



Article

Higher Temperatures Decrease Fruit Size in Strawberry Growing in the Subtropics

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Abstract: Five strawberry (*Fragaria × ananassa* Duch.) cultivars were grown in Queensland, Australia to determine whether higher temperatures affect production. Transplants were planted on 29 April and data collected on growth, marketable yield, fruit weight and the incidence of small fruit less than 12 g until 28 October. Additional data were collected on fruit soluble solids content (SSC) and titratable acidity (TA) from 16 September to 28 October. Minimum temperatures were 2 °C to 4 °C higher than the long-term averages from 1965 to 1990. Changes in marketable yield followed a dose-logistic pattern ($p < 0.001$, $R^2_s = 0.99$). There was a strong negative relationship between fruit weight (marketable) and the average daily mean temperature in the four or seven weeks before harvest from 29 July to 28 October ($p < 0.001$, $R^2_s = 0.90$). There were no significant relationships between SSC and TA, and temperatures in the eight days before harvest from 16 September to 28 October ($p > 0.05$). The plants continued to produce a marketable crop towards the end of the season, but the fruit were small and more expensive to harvest. Higher temperatures in the future are likely to affect the economics of strawberry production in subtropical locations.

Keywords: climate; cultivar; fruit growth; harvest; strawberry; temperature; yield



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1. Introduction

Global climate change is expected to increase both the temperature and the concentration of CO₂ (carbon dioxide) in the atmosphere. These changes will increase CO₂ assimilation in the leaves of many crops; however, this increase will be off-set by excessive leaf production and decreases in flower and fruit development [1–3]. Overall, higher temperatures will have a greater effect on productivity than higher concentrations of CO₂. The impact of temperature on plant development can be due to higher average temperatures or short-term increases in temperatures above the optimum range [4,5].

Some crop models predict higher yields in the short-term with climate change and lower yields in the long-term, while other models predict lower yields across both periods or even under current conditions [6–14]. There can be difficulties in predicting yields under climate change because the changes in CO₂ and temperature, etc. vary across different regions. There are also uncertainties in how individual crops respond to growing conditions. Keeping global warming to within 1.5 °C is less problematic than global warming to within 2.0 °C [15].

Qian et al. [16] predicted that the yields of canola (*Brassica napus* L.) would decrease by 24 to 42% across three regions in Canada from 2041 to 2070. Kinose et al. [17] predicted that the yields of rice (*Oryza sativa* L.) in Indonesia would decrease under 14 climate scenarios, mainly because of higher temperatures. The mean reduction in yield was 12.1% for all of the country from 2039 to 2042 compared with current production. Cammarano et al. [18] predicted that the yields of barley (*Hordeum vulgare* L.) would decrease by 27% in a dry location in the Mediterranean basin by 2050 and increase by 4 or 8% in two wetter locations.

Varma and Beber [19] modelled the productivity of banana (*Musa* spp.) across 27 countries under climate change. They reported that annual yields had increased by an average of 1.37 t/ha since 1961, but this was expected to fall to 0.59 t/ha by 2050. A review

of agriculture production in California indicated that climate change will reduce the yields of many fruit and vegetables [20]. Production in some areas will be more susceptible to changes in the climate than in other areas.

There is some information on the impact of climate change on strawberry (*Fragaria × ananassa* Duch. and related species). Several reviews suggest that increases in the concentration of CO₂ and temperature will alter the production season and the pattern of plant development in different growing areas [21–27]. Two analyses in California suggested that yields would decline by 10% by 2050 and by 43% by 2070 to 2099 [28,29]. High temperatures and low rainfall in November were associated with low yields in this area from 1980 to 2003 [30]. Grez et al. [31] indicated that global warming will decrease the productivity of *F. chiloensis* in its native habit in Chile. The natural distribution of tetraploid species of *Fragaria* will shrink under climate change in Yunnan Province, China [32]. In contrast, the habitat for diploid species will expand.

Gamboa-Mendoza et al. [33] showed that plants of *F. mexicana* grown at 5.1 °C above ambient in Mexico had 41% fewer flowers than plants at ambient temperatures (mean daily temperature of 19.6 °C) and 38% fewer fruit. In some studies, elevated temperatures overrode the benefits of elevated concentrations of CO₂ on growth and productivity. For instance, Sun et al. [34] demonstrated that yields at elevated CO₂ (720 ppm versus 360 ppm) and temperatures (25 °C/20 °C) were 12% lower than those at elevated CO₂ and standard temperatures (20 °C/15 °C).

Higher temperatures under climate change will reduce the accumulation of sugars in the fruit and reduce fruit size. MacKenzie et al. [35] indicated that there was a strong negative relationship between soluble solids content (SSC) and mean temperature in the eight days before harvest in Florida ($R^2 = 0.73$). Menzel [36] demonstrated that average fruit fresh weight decreased by more than 50% as the temperature increased from 16 °C to 20 °C in Queensland.

