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Temperature Has a Greater Effect on Fruit Growth than Defoliation or Fruit Thinning in Strawberries in the Subtropics

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Received: 16 May 2019; Accepted: 14 June 2019; Published: 18 June 2019

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Abstract: Fruit size declines in strawberries (*Fragaria* × *ananassa* Duch.) as the season progresses in many subtropical areas, possibly due to inadequate leaf area, over-cropping, or high temperatures. An experiment was conducted to investigate the importance of these factors on fruit growth in 'Festival' in Queensland, Australia. Groups of plants were defoliated to remove half of the mature leaves on each plant, thinned to remove all the inflorescences on each plant, or defoliated and thinned. Control plants were left intact. Defoliation, thinning, or defoliation + thinning decreased yield (total and/or marketable) by 15% to 24% compared with the control. Defoliation, or defoliation + thinning decreased average fruit weight (total and/or marketable fruit) by 1 to 2 g compared with the control, whereas thinning had the opposite effect. The incidence of small fruit increased towards the end of the season. There were strong relationships between fruit weight and average daily mean temperature in the seven weeks before harvest (R^2s greater than 0.80). Fruit weight decreased from 24 g to 8 g as the temperature increased from 16 °C to 20 °C. This response was not affected by defoliation or thinning. The strong effect of temperature on fruit size indicates a problem for production in the future in the absence of heat-tolerant cultivars.

Keywords: crop load; defoliation; *Fragaria* × *ananassa* Duch.; fruit growth; fruit thinning; leaf area; temperature; yield

1. Introduction

One of the major issues affecting strawberry cultivation in the subtropics is the production of small fruit [1–4]. In Queensland, Australia, the incidence of small fruit increases as the season progresses, with more than half the fruit smaller than 12 g in October. A high incidence of small fruit reduces marketable yields and increases the costs of harvesting. A study in Italy showed that for each one gram decrease in average fruit fresh weight, the cost of harvesting was increased by about €500/ha [5]. Small fruit at the end of the season could be due to inadequate leaf area, over-cropping, or high temperatures [4,6].

Strawberry fruit are initiated from inflorescences called cymes, with a hierarchy of fruit decreasing in size with inferior positions of the flowers [7]. A primary flower is produced at the end of the cyme, with secondary, tertiary, and possibly quaternary and quinary flowers produced from the axes of the cymes below the preceding blooms [8]. There are more ovules and more pollen in the primary flower than in the lower-order flowers [9]. The berry is an aggregate fruit originating from the receptacle tissue, and has a number of ovaries, which develop into one-seeded fruit or achenes. The achenes are composed of a seed and ovary tissue and originate at the base of each pistil [10]. Each berry can have up to 500 achenes, depending on the cultivar and growing conditions. The number of achenes reflects the number of pistils in the developing flower, and typically decreases with the ranking of the fruit on the cyme. Berry weight increases with the number of achenes per fruit and decreases with the number of achenes per unit area of fruit surface [11,12]. Auxins have a major role in vegetative and reproductive development in strawberries and affect the development of the flowers and fruit [13]. Auxins produced in the young leaves are transported through the vascular system to the shoot apical meristem and are essential for floral induction and differentiation [14]. Auxins produced from the achenes are essential for fruit set and fruit growth [15].

The development of the flowers and fruit is dependent on carbohydrates produced in the leaves. Experiments have been conducted to explore the relationship between fruit growth, photosynthesis, and the demand for carbohydrates by the developing crop. In most studies, defoliation or thinning had a small effect on average fruit weight [16–19]. This might have been because the treatments were not severe enough to affect the distribution of carbohydrates to the fruit.

Temperature is the main environmental factor influencing the growth of the cymes, flowers, and fruit. Miura et al. [20] indicated that average fruit weight for the whole cyme was lower at 19 °C (7.3 ± 0.3 g) than at 15 °C (8.2 ± 0.4 g), suggesting a direct effect of temperature on the flowers and fruit rather than on the structure of the cyme. Kumakura and Shishido [21] found that fruit weight decreased as the mean temperature in glasshouses increased from 15 °C to 20 °C to 25 °C. The weight of the fruit from the primary flower was about 35 g, 20 g, and 11 g at the three temperatures. A similar response occurred in the flowers in the lower positions on the cyme.

This paper reports on a study to investigate the importance of leaf area, over-cropping, and high temperatures on fruit growth of strawberries in Queensland. Half the mature leaves or all the cymes (inflorescences) were removed from groups of plants, or both treatments applied. Information was collected on plant growth, yield, and fruit weight, and the relationship between fruit weight and temperature over the season determined. None of the previous studies in strawberries examined whether leaf area or crop load affected the relationship between fruit size and temperature. The defoliation and thinning treatments were also more severe than in many of the earlier experiments.

