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No Evidence of Excessive Leaf Production by Strawberries Grown in the Subtropics

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Abstract: Fruit growth in most plants is strongly dependent on photosynthates produced in the leaves. However, if there are too many leaves, the lower part of the canopy becomes heavily shaded and yields are reduced. Experiments were conducted to determine if cultivars of strawberry (*Fragaria* × *ananassa* Duch.) grown in Queensland, Australia have excessive leaf production for adequate cropping. Seven cultivars and breeding lines were planted from March to May from 2004 to 2016 and the number of fully-expanded leaves, dry weight of the flowers and fruit, and yield/plant recorded (n = 23). Information was collected on daily maximum and minimum temperatures and solar radiation. Increases in the number of leaves/plant over the season followed a linear pattern (range in R^2 from 0.81–0.99), with the relationship generally similar or better than a dose-logistic (sigmoid) function (range in R^2 from 0.79–0.99). There were strong linear relationships between the number of leaves/plant and growing degree-days (GDDs), using a base temperature of 7 °C (range in R^2 from 0.81–0.99). In contrast, there was no relationship between the number of leaves/plant produced each day and average season daily mean temperature (15.7 °C to 17.8 °C) or radiation (13.0 to 15.9 MJ/m^2/day) (R^2 < 0.10). Potential yield as indicated by the dry weight of the flowers and immature fruit/plant increased up to 40 to 45 leaves/plant (R^2 = 0.49 or 0.50) suggesting that the cultivars do not have excessive leaf production. There was no relationship between yield and the number of leaves/plant (R^2 < 0.10) because rain before harvest damaged the fruit in some years. These results suggest that the development of new cultivars with more leaves/plant might increase cropping of strawberries growing in the subtropics.

Keywords: growth analysis; growing degree-day; leaf production; productivity; solar radiation; temperature; yield

1. Introduction

The modern strawberry plant (*Fragaria* × *ananassa* Duch.) is widely cultivated throughout the world, and has a total production of about eight million tons [1]. The crop is grown most extensively in the temperate regions of northern Europe, northern America and China, with significant plantings in Spain, California, and other places that have a Mediterranean climate. There are a few subtropical areas such as Florida and Queensland that produce berries over winter [2,3].

Strawberry is an herbaceous perennial plant with a shortened central stem or crown, from which the new leaves, roots, stolons and inflorescences (cymes) emerge [4]. Axillary buds at the top of the crown produce new crowns or stolons or remain dormant, depending on environmental conditions. Productivity is related to the production of new crowns, leaves and inflorescences, and varies with the cultivar, irrigation, fertilizing and environment [5,6]. Low yields can be related to poor leaf or flower initiation or poor fruit set. A study of the architecture of commercial strawberries in Italy showed that there were 1 to 3 crowns/plant, 2 to 5 inflorescences/crown, and 10 to 13 primary inflorescences/plant [7]. A similar study in Finland showed that plants under different photoperiods had 4 to 12 crowns/plant and 1 to 10 inflorescences/plant [8]. Across several studies, there was a strong negative relationship (R^2 = 0.70) between yield and the proportion of flowers removed from individual cymes or plants [9–14], suggesting insufficient flowers or fruit for acceptable fruit production.

Fruit development in strawberry is mainly dependent on current CO_2 assimilation in the leaves. Choi et al. [15] showed that there was a strong relationship between yield under different growing conditions and net CO_2 assimilation per leaf area in Korea (R^2 = 0.93). Researchers have shown that there were positive linear relationships between yield and leaf production in different cultivars, quadratic relationships, negative linear relationships or no relationships [16–25]. A positive linear relationship suggests that the plants do not have too many leaves for adequate flower and fruit production. A negative linear relationship or a quadratic relationship suggests that some cultivars have too many leaves, associated with over-crowding, shading or competition between the leaves and the fruit [17,26]. Lack of a relationship between yield and leaf production could indicate that yield was limited by the number of flowers and fruit/plant.

