and temperature in strawberry. Leaf growth follows a linear, sigmoid or Gaussian pattern over the season or is variable depending on the weather. There was a linear increase in leaf growth with temperatures below 26°C, and a linear decrease in growth with temperatures above 26°C. In other studies, the mean lower optimum for 90% of maximum growth was 18.3° ± 3.9°C, the median was 19.6°C, and the range was from 7.2° to 22.0°C (N = 11). The mean higher optimum was 27.3° ± 3.6°C, the median was 27.4°C, and the range was from 21.1° to 33.5°C (N = 12). Leaf growth was higher under 30°C and lower above 30°C. Limited studies suggest that elevated CO<sub>2</sub> will not counteract the impact of high temperatures on growth. Climate change will increase leaf growth in cool areas and decrease growth in warm areas. The decrease in leaf growth in locations with temperatures above 30°C will contribute to lower yields under global warming.

## ARTICLE HISTORY

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## KEYWORDS

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

## Introduction

One of the unique features of land plants is their ability to produce new leaves from the shoot apical meristem (Ambrose & Ferrándiz, 2013; Byrne & Katsanis, 2006; Manuela & Xu, 2020; Xue et al., 2020). In most species, the leaves are the main site for the photosynthesis that drives the growth of new tissues. The morphology and anatomy of leaves varies across species and ecosystems (Bhatia et al., 2021; Castro Sánchez-Bermejo et al., 2023; Dong & He, 2019; Kobayashi et al., 2020; Nakayama et al., 2023; Peng et al., 2023; Runions et al., 2017; Zhou & Lin, 2023). Li et al. (2017) proposed that the evolution resulted in optimum combinations of different leaf traits that were better adapted to the environment.

Strawberry (*Fragaria ×ananassa* Duch.) is one of the most important fruit crops grown around the globe. Total production is 14.5 million tonnes each year, with China, the United States, Egypt, Mexico, Turkey and Spain all major producers (Fan et al., 2022; Guevara-Terán et al., 2023; Hummer et al., 2023; Lu et al., 2023b; Wu et al., 2020). Overall, 43% of production is in Asia, 27% in the Americas and 24% in Europe. In Africa, Egypt ranks first with 468,248 tonnes per year. In Central and South America, Mexico (557,514 tonnes) and Brazil (218,881 tonnes) are the largest producers. Cultivation is concentrated in the northern hemisphere and accounts for 98% of the crop (Ngouana et al.,


2023). There are no genetic or climatic issues restricting cultivation in the southern hemisphere. The total value of the crop across the globe is US\$14 billion (Hernández-Martínez et al., 2023b).

There is a range of cultivars, including those that are adapted to cold winters and frosts in spring or heat in summer (Dash et al., 2023; Faehn et al., 2023; Gambardella et al., 2021; Knapp et al., 2023; Krüger et al., 2012; Łysiak & Szot, 2023; Mbarushimana et al., 2022; Patel et al., 2023; Roussos et al., 2020; Salimi et al., 2024; Van Delm et al., 2017). Cultivars vary in their need for chilling for flower initiation and the time of flowering and ripening (Cockerton et al., 2023; Hummer et al., 2023; James et al., 2022; Read et al., 2023; Toda et al., 2023). Most of the production is focused in areas with a temperate or Mediterranean climate, between latitudes 28° and 60°N, with average temperatures in mid-summer of 15° to 30°C.

The genus *Fragaria* includes several other species such as *F. vesca*, *F. pentaphylla*, *F. chiloensis* and *F. virginiana* which are grown commercially or have contributed to the improvement of common strawberry (Bird et al., 2021; Chini et al., 2023; De Kort et al., 2022; Fan & Whitaker, 2024; López et al., 2022; Ma et al., 2023; Pincot et al., 2021; Porter et al., 2023; Qiao et al., 2021; Still et al., 2023; Zhang et al., 2023b). The United States Department of Agriculture at Corvallis in

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Oregon has 2,013 active strawberry accessions, representing 46 taxa, including species and subspecies (Diaz-Lara et al., 2021). New species are still being described (e.g. *F. emeiensis* by Qiao et al., 2021).

Climate change has increased the temperature and the concentration of CO<sub>2</sub> in the atmosphere in the last 100 years compared with earlier periods (Dusenge et al., 2019; Eller et al., 2020). These changes in environmental conditions affect the growth and yield of crop and wild plants.

There is a strong relationship between yield and leaf production in strawberry. Sproat et al. (1936) removed leaves from four cultivars in Maryland, United States in September and counted the number of leaves and berries produced on the plants to June. There were positive linear relationships between yield and the number of leaves per plant ( $p = 0.001$  to 0.020,  $R^2$ s = 0.73 to 0.88). No optimum leaf production was established, with yield increasing with the maximum number of leaves in each cultivar. The cultivars produced 1.1 to 2.8 berries per leaf. Casierra-Posada et al. (2013) examined the effect of defoliation on yield in a greenhouse in Tunja, Colombia. One or two leaflets were removed from each compound leaf as they emerged to attain a 38 or 67% reduction in the leaf area per plant. The light defoliation decreased yield by 24% compared with the control, while the severe defoliation decreased yield by 50%. High temperatures can have a direct effect on the yield of strawberry by reducing fruit weight (Le Mièrre et al., 1998; Menzel, 2021, 2023). Productivity is also dependent on the initiation of new crowns and flowers (Menzel, 2022).

This review examines leaf growth in strawberry. The main objective of the review was to determine the relationship between growth and temperature. Information was collected to examine whether high concentrations of CO<sub>2</sub> under climate change will counteract the impacts of high temperatures on growth. The effects of climate change on leaf growth in different growing areas is discussed.

### Initiation and development of the leaves in strawberry

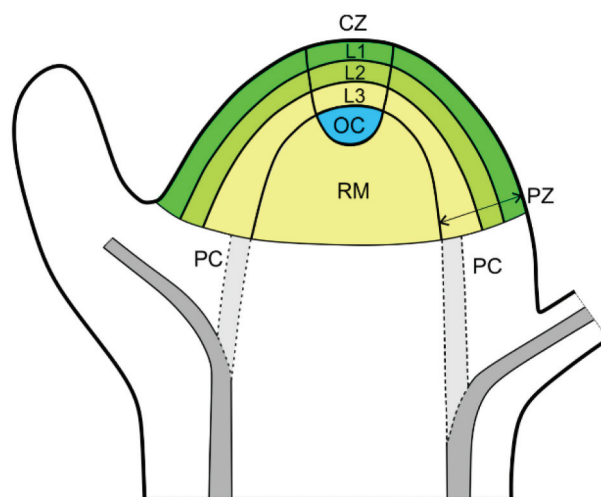
Leaf development in strawberry varies with the species, cultivar and environment. The cultivated (*F. ×anannassa*) and woodland strawberries (*F. vesca*) have trifoliate leaves, which consist of a terminal leaflet flanked by a pair of symmetrical lateral leaflets and have long petioles (Han & Kang, 2023; Lu et al., 2023a; Pi et al., 2023). The wild species, *F. pentaphylla* from south-west China has three major leaflets and two smaller ones, for a total of five leaflets (Chatterjee et al., 2011).

New tissues develop from meristems in plants (Banasiak & Gola, 2023; Erickson & Michelini, 1957). In strawberry and other plants, the shoot apical

meristem (SAM) is located at the tip of the growing stem and is comprised of a central zone (CZ), an organising centre (OC) and a peripheral zone (PZ) (Banasiak & Gola, 2023; Figure 1; Li et al., 2019). The outermost cell layers of the SAM (L1 and L2) and the inner meristem are termed the tunica and the corpus, respectively (Guo et al., 2022; Pernisová & Vernoux, 2021). Cells in the central zone divide at a low rate and remain in an undifferentiated state (Kalve et al., 2014). In contrast, cells in the peripheral zone divide faster and differentiate into leaves, axillary nodes and flowers.

In strawberry, the SAM remains vegetative producing new leaf primordia and branches or branch crowns (Hou & Huang, 2005; Wang et al., 2023). Alternatively, it differentiates into a terminal inflorescence (Fan et al., 2022; Lembinen et al., 2023; Samad et al., 2022). The plants have axillary buds (AXBs) in the axils of the leaves (Qiu et al., 2019; Zhu & Wagner, 2020; Andrés et al., 2021; Muñoz-Avila et al., 2022; Labadie et al., 2023a, Labadie et al., 2023b). These buds remain dormant or produce branch crowns or stolons. The vegetative SAM has little swelling, whereas the first evidence of floral initiation is characterised by a mounding of the apex (Kurokura et al., 2006; Manakasem & Goodwin, 1998).

The SAM is buried by the young leaves and is surrounded by a young leaf primordium. Leaf development is separated into three stages, including initiation, morphogenesis and differentiation (Dengler & Tsukaya, 2001; Efroni et al., 2010; Poethig, 1997). These stages correspond to the leaf primordia



**Figure 1.** Diagram of the shoot apical meristem (SAM) in the model plant *Arabidopsis*, showing structural and functional zonation. L1 and L2 refer to the layers of the initial cells giving rise to two tunica layers shown in green and L3 to the internal layer of the initial cells for the corpus shown in yellow. Vascular strands are shown in grey. The procambium which reaches the internal parts of the peripheral zone of the meristem is shown in light grey. Differentiating vascular traces are shown in dark grey. CZ = central zone; OC = organising centre; PC = procambium; PZ = peripheral (organogenic) zone; and RM = rib meristem. From Banasiak and Gola (2023).

emerging from the SAM, outgrowth of leaf margins, and rapid expansion of the leaf blade and maturation. Pi et al. (2023) described early leaf development in *F. vesca*. A leaf primordium is initiated first, followed by two stipule primordia and two leaflet primordia. Trichomes were initiated on the adaxial or upper side of the leaves. Later, serrations appeared on the margins of the leaflets. The basic morphology of the leaf was established at this stage. Carisse and Bouchard (2010) divided leaf growth in strawberry into seven stages from the new leaf completely folded (Stage 1) to the leaf fully expanded and mature (Stage 7). Asalf et al. (2014) had a similar description of development from the leaflets light green and not separated (Stage 1) to the leaflets fully expanded and dark green (Stage 7). There is competition between the new tissues in the SAM. Arney (1968) demonstrated that removing some of the leaf primordia of strawberry accelerated cell division and the initiation of new leaves at the apex. Leaves emerged every  $12.2 \pm$  days in intact plants compared with  $6.0 \pm 2.8$  days where three or four older leaves were removed.