Fernandes Filho et al. [37] used variations in seasonal temperatures to characterize the response of potato (*Solanum tuberosum* L.) to higher temperatures in Brazil. The plants were grown across three seasons from January to May 2017, May to September 2017, and November 2017 to February 2018, representing moderate heat stress, no heat stress, and severe heat stress. Mean tuber yield was reduced by 2.4% under moderate stress compared with no stress and by 70.2% under severe stress.

This paper reports on the effect of temperature on the performance of five strawberry cultivars growing in the field in subtropical Queensland, Australia. Information was collected on plant growth, marketable yield, fruit size, fruit soluble solids content (SSC) and fruit titratable acidity (TA). Changes in the growth of the plants over the season were used to evaluate the sensitivity of the plants to higher temperatures.

2. Materials and Methods

2.1. Experimental Design and Growing Conditions

Containerized transplants of ‘Festival’, ‘Brilliance’, ‘Red Rhapsody’ ‘Scarlet Rose’ and ‘Sundrench’ were planted on 29 April 2020 at Nambour in south-east Queensland, Australia (latitude 26.6° S, longitude 152.9° E, and elevation 29 m). The first two cultivars were developed in Florida [38,39], while the other three cultivars were developed in Queensland [40]. The transplants were grown in 72 cell-trays with 41 cm³ cells at Armidale in northern New South Wales (latitude 30.3° S, longitude 151.4° E, and elevation 980 m) and were supplied with three to four leaves/plant. Average (\pm SE or standard error) dry weight of the transplants was 1.1 ± 0.1 g/plant. Nambour has a warm subtropical climate, with relatively wet summers, autumns, and winters, and relatively dry springs. The soil at the experimental site was a sandy, clay loam, with moderate fertility and water-holding capacity. The cultivars were planted out in a randomized block design, with six replications.

The new plants were planted through plastic, in double-row beds 70 cm wide and 130 cm apart from the centres. The plants were grown at an inter-row spacing of 30 cm and at an intra-row spacing of 30 cm. This layout provided 77 rows with 666 plants/row

for each ha, giving a density of 51,282 plants/ha. The plants were irrigated through drip-tape placed under the plastic when the soil water potential in the root-zone decreased below -10 kPa [41,42]. Nitrogen and other nutrients were applied by fertigation [42]. The plants received a total of 117 kg/ha of N, 24 kg/ha of P, 165 kg/ha of K, 7 kg/ha of Ca, 13 kg/ha of Mg, 1.8 kg/ha of B, 0.14 kg/ha of Cu, 0.28 kg/ha of Fe, 0.14 kg/ha of Mn, and 0.05 kg/ha of Zn. The main disease affecting the crop was grey mould incited by *Botrytis cinerea*. The plants received weekly applications of multi-site fungicides such as captan and thiram, and applications of site-specific fungicides such as iprodione, fenhexamid, cyprodinil + fludioxonil, and penthiopyrad during wet weather [43].

2.2. Data Collection

Data were collected on the number of leaves/plant, leaf area/plant and plant dry weight (leaves, crowns, and roots) on 26 August and 28 October. Fruit were harvested every week for an assessment of marketable yield (fresh weight) and average fruit fresh weight from 8 July to 28 October. Mature fruit were classified as those that were at least three-quartered coloured. Average seasonal fruit fresh weight was the long-term average value of fruit fresh weight in a cultivar pooled across all harvests (marketable fruit). A record was kept of the number of fruit that were small (less than 12 g fresh weight). Fruit that were affected by rain and/or grey mould or misshapen, or that had other defects (mainly other disease, surface bronzing, or bird damage) were considered non-marketable. Fruit that were small and misshapen were rated as misshapen.

The concentrations of non-structural carbohydrates (starch, sucrose, fructose, glucose and maltose) in the leaves, and in the crowns and roots were determined in the plants harvested on 26 August and 28 October [44]. The analysis for starch was conducted using a Megazyme total starch assay kit using the alpha amylase/amyloglucosidase method (www.megazyme.com, accessed on 15 March 2019). The analysis for soluble sugar profile was conducted using HPLC (high performance liquid chromatography). The sugars were extracted and analysed by HPLC using the relevant reference standards. The data on non-structural carbohydrates are presented on a dry weight basis (DW).

Data were collected on fruit total soluble solids content (SSC) and titratable acidity (TA) as citric acid measured at 20 °C weekly from 16 September to 28 October [45]. These authors indicated that SSC was strongly correlated with the concentrations of sugars (fructose, glucose and sucrose) in strawberry. The sugars accounted for about 90% of the soluble solids in the fruit. Three to six fruit from each plot were placed in small snap lock resealable bags (18 cm × 17 cm, Glad, Sydney, Australia), and frozen at -18 °C until used for chemical analysis. The data on fruit chemistry are presented on a fresh weight basis (FW).

Daily maximum and minimum temperatures, rainfall, and solar radiation data were collected at the site from May to October from the Bureau of Meteorology (www.bom.gov.au, accessed on 15 March 2019). The temperature data were compared with the long-term data for Nambour from 1965 to 1990.