The results of the current work show that fruit weight varied by a factor of three with changes in temperature over the season but by only a few grams with different leaf areas or crop loads. Temperature had a greater effect on fruit size than defoliation or thinning, with the response to temperature similar in the different treatments. The strong effect of temperature on fruit size indicates a problem for production in the future in the absence of heat-tolerant cultivars.

2. Materials and Methods

An experiment was conducted to investigate the importance of leaf area, crop load, and temperature on fruit development in 'Festival' strawberries in south-east Queensland, Australia. Bare-rooted transplants were planted in the open field in Nambour (latitude 26.6° S, longitude 152.9° E, elevation 29 m) in mid-April in 2016. The transplants were grown at Stanthorpe in southern Queensland (latitude 28.6° S, longitude 152.0° E, elevation 872 m) and had three to four leaves on each plant.

The plants were maintained using standard agronomic practices for this region [22]. The new plants were planted through plastic, in double-row beds 70 cm wide and 130 cm apart from the centers. The plants were grown at an inter-row spacing of 30 cm and at an intra-row spacing of 30 cm. This lay-out 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 [22]. The plants were fertilized through the irrigation and received 117 kg N/ha, 24 kg P/ha and 165 kg K/ha and other nutrients as described previously [23]. The main disease affecting the crop was grey mold incited by *Botrytis cinerea*, with the plants receiving 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 [22].

Half the mature leaves were removed at random from a group of plants, or all the cymes (inflorescences) removed, or both treatments applied on 28 June. Control plants were left undefoliated and unthinned. The treatments were applied once. Information was collected on the number of leaves, leaf area, and dry weight of the leaves, crowns, roots, flowers, and immature fruit every three weeks, and on yield, fruit production, and average fruit fresh weight every week over the following 16 weeks until late October. Fruit were classified as mature when they were 75% colored, and as marketable (12 g or greater) or non-marketable (less than 12 g). The percentage of fruit that were non-marketable was calculated from the total number of fruit/plant and the number of non-marketable fruit/plant. Fruit that were damaged by rain or disease were not included in the analysis.

The experiment was arranged in a latin-square design, with four replicate blocks per treatment. There were two sections in each block, one for recording plant growth, and an adjacent one for recording yield, fruit production, and fruit weight. For the growth data, there were four plots × two plants in each plot and eight plants per treatment. For yield, fruit production, average fruit weight, and the percentage of non-marketable fruit, there were four plots × 14 plants in each plot and 56 plants per treatment. Data on growth were analyzed by latin-square analysis of variance (ANOVA) using GenStat (Version 15; VSN International, Hemel Hempstead, UK), pooled over the six harvests. Data on yield, fruit production, average fruit weight and the percentage of non-marketable fruit were analyzed by latin-square ANOVA. Data on yield, fruit production, and average fruit fresh weight were separated into marketable, non-marketable, and total components. Data on average fruit weight were analyzed only for the last 11 weeks of the experiment when fruit were harvested from all the treatments. Treatment means were separated by calculating least significant differences (LSDs) from the ANOVAs.

Additional data are presented for the control plants, including the seasonal changes in yield, fruit production, average fruit weight, and the percentage of non-marketable fruit. Daily maximum and minimum temperatures were collected at the site, and average values calculated in the five to seven, four, and seven weeks before harvest, covering flower development, fruit development, and flower and fruit development [24–26].

The relationship between the percentage of marketable fruit and average fruit weight in the controls was determined by regression analysis and fitted using the Marquart-Levenberg algorithm from the graphics software program SigmaPlot (Version 12; Systat, Chicago). The relationships between average fruit weight and yield reflected by the number or total weight of fruit/plant in the controls was determined by regression analysis. The relationship between fruit weight and average daily mean temperature in the different periods before harvest was also determined. First, the relationships in the control and the defoliation treatments were determined for the whole 16-week season. Second, the relationships in the controls, and in the defoliation, thinning, and defoliation + thinning treatments were determined over the last 11 weeks of the season when fruit were harvested from all the plots. The different regressions were analyzed in Groups using GenStat (control and defoliated for the whole experiment, and all the treatments for the last 11 weeks of the experiment) to test whether the intercepts and slopes of the different regressions were significantly different.

3. Results

The average maximum temperature ranged between 20.0 °C to 28.7 °C during the experiment, the average minimum temperature ranged between 8.8 °C to 18.3 °C, and the average mean temperature ranged between 15.1 °C to 22.1 °C (Figure 1). The average maximum daily temperature during the coolest period of flower and fruit development (seven weeks) ranged between 16.4 °C to 30.0 °C, the average minimum daily temperature ranged between 3.9 °C to 19.4 °C, and the average mean daily temperature ranged between 11.2 °C to 24.7 °C. The corresponding ranges for the warmest developmental period were 21.1 °C to 33.3 °C, 8.0 °C to 17.7 °C, and 16.8 °C to 25.0 °C.