The interval between successive leaf primordia varies with the environment, especially the photoperiod and temperature. Arney (1953b) showed that new leaves emerged every  $8.7 \pm 0.6$  days to  $17.6 \pm 1.3$  days across three experiments in the United Kingdom. The temperature ranged from  $4.4^\circ$  to  $23.9^\circ\text{C}$  during these studies. Bodson and Verhoeven (2005) indicated that new leaves emerged every 7.5 days in a chamber in Belgium. Several authors have reported that the rate of leaf emergence was constant over the season in Brazil (e.g. Rosa et al., 2011; Mendonça et al., 2012c; Cocco et al., 2016; Diel et al., 2017a, 2017b). In these experiments, the rate of leaf emergence was expressed on a thermal time basis (degree-days). In an experiment in chambers in Taiwan, a new leaf emerged every 14.8 to 20.9 days, with warm days slowing leaf emergence (Wang & Chen, 2022).

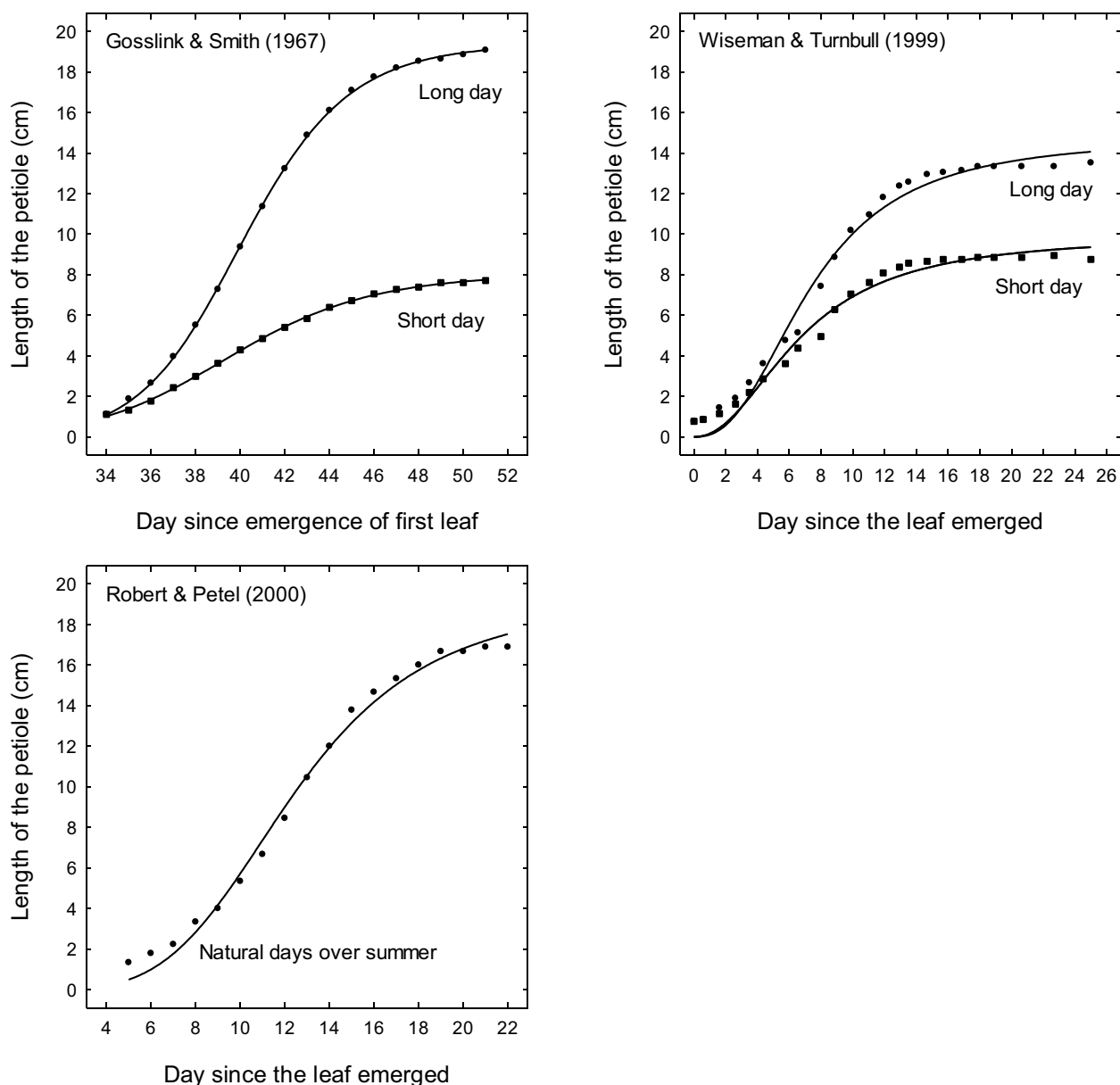
Leaf development can be assessed by calculating the plastochron index or the phyllochron, with confusion in the literature between the two indices (Meicenheimer, 2014; Nosaka-Takahashi et al., 2022). In some studies, they are used interchangeably. The plastochron index (PI) or phyllotaxis index was developed by Erickson and Michelini (1957) and estimates the stage of development for leaf primordia, expanding leaves or other tissues (Ade Ademilua & Botha, 2005; Lee et al., 2009; Meicenheimer, 2014). In plants, the phyllochron is defined as the interval between emergence of successive leaves along a growing axis (Fournier et al., 2005; Itoh & Sano, 2006; Plancade et al., 2023; Wilhelm & McMaster, 1995). The time between successive leaves is calculated in days or in degree-days (Martins et al., 2023). The interval is not constant over the season and varies with

the growth stage, environment and cultivation practices (e.g. Davidson et al., 2015, 2017, 2019 in peach).

The growth of individual leaves and their relationship with cell division and expansion have been explored in strawberry (Arney, 1954; Arney 1955, 1956; Gosselink & Smith, 1967; Guttridge & Thompson, 1959, 1963; Nishizawa, 1990, 1992, 1994; Robert & Pétel, 2000; Wiseman & Turnbull, 1999). The results of these experiments indicate that leaf growth involves changes in cell division and cell expansion. Overall, cell expansion is more important than cell division. Changes in the growth of the leaves or individual sections of a leaf follow a sigmoid pattern, with longer petioles under long photoperiods than under short photoperiods (Figure 2) and under high than low  $\text{CO}_2$  (Li et al., 2020). Gosselink and Smith (1967) grew 'Sparkle' under short or long days (12 or 14 h) in a greenhouse with the night temperature set at  $21^\circ \pm 1^\circ\text{C}$ . Wiseman and Turnbull (1999) grew 'Earlisweet' in growth chambers under short or long days (8 or 16 h) at  $25^\circ/20^\circ\text{C}$ . Robert and Pétel (2000) grew 'Elsanta' outside in France under a natural photoperiod during summer.

There are changes in the rates of cell division and enlargement as the leaves of strawberry develop and differences between successive leaves and between parts of a leaf. Arney (1953a, 1954) proposed that elongation of the leaves was dependent on both the number and size of the cells in the petiole. However, cell division was more important. Initial growth mainly involved cell division, while growth after emergence mainly involved cell enlargement. The size of the leaves was related to the duration of cell division. Short days decreased the size of the leaves by curtailing the period of cell division (Arney, 1968). Temperatures below  $7^\circ\text{C}$  decreased the size of leaves by decreasing cell enlargement and less importantly the rate of cell division. The longer petioles under low light compared with high light ( $\times 1.30$ ) in strawberry reflected increases in both the number of epidermis cells ( $\times 1.21$ ) and the length of the cells ( $\times 1.16$ ) (Guttridge & Thompson, 1959). Furthermore, long petioles were produced under long days compared with short days (Nishizawa, 1990, 1992, 1994) (Table 1). This response reflected increases in both cell division and cell expansion, with the response depending on when the new leaves emerged. Robert and Pétel (2000) examined the growth of 'Elsanta' strawberry in an open field in France. They showed that elongation of the petiole was primarily due to cell multiplication which took place in the upper part of the petiole. In contrast, the increase in the diameter of the petiole was mainly due to increases in the size of the parenchyma cells.

The life-span of leaves varies across species and growing conditions (Kikuzawa et al., 2013). Arney (1947) demonstrated that the leaves of commercial strawberry



**Figure 2.** Changes in the elongation of the leaf petiole in strawberry. There were dose-logistic relationships between growth and time ( $p < 0.001$ ,  $R^2$ s = 0.97 to 0.99). Data are from Gosslink and Smith (1967), Wiseman and Turnbull (1999) and Robert and Pétel (2000).

**Table 1.** Effect of photoperiod on the changes in petiole elongation, epidermal cell length and the number of epidermal cells in 'Donner' strawberry in Japan. Data on the number of epidermal cells were obtained from dividing the length of the petiole by the length of the epidermal cells.

| Leaf    | Photoperiod | Length of petiole (cm) | Length of epidermal cell ( $\mu\text{m}$ ) | Number of epidermal cells |
|---------|-------------|------------------------|--|---------------------------|
| Leaf 9  | 9 h         | 9.8                    | 11.6                                       | 845                       |
|         | 16 h        | 14.7**                 | 17.8**                                     | 846                       |
| Leaf 10 | 9 h         | 9.7                    | 10.8                                       | 915                       |
|         | 16 h        | 18.8**                 | 17.0**                                     | 1121*                     |
| Leaf 11 | 9 h         | 9.2                    | 9.0  | 1017                      |
|         | 16 h        | 18.3**                 | 14.9**                                     | 1245*                     |

Differences between paired means are indicated (\*\*equals  $p < 0.01$  and \* equals  $p < 0.05$ ). Data are from Nishizawa (1994).

turned yellow after  $87.0 \pm 20.1$  days in Southampton in the United Kingdom, the median time was 84.5 days, and the range was from 55.0 to 126.0 days. Jurik and Chabot (1986) reported 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.

Shiklomanov et al. (2020) conducted a meta-analysis of leaf growth across species. They found that the lifespan of the leaves ranged from 16 weeks in needle leaf deciduous trees to 298 weeks in evergreen shrubs.