Temperature is one of the main factors affecting leaf production in strawberry. Darrow [27] found that leaf expansion was greatest when average temperatures during the day in Maryland in the United States were between 20 °C and 26 °C, with an optimum temperature of 23 °C. Similar work in the United Kingdom by Arney [28] showed that leaf emergence ceased in 'Royal Sovereign' when the daily mean temperature fell to 5 °C, and was most rapid at 24 °C. Went [29] reported that the rate of leaf emergence increased as temperatures increased from 10 °C to 20 °C in growth chambers in California, but at the highest temperature, leaf abscission was accelerated. The greatest number of leaves/plant was found between 10 °C and 17 °C. Le Mière et al. [30] indicated that waiting-bed plants in glasshouses in the United Kingdom produced 1.1 leaves/week at 12 °C and 1.8 leaves/week at 28 °C. The optimum temperature for leaf production varies from 10 °C to 28 °C or higher, reflecting cultivars adapted to different conditions.

Leaf initiation is related to solar radiation in some crops [31–33], although there is little information in strawberries. Jurik et al. [34] found that plants of *F. virginiana* produced 19.7 ± 3.8 leaves under high light (PPF or photosynthetic photon flux of 406 μmol/m^2/s) and 5.4 ± 1.1 leaves under low light (PPF of 80 μmol/m^2/s) in growth chambers. Wright and Sandrang [35] indicated that plants of commercial strawberry produced 50 leaves under full sun and 20 leaves under 30% full sun in the United Kingdom.

This paper reports on a study that examined the relationship between productivity and leaf growth in strawberries in Queensland, Australia. The main objective of the work was to determine whether the cultivars produce too many leaves for adequate flower and fruit production. The dry weight of the flowers and immature fruit was used to estimate potential yield because rain damage and fruit diseases before harvest reduce yields in Queensland [3]. Other studies have shown that flower production can be used to estimate yield [36]. The second objective of the study was to determine if leaf production was affected by temperature and solar radiation.

2. Materials and Methods

Experiments were conducted to investigate the relationship between productivity and leaf growth in strawberries in south-east Queensland, Australia over several seasons. Various cultivars and breeding lines were planted in Nambour (latitude 26.6° S, longitude 152.9° E, and elevation 29 m) between 17 March and 5 May from 2004 to 2016 (Table 1). The transplants were grown at Stanthorpe in southern Queensland (latitude 28.6° S, longitude 152.0° E, and elevation 872 m) and had three to four leaves. The soil at the experimental site at Nambour was a sandy clay loam and was well drained.

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 [37]. 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 [37]. 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 [3].

Table 1. Details of the experiments conducted to investigate productivity and leaf growth in strawberries in Queensland.

Experiment	Year	Cultivars	Time of Planting	Replication (*n*)	Period of Leaf Growth
1	2004	Festival & Sugarbaby	20 April	2	13 May to 5 August
2	2005	Festival, Rubygem & Sugarbaby	19 April	4	25 May to 3 October
3	2006	Festival & Rubygem	11 April	4	16 May to 26 September
4a	2007	Festival	22 March	4	15 May to 9 October
4b	2007	Festival	29 April	4	15 May to 9 October
5a	2008	Festival	17 March	5	17 May to 1 October
5b	2008	Festival	28 April	5	17 May to 1 October
6a	2009	Festival	16 March	5	5 May to 28 September
6b	2009	Festival	28 April	5	5 May to 28 September
7a	2010	Festival	31 March	4	12 May to 6 October
7b	2010	Festival	28 April	4	12 May to 6 October
8a	2010	Fortuna	7 April	4	19 May to 10 October
8b	2010	Fortuna	5 May	4	19 May to 10 October
9a	2011	Festival	30 March	4	11 May to 5 October
9b	2011	Festival	27 April	4	11 May to 5 October
10a	2011	Fortuna	6 April	4	18 May to 12 October
10b	2011	Fortuna	4 May	4	18 May to 12 October
11	2012	Festival, Rubygem & two breeding lines	21 March	4	28 May to 5 October
12	2013	Festival, Rubygem & two breeding lines	21 March	4	23 April to 9 October
13	2014	Festival, Fortuna & Winter Dawn	10 April	4	19 May to 8 October
14a	2015	Festival	20 April	6	15 June to 19 October
14b	2015	Festival	29 April	6	15 June to 19 October
15	2016	Festival	13 April	4	29 June to 3 October