2.3. Data Analysis

There were two sections in each experimental block, one for recording plant growth and concentrations of non-structural carbohydrates, and an adjacent one for recording yield, fruit size, SSC, and TA. There were 22 plants/plot for the yield, fruit size, SSC, and TA data and 2 plants/plot for the growth data.

Data on plant growth, concentrations of non-structural carbohydrates, marketable yield, and mean average seasonal fruit fresh weight, percentage of small fruit, SSC, and TA were analysed by one-way analysis of variance (ANOVA, five cultivars × six blocks) using GenStat (Version 18; VSN International, Hemel Hempstead, UK). The data on plant growth and non-structural carbohydrates for each harvest were analysed separately. Treatment means were separated by calculating least significant differences (LSDs) from the ANOVAs.

The seasonal changes in marketable yield were determined by regression analysis and fitted using the Marquardt-Levenberg algorithm from the graphics' software program SigmaPlot (Version 15; Systat, Chicago, IL, USA). This algorithm was developed several decades ago and is widely used in regression analysis and modelling [46–48]. The relationships between average fruit fresh weight and the average daily mean temperature in the five to seven weeks before harvest, four weeks before harvest and seven weeks before harvest were analysed by regression. These periods covered flower development, fruit development, and flower and fruit development [49–51]. The relationships between SSC and TA, and the average daily mean temperature in the eight days before harvest were also analysed by regression [35].

3. Results

3.1. Weather

Average daily maximum temperatures ranged from 21.3 °C to 26.6 °C and average daily minimum temperatures ranged from 10.1 °C to 15.7 °C (Table 1). The average daily mean temperature in the eight days before fruit harvest increased from 15 °C to 21 °C from 8 July to 28 October (Linear model, $p < 0.001$, $R^2 = 0.78$, $n = 14$). Maximum temperatures were close to the long-term averages from 1965 to 1990, while minimum temperatures were 2 °C to 4 °C higher. Mean monthly daily solar radiation ranged from 12.4 to 20.6 MJ/m² and total monthly rainfall ranged from 17 to 113 mm (Table 1). Values of solar radiation were close to long-term averages, whereas it was wetter in July and October than the long-term average, and drier in May, June, and August.

Table 1. Average monthly daily temperatures and daily solar radiation, and total monthly rainfall in the study with the strawberries in Queensland. Long-term average temperatures (1965 to 1990), solar radiation (2004 to 2019), and rainfall (2007 to 2019) also presented.

Period	May	June	July	August	September	October
<i>2020</i>						
Mean daily max. temperature (°C)	23.2	22.2	21.3	23.3	24.6	26.6
Mean daily min. temperature (°C)	13.5	13.0	11.2	10.1	13.7	15.7
Mean daily solar radiation (MJ/m ²)	13.3	12.4	13.5	16.3	17.4	20.6
Total monthly rainfall (mm)	51	59	113	17	76	112
<i>Long-term average</i>						
Mean daily max. temperature (°C)	23.5	21.3	20.8	22.3	24.6	26.5
Mean daily min. temperature (°C)	11.7	8.5	7.0	7.4	9.8	13.2
Mean daily solar radiation (MJ/m ²)	13.7	11.7	13.1	16.1	18.9	20.9
Total monthly rainfall (mm)	108	115	50	58	90	80

3.2. Plant Growth

On both harvests, there were only small differences in the number of leaves/plant, crown dry weight/plant and root dry weight/plant across the five cultivars (Table 2). In contrast, leaf area/plant was higher in 'Festival' and leaf dry weight/plant was higher in 'Festival' and 'Red Rhapsody' than in the other cultivars. Plant growth was higher in October than in August, especially the growth of the leaves (Table 2).

The main non-structural carbohydrates measured in the leaves were glucose (mean concentration of $3.6 \pm 0.1\%$ DW or dry weight), fructose ($2.6 \pm 0.1\%$), and starch ($1.0 \pm 0.02\%$), with lower concentrations of sucrose and maltose ($<0.1\%$). The mean concentration of all the sugars measured was $6.2 \pm 0.2\%$, and the mean concentration of the non-structural carbohydrates measured was $7.2 \pm 0.2\%$. The main carbohydrates measured in the crowns and roots were glucose ($1.4 \pm 0.05\%$), fructose ($1.6 \pm 0.07\%$), and starch ($1.2 \pm 0.02\%$). The mean concentration of all the sugars was $3.2 \pm 0.1\%$, and the mean concentration of the non-structural carbohydrates was $4.4 \pm 0.1\%$. The soluble sugars accounted for more than 70% of the carbohydrates analysed in the leaves, crowns, and roots.

Table 2. Variations in the number of leaves/plant, leaf area/plant and plant dry weight (leaves, crowns, and roots) in five strawberry cultivars in Queensland. Data are the means of six replicates per cultivar and were collected on 26 August or on 28 October. Means in a column for each harvest followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Means \pm (SE or standard error) across all the cultivars for each harvest also presented.