Several genes regulate leaf development in the woodland strawberry (*F. vesca*) which is a diploid

**Table 2.** Genetic control of leaf growth in the woodland strawberry, *F. vesca*. Data are from the sources indicated in the Table.

| Reference                | Regulator                                   | Leaf trait  |
|--------------------------|---|---|
| Chatterjee et al. (2011) | <i>KNOX</i>                                 | Growth of the petioles & the number of serrations on the leaf margins.    |
| Zheng et al. (2019)      | <i>Fvemir164a</i>                           | Number of serrations on the leaf margins.                                 |
| Li et al. (2022)         | <i>Fvemir167b</i>                           | Leaf initiation.  |
| Han and Kang (2023)      | <i>FveKNOXs, FveLFYa &amp; SIMPLE LEAF1</i> | Complexity of leaf morphology.  |
| Lu et al. (2023a)        | <i>FveYUC4</i>                              | Width of the leaf blade & number of serrations on the leaf margins.       |
| Pi et al. (2023)         | <i>FveLFYa</i>                              | Number of leaflets per leaf.  |
| Wang et al. (2023)       | <i>FvePHP</i>                               | Size of the leaf cells & size of the leaves.                              |
| Zhang et al. (2023a)     | <i>FveLFYa</i>                              | Size & number of leaflets.  |
| Zhang et al. (2023c)     | <i>CYP734A129</i>                           | Length of the petioles & leaf blades.                                     |
| Luo et al. (2024)        | <i>SIMPLE LEAF1 &amp; SALAD</i>             | Complexity of leaf morphology & number of serrations on the leaf margins. |

(Table 2). New germinated plants of this species give rise to two to four simple leaves and then develop trifoliate compound leaves, all of which have serrated margins. The diploid strawberry has emerged as a model for research on leaf and flower development and fruit ripening in plants. The genes isolated from this species control various aspects of development, including the size of the leaf cells, the number and the size of the leaves or leaflets, the expansion of the petiole and lamina, the number of serrations on each leaflet and fusion of the leaflets.

The new leaves in strawberry plants are initiated from the SAM, with future development dependent on cell division and cell expansion. Overall, leaf growth is more dependent on cell expansion. The rate of leaf appearance and development varies with changes in solar radiation, photoperiod and temperature. Several genes are involved in leaf development in the woodland strawberry. Similar studies are missing in commercial strawberry.

### Changes in leaf growth over the season

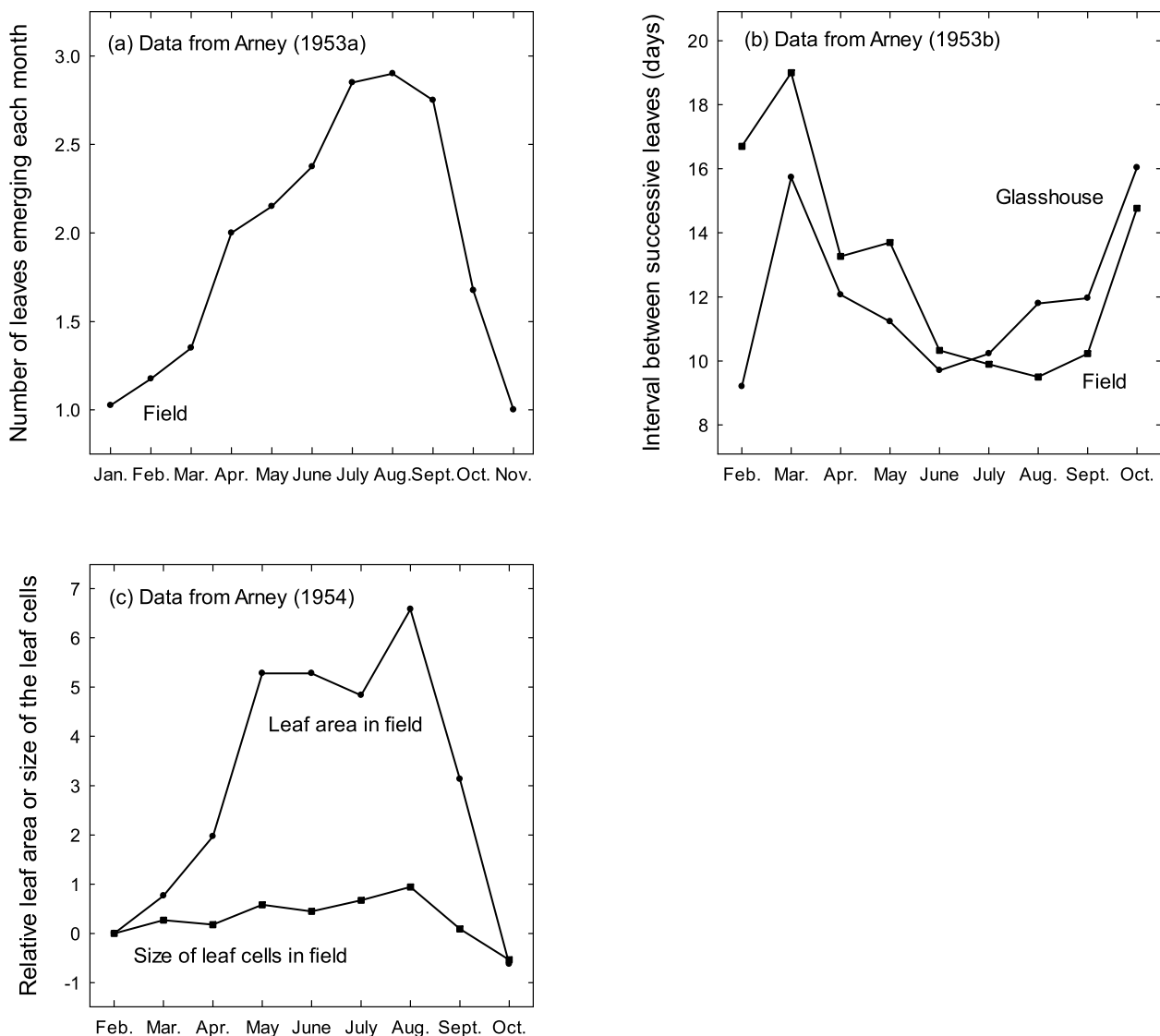
The changes in leaf growth in strawberry over the season vary across experiments, reflecting the cultivar, environment and the method used to assess growth. A linear increase in leaf production suggests that the environment is ideal for growth or that the fruit do not compete with the leaves for photosynthates. In contrast, a period of slow growth suggests that conditions are not ideal for growth or that the fruit compete with the leaves for photosynthates.

Arney (1953a,b) studied the growth of 'Royal Sovereign' strawberry over several seasons in the United Kingdom, with data collected from plants in a glasshouse and in a field. The maximum rate of leaf emergence occurred from April to September, with a lower rate from October to March (Figure 3a). A leaf emerged every eight to ten days from June to August. More leaves were initiated each month in the glasshouse than in a field, but only from February to May (Figure 3b). Overall, plants in the field produced more leaves. The interval between successive leaves was negatively correlated with temperature ( $r = -0.77$ ), but not with rainfall or hours of sunshine. Temperatures below 5°C inhibited the emergence of new leaves.

Menzel and Smith (2012) examined the phenology of 'Festival' strawberry in Queensland, Australia. There were linear increases in leaf production when the transplants were planted on 31 March (Figure 4). In contrast, there were sigmoid relationships when the transplants were planted on 14 or 28 April. Maximum leaf growth was greater in the first planting than in the second or third. Yield was greater in the first planting (875 g per plant versus 689 g per plant or 643 g per plant; LSD,  $p = 0.05$ , 104). Ran (2014) collected data on the growth of 'Elsanta' in Finland. The temperature in the greenhouse was maintained at  $19.7^\circ \pm 2.0^\circ\text{C}$  during the experiment, which ran from 15 February to 28 May. Supplementary lighting was provided during periods of overcast weather. There was a linear increase in leaf production during the experiment (Figure 5). In contrast, the length of the petioles peaked six to ten weeks after planting and then decreased. Berry yield per week peaked at the same time. The plants produced a maximum of 17.4 leaves per plant, with a maximum petiole length of 25.9 cm.

Jahn and Dana (1970) investigated changes in growth in three strawberry cultivars in Wisconsin. There were sigmoid relationships between leaf growth and the day since emergence of the first leaf (Figure 6). The cultivars produced 16.9 to 23.1 leaves per plant over 120 days. Pérez de Camacaro et al. (2002) examined strawberry phenology in the United Kingdom. There were sigmoid relationships between leaf production and time in 'Elsanta' and 'Bolero' over six months (Figure 6). The rate of leaf emergence was rapid from May to September and slow from October to November. Bodson and Verhoeven (2005) studied strawberry growth in Belgium. The plants were cultivated in chambers and exposed to the regular decrease in photoperiod and temperatures recorded during summer and fall in the area. There was a sigmoid relationship between leaf production and time (Figure 6). There was a rapid increase in leaf emergence from July to September and a slow increase from October to November. The plants produced an average of 21.1 leaves at the end of the experiment.

Atkinson et al. (2006) examined the behaviour of two strawberry cultivars in chambers in the United Kingdom. There was a linear relationship between leaf production and time in 'Elsanta' and a sigmoid



**Figure 3.** Leaf growth in 'Royal Sovereign' strawberry in the United Kingdom: (a) Changes in the number of new leaves emerging in a field; (b) Changes in the interval between successive leaves in a glasshouse and a field; and (c) relative size of the leaves and leaf cells in a field. Data are from Arney (1953a,b) and Arney (1954).