The plants in each experiment were laid out in randomized blocks, with two to six replicates (mostly four) (Table 1). There were two sections in each block, one for recording plant growth and an adjacent one for recording yield. Data were collected on the number of fully-expanded leaves/plant and on the dry weight of the flowers and immature fruit from two or three plants in each block selected at random every three weeks from April to October (Table 1). The number of fully-expanded leaves/plant is the net rate of leaf production taking into account the emergence of new leaves and the abscission of old leaves [38]. The dry weight of the flowers and immature fruit was used as an index of potential productivity and is less affected by wet weather than the final fruit harvest [39]. Fruit were harvested once or twice per week for an assessment of yield (fresh mass, FM) from 10 to 40 plants/plot. Mature fruit were classified as those that were at least 75% colored, and fruit with visual symptoms of damage or disease were rejected as non-marketable.

Information was collected on daily maximum and minimum temperatures and solar radiation at the site from the Australian Bureau of Meteorology (www.bom.gov.au). The number of growing degree-days (GDDs), using a base temperature of 7 °C was calculated over the season. The daily mean temperature was calculated from the average of the product of the maximum and minimum temperature [40]. During the experiments, the daily mean temperature was always above 7 °C. Maximum and minimum temperatures were given similar weight in the calculation and there was no attempt to include an upper limit to leaf growth [41] or to take into account minima below 7 °C [42].

The maximum number of leaves/plant, the average dry weight of the flowers and immature fruit over the season, and yield/plant in the experiments are presented as treatment means with standard errors (SEs) calculated from GenStat (Version 15, VSN International, Hemel Hempstead, UK). Changes in the number of leaves/plant over the season and with GDD were analyzed by regression and fitted using the Marquart-Levenberg algorithm from the graphics software program SigmaPlot (Version 12, Systat, Chicago, IL, USA), and are presented as means for each sampling time and SEs. The average rate of leaf production (number of leaves/day) and the interval between successive leaves in days and GDDs were calculated from these regressions. Ninety-five percent confidence intervals (CIs) were calculated for these parameters from the standard errors of the slopes of the regressions (CI = SE × $t_{0.05}$, df). The degrees-of-freedom (df) used for the t-value was the number of observations in the regression minus two.

The relationships between the average rate of leaf production/plant/day and average daily mean temperature, average solar radiation and the product of mean temperature × solar radiation were analyzed by using regression. The relationships between the average weight of the flowers and immature fruit (potential yield) and final yield, and the maximum number of leaves/plant were also determined.

3. Results

The average daily mean temperature ranged from 15.7 °C to 17.8 °C in the experiments, the average daily solar radiation ranged from 13.0 to 15.9 MJ/m^2, and the average product of daily mean temperature × solar radiation ranged from 218 to 281 °C MJ/m^2 (Table 2). During the experiments, the daily mean temperature was always above 7 °C. The highest daily maximum temperature ranged from 27.0 °C to 35.7 °C, and the lowest daily minimum temperature ranged from –0.6 °C to 6.0 °C. There was no relationship between average daily mean temperature and average daily radiation (R^2 < 0.10).

Table 2. Temperatures and solar radiation in the experiments with the strawberries in Queensland. Details of the experiments are provided in Table 1.

Experiment	Period of Leaf Growth (days)	Average Daily Mean Temp. (°C)	Average Daily Solar Radiation (MJ/m^2)	Total Daily Mean Temp. × Solar Radiation (°C MJ/m^2)
1	85	15.7	14.0	218
2	132	16.5	15.4	257
3	130	16.5	15.1	249
4a	148	16.8	14.9	257
4b	148	16.8	14.9	257
5a	138	16.9	14.1	240
5b	138	16.9	14.1	240
6a	147	17.8	15.1	273
6b	147	17.8	15.1	273
7a	148	17.5	13.2	231
7b	148	17.5	13.2	231
8a	145	17.5	13.0	229
8b	145	17.5	13.0	229
9a	148	16.5	14.5	242
9b	148	16.5	14.5	242
10a	148	16.6	14.5	245
10b	148	16.6	14.5	245
11	131	16.9	15.1	259
12	140	17.6	13.6	240
13	142	17.5	15.0	263
14a	127	17.4	15.9	281
14b	127	17.4	15.9	281
15	96	17.7	15.1	268
Mean (± SE)	*137 ± 3*	*17.1 ± 0.1*	*14.5 ± 0.2*	*250 ± 4*

Changes in the number of leaves/plant over the season followed a linear pattern (R^2s = 0.81−0.99), with the relationship generally similar or better than a dose-logistic (sigmoid) function (R^2s = 0.79−0.99) (Table 3). There was an average (± SE) of 0.16 ± 0.01 leaves/plant/day, 27.4 ± 1.4 leaves/plant at the end of the season, and 6.4 ± 0.3 days between successive leaves.