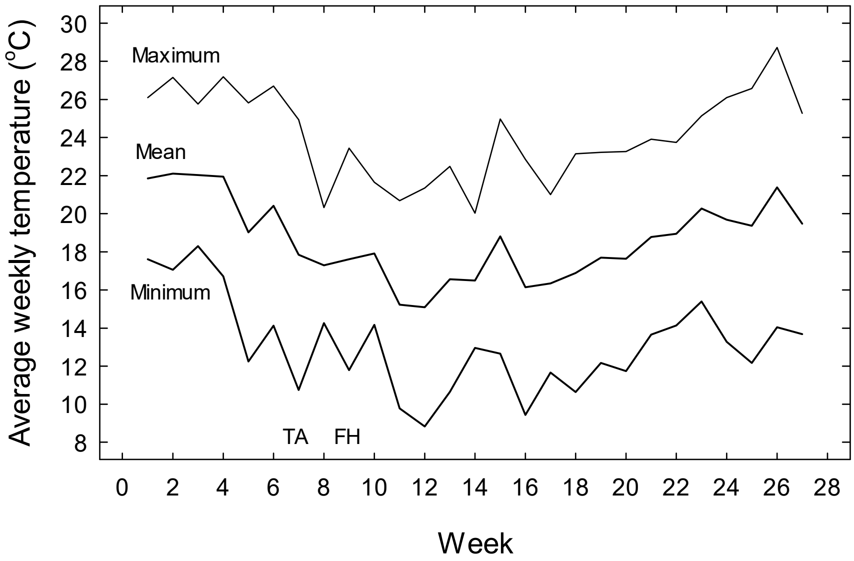

Figure 1. Changes in average weekly maximum, minimum, and mean daily temperatures during the experiment with the strawberries in Queensland. The different treatments were applied on 28 June, equivalent to week 7.5 (Treatments applied or TA), and the first fruit were harvested was on 7 July, equivalent to week 9 (First harvest or FH). The plants were planted on April 13 (start of week one).

There were 12.8 ± 0.7 leaves/plant (mean ± SE) on the controls at the start of the experiment on 28 June about ten weeks after planting, 10.1 ± 1.8 visible flowers and immature fruit/plant, but no mature fruit. Defoliation decreased all components of plant growth compared with the control (Table 1). Thinning had no significant ($p > 0.05$) effect on leaf and root growth compared with the control, increased the weight of the crowns, and decreased the weight of the flowers and the fruit (immature + mature fruit). Defoliation + thinning had no significant ($p > 0.05$) effect on leaf production compared with the control, and decreased leaf area and the dry weight of the leaves, flowers, and fruit (Table 1).

Defoliation decreased marketable and total yield compared with the control (Table 2). This response was associated with fewer marketable fruit after defoliation, but a similar total number of fruit in the two treatments. Thinning, or defoliation + thinning decreased fruit number and yield (marketable and total) compared with the control. Defoliation, and defoliation + thinning decreased average fruit weight (total and/or marketable fruit) compared with the control, whereas thinning had the opposite effect (Table 3). The four treatments had similar non-marketable fruit weights. Defoliation increased the percentage of non-marketable fruit compared with the other treatments, including the control (Table 3).

Table 1. Effect of defoliation and thinning on average seasonal growth in 'Festival' strawberries in Queensland. The plants had half of the mature leaves removed or all the cymes removed in June. Data are the means (± SDs) of four replicates per treatment, pooled over six harvests. Means in a column not sharing common letters are significantly different at $p < 0.05$.

Treatment	No. of Leaves/Plant	Leaf Area (cm^2/Plant)	Dry Weight (g/Plant)					
			Leaves	Crowns	Roots	Flowers & Immature Fruit	Flowers & All Fruit	Plant
Control	19.9 ± 1.3 b	2066 ± 106 c	16.9 ± 1.3 c	5.9 ± 0.9 b	2.4 ± 0.4 b	8.1 ± 0.7 b	13.0 ± 0.4 c	38.3 ± 2.4 c
Defoliation	14.6 ± 1.4 a	1436 ± 149 a	10.9 ± 0.9 a	4.9 ± 0.5 a	1.7 ± 0.1 a	6.7 ± 0.7 a	11.1 ± 0.8 b	28.6 ± 1.9 a
Thinning	19.9 ± 1.0 b	2186 ± 200 c	18.4 ± 1.9 c	6.9 ± 0.6 c	2.3 ± 0.2 b	7.6 ± 1.2 ab	10.5 ± 1.4 ab	38.1 ± 2.9 c
Defoliation + thinning	17.6 ± 2.8 ab	1744 ± 267 b	14.2 ± 2.2 b	6.2 ± 0.5 bc	2.3 ± 0.2 b	6.9 ± 1.1 a	9.7 ± 1.2 a	32.5 ± 3.9 b