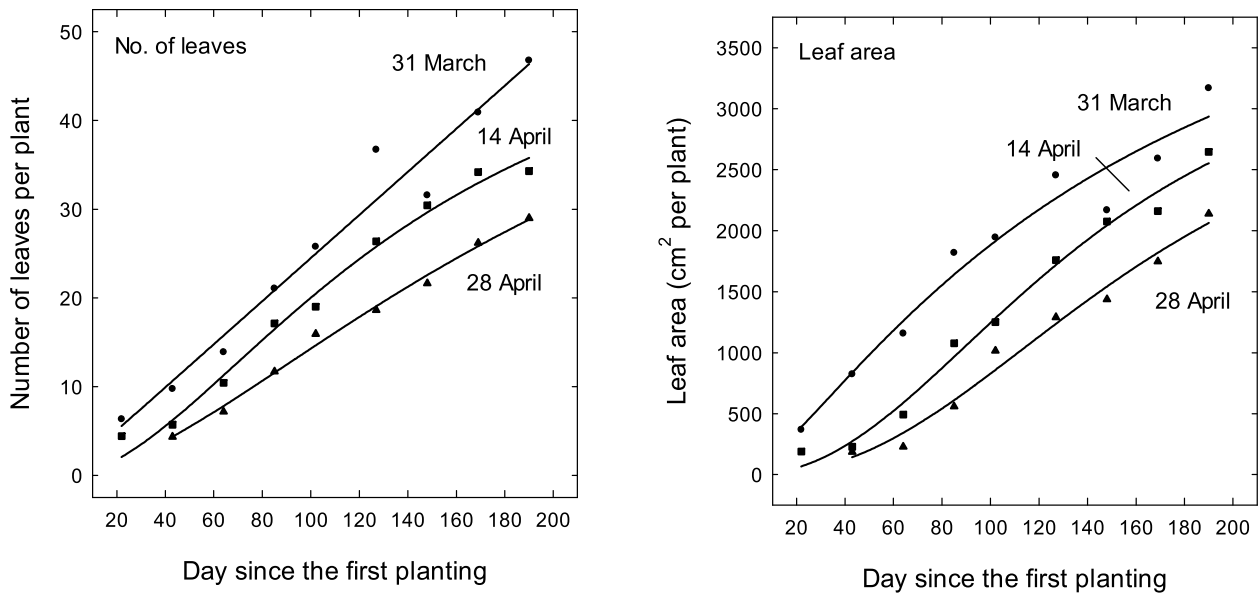
relationship in 'Flamenco' (Figure 6). Maximum leaf production was 6.1 leaves per plant in 'Elsanta' and 7.4 leaves per plant in 'Flamenco'. Jo and Shin (2022) studied the performance of 'Seolhyang' in a greenhouse in Korea. There was a linear increase in leaf production over 148 days (Figure 6). The plants produced 19.2 leaves by the end of the experiment. Fall and Carisse (2022) investigated the performance of 'Seascape' in Quebec, Canada over two seasons. The relationship between leaf production and time was described by a Gaussian function (Figure 6). There was an exponential increase in growth for the first 80 days and a decrease over the last 40 days. The maximum number of leaves produced was 25.9 leaves per plant. Butler et al. (2002) grew 'Chandler' in North Carolina and recorded growth over the season. Leaf area expansion was slow from October to February and rapid from April to May. Average leaf area expansion was 1,165 cm<sup>2</sup> per plant at the end of the season. Mochizuki et al. (2013) indicated a similar lull in leaf

growth in two strawberry cultivars in a greenhouse in Korea. Growth was slow in January and faster before and after this period. 'Benihoppe' produced 12.6 leaves per plant and 'Toyonoka' produced 11.6 leaves per plant.

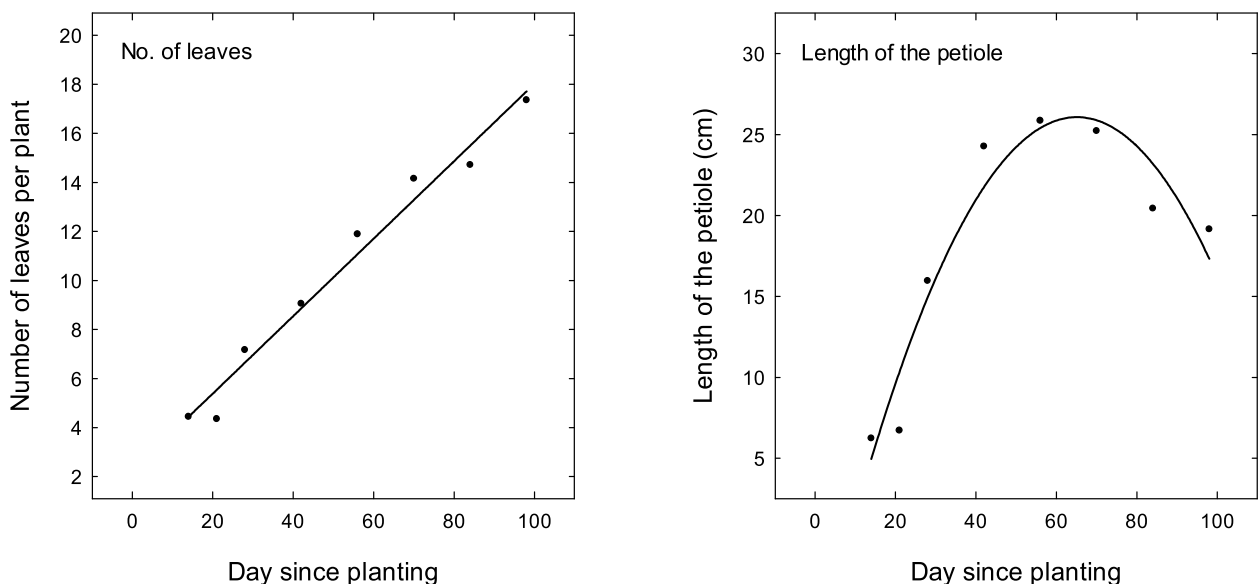
Leaf growth in strawberry is affected by seasonal weather. Under optimum conditions, the changes in leaf growth follow a linear or sigmoid pattern. In contrast, low light levels, short days and low temperatures slow the rate of leaf development.

### Genetics and heritability of leaf growth

Growth and development in plants are dependent on genetics and the environment. Plant breeders can estimate the heritability of traits to determine the relative role of these two factors. There are two types of heritability. Broad-sense heritability ( $H^2$ ) estimates the ratio of genotypic to phenotypic variance in a trait, while narrow-sense heritability ( $h^2$ ) estimates the ratio



**Figure 4.** Seasonal changes in leaf growth in 'Festival' strawberry in Queensland, Australia. The transplants were planted on 31 March, 14 April or 28 April. There were linear or dose-logistic relationships between growth and the day since the first planting ( $p < 0.001$ ,  $R^2$ s = 0.95 to 0.98). Data are from Menzel and Smith (2012).



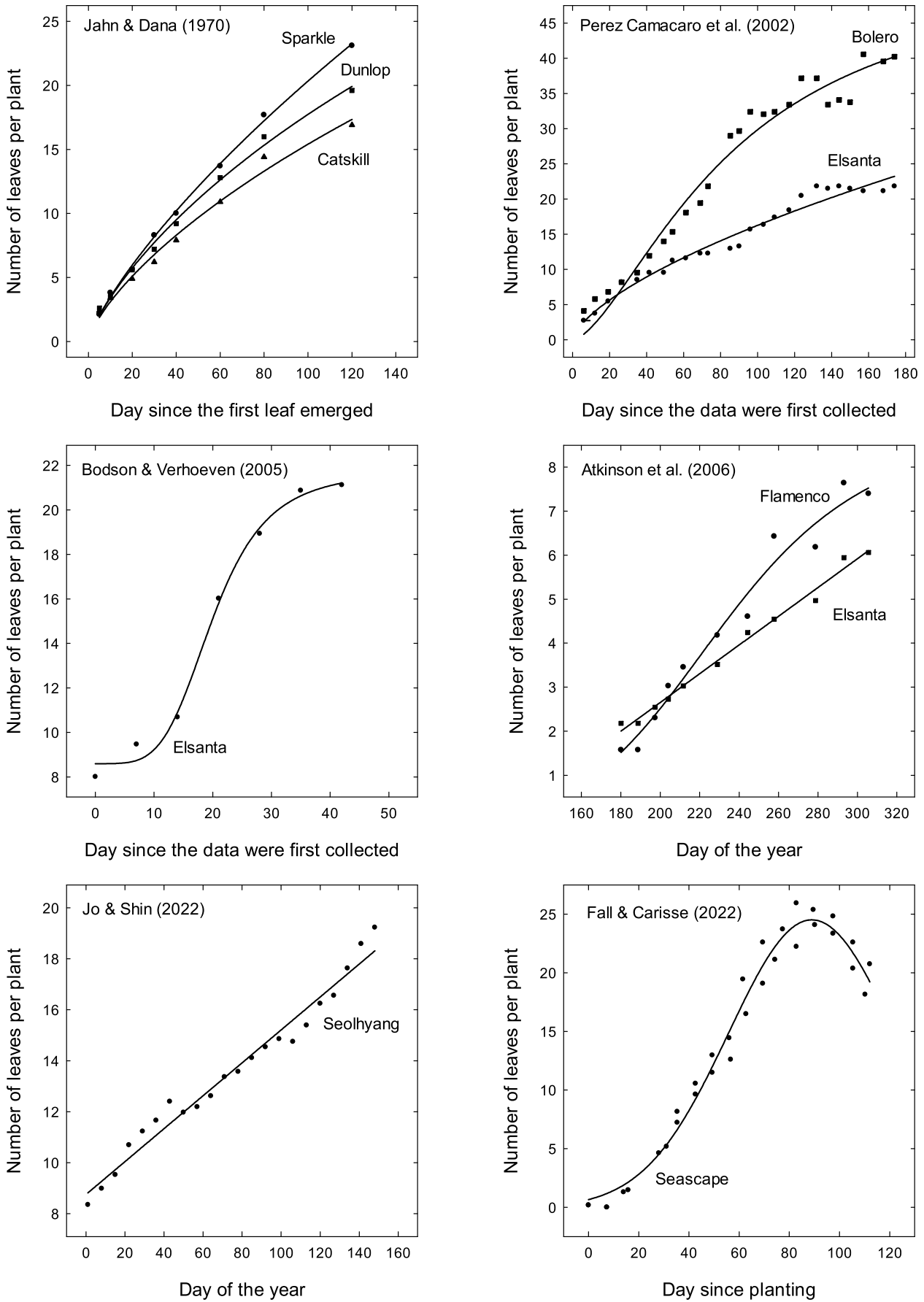
**Figure 5.** Seasonal changes in leaf growth in 'Elsanta' strawberry in Helsinki, Finland planted on 15 February. There was a linear relationship between leaf production and the day since planting ( $p < 0.001$ ,  $R^2 = 0.97$ ) and a quadratic relationship between the length of the petiole and the day since planting ( $p = 0.002$ ,  $R^2 = 0.89$ ). Data are from Ran (2014).