Table 3. Pattern and rate of leaf production in strawberries in Queensland. The number of leaves/day was calculated from the slope of the linear relationship between the number of leaves/plant and the day since planting. The interval between successive leaves was calculated from the slope of the linear relationship between day since planting and the number of leaves/plant. The number of growing degree-days (GDDs) between successive leaves was calculated from the slope of the linear relationship between GDDs and the number of leaves/plant, using a base temperature of 7 °C. Data are presented as mean values ± SEs (standard errors). Confidence intervals were calculated from the SEs. Details of the experiments are provided in Tables 1 and 2.

Experiment	R^2 from the Linear Relationship between No. of Leaves & Day Since Planting	R^2 from the Dose-Logistic Relationship between No. of Leaves & Day Since Planting	No. of Observations (*n*)	No. of Leaves/Day	Confidence Interval (95%)	Days between Successive Leaves	Confidence Interval (95%)	GDDs between Successive Leaves	Confidence Interval (95%)
1	0.92	0.99	5	0.13 ± 0.02	0.06	7.0 ± 1.0	3.3	56 ± 7	23
2	0.86	0.79	5	0.14 ± 0.03	0.09	6.2 ± 1.2	3.9	53 ± 12	37
3	0.97	0.97	8	0.18 ± 0.01	0.03	5.6 ± 0.4	0.9	49 ± 4	9
4a	0.91	0.95	8	0.20 ± 0.02	0.06	4.7 ± 0.6	1.4	41 ± 7	16
4b	0.87	0.87	8	0.15 ± 0.02	0.05	5.8 ± 0.8	2.1	52 ± 9	23
5a	0.89	0.89	8	0.11 ± 0.01	0.04	8.1 ± 1.1	2.6	76 ± 12	29
5b	0.96	0.93	8	0.10 ± 0.01	0.019	9.7 ± 0.7	1.8	93 ± 8	18
6a	0.81	0.89	8	0.14 ± 0.03	0.06	5.9 ± 1.1	2.6	61 ± 11	27
6b	0.95	0.93	8	0.14 ± 0.01	0.03	6.8 ± 0.6	1.4	69 ± 7	17
7a	0.94	0.94	8	0.25 ± 0.02	0.06	3.9 ± 0.4	0.9	39 ± 4	9
7b	0.99	0.99	8	0.17 ± 0.01	0.01	5.8 ± 0.2	0.5	59 ± 2	6
8a	0.96	0.97	8	0.21 ± 0.01	0.04	4.6 ± 0.3	0.8	46 ± 4	11
8b	0.97	0.96	8	0.16 ± 0.01	0.03	6.2 ± 0.4	1.0	64 ± 3	8
9a	0.99	0.99	8	0.16 ± 0.005	0.01	6.3 ± 0.2	0.4	57 ± 2	5
9b	0.98	0.98	8	0.13 ± 0.01	0.02	7.7 ± 0.4	0.9	70 ± 4	9
10a	0.91	0.91	8	0.13 ± 0.02	0.04	7.0 ± 0.8	2.0	65 ± 7	18
10b	0.99	0.98	8	0.11 ± 0.004	0.01	9.3 ± 0.4	0.9	87 ± 3	6
11	0.98	0.98	6	0.17 ± 0.002	0.004	5.9 ± 0.4	1.1	57 ± 4	12
12	0.99	0.99	6	0.21 ± 0.01	0.03	4.7 ± 0.2	0.6	48 ± 3	7
13	0.99	0.99	6	0.16 ± 0.005	0.01	6.3 ± 0.2	0.5	63 ± 2	5
14a	0.98	0.99	6	0.16 ± 0.01	0.02	6.3 ± 0.3	0.9	64 ± 4	12
14b	0.97	0.98	6	0.14 ± 0.01	0.03	6.8 ± 0.6	1.6	69 ± 8	23
15	0.97	0.98	6	0.15 ± 0.01	0.03	6.6 ± 0.5	1.4	69 ± 6	18
Mean (± SE)				*0.16 ± 0.01*		*6.4 ± 0.3*		*63 ± 3*	