Table 2. Effect of defoliation and thinning on yield and fruit production in 'Festival' strawberries in Queensland. The plants had half of the mature leaves removed or all the cymes removed in June. Data are the means (± SDs) of four replicates per treatment. Means in a column not sharing common letters are significantly different at $p < 0.05$. MKT = marketable fruit and Non-MKT = non-marketable fruit (less than 12 g).

Treatment	Yield (g/Plant)			Number of Fruit/Plant		
	MKT	Non-MKT	Total	MKT	Non-MKT	Total
Control	853 ± 60 c	138 ± 10 b	991 ± 61 c	41.9 ± 2.9 b	16.8 ± 1.4 b	58.6 ± 3.4 b
Defoliation	676 ± 53 a	157 ± 18 c	834 ± 71 b	34.7 ± 2.9 a	19.7 ± 2.1 c	54.4 ± 4.8 b
Thinning	725 ± 46 b	118 ± 11 a	843 ± 52 b	34.5 ± 1.7 a	13.4 ± 1.2 a	47.9 ± 2.6 a
Defoliation + thinning	651 ± 68 a	130 ± 23 ab	780 ± 89 a	33.6 ± 3.3 a	15.2 ± 2.6 ab	48.8 ± 5.8 a

Table 3. Effect of defoliation and thinning on average fruit fresh weight and the percentage of fruit that were non-marketable in 'Festival' strawberries in Queensland. The plants had half of the mature leaves removed or all the cymes removed in June. Data are the means (± SDs) of four replicates per treatment. Means in a column not sharing common letters are significantly different at $p < 0.05$. MKT = marketable fruit and Non-MKT = non-marketable fruit (less than 12 g). The percentage of fruit that were non-marketable was calculated from the total number of fruit/plant and the number of non-marketable fruit/plant.

Treatment	Average Fruit Fresh Weight (g)			Percentage of Fruit That Were Non-Marketable
	MKT	Non-MKT	Total	
Control	19.0 ± 0.3 b	8.9 ± 0.1 a	16.4 ± 0.3 b	28.6 ± 1.8 a
Defoliation	18.3 ± 0.6 a	9.1 ± 0.3 a	15.3 ± 0.8 a	36.2 ± 0.7 b
Thinning	19.9 ± 0.5 c	8.8 ± 0.2 a	17.4 ± 0.3 c	27.9 ± 1.3 a
Defoliation + thinning	18.6 ± 0.3 a	8.8 ± 0.3 a	15.9 ± 0.5 ab	31.0 ± 2.2 a

Both marketable and total yield in the control peaked 65 to 86 days after the treatments were applied, and then declined (Figure 2). Fruit fresh weight (marketable and total) in the control was generally higher up to day 65 and generally lower after that period (Figure 3). These responses were associated with a strong increase in the percentage of fruit that were non-marketable after day 65 (Figure 3). There was a strong negative relationship between the percentage of fruit that were non-marketable and average fruit fresh weight (marketable + non-marketable) (TOTAL AVWT) (Figure 4). About 80% of the fruit were rejected when the average weight of the fruit was 8 g. There were weak negative relationships between average fruit weight (TOTAL AVWT) and the total number or weight of fruit/plant for the first twelve harvests (R^2 = 0.37 or 0.22), and no relationship for the last four harvests (Figure 5).