of additive genetic to phenotypic variance (Clóvis et al., 2021; Larios et al., 2023). Heritability is not fixed and varies with the population, environment and the statistical method used in the analysis in strawberry (Osorio et al., 2021). The heritability of leaf and canopy growth in strawberry was investigated across studies (Table S1,  $N = 28$ ). The mean  $h^2$  was  $0.28 \pm 0.11$ , the median was 0.27, and the range was from 0.14 to 0.52 ( $N = 14$ ) (Figure 7). The mean  $H^2$  was  $0.40 \pm 0.22$ , the median was 0.33, and the range was from 0.14 to 0.74 ( $N = 13$ ). Values of heritability for leaf or canopy growth are lower than those for yield, although the data for yield are variable

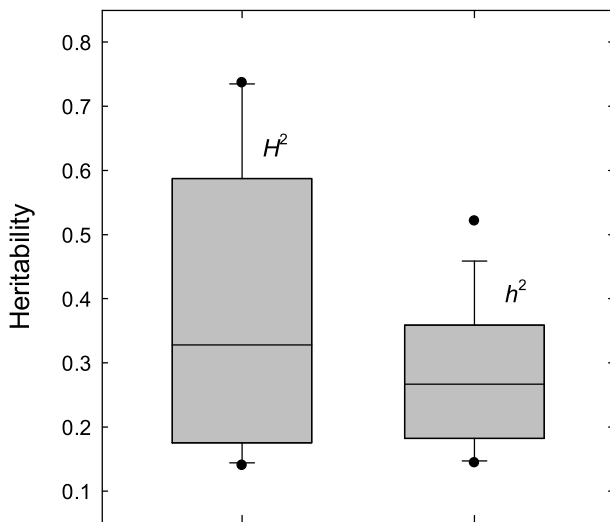
(Andrade Júnior et al., 2020; Barth et al., 2020, 2022; Chiomento et al., 2024; Feldmann et al., 2024; Osorio et al., 2021; Rutz et al., 2023).

Leaf initiation, leaf area expansion and leaf dry matter production vary across different strawberry cultivars. Examples of the variations in leaf growth are provided for two main growing areas. Guan et al. (2020) examined the performance of strawberry in Florida. The genotypes were selected to represent the range in the size of the plants in the University of Florida breeding germplasm, with two other genotypes representing other programmes. Mean leaf dry weight was  $15.7 \pm 9.2$  g per plant, the median was





**Figure 6.** Seasonal changes in leaf growth in strawberry. There were linear, dose-logistic or Gaussian relationships between growth and time ( $p < 0.001$ ,  $R^2 = 0.96$  to  $0.99$ ). Data are from Jahn and Dana (1970), Pérez de Camacaro et al. (2002), Bodson and Verhoeven (2005), Atkinson et al. (2006), Jo and Shin (2022) and Fall and Carisse (2022).



**Figure 7.** Box plots showing the distribution of heritability for leaf or canopy growth in strawberry.  $H^2$  is broad-sense heritability (total genetic variability) and  $h^2$  is narrow-sense heritability or heritability (additive genetic variability). Data are from the various authors shown in Table S1.

12.3 g per plant, and the range was from 7.1 to 41.4 g per plant ( $N = 16$ ) (Figure 8). Mean leaf area was  $1,554 \pm 1,009 \text{ cm}^2$  per plant, the median was  $1,247 \text{ cm}^2$  per plant, and the range was from 765 to  $4,256 \text{ cm}^2$  per plant. Leaf dry weight and leaf area expansion were variable across the group. Grant et al. (2010) collected data on the growth of ten cultivars in a tunnel in the United Kingdom. The cultivars included three cultivars that were grown in the area at that time ('Elsanta', 'Florence' and 'Symphony'), two locally-bred cultivars unrelated to the first three ('Delia' and 'Emily'), two cultivars bred in the 1950s and 1960s from the United Kingdom ('Cambridge') and Canada ('Totem'), along with 'Hapil' from Belgium, 'Idea' from Italy and 'Elvira'. There was a range in growth across the group. Mean leaf production was  $16.7 \pm 4.5$  leaves per plant, the median was 15.5 leaves per plant, and

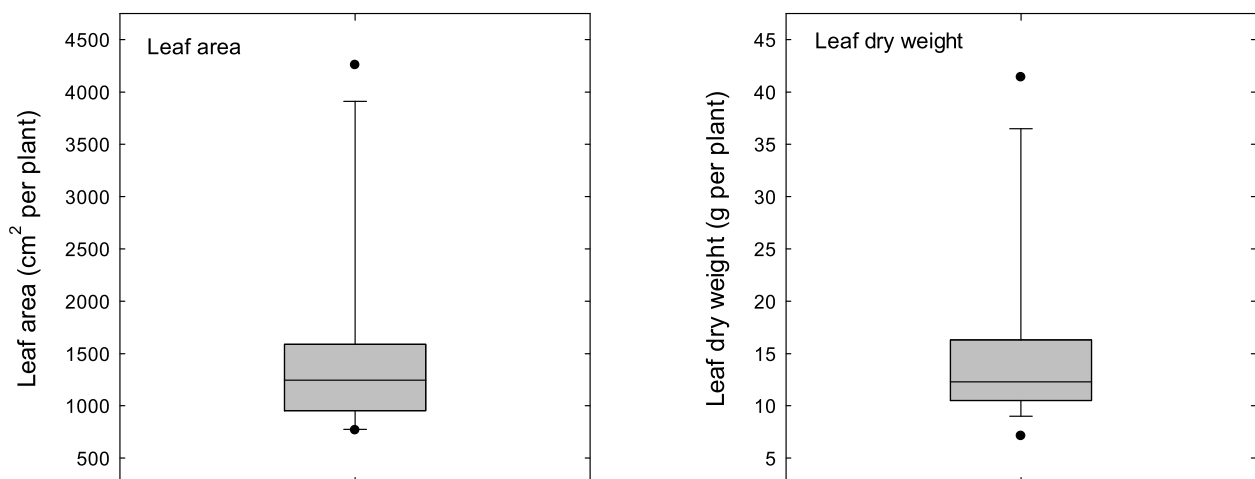
the range was from 11.0 to 25.0 leaves per plant. Mean leaf area was  $1,390 \pm 325 \text{ cm}^2$  per plant, the median was  $1,500 \text{ cm}^2$  per plant, and the range was from 900 to  $1,900 \text{ cm}^2$  per plant. Mean leaf dry weight was  $16.7 \pm 3.7 \text{ g}$  per plant, the median was 16.9 g per plant, and the range was from 11.6 to 22.1 g per plant. These results demonstrate the impact of breeding and selection on leaf growth in strawberry in temperate and subtropical areas. Guan et al. (2020b) and Grant et al. (2010) did not provide information on heritability of the leaf traits.

Genome-wide associated studies can be used to develop populations and cultivars of strawberry with desirable characteristics such as higher yields, better flavour, better post-harvest life or disease resistance (Jiménez et al., 2023; Oh et al., 2021; Petrasch et al., 2022; Pincot et al., 2018). There is little research in this area to assess the genetics of leaf or canopy growth.

Leaf growth varies across cultivars of commercial strawberry. Heritability for leaf or canopy growth in strawberry is low to intermediate across studies. Values of heritability are lower than those for yield in the crop.

### Effect of temperature on anatomy of the leaves

The anatomy and morphology of leaves varies with the species and environment (Feng et al., 2023; Huang et al., 2022; Poorter et al., 2010; Shipley, 2006; Siefert et al., 2015). Environmental conditions effect leaf development in strawberry, with changes in anatomy and ultrastructure under various water applications, light levels, photoperiods and temperatures (Chabot, 1978; Went, 1957; Xu et al., 2022). Arney (1954) studied the growth of 'Royal Sovereign' strawberry in the United Kingdom. He found that the leaves were larger from May to August than at other times



**Figure 8.** Box plots showing the variation in leaf growth in 16 genotypes of strawberry in Florida. Data are from Guan et al. (2020b).

(Figure 3c). There were small variations in the size of individual cells in the leaf, suggesting that the changes in leaf size were due to different rates of cell division during the initiation of the leaf primordia (Figure 3c). The larger leaves produced from May to August reflected longer days and warmer conditions. Went (1957) indicated that the length of the petioles of strawberry doubled as the temperature increased from 10° to 20°C in chambers in California.

Bodson and Verhoeven (2005) studied changes in the growth of commercial strawberry in Belgium. The plants were grown in chambers and exposed to the regular decrease in photoperiod and temperatures recorded during summer and fall in the area. They found that the petioles became shorter when leaf emergence was delayed, and the leaves became smaller. Leaves emerging on 31 July, 14 August, 15 September or 19 October had petioles that were  $14.8 \pm 0.7$  cm,  $13.2 \pm 1.0$  cm,  $5.6 \pm 1.6$  cm or  $3.2 \pm 1.0$  cm. The total area of the leaves was  $93 \pm 5$  cm<sup>2</sup>,  $106 \pm 6$  cm<sup>2</sup>,  $63 \pm 3$  cm<sup>2</sup> or  $20 \pm 1$  cm<sup>2</sup>. Robert et al. (1999) conducted similar work with four cultivars of commercial strawberry further south at two sites in France. There were negative linear relationships between the length of the leaf petiole and the day of leaf emergence ( $p < 0.001$ ,  $R^2 = 0.90$  or  $0.97$ ). The length of the petiole ranged from 2.7 to 11.0 cm at Avignon and from 4.1 to 11.7 cm at Clermont-Ferrand. Tolvanen (2020) studied the morphology of 12 clones of *F. vesca* in a field and a glasshouse in Finland. The clones were collected from Norway, Finland, Germany, Italy and Spain. Leaves produced in summer were larger than those in winter and were larger when grown at 16°C than at 6°C. The shortest petioles were 3.5 cm long and the longest petioles were 9.5 cm long. A similar study with 15 clones of the woodland strawberry in this area indicated that leaf development in spring would be quicker under global warming (Liu, 2022). Additionally, leaves initiated in winter would senesce earlier.