Examples are provided on the number of leaves/plant for 'Festival' planted in 2010 and 'Fortuna' planted in 2011 (Figure 1). These examples cover the range in response across the various experiments, with different cultivars, different years and different times of planting (Table 1). There were linear increases in the number of leaves/plant in all the other experiments. The responses (linear regressions) over time were similar in these experiments to those shown for 'Festival' planted in 2010 and 'Fortuna' planted in 2011 (Figure 1). Thus, the changes for these other 19 experiments are not presented. Across the different experiments, there were differences in the rate of leaf production per day and differences in the maximum number of leaves/plant at the end of the growing season and these data are shown in Tables 3 and 4.

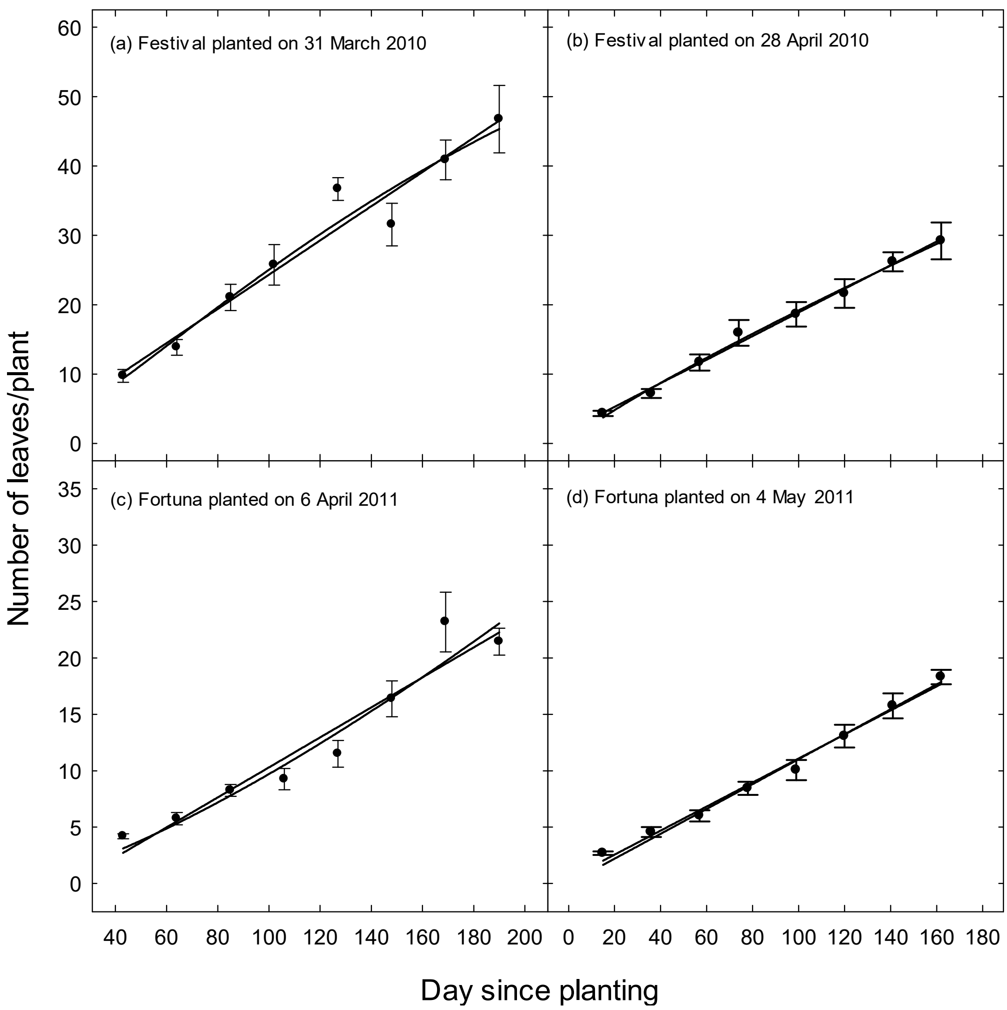

Figure 1. Changes in leaf production in (**a**,**b**) 'Festival' and (**c**,**d**) 'Fortuna' strawberries in Queensland in 2010 and 2011. Data are the means and standard errors (SEs) of four replicates per treatment. Linear and dose-logistic models shown, with information on the regressions provided in Table 3 (Experiments 7a, 7b, 10a and 10 b).