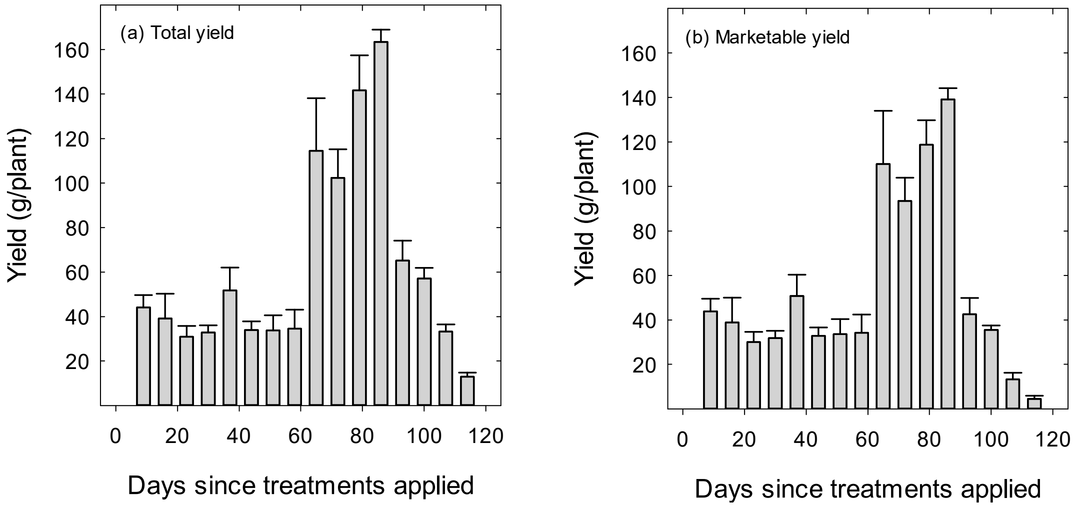

Figure 2. Changes in (**a**) total and (**b**) marketable yield in 'Festival' strawberries in Queensland. Data are the means and standard errors (SEs) of four control plants (N = 16 harvests). Marketable fruit included fruit weighing 12 g or heavier. The experiment started on 28 June.

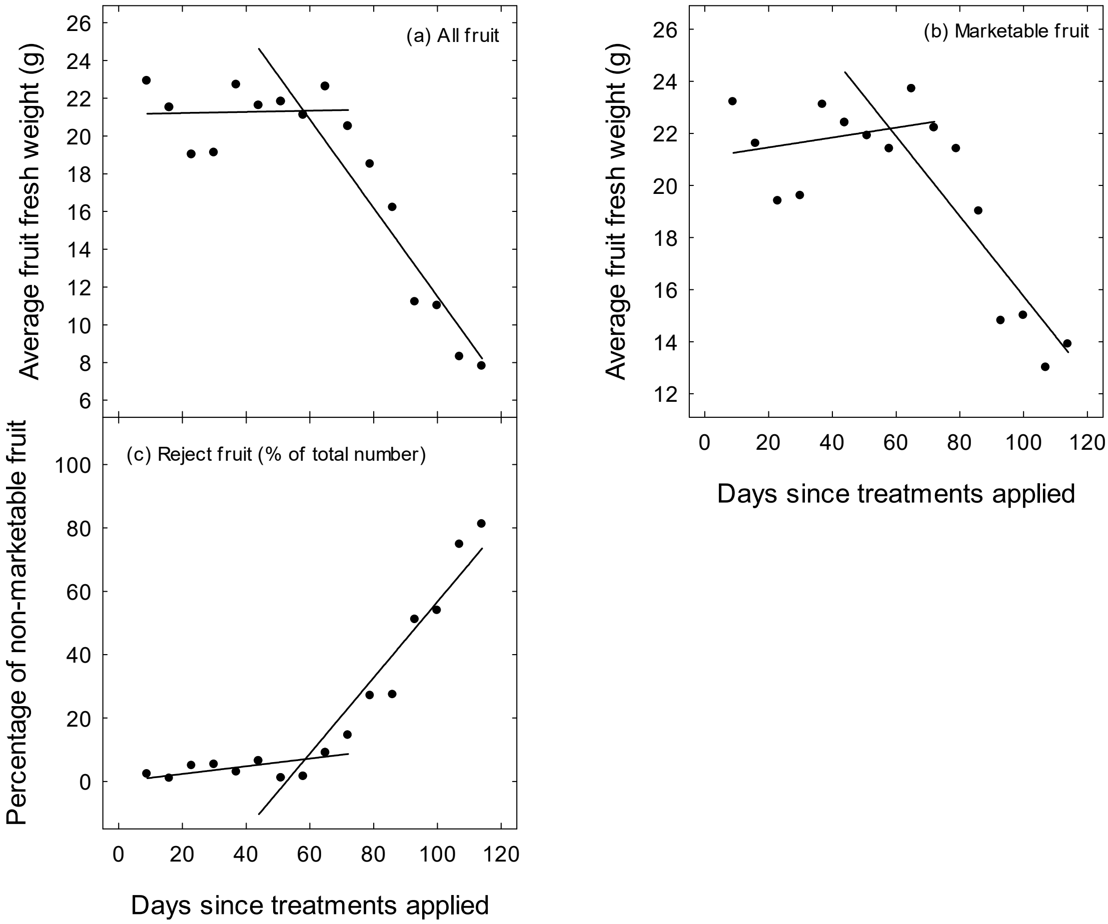

Figure 3. Changes in (**a**) average fruit fresh weight (all fruit), and (**b**) average fruit weight (marketable fruit weighing 12 g or heavier) and (**c**) the percentage of non-marketable fruit in 'Festival' strawberries in Queensland. Data are the means of four control plants (n = 16 harvests). The experiment started on 28 June. The percentage of fruit that were non-marketable was calculated from the total number of fruit/plant and the number of non-marketable fruit/plant. Linear-linear relationships shown.