Chabot and Chabot (1977) grew plants of *F. vesca* in artificially-lit chambers set at 10°/2°, 20°/10°, 30°/20° or 40°/30°C. The greatest differences in anatomy were noted at the extremes of temperature. Some of the cells in the leaves died at the highest temperatures. The plants under extreme cold had thick leaves, but poor internal development (Figure 9). The authors provided data on various aspects of development (Table 3). Leaves became thinner over most of the range in temperature, but they became thicker at the highest temperatures (40°/30°C). Specific leaf weight increased over the same range and then decreased. There was no consistent pattern in the percentage of epidermis, mesophyll or intercellular air space in the leaf on a volume basis. Changes in mesophyll surface area per leaf surface area were small. Mesophyll cell volume changed across the treatments, but without a clear pattern. It was suggested that changes in the

ratio of surface to volume indicated a decrease in the size of the cells with increasing temperatures. Abdelrahman (1984) examined the effect of temperature on leaf anatomy in three cultivars of commercial strawberry, with the chambers set at 20°/10°, 30°/20° or 40°/30°C. Overall, the response of the plants was similar with that recorded for *F. vesca* by Chabot and Chabot (1977). The plants at 30°/20°C had thinner leaves than those at the other temperatures (Table 4). The plants at 40°/30°C had a lower proportion of mesophyll in the leaf than the others, and a higher proportion of intercellular space.

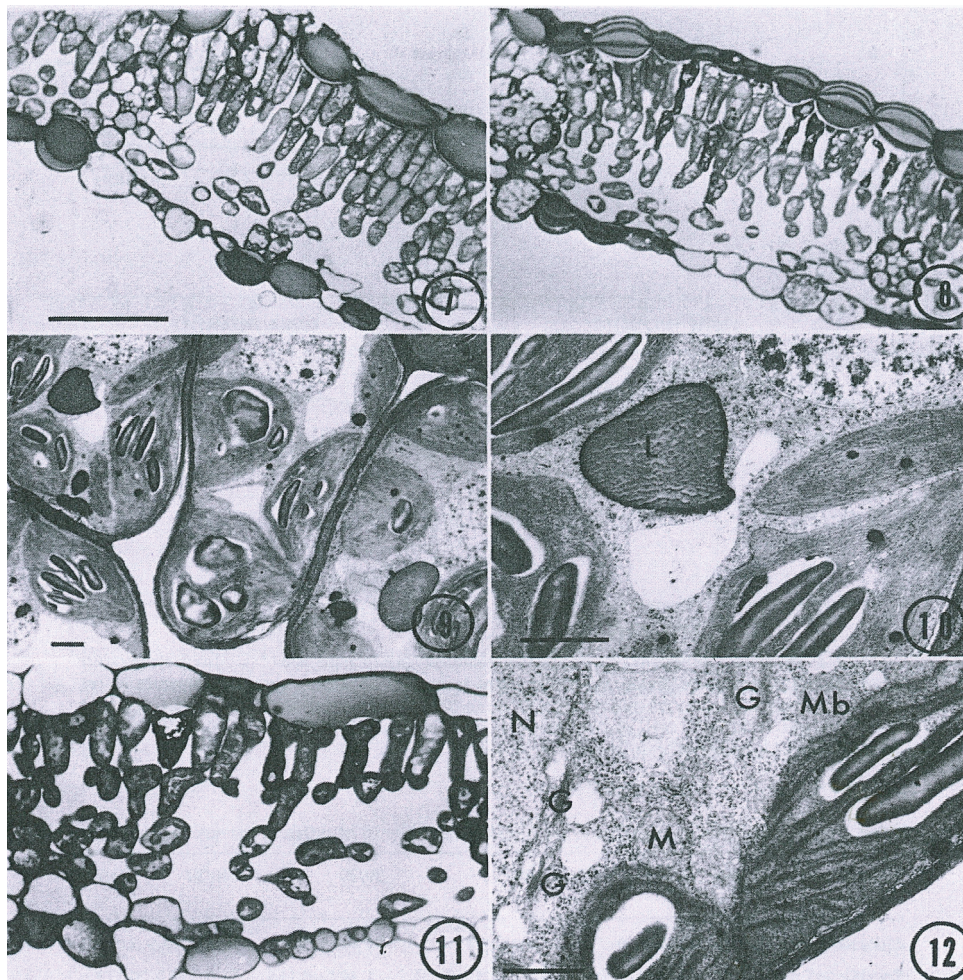
Temperature affects the anatomy of strawberry leaves. Development is acceptable at intermediate temperatures but declines at extreme temperatures. Some of the leaf cells die at high temperatures, whereas leaf development is stunted at low temperatures.

### Base temperature for leaf growth in strawberry

Temperature has a strong effect on the development of plants, with different optima for growth depending on the species and ecosystem (Huang et al., 2019). Leaf initiation occurs over a wider range of temperatures than leaf area expansion, with leaf initiation having a lower base temperature and a higher optimum temperature (Kim et al., 2012; Milford et al., 1985). Some species have a base temperature for leaf initiation close to freezing (e.g. Gallagher, 1979 for winter wheat in the United Kingdom; and Lainé et al., 2023 for maize across the globe). In other species, growth continues above 40°C (e.g. de Freitas et al., 2017 for *Corymbia citriodora* and *Eucalyptus urophylla* in Brazil).

Strawberry plants are adapted to a range of environmental conditions and grow in locations with temperatures from close to freezing up to 40°C (Guan et al., 2023; Jiang et al., 2023; Lustosa da Silva et al., 2023; Madhavi et al., 2023; Nascimento et al., 2023; Neri et al., 2012; Rosa et al., 2013; Sammarco et al., 2022; Soppelsa et al., 2023; Thammasophon et al., 2023; Yao et al., 2009). Critical temperatures include the base temperature ( $T_b$ ) where growth stops at low temperatures and the maximum temperature ( $T_{max}$ ) where growth stops at high temperatures (Roth et al., 2022; Slafer & Rawson, 1995; Wang et al., 2017; Weikai & Hunt, 1999). There are also the lower and upper temperatures associated with maximum growth for strawberry ( $T_{lower}$  and  $T_{upper}$ ).

Different base temperatures for growth have been suggested, including temperatures close to freezing and up to 7°C. Rosa et al. (2011) conducted an experiment to examine the relationship between leaf production and temperature in Brazil. The best estimate of the  $T_b$  was calculated by using the Mean Square Error (MSE) from the linear regression between the number of leaves per plant and degree-days. The temperature



**Figure 9.** Effect of temperature on leaf anatomy in *F. vesca* in New York, United States: (Part 7) Leaves at 30°/20°C have two layers of palisade. Bar equals 50  $\mu\text{m}$ .  $\times$  344 magnification; (Part 8) Leaves at 40°/30°C have several damaged cells, with dense black cytoplasm.  $\times$  344 magnification. (Part 9) Healthy cells of leaves at 40°/30°C have lipid in the cytoplasm. Bar equals 1  $\mu\text{m}$ .  $\times$  4,730 magnification; (Part 10) Higher magnification of Part 9 illustrates the extensive membrane development of the chloroplasts at 40°/30°C. A lipid droplet (L) is present. Bar equals 1  $\mu\text{m}$ .  $\times$  13,330 magnification; (Part 11) Leaves at 10°/2°C are thick with a large intercellular air space. Some damage is illustrated by the black cells.  $\times$  344 magnification; and (Part 12) a characteristic feature of the leaves at low temperature is the prominence of multiple Golgi bodies (G) with distended vesicles. Microbodies (Mb) and mitochondria (M) are in contact with a chloroplast. The chromatin in the nucleus (N) is dispersed. The chloroplasts have fewer membranes and grana stacks than at higher temperatures. Bar equals 1  $\mu\text{m}$ . Data are from Chabot and Chabot (1977).

**Table 3.** Effect of temperature on leaf anatomy in the woodland strawberry, *F. vesca* in New York, United States. Data are from Chabot and Chabot (1977). Some of the treatment means are presented with standard errors (s.e.).

| Parameter  | 10°/2°C         | 20°/10°C        | 30°/20°C        | 40°/30°C        |
|--|-----------------|-----------------|-----------------|-----------------|
| Leaf thickness ( $\mu\text{m}$ )   | 124 $\pm$ 7     | 111 $\pm$ 8     | 97 $\pm$ 6      | 115 $\pm$ 10    |
| Specific leaf weight (g per $\text{dm}^2$ )                                      | 1.28 $\pm$ 0.06 | 1.30 $\pm$ 0.13 | 1.39 $\pm$ 0.16 | 1.19 $\pm$ 0.12 |
| Cell volume/leaf volume (%)  |                 |                 |                 |                 |
| Epidermis  | 25              | 28              | 29              | 28              |
| Mesophyll  | 34              | 50              | 46              | 44              |
| Intercellular space  | 41              | 22              | 26              | 28              |
| Mesophyll volume/leaf surface area ( $\mu\text{m}^3$ per $\mu\text{m}^2$ )       | 42 $\pm$ 6      | 55 $\pm$ 4      | 45 $\pm$ 5      | 51 $\pm$ 5      |
| Mesophyll surface area/leaf surface area ( $\mu\text{m}^2$ per $\mu\text{m}^2$ ) | 15 $\pm$ 1      | 19 $\pm$ 3      | 19 $\pm$ 2      | 23 $\pm$ 2      |

associated with the lowest MSE was considered the best estimate of  $T_b$  and was 0°C, although this is low for a subtropical plant.

Krüger et al. (2012) and Alvarado-Raya et al. (2019) used a  $T_b$  of 3.0°C to analyse strawberry growth, based on the earlier study by Døving and Mage (2001) in Norway. Døving and Mage (2001) noted that the mean temperature in April ranged from 3.0° to 7.2°C and

that the lower limit for growth was within this interval. Hernández-Martínez et al. (2023a) used a base temperature of 3°C for modelling the growth of strawberry in Alabama. Bonhomme (2000), Parent et al. (2019) and Raper et al. (2023) noted several issues when relating growth to temperature. These include the range in temperatures used, the time interval when measurements are taken, and differences between day

**Table 4.** Effect of temperature on leaf anatomy in commercial strawberry, *F. xananassa* in Kansas, United States. Data are from Abdelrahman (1984).

| Parameter                      | 20°/10°C | 30°/20°C | 40°/30°C | Significance |
|--------------------------------|----------|----------|----------|--------------|
| Leaf thickness (µm)            | 190      | 150      | 203      | $p < 0.01$   |
| Height of upper epidermis (µm) | 40.0     | 30.8     | 45.5     | $p < 0.05$   |
| Height of lower epidermis (µm) | 28.0     | 21.8     | 19.3     | n.s.         |
| Length of palisade cells (µm)  | 10.6     | 10.4     | 8.8      | n.s.         |
| Width of mesophyll cells (µm)  | 14.7     | 15.1     | 11.9     | n.s.         |
| Cell volume/leaf volume (%)    |          |          |          |              |
| Epidermis                      | 30.0     | 32.4     | 30.4     | n.s.         |
| Mesophyll                      | 28.6     | 29.0     | 33.2     | $p < 0.01$   |
| Intercellular space            | 41.5     | 38.6     | 36.7     | $p < 0.05$   |

Data are the means of three cultivars. n.s. = not significant ( $p > 0.05$ ).

and night temperatures. Locatelli et al. (2023) used a  $T_b$  of 5°C for plant phenology in a study with 13 cultivars of commercial strawberry in a greenhouse in Italy. This value was based on an earlier investigation with four cultivars in the field in Norway (Opstad et al., 2011). There was a closer correlation between strawberry plant phenology and thermal time using a  $T_b$  above 0°C than using one of 0°C.