There were strong linear relationships between the number of leaves/plant and growing degree-days (GDDs) in the experiments (R^2s = 0.81-0.99), with a new leaf produced every 63 ± 3 GDDs (Table 3). Examples are provided on the number of leaves/plant with GDD for 'Festival' in 2010 and 'Fortuna' in 2011 (Figure 2). There was no relationship (n = 23, R^2s < 0.10) between the mean rate of leaf production and average temperatures and radiation in the experiments (data not presented).

Table 4. Mean maximum number of leaves, average dry weight of the flowers and immature fruit, and yield in the different experiments with the strawberries in Queensland. Data are presented with standard errors (SEs). Details of the experiments are provided in Tables 1 and 2.

Experiment	Max. No. of Leaves/Plant	Average d. wt. of the Flowers & Immature Fruit (g/plant)	Average Yield (g/plant)
1	17.2 ± 2.9	-	189 ± 0
2	25.4 ± 1.3	-	702 ± 32
3	26.9 ± 1.9	-	480 ± 32
4a	34.2 ± 0.9	6.8 ± 0.2	727 ± 21
4b	23.4 ± 0.7	4.1 ± 0.2	560 ± 26
5a	22.2 ± 1.3	7.3 ± 0.3	1092 ± 41
5b	18.8 ± 1.6	3.5 ± 0.1	510 ± 14
6a	30.8 ± 2.2	7.2 ± 0.2	934 ± 18
6b	24.3 ± 2.5	4.0 ± 0.3	555 ± 19
7a	46.8 ± 3.6	9.5 ± 0.4	876 ± 49
7b	29.0 ± 2.7	5.1 ± 0.2	642 ± 23
8a	32.1 ± 2.2	7.1 ± 0.7	827 ± 58
8b	26.5 ± 1.9	3.9 ± 0.3	478 ± 24
9a	28.4 ± 1.3	7.2 ± 0.1	966 ± 39
9b	22.2 ± 0.7	4.0 ± 0.1	740 ± 16
10a	21.4 ± 1.4	5.0 ± 0.3	823 ± 72
10b	18.3 ± 0.5	3.0 ± 0.2	643 ± 15
11	37.1 ± 1.8	10.6 ± 0.1	720 ± 28
12	34.5 ± 0.5	9.0 ± 0.2	480 ± 15
13	30.4 ± 0.9	5.9 ± 0.2	796 ± 25
14a	28.0 ± 2.1	9.2 ± 0.3	1123 ± 43
14b	26.0 ± 1.6	8.7 ± 0.3	1037 ± 44
15	27.1 ± 1.4	8.1 ± 0.4	991 ± 38
Mean (± SE)	*27.4 ± 1.4*	*6.5 ± 0.5*	*734 ± 49*