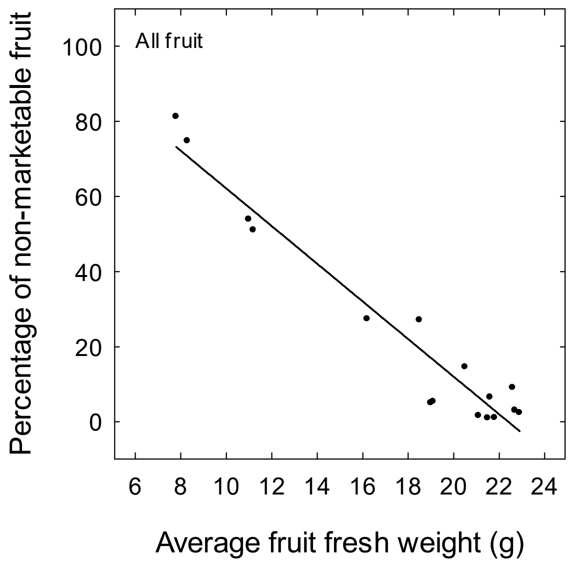

Figure 4. Relationship between the percentage of non-marketable fruit weighing less than 12 g (Non-MKT) and average fruit fresh weight (marketable + non-marketable) (TOTAL AVWT) in 'Festival' strawberries in Queensland. Data are the means of four control plants (N = 16 harvests). Non-MKT = 112.3 − 5.0 × TOTAL AVWT (R^2 = 0.94).

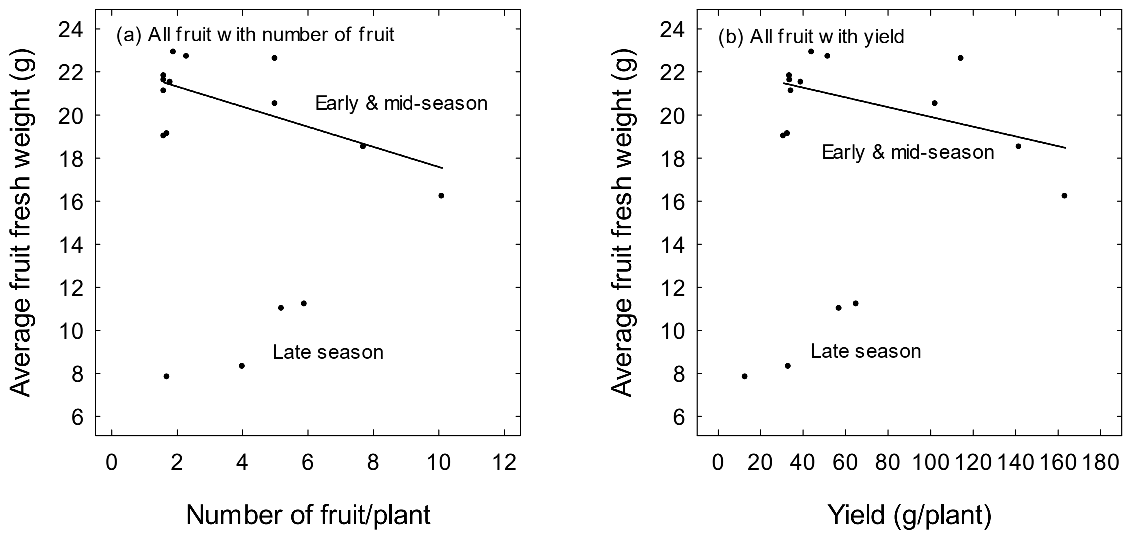

Figure 5. Relationship between average fruit fresh weight (marketable + non-marketable) (TOTAL AVWT), and (**a**) the total number of fruit/plant (Number) or (**b**) total yield/plant (Yield) in 'Festival' strawberries in Queensland. Data are the means of four control plants, and have been separated into early and mid-season harvests over the first twelve weeks (n = 12 harvests), and harvests over the last four weeks (n = 4 harvests). Regressions for the early and mid-season: TOTAL AVWT = 22.3 − 0.47 × Number (R^2 = 0.37), and TOTAL AVWT = 22.2 − 0.03 × Yield (R^2 = 0.22).

There were strong negative relationships between average fruit weight and average daily mean temperature in the seven weeks before harvest (Figure 6; Table 4). Fruit weight decreased from 24 g to 8 g as the temperature increased from 16 °C to 20 °C. This response occurred across all the treatments, and was similar when the data for the control and the defoliation treatments were used for part or the whole season. The relationship between fruit weight and temperature was stronger (higher R^2) in the seven weeks before harvest than in the four or five to seven weeks before harvest (data not presented). The earlier period covered fruit development and the later period covered flower development.