Cultivar & Time of Sampling	No. of Leaves/Plant	Leaf Area (cm ² /plant)	Leaf Dry Weight (g/plant)	Crown Dry Weight (g/plant)	Root Dry Weight (g/plant)
<i>26 August</i>					
Festival	15.3 b	1450 c	12.4 c	2.5 bc	1.2 bc
Brilliance	13.8 ab	843 a	7.3 a	1.9 a	0.7 a
Red Rhapsody	13.4 ab	1138 b	11.1 c	2.6 c	1.5 c
Scarlet Rose	11.4 a	990 a	9.3 b	2.0 ab	0.9 ab
Sundrench	14.9 b	1008 ab	9.0 ab	1.8 a	1.0 ab
Mean \pm SE	13.8 \pm 0.6	1086 \pm 92	9.8 \pm 0.8	2.2 \pm 0.1	1.1 \pm 0.1
<i>28 October</i>					
Festival	25.1 b	1249 c	17.2 c	4.8 b	1.7 b
Brilliance	24.9 b	1280 a	10.4 a	3.4 a	1.1 a
Red Rhapsody	22.5 ab	1710 b	16.8 c	4.4 b	2.1 c
Scarlet Rose	19.5 a	1642 b	14.8 b	3.5 a	1.2 a
Sundrench	21.2 a	1142 a	9.8 a	2.9 a	1.5 b
Mean \pm SE	22.6 \pm 1.0	1585 \pm 159	13.8 \pm 1.4	3.8 \pm 0.3	1.5 \pm 0.2

There were only small differences in the concentrations of non-structural carbohydrates across the five cultivars (Table 3). The total concentration of non-structural carbohydrates in the leaves in October was lower in 'Brilliance' and 'Red Rhapsody' and higher in 'Festival' and 'Sundrench'. The mean concentrations of non-structural carbohydrates across the cultivars were lower on 28 October than on 26 August (Table 3).

Table 3. Variations in the concentration of non-structural carbohydrates in the leaves, crowns, and roots in five strawberry cultivars in Queensland. The plants were harvested on 26 August or on 28 October. Data are the means of six replicates per cultivar. 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. Means \pm (SE or standard error) across all the cultivars for each harvest also presented. DW = dry weight.

Cultivar	Concentration of Non-Structural Carbohydrates (% DW)			
	Leaves on 26 August	Crowns and Roots on 26 August	Leaves on 28 October	Crowns and Roots on 28 October
Festival	8.9 a	4.8 a	7.1 b	3.8 a
Brilliance	7.7 a	4.9 a	5.6 a	3.5 a
Red Rhapsody	8.2 a	5.3 a	5.9 a	3.6 a
Scarlet Rose	7.7 a	4.5 a	6.3 ab	3.5 a
Sundrench	7.9 a	5.4 a	7.1 b	4.3 a
Mean \pm SE	8.1 \pm 0.3	5.0 \pm 0.1	6.4 \pm 0.2	3.7 \pm 0.1

3.3. Yield and Fruit Quality

Total marketable yield was lower in 'Brilliance' than in the other cultivars (Table 4). Mean seasonal average fruit fresh weight was lower in 'Festival' and 'Brilliance' and higher in 'Red Rhapsody', 'Scarlet Rose', and 'Sundrench'. The reverse was true for the mean incidence of small fruit (higher in 'Festival' and 'Brilliance') (Table 4). Mean soluble solids content (SSC) was lower in 'Sundrench', intermediate in 'Brilliance' and 'Red Rhapsody' and higher in 'Festival' and 'Scarlet Rose' (Table 4). Mean titratable acidity (TA) was lower in 'Brilliance' and 'Sundrench', intermediate in 'Festival' and 'Red Rhapsody', and higher in 'Scarlet Rose'. Average seasonal SSC increased from 7.0 to 9.0% as average seasonal TA

increased from 0.55 to 0.85% (linear model, $p < 0.001$, $R^2 = 0.60$, $n = \text{five cultivars} \times \text{six blocks or 30 samples}$).

Table 4. Variations in total marketable yield, mean seasonal average fruit fresh weight (marketable), percentage of small fruit (<12 g fresh weight), fruit soluble solids content (SSC), and fruit titratable acidity (TA) in five strawberry cultivars in Queensland. Average seasonal fruit fresh weight is the long-term average value of fruit fresh weight in a cultivar pooled across all harvests (marketable fruit). Soluble solids content and titratable acidity were measured over seven harvests from 16 September to 28 July. Data are the means of six replicates per cultivar. 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.