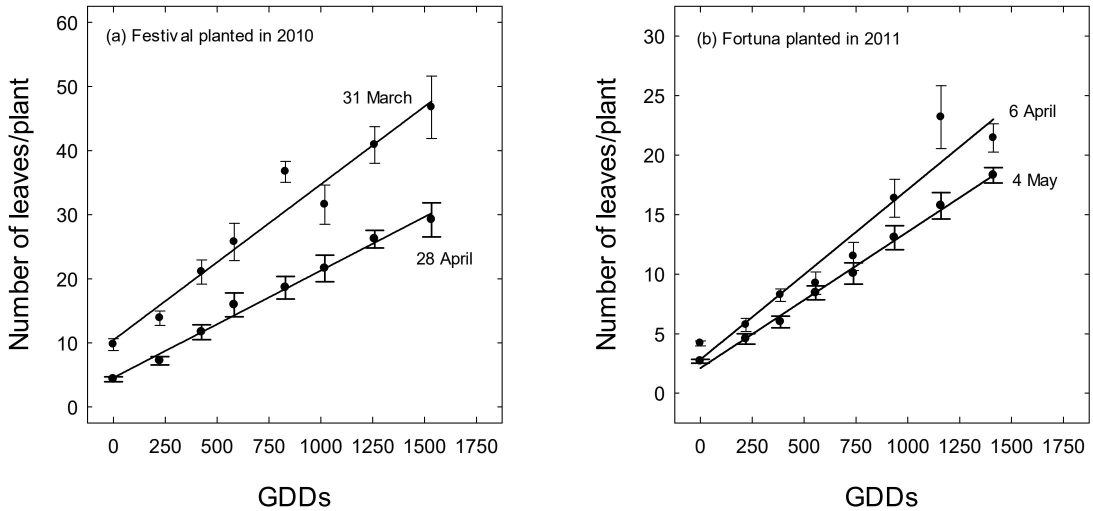

Figure 2. Changes in leaf production in (**a**) 'Festival' and (**b**) 'Fortuna' strawberries planted at two different times with growing degree-days (GDDs) in Queensland in 2010 and 2011. The base temperature used to calculate GDD was 7 °C. Data are the means and standard errors (SEs) of four replicates per treatment. The early and late plantings of 'Festival' in 2010 relate to Experiments 7a and 7b, while the early and late plantings of 'Fortuna' in 2011 relate to Experiments 10a and 10b. Linear models are shown.

Average yield (± SE) was 734 ± 49 g/plant in the experiments and average mean seasonal dry weight of the flowers and immature fruit was 6.5 ± 0.5 g/plant (Table 4). The dry weight of the flowers and immature fruit (potential yield) increased by a factor of more than two as leaf production increased from 20 leaves/plant to 40 to 45 leaves/plant (Figure 3). In contrast, there was no relationship between final yield and the number of leaves/plant ($R^2 < 0.10$)

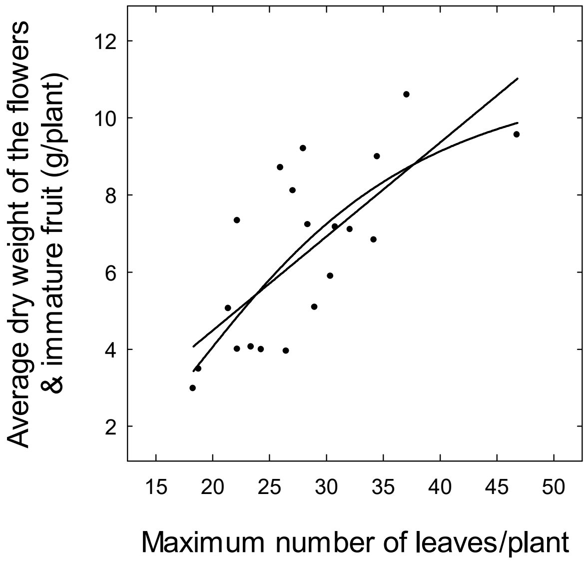

Figure 3. Relationships between average dry weight of the flowers and immature fruit (potential yield, DW) and maximum number of leaves/plant (No. leaves) in strawberries in Queensland. Data are the means of two to six replicates (mostly four) per treatment. Linear and dose-logistic models shown. DW = −0.38 + 0.24 × No. leaves (R^2 = 0.49, n = 20). DW = 11.57/{1 + exp. [2.79 (No. leaves − 24.92)]} (R^2 = 0.50, n = 20).

4. Discussion

The strawberries produced a new leaf every four to ten days, however, there was no evidence that the plants produced too many leaves for acceptable flower and fruit production. Potential yield as indicated by the dry weight of the flowers and immature fruit increased up to 40 to 45 leaves/plant.

Strawberry fruit are dependent on carbohydrates produced by the leaves during photosynthesis. The carbohydrates can come from current photosynthesis or from reserves stored in the crowns and roots [43,44]. In the United States, only 25% of the carbohydrates required for the first seven days of fruit growth was supplied from CO_2 assimilation during that time, with the majority supplied from reserves [45]. In a similar experiment in Japan, about 25% of ^{14}C from the uppermost leaf was translocated to the inflorescences at anthesis and 60% to 80% to the ripening fruit [46].