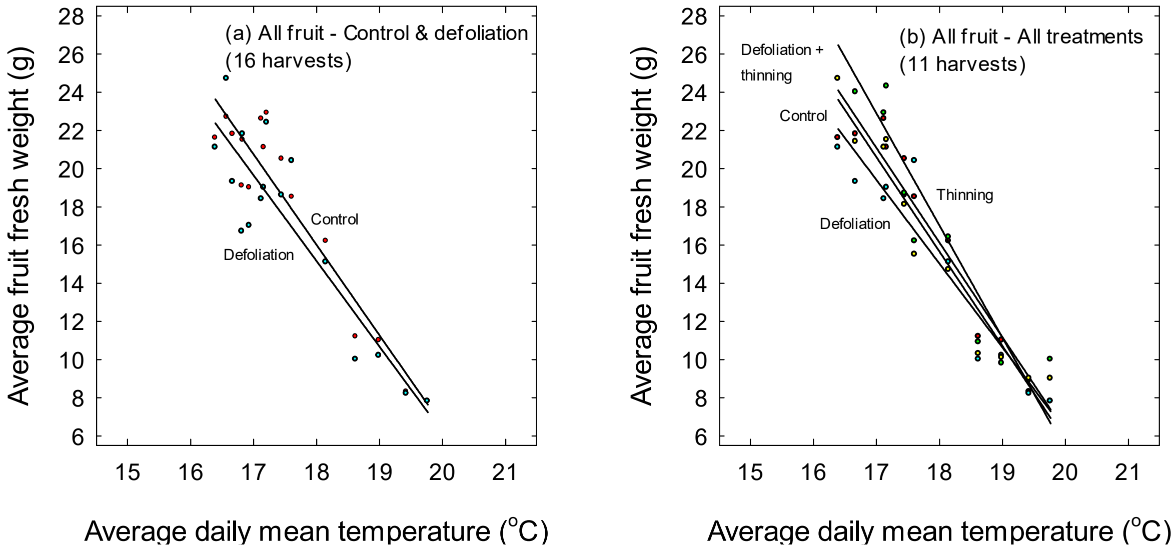

Figure 6. Relationship between average fruit fresh weight (marketable + non-marketable) and average daily mean temperature in the seven weeks before harvest in 'Festival' strawberries in Queensland. Data show the relationships for the four different treatments. First (**a**), there are the relationships for the whole 16-week season in the control (red) and the defoliation treatment (blue) (n = 16 harvests). Second (**b**), there are the relationships when the fruit were harvested from all the treatments over the last 11 weeks in the control, and in the defoliation, thinning (green), and defoliation + thinning (yellow) treatments (n = 11 harvests). Data are the means of four replicates per treatment. The regressions are shown in Table 4.

Table 4. The intercepts and constants (± standard errors or SEs) determined from the relationships between average fruit fresh weight and average daily mean temperature shown in Figure 6. The relationships were determined for the whole 16-week season, or for the last 11 weeks when fruit were harvested from all the treatments. An analysis of regressions by Groups showed that the intercepts and slopes for the control and defoliation treatment for the whole experiment were not significantly different ($p > 0.05$), nor for all four treatments over the last 11 weeks of the experiment.

Treatment	Period	Intercept	Constant	R^2 Value
Control	Whole season	101.3 ± 7.4	−4.7 ± 0.4	0.89
Defoliation	Whole season	96.0 ± 9.9	−4.5 ± 0.6	0.81
All data	Whole season	98.7 ± 6.1	−4.6 ± 0.3	0.85
Control	Part season	105.3 ± 7.5	−5.0 ± 0.4	0.93
Defoliation	Part season	94.0 ± 8.4	−4.4 ± 0.5	0.90
Thinning	Part season	122.7 ± 11.2	−5.9 ± 0.6	0.90
Defoliation + thinning	Part season	104.6 ± 7.6	−4.9 ± 0.4	0.93
All data	Part season	106.7 ± 4.8	−5.0 ± 0.3	0.89

4. Discussion

Temperature had a greater effect on fruit size than defoliation or thinning. Average fruit weight decreased from 24 g to 8 g as the average daily mean temperature increased over the season from 16 °C to 20 °C. In contrast, fruit weight varied by only 1 to 2 g with defoliation and thinning. A high incidence of small fruit at the end of the season was related to high temperatures rather than to an inadequate leaf area or over-cropping.