Cultivar	Marketable Yield (g/plant)	Av. Fruit Fresh Weight (g)	Percentage of Small Fruit	Soluble Solids Content (%)	Titratable Acidity (%)
Festival	616 b	20.3 a	29.0 c	8.3 c	0.64 b
Brilliance	457 a	22.7 b	28.2 c	7.3 b	0.57 a
Red Rhapsody	617 b	23.9 c	16.2 a	7.3 b	0.64 b
Scarlet Rose	592 b	24.4 cd	21.7 b	8.9 d	0.83 c
Sundrench	656 b	25.5 d	16.0 a	6.8 a	0.57 a

Changes in accumulated marketable yield over the season followed a sigmoid (dose-logistic) pattern ($p < 0.001$, $R^2 = 0.99$, Figure 1, Table 5) and were generally similar across the five cultivars. S_m is the maximum yield, k is a rate constant (yield/day), and m describes the time to reach the maximum increase in yield. All the cultivars were producing a marketable crop at the last harvest on 28 October, although at a lower rate than earlier in the month. The maximum yield in the regressions reflected the absolute yields of the cultivars ('Brilliance' lower and the other cultivars higher).

Table 5. Details of the relationships between the seasonal changes in accumulated marketable yield and day since planting in the five strawberry cultivars in Queensland shown in Figure 1. Yield (g/plant) = $S_m / (1 + \exp. (-k \times (\text{Day}-m)))$. S_m is the maximum yield, k is a rate constant (yield/day), and m describes the time to reach the maximum increase in yield (days). SE = standard error. $p < 0.001$ in all cases.

Cultivar	$S_m \pm SE$	$k \pm SE$	$m \pm SE$	R^2 Value
Festival	670 \pm 12	0.050 \pm 0.002	129 \pm 1	0.99
Brilliance	481 \pm 11	0.047 \pm 0.002	125 \pm 1	0.99
Red Rhapsody	698 \pm 13	0.046 \pm 0.001	139 \pm 1	0.99
Scarlet Rose	643 \pm 14	0.049 \pm 0.002	133 \pm 1	0.99
Sundrench	679 \pm 12	0.052 \pm 0.002	127 \pm 1	0.99

Average fruit fresh weight varied over the growing season (Figure 2). There was a strong negative relationship between fruit size and the day of sampling for the last fourteen harvest. Fruit were relatively small during the first three harvests when the plants were small and these data were not included in the regression. There were moderate to strong negative relationships between average fruit weight (marketable) and the average daily mean temperature before harvest from 29 July to 28 October (Figure 3). Fruit size was more closely related to temperatures during fruit development (four weeks before harvest) or during flower and fruit development (seven weeks before harvest) than during flower development alone (five to seven weeks before harvest).