The relationship between yield and leaf production can be investigated by removing leaves on a plant and recording the impact on yield. Sproat et al. [47] removed leaves from four strawberry cultivars in Maryland in September and counted the number of leaves and berries produced on the plants to June. There were linear relationships between yield and the number of leaves/plant (R^2s = 0.73–0.88). No optimum was established, with yield increasing up to 28 to 55 leaves/plant, depending on the cultivar. The cultivars produced 1.1 to 2.8 berries/leaf. Several other authors have examined the effect of defoliation on the yields of strawberries [13,48–50]. Across these studies, a mean (± SE) 50 ± 4% decrease in the number or area of leaves/plant was associated with 26 ± 5% decrease in yields relative to non-defoliated controls.

In the current study, potential yield increased with increasing number of leaves/plant, with no evidence of excessive leaf production. In the United Kingdom and the United States, shading of the lower leaves by the upper leaves decreased yields and cultivars with more open canopies had higher yields than those with dense canopies [35,51,52]. Srinivasan et al. [53] suggested that decreasing, not increasing, leaf area will raise crop yields under climate change. They found that removing some of the leaves from soybean plants in Illinois, United States increased yields by 8% to 10% compared with control plants. Similar studies with maize in China indicated that removing a few leaves increased yields by 12% to 15% [54].

There was a linear increase in the number of leaves/plant in the experiments. Leaf production was nearly linear over 120 days in Wisconsin, with a leaf produced every six to thirteen days [55]. Leaf production was linear over 64 days in one cultivar in the United Kingdom and linear over 96 days in two cultivars [56]. A leaf was produced every two to five days during the main period of growth. Arney [28,57,58] found that a leaf emerged every eight to ten days in 'Royal Sovereign' from June to September in the United Kingdom. All the previous studies involved strawberries growing over summer in temperate areas. The average rate of leaf production in Queensland is similar to that reported in the United States and the United Kingdom.

There were strong relationships between the number of leaves/plant and growing degree-days (GDDs), with a new leaf emerging after 39 to 93 GDDs and a mean of 63 ± 3 GDDs. This analysis used a base temperature of 7 °C as proposed in Brazil, with a new leaf emerging after 57 to 200 GDDs and a mean of 116 ± 8 GDDs [59]. These researchers used a range of cultivars and a range of different nursery plants. Overall, leaf production was more rapid in Queensland than in Brazil. Other base temperatures have been suggested for the growth of strawberries, including 0 °C in Brazil [25] and 3 °C in Norway [60], but these temperatures appear too low for a species in the subtropics.

There was no relationship between the number of leaves/day and average temperatures or solar radiation in the current experiments. Various optimum temperatures have been proposed for leaf production in strawberry, but no critical upper threshold when leaf production ceases has been suggested. Maximum leaf production occurred with different mean temperatures ranging from 10 °C to higher than 28 °C in cultivars adapted to temperate or Mediterranean conditions [28–30]. The minimum daily solar radiation for leaf production has not been established for strawberries.

There was no relationship between yield and the number of leaves/plant, because rain or disease affected the fruit before they were harvested in some years. Previous research in Queensland demonstrated that up to 60% of the fruit were damaged by rain or disease during wet weather [61].

5. Conclusions

Strawberries in Queensland produced a leaf every four to ten days, however, there was no evidence that the plants had too many leaves for adequate flower and fruit production. The dry weight of the flowers and immature fruit (potential yield) increased up to 40 to 45 leaves/plant. There was no relationship between yield and the number of leaves/plant, because rain before harvest damaged the fruit in some years. A new leaf was produced after every 63 ± 3 GDDs using a base temperature of 7 °C. In contrast, there was no relationship between the numbers of leaves/day and average season daily mean temperature (15 °C to 17.8 °C) or radiation (13.0 to 15.9 MJ/m^2)**.** These results suggest that the development of new cultivars with more leaves/plant might increase cropping of strawberries growing in the subtropics. Another approach would be to develop cultivars with larger leaves [62] or cultivars with longer leaf spans [38,63], which would increase seasonal carbohydrate production.

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