A range of authors in south America used a  $T_b$  of 7.0°C (Antunes et al., 2006; Cocco et al., 2016; da Costa 2014a, 2014b; da Costa et al., 2017; Diel et al., 2017a, 2017b; Mendonça et al., 2012a, 2012b, 2012c; Mendonça et al., 2017; Tazzo et al., 2015; Thiesen et al., 2018). However, the basis of this decision is unclear, with the reports referring to a few obscure studies (Antunes et al., 2006; Mendonça et al., 2012a; Ronque, 1998; Verdial, 2004). Ronque (1998) and Antunes et al. (2016) indicated that the plants required 380 to 700 hours of temperatures between 2°C and 7°C for successful cropping and this analysis follows similar studies in the area relating yield, flowering and temperatures below 7°C in temperate crops (Caramori et al., 2008; Petri et al., 2021). Fontana et al. (2016) and Olivoto et al. (2022) reported on the relationship between leaf production and temperature in Brazil, but they did not indicate the  $T_b$  used to calculate degree-days.

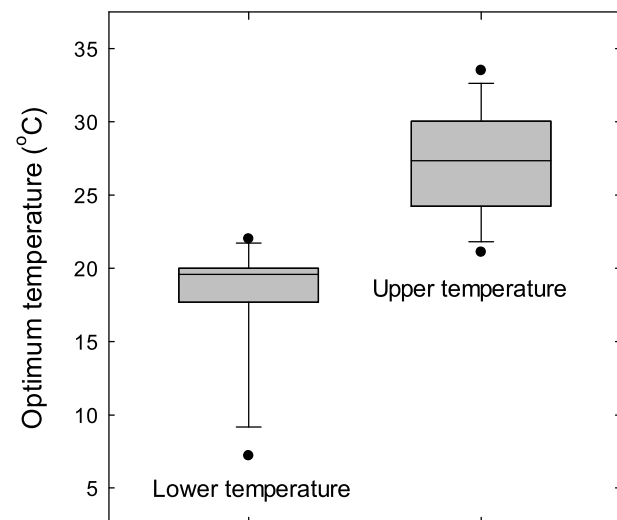
A range of base temperatures have been used to model plant and leaf growth in strawberry. These models include temperatures from freezing up to 7°C. The correct temperature is probably closer to the higher estimate than to the lower estimate.

### Relationship between leaf growth and temperature

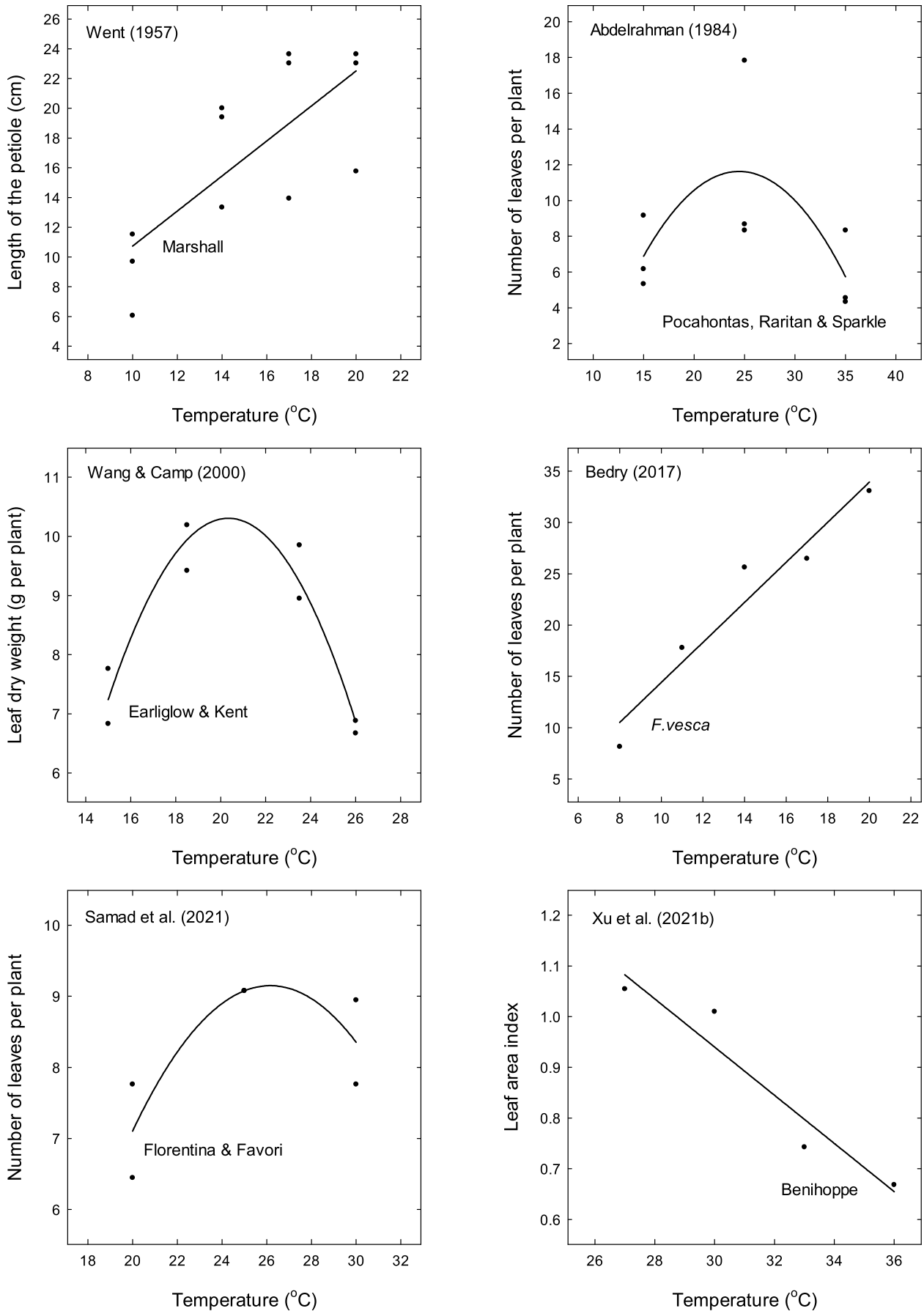
The relationship between leaf growth and temperature in strawberry was investigated over several studies (Table S2,  $N = 46$ ). There was a mixed response across the experiments. In the first two groups, there was a linear decrease or increase in growth as temperatures increased and no optimum was established. In the third group, there was a quadratic relationship between growth and temperature and an optimum range associated with

90% of maximum growth was calculated. The mean lower optimum ( $T_{lower}$ ) for 90% of maximum growth was  $18.3^\circ \pm 3.9^\circ\text{C}$ , the median was  $19.6^\circ\text{C}$ , and the range was from  $7.2^\circ$  to  $22.0^\circ\text{C}$  ( $N = 11$ ) (Figure 10). The mean higher optimum ( $T_{upper}$ ) was  $27.3^\circ \pm 3.6^\circ\text{C}$ , the median was  $27.4^\circ\text{C}$ , and the range was from  $21.1^\circ$  to  $33.5^\circ\text{C}$  ( $N = 12$ ). In the group showing a positive linear response, the highest temperature was lower than  $26^\circ\text{C}$ , while in the group showing a negative linear response, the lowest temperature was higher than  $26^\circ\text{C}$ . Overall, growth was higher below  $30^\circ\text{C}$  and lower above  $30^\circ\text{C}$ . Variations in the response across the studies reflect different cultivars, environments and the method used to measure growth.

Some examples of the response to temperature are provided (Figure 11). Abdelrahman (1984) examined the performance of three commercial cultivars in chambers in Kansas, United States set at  $20^\circ/10^\circ\text{C}$  to  $40^\circ/30^\circ\text{C}$ . The number of leaves per plant was highest when the mean temperature ranged from  $19.6^\circ$  to  $29.3^\circ\text{C}$ . Wang and Camp (2000) conducted a similar experiment in Maryland, with the chambers set at  $18^\circ/12^\circ\text{C}$  to  $30^\circ/22^\circ\text{C}$ . Leaf dry weight per plant was



**Figure 10.** Box plots showing the distribution of the lower ( $T_{lower}$ ) and upper optimum temperatures ( $T_{upper}$ ) for 90% of maximum leaf growth in strawberry ( $N = 11$  or  $12$ ). Data are from the various authors shown in Table S2.