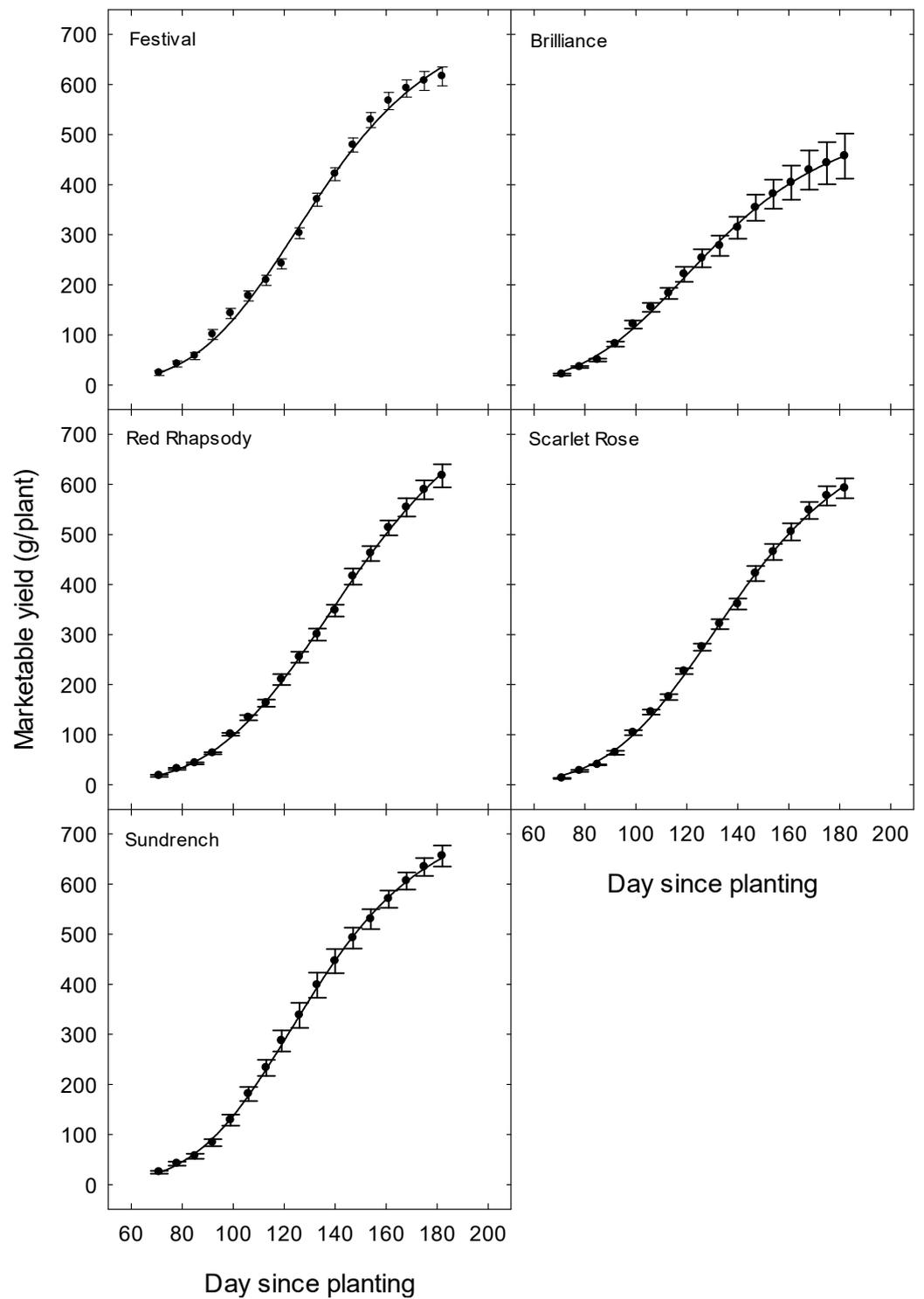


Figure 1. Seasonal changes in accumulated marketable yield in five strawberry cultivars in Queensland. Data are the means (\pm SE or standard error) of six replicates per cultivar. Day 1 was the date of planting on 29 April and Day 182 was the last harvest on 28 October ($n = 17$). Details of the regressions are shown in Table 5.

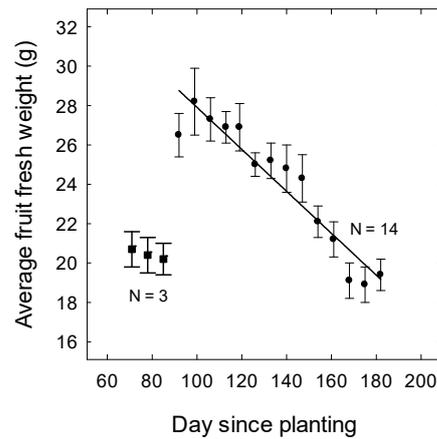


Figure 2. Seasonal changes in average fruit fresh weight (marketable fruit weighing at least 12 g) (AFWT) in strawberries in Queensland. Data are the means (\pm SE or standard error) of five cultivars with six replicates for each cultivar. Day 1 was the date of planting on 29 April and Day 182 was the last harvest on 28 October ($n = 17$). For the last 14 harvests, $AFWT (g) = Intercept - 0.107 \times Day$ ($p < 0.001, R^2 = 0.89$). Average fruit fresh weight was low for the first three harvests (not included in regression).