Removing the leaves, flowers, and fruit changed plant growth. There was some recovery in the plants after the treatments were applied, with new leaves and flowers initiated in the defoliated and thinned plants. Total yield was reduced by 15% when plants were defoliated or thinned compared with the control, and by 24% when they were defoliated and thinned. Lyu et al. [19] removed old leaves from mid-November until early March from plants in Taiwan and found that yield was lower in the defoliated plants (144 g) than in the control (238 g).

The flowers and fruit are dependent on carbohydrates produced by the leaves [27]. Defoliation, and defoliation + thinning decreased fruit weight by 1 or 2 g compared with the control, whereas thinning had the reverse effect. In the current experiment, the plants were able to produce new leaves and flowers after the treatments were applied. The effect of defoliation on yield was greater than the effect on fruit size as reported by Lyu et al. [19]. They found that removing old leaves decreased yield (see above) but only had a small effect on fruit weight (14.4 g in the defoliated plant and 16.0 g in the control). Hortyński et al. [28] examined the relationship between fruit size and leaf area in seven cultivars with small leaves and six cultivars with large leaves in Poland. Mean fruit weight was 7.6 g and 9.1 g in the two groups of plants. Further studies are required to determine whether this response occurs in cultivars grown in Queensland.

Research has been conducted to investigate the effect of thinning on fruit size in strawberries. Janick and Eggert [16] and Khanizadeh et al. [17] showed that removing the primary and/or secondary flowers had little or no effect on the size of fruit produced from the remaining flowers, with fruit weight varying by less than 2 g in the treatments. The current experiment was different to these studies, with all the flowers and fruit on an individual plant removed in June. However, the effect of thinning on fruit size was similar to the earlier studies, and relatively small. Fruit size is not affected by competition between developing fruit unless there is a high fruit to leaf ratio. The main factor affecting fruit size in an individual cultivar is the position of the flower within the cyme.

The incidence of small fruit increases as the season progresses in Queensland [4]. This response could be due to an inadequate leaf area, over-cropping, or high temperatures. In the current experiment, there were only moderate relationships between fruit weight and yield as reflected by the total number or weight of fruit in the early and middle part of the season (R^2s below 0.40). There were no significant relationships between fruit size and crop load at the end of the season. Studies in Florida demonstrated that lower soluble solids content (SSC) in the fruit were associated with warm weather rather than heavy cropping [29].

There was a strong negative relationship between fruit size and average daily mean temperature in the seven weeks before harvest. Fruit weight decreased from 24 g to 8 g as the temperature increased from 16 °C to 20 °C. Changes in leaf area and crop load with defoliation and thinning did not affect the relationship between fruit size and temperature. The best relationship included temperatures covering flower and fruit development, suggesting that temperatures before and after flowering affect fruit growth. Temperature is one of the important factors influencing photosynthesis and carbohydrate production in strawberries. The optimum temperature for net CO_2 assimilation per leaf area is about 25 °C, although values do not differ greatly from 16 °C to 32 °C [30,31]. Average maximum temperatures in the current experiment ranged from 20 °C to 30 °C, suggesting that temperatures were close to optimum for photosynthesis in the leaves.

'Festival' was developed in Florida [32], with fruit size more sensitive to temperature than cultivars used in Japan, the United Kingdom and Germany [21,33,34]. There has been no effort to breed heat-tolerant cultivars in Queensland. Shaw and Larson [35] indicated that average fruit weight nearly doubled in strawberry cultivars developed over 50 years of breeding in California. Mean (± SE) average fruit weight was 14.9 ± 0.4 g for cultivars released from 1945 to 1966 and 24.8 ± 0.7 g for cultivars released from 1993 to 2004. Fruit weight increased by 2.6 grams per year in cultivars released from 1975 to 2008 in the plant improvement program in Florida, indicating the benefit of breeding and selection [36].

5. Conclusions

The results of this study showed that temperature had a greater effect on fruit size than defoliation or thinning. Fruit weight decreased from 24 g to 8 g as the average daily mean temperature in the seven weeks before harvest increased from 16 °C to 20 °C. In contrast, defoliation, thinning, or defoliation +

thinning increased or decreased fruit weight by 1 to 2 g compared with the control. A high incidence of small fruit at the end of the season was related to high temperatures rather than to an inadequate leaf area or over-cropping. The strong effect of temperature on fruit growth indicates that production might be a problem in the future in the absence of heat-tolerant cultivars.

Funding: The Queensland government funded the research through the Department of Agriculture and Fisheries. The research also received funds from the Florida Strawberry Growers' Association' (FSGA) to support the project "Strawberry production in Queensland and Florida under a warming climate". Many thanks to the farm staff at Nambour for help with growing the strawberry plants.

Conflicts of Interest: The author declares no conflict of interest.

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