**Figure 11.** Relationship between leaf growth and temperature in strawberry. There were linear or quadratic relationships between growth and temperature. Data are from Went (1957) ( $p = 0.005$ ,  $R^2 = 0.52$ ), Abdelrahman (1984) ( $p = 0.183$ ,  $R^2 = 0.24$ ), Wang and Camp (2000) ( $p = 0.002$ ,  $R^2 = 0.88$ ), Bedry (2017) ( $p = 0.007$ ,  $R^2 = 0.92$ ), Samad et al. (2021) ( $p = 0.150$ ,  $R^2 = 0.53$ ) and Xu et al. (2021) ( $p = 0.041$ ,  $R^2 = 0.88$ ). Data are from Table S2.

highest when the mean temperature ranged from 17.0° to 23.5°C. Samad et al. (2021) grew two cultivars in greenhouses in Sweden set at 20°C to 30°C. The number of leaves per plant was highest from 22.0° to 29.9°C. Bedry (2017) grew plants of *F. vesca* in chambers in the United Kingdom set at 8° to 20°C. There was a positive linear relationship between the number of leaves per plant and temperature (Figure 11). Leaf production in the treatments ranged from 8.1 to 33.1 leaves per plant. Went (1957) noted a similar relationship between strawberry leaf growth and temperature in chambers in California. The plants were grown at 10°, 14°, 17° or 20°C under photoperiods of 8, 12 or 16 hours. Leaf elongation increased as the temperature increased. The length of the leaf petioles in the treatments ranged from 6.1 to 23.6 cm. Xu et al. (2021) noted a different response in China. They grew plants in greenhouses set at 32°/22°C to 41°/31°C. There was a strong negative linear relationship between growth and the mean temperature in the regimes. Leaf area index (LAI) ranged from 0.67 to 1.05 in the treatments. The results of these experiments demonstrate the range in the response to temperature.

Temperature affects leaf initiation, expansion and dry matter production in strawberry. Growth is better below 30°C than above 30°C. Most of the research has investigated the response of commercial strawberry, with limited data collected on the woodland strawberry or other wild species.

### Interaction between CO<sub>2</sub> and temperature on leaf growth

In addition to rises in global temperatures, future climate change scenarios include increases in the concentration of CO<sub>2</sub> in the atmosphere and changes in the patterns and intensities of precipitation (Abbass et al., 2022; Nunes, 2023; Solomon et al., 2009). Higher concentrations of CO<sub>2</sub> and temperatures affect the physiology and growth of plants, however, there are few studies where the effect of both warming and CO<sub>2</sub> enrichment have been investigated.

Dieleman et al. (2012) conducted a meta-analysis on the effect of climate change on plants, where elevated CO<sub>2</sub> was combined with elevated temperatures. For above-ground biomass, the weighted meta-analysis estimates of the responses to elevated CO<sub>2</sub> and warming were higher (19.1% increase) than the median effect estimates (8.6% increase). As a meta-analysis gives more weight to larger studies (i.e. studies with more replicates per treatment), this indicated that larger studies had larger responses. However, while the median effect estimates were smaller, the number of studies reporting positive responses was larger than those reporting negative responses. A positive effect of combining warming with elevated CO<sub>2</sub> on biomass was supported by both analyses. Dieleman et al.

(2012) conducted further analyses to determine which factor dominated the response when elevated CO<sub>2</sub> was combined with warming. Uncertainties in the combined treatment (elevated CO<sub>2</sub> and temperatures) were larger than those in single factor experiments (elevated CO<sub>2</sub> or elevated temperatures). In other words, the responses to the combined treatment were less consistent across experiments. Second, the response in the combined treatment was more similar to that of elevated CO<sub>2</sub>-only than to warming-only. This suggested that over all multi-factor experiments, CO<sub>2</sub> affected growth more than warming.

There is limited information on the effect of CO<sub>2</sub> and temperature on strawberry and the results of the studies are inconclusive.

Balasoorya et al. (2018) grew two strawberry cultivars ('Albion' and 'San Andreas') in chambers in Victoria, Australia. The plants were grown at 25° or 30°C and at concentrations of CO<sub>2</sub> of 400, 650 or 950 ppm. Maximum leaf production occurred at 25°C combined with 650 ppm CO<sub>2</sub> (16 ± 2 leaves per plant), with fewer leaves in the other regimes (9 ± 3 leaves per plant to 11 ± 3 leaves per plant) ( $p < 0.05$ ). Canopy area per plant was higher at 25°C and 650 ppm CO<sub>2</sub> (722 ± 108 cm<sup>2</sup> versus 436 ± 92 cm<sup>2</sup> to 626 ± 101 cm<sup>2</sup>) ( $p < 0.05$ ). The number of leaves per plant was slightly higher at 25°C (12 ± 1.5) than at 30°C (10 ± 0.6), and higher at 650 ppm CO<sub>2</sub> (13 ± 2.5) than at 400 or 900 ppm CO<sub>2</sub> (11 ± 0 or 11 ± 0.4). Canopy area per plant followed the same trend. Productivity was low, with yields below 100 g per plant. There was no evidence that growth was promoted under high CO<sub>2</sub> and temperatures.

Sammarco et al. (2023) examined the effect of CO<sub>2</sub> and temperature on the growth of the woodland strawberry in greenhouses in Czechia. The experimental set-up was different to that used to study the response of commercial strawberry (Balasoorya et al., 2018). The wild plants were grown at ambient temperature and 400 ppm CO<sub>2</sub> (control), at 4°C above ambient and 400 ppm CO<sub>2</sub>, or at 4°C above ambient and 800 ppm CO<sub>2</sub>. The mean daily temperature in the control chamber was 16.2°C, and 20.1°C or 20.2°C in the warmer chambers with and without high CO<sub>2</sub>. The authors assessed growth using a biomass index calculated by multiplying the number of leaves per plant by the length of their longest leaf. The authors indicated that there was a strong relationship between total plant dry weight and this index ( $p < 0.001$ ,  $R^2 = 0.75$ ,  $N = 453$  plants). The biomass index was higher when elevated temperatures were combined with elevated CO<sub>2</sub> (about 14.2 units) than under ambient temperatures and CO<sub>2</sub> (6.4 units) or under elevated temperatures and ambient CO<sub>2</sub> (6.1 units) ( $p < 0.001$ ). Yield was higher when elevated temperatures were combined with elevated CO<sub>2</sub> (about 100 fruit per plant versus 68 fruit per plant or 42 fruit per plant) ( $p < 0.001$ ).

Growth and yield were higher under elevated temperatures and CO<sub>2</sub>. However, the mean temperatures in the warm glasshouses were relatively low (about 20°C). The effect of high temperatures and CO<sub>2</sub> on growth requires further research. It is not known if the response of commercial strawberry reflects those of woodland strawberry.

Future climate change scenarios involved higher concentrations of CO<sub>2</sub> in the atmosphere and higher temperatures. Limited information suggests that the higher CO<sub>2</sub> will not counteract the negative impacts of higher temperatures on leaf growth in strawberry.

### Impact of global warming on leaf growth in different producing areas

The effect of temperature on leaf growth in strawberry varies across studies. Growth is higher below 30°C and lower above 30°C (Table S2). The impact of high temperatures on growth is dependent on the seasonal changes in temperature in the growing areas.

Studies across central and northern Europe suggest that temperatures do not get high enough to impact leaf growth during most of the season (Klakotskaya et al., 2023; Krüger et al., 2012, 2021, 2022). For example, in Norway, Denmark, Germany, Switzerland and Italy, average daily minima ranged from 7.2° ± 2.1°C to 9.9° ± 1.0°C, while maxima ranged from 19.0° ± 0.7°C to 26.8° ± 0.8°C (Krüger et al., 2012). In contrast, conditions in southern Spain are mixed with temperatures exceeding 30°C for part of the strawberry season (Fernández-Cabanás et al., 2022; García-Tejero et al., 2018; Gavilán et al., 2015; Lozano et al., 2016). Much of the production in this area is under protected cropping, with temperatures higher under plastic tunnels than outside if ventilation is inadequate. Temperatures were variable and ranged from 2° to 41°C in a study in a greenhouse in Seville (Fernández-Cabanás et al., 2022), suggesting an impact of high temperatures on leaf growth.

California accounts for the bulk of the strawberry crop in the United States. The unique coastal environment offers optimum conditions as exposure to the western ocean moderates extreme temperatures, with warm sunny days and cool foggy nights (Maskey et al., 2019). The nursery plants are planted in the fall and bear fruit over the following spring and summer. Average maximum/minimum temperatures in Oxnard in December are 18.9°/7.2°C, while average maximum/minimum temperatures in August during the peak season are 23.3°/15.5°C. Temperatures under plastic tunnels are often higher than those outside, especially if the plastic is new and transmits much of the sunlight (Daugovich & Larson, 2009; Larson et al., 2009). Florida produces berries over winter, opposite to the production on the western seaboard in California. Agehara and Nunes (2021) examined

the performance of strawberry plants in Balm, Florida. They indicated that average maxima/minima over the entire season were 25.2°/13.8°C in the first year and 26.2°/13.6°C in the second year. Average maximum/minimum temperatures in the area in January are 22°/10°C, while average maximum/minimum temperatures in April (end of season) are 28°/16°C. Temperatures are generally suitable for leaf growth.

Strawberries are produced throughout Central and South America, with the impact of temperature on growth varying across the region. Alvarado-Raya et al. (2019) reported on the growth of plants in tunnels in Chapingo in central Mexico at an elevation of 2,250 m. Throughout the experiment, the average daily mean temperature was 16.4°C, the maximum was 30.0°C and the minimum was 10.5°C. The highest temperature recorded was 37.8°C. These data suggest that conditions under the tunnel were too high for maximum growth at times. Further south in Venezuela where strawberries are grown at elevations of 200 to 1,800 m, average maxima ranged from 22° to 25°C and minima ranged from 8° to 18°C (Pérez de Camacaro et al., 2017). Conditions at this location appear adequate for leaf growth. Palombini et al. (2023) showed that maxima exceeded 30°C for part of the season in a greenhouse in Vacaria, Brazil at an elevation of 970 m, suggesting an impact of temperature on leaf growth.

The impacts of global warming on leaf growth in strawberry vary across areas. In cool-growing locations (e.g. Norway), temperatures do not get high enough to impact leaf growth. In contrast, in warm-growing locations (e.g. Spain), temperatures are above the optimum for leaf growth for part of the season.

### Conclusions

Leaf growth in strawberry is sensitive to temperature, with growth higher under 30°C and lower above 30°C. Limited data suggest that elevated concentrations of CO<sub>2</sub> will not counteract the impact of high temperatures on growth. The effect of global warming on growth varies across areas. Higher temperatures in cool-growing locations under climate change are likely to increase leaf growth. In contrast, higher temperatures in warm-growing locations are likely to decrease growth. The decrease in leaf growth in areas with temperatures above 30°C is likely to contribute to lower yields under global warming. Higher temperatures also have a direct impact on fruit growth. Consequently, there is an urgent need to develop heat-tolerant cultivars with acceptable growth and yields for sustainable production in warm locations.



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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.

## Disclosure statement

No potential conflict of interest was reported by the author.

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