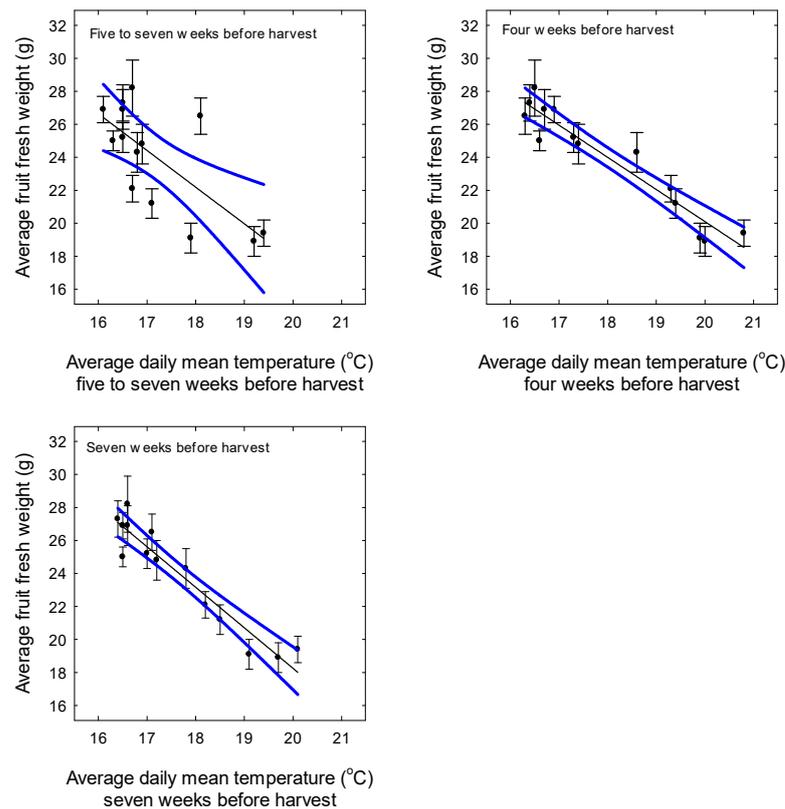


Figure 3. Relationship between average fruit fresh weight (marketable fruit weighing at least 12 g) (AFWT) and average daily mean temperature (Temperature) during different periods before harvest from 29 July to 28 October in strawberries in Queensland. These periods covered flower development (five to seven weeks before harvest), fruit development (four weeks before harvest), and flower and fruit development (seven weeks before harvest). Data are the means (\pm SE or standard error) of five cultivars with six replicates for each cultivar. $AFWT (g) = Intercept - 2.22 \times Temperature_{Weeks5-7}$ ($p < 0.001, R^2 = 0.48, n = 14$). $AFWT (g) = Intercept - 1.95 \times Temperature_{Weeks4}$ ($p < 0.001, R^2 = 0.90, n = 14$). $AFWT (g) = Intercept - 2.45 \times Temperature_{Weeks7}$ ($p < 0.001, R^2 = 0.90, n = 14$). Blue lines indicate 95% confidence intervals.

There were no significant relationships between SSC and TA, and average mean temperature from 16 September to 28 October ($p > 0.05$, $n = 7$). The average daily mean temperature eight days before harvest over this period ranged from 18.2 °C to 22.2 °C. Average SSC was lower on 28 October ($6.7 \pm 0.3\%$) than from 16 September to 21 October ($7.4 \pm 0.3\%$ to $8.5 \pm 0.4\%$).

4. Discussion

There were large changes in plant growth, marketable yield, and fruit size in the strawberry as the temperatures increased in Queensland. Higher temperatures generally had a negative effect on the performance of the plants. The plants continued to produce a marketable crop towards the end of the season. However, the fruit were small and more expensive to harvest. These results suggest that the economics of production in this area may already be affected by rises in temperature.

Plant growth was higher in October than in August, especially leaf production, leaf area expansion, and leaf dry weight. These results suggest that temperatures towards the end of the experiment were still optimal for leaf growth. There is little information on the effect of temperature on the growth of strawberry in the subtropics. Some authors provide data on the growth of plants under controlled-temperature conditions.

Wang and Camp [52] grew 'Earliglow' and 'Kent' in growth chambers set at different temperatures. Leaf dry weight/plant was higher at 25 °C/15 °C or 25 °C/22 °C and lower at 18 °C/12 °C or 30 °C/22 °C. Crown dry weight/plant was higher at 18 °C/12 °C, 25 °C/15 °C, or 25 °C/22 °C. Root dry weight was higher at 18 °C/12 °C. Kadir et al. [53] showed that leaf growth in 'Chandler' and 'Sweet Charlie' was higher at 30 °C/25 °C and lower at 20 °C/15 °C or 40 °C/35 °C. Root growth was best at the lowest temperature regime. Menzel [54] investigated the effect of temperature on the growth of 'Festival' in controlled-temperature glasshouses. Leaf dry weight/plant was a maximum at 25 °C and lower at 15 °C, 20 °C, or 30 °C. In contrast, crown and root dry weight/plant were a maximum at 20 °C.

There were variations in the concentrations of non-structural carbohydrates across the three plant parts and across the two harvests. The concentrations of non-structural carbohydrates were lower in the crowns and roots than in the leaves, and lower on 28 October than on 26 August. The concentration of non-structural carbohydrates in the plants reflects the balance between photosynthesis, respiration, and growth. If photosynthesis exceeds respiration and growth, then carbohydrates accumulate in the plant. If photosynthesis is lower than respiration and growth, then carbohydrates dissipate in the plant. In many crops, including strawberries, the concentration of non-structural carbohydrates is higher at low temperatures than at high temperatures, provided CO₂ assimilation continues [55]. The lower concentrations of non-structural carbohydrates in the plants in October reflect higher temperatures and stronger growth at the end of the season.

The plants continued to produce a marketable crop towards the end of the season, although at a lower rate. Overall, the five cultivars had similar patterns of cropping, but with differences in total marketable yield. Average marketable yield across the cultivars was 588 g/plant. There are few studies reporting on the productivity of strawberry cultivars in the subtropics. Average marketable yields across four cultivars in a previous study in Queensland ranged from 657 to 1064 g/plant in the first season and from 416 to 605 g/plant in the second season [41]. Marketable yields across three cultivars and three seasons in Florida ranged from 412 to 1014 g/plant, with a mean (\pm SE) of 797 ± 66 g/plant [38]. Yields peaked in February and declined in March in Florida.

Kruger et al. [56] indicated that yields across several sites in Europe were more affected by season and growing conditions than latitude. Average daily mean temperature decreased by 2 °C from north to south. In contrast, there were strong negative relationships between SSC and average maximum and minimum temperatures in the week before harvest ($p < 0.001$, $r = -0.70$ to -0.82)

In the current experiment, average fruit weight (marketable) decreased from late July to late October. There was a strong negative relationship between average fruit weight and the average daily mean temperature during fruit development (four weeks before harvest) or during flower and fruit development (seven weeks before harvest). Menzel [36] indicated that average fruit fresh weight decreased as the average mean daily temperature increased from 16 °C to 20 °C in Queensland.

Le Mière et al. [57] studied the effect of temperature on strawberry in glasshouses in the United Kingdom. The plants were grown at constant temperatures ranging from 12 °C to 28 °C. Yield decreased from 200 g/plant to 50 g/plant as the temperature increased, while average fruit fresh weight decreased from 14 g to 5 g. The number of fruit per plant decreased from 15/plant to 8/plant. Lower yields at high temperatures were due to fewer and smaller fruit. High temperatures affected dry matter production in individual fruit, independently of the effect of temperature on total fruit production.

Strawberry fruit are produced from inflorescences called cymes, with a hierarchy of fruit decreasing in size with inferior positions of the flowers [36]. A primary flower is initiated at the end of the cyme, with secondary, tertiary, and possibly quaternary and quinary flowers initiated from the axes below the preceding blooms. No information was collected on the development of the cymes in the current experiment. Further research is required to separate the effect of temperature on the development of the cymes and on the development of individual fruit.

Commercial fruit production continued to the end of the season in Queensland. However, average fruit weight decreased. Plants with small fruit cost more to harvest than plants with large fruit. Harvesting accounts for up to 60% of variable costs for growing strawberries in Japan, California, Florida, and Queensland [58,59]. Studies in the United Kingdom demonstrated that ‘Malling Centenary’ has larger fruit than many earlier cultivars and lower harvesting costs [60,61]. Harvesting rates in the new cultivar were 30 to 40 kg/hour under table-top production compared with 25 to 30 kg/hour in the earlier cultivars. A study in Italy showed that for each one gram decrease in average fruit fresh weight, the cost of harvesting was increased by €500/ha [62]. Herrington et al. [63] indicated the cost of harvesting in Australia increased by \$AU600/ha for each one gram decrease in fruit weight from 30 g to 17 g.

The soluble solids content (SSC) and titratable acidity (TA) of the fruit varied across the different cultivars. In contrast, there was no significant relationships between SSC and TA, and the temperature from 16 September to 28 October. Fruit SSC was lower in the last harvest on 28 October than in the earlier harvests. Average SSC across the cultivars ranged from 6.8 to 8.9%, while average TA ranged from 0.57 to 0.82%. In an earlier study in Queensland, SSC ranged from 6.8 to 8.1% in the first season and from 7.0 to 8.8% in the second season [41]. In the same study, TA ranged from 0.61 to 0.65% and from 0.61 to 0.71%.

MacKenzie et al. [35] investigated the effect of temperature on fruit growth and carbohydrate accumulation in strawberry in Florida. Individual flowers on plants in the field were transferred to glasshouses set at 15 °C or 22 °C. The weight and SSC of individual fruit were recorded at harvest over two seasons. Temperature did not affect fruit fresh weight, probably because temperatures were only manipulated for a few days after the flowers opened. In contrast, SSC was lower at the higher temperature (5.2%) than at the lower temperature (6.5%). In a related work, the authors found a strong negative relationship between SSC and temperature in the eight days before harvest in the field. Soluble solids content decreased from a 9.5% at 11 °C to 6.0% at 21 °C. The data in the current experiment were too variable to determine the relationship between SSC and temperature.

Higher temperatures affect many aspects of plant development in strawberry. In most cultivars, there is a broad temperature optimum for growth [49] and flowering [64–66] and a narrow optimum for average fruit weight [32]. Sønsteby and Heide [66] indicated that floral induction in six cultivars in Norway exhibited a broad optimum from 15 °C

to 21 °C and was reduced or suppressed at 9 °C or 27 °C. In a later study, Heide and Sønsteby [67] suggested that inadequate winter chill was the main limiting factor for berry crops under climate change in northern Europe. A 2 °C increase in temperature was expected to lead to smaller leaves and inflorescences in spring. In warmer areas such as Queensland and Florida, fruit size and fruit SSC are likely to be the main limiting factors under global warming.

5. Conclusions

Temperature was correlated with the growth and development of the strawberry plants in Queensland. Average daily maximum/minimum temperatures were 23.2 °C/13.5 °C in May, 22.2 °C/13.0 °C in June, 21.3 °C/11.2 °C in July, 23.3 °C/10.1 °C in August, 24.6 °C/13.7 °C in September, and 26.6 °C/15.7 °C in October. Minimum temperatures were 2 °C to 4 °C higher than the long-term averages from 1965 to 1990. The plants continued to produce a marketable crop towards the end of the season. However, the fruit were small and more expensive to harvest. There was a strong negative relationship between average fruit weight and the average daily mean temperature during fruit development (four weeks before harvest) or during flower and fruit development (seven weeks before harvest). These results suggest that the economics of strawberry production in this area is already affected by rises in temperature. Global warming will reduce the profitability of strawberry in the subtropics in the absence of heat-tolerant cultivars or other mitigating strategies.

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