

NET PHOTOSYNTHESIS AND PHOTOSYNTHATE PARTITIONING/OF
DAY-NEUTRAL AND JUNE BEARING STRAWBERRY PLANTS AS INFLUENCED
BY FRUITING

by

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(ABSTRACT)

Net photosynthesis (Pn) and photosynthate partitioning were compared between fruiting and deblossomed strawberry plants. Throughout a six-week fruiting cycle, Pn (leaf area basis), specific leaf weight (SLW), and chlorophyll content were determined at 7-day intervals for an early-formed leaf (old leaf) and for the most recently expanded leaf (young leaf) of fruiting and deblossomed day-neutral plants (cv. Tribute). During the fifth week of the fruiting cycle, Pn of the young leaf was higher for fruiting plants than for deblossomed plants. Pn of the old leaf was not different between treatments during any week. During weeks 4 and 5, the young leaf of the deblossomed plants had a higher SLW than that of fruiting plants; SLW of the old leaf was higher for deblossomed plants during weeks 4-6. The young leaf of the deblossomed plants had a higher chlorophyll content than

that of fruiting plants during weeks 1 and 4. Chlorophyll content of the old leaf was higher for deblossomed plants during weeks 1, 2, and 4. There were no differences between treatments for stomatal conductance for CO₂ or dark respiration during any week of the fruiting cycle.

In another experiment, deblossoming day-neutral strawberry plants (cv. Tribute) increased the amount of ¹⁴C translocated to the newly-emerging leaves 48 hrs after treatment with ¹⁴CO₂. During weeks 3-6 of the fruiting cycle, leaves of deblossomed plants had a greater total area, dry weight, and total non-structural carbohydrate (TNSC) content than leaves of fruiting plants. Pn on a whole-plant basis was higher for deblossomed plants than fruiting plants. This was largely due to the greater leaf area of the deblossomed plants, since total leaf area was highly correlated with Pn (whole plant basis). Pn (whole plant basis) was highly correlated with total dry weight and TNSC of plants in both treatments. Thus, deblossoming changed Pn and dry matter partitioning of strawberry plants. The additional leaf area and greater Pn rates (whole plant basis) obtained by deblossoming strawberry plants may result in increased yields during subsequent fruiting cycles.

DEDICATION

This dissertation is dedicated to my closest friend,

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Chapter I
LITERATURE REVIEW

INTRODUCTION

In the United States, strawberries (Fragaria x ananassa Duch.) are grown commercially on about 14,000 hectares in 35 states (2, 13, 36). Fruit yield per hectare varies considerably among states; in 1980, California produced 52.7 tons of strawberries per hectare, about 8.5 times the average yield per hectare of other states (36). California, the leading state in strawberry production, accounts for 74 % of the commercial strawberry crop, although it comprises only 35 % of the total acreage (36). Enormous gains in strawberry yields in California over the years, may be attributed to concentrated research efforts in physiology, breeding, and management of strawberry plants. From the example set by California, it would seem that a tremendous potential exists for increasing strawberry productivity in the eastern United States. This may be achieved through a better understanding of the effects of environmental and cultural factors on the physiology of strawberry plants.

The productivity of strawberry plants, like other crops, hinges on net photosynthesis (Pn) and photosynthate partitioning (37). Basic research in photosynthesis over the years has revealed many possible approaches toward increasing efficiency of CO₂ assimilation. One factor entails altering the ratio of vegetative to reproductive structures at specific times during plant development (14). Significant increases in strawberry yield may be obtainable by maximizing the photosynthetic efficiency.

The presence of plant organs with a net demand for assimilates ("sinks"), such as fruit, have been shown to increase Pn of several horticultural crops (10, 27, 30,). There have been some reports on the effects of fruiting on Pn and photosynthate partitioning of strawberry plants (5, 6, 9, 11, 12, 17, 18) , but most of this work was done with Junebearing cultivars.

Day-neutral strawberry cultivars were first released on the commercial market in 1979 (3). The 2 day-neutral cultivars adapted for the eastern United States, 'Tribute' and 'Tristar', were developed in 1976 (7) and released on the commercial market in 1981. Day-neutral strawberry cultivars are capable of fruiting in successive 6-week cycles (6) regardless of photoperiod (8). Thus, they offer an exciting possibility for home gardeners as well as specialized pick-your-own markets.

Little is known about the effects of fruiting on Pn and photosynthate partitioning of day-neutral strawberry cultivars. Also, the literature contains conflicting reports which may be due to cultivar or environmental differences among studies. Thus, there is a need to further elucidate the effects of sink removal on Pn and assimilate partitioning of day-neutral strawberry plants. This knowledge may eventually allow growers to manipulate these crops in order to maximize their yields.

EFFECTS OF FRUITING ON NET PHOTOSYNTHESIS

The presence of fruit has been shown to increase Pn of many plant species, including sweet pepper (30), soybean (27), eggplant (17), pea (10), and strawberry (6, 11, 17). Hoffmann and Lenz (17) discovered that fruiting strawberry plants of a Junebearing cultivar had higher Pn rates than defruited plants. Forney and Breen (11) observed that fruiting strawberry plants of the day-neutral cultivar Brighton had higher Pn rates than deblossomed plants from 67 days after planting until the end of the fruiting period.

Choma et al. (6) also found Pn (leaf area basis) of the day-neutral strawberry cultivar Hecker to be greater for fruiting plants than deblossomed plants 5 out of 6 weeks of a fruiting cycle. Deblossomed plants, however, had a great-

er leaf area. Thus, on a whole plant basis, Pn was similar for fruiting and deblossomed plants. A subsequent study by Durner et al. (8), compared Pn of Junebearing, everbearing, and day-neutral cultivars grown under short days and simulated long days. Their data did not support the hypothesis that the presence of fruit increases Pn. It is unclear, however, if the discrepancies between these studies were due to photoperiod, light level, or cultivar differences.

Stomatal conductance for CO₂ (g_s) has been correlated with Pn for several crops, including soybeans (23), and strawberry plants (11). Fruiting strawberry plants (11), apple trees (32) and soybeans (23) had higher g_s rates than deblossomed plants. Thus the higher Pn rates for the fruiting plants were, in part, attributed to increased g_s.

Specific leaf weight (SLW) has been positively correlated with Pn of apple leaves (26) and strawberry plants (5). The positive correlation for strawberry plants was due to an increase of mesophyll cell volume as SLW increased (5). Forney and Breen (12) found that SLW of 'Brighton' strawberry plants increased steadily in non-fruiting plants but ceased increasing during rapid fruit growth in fruiting plants. Monselise and Lenz (28) discovered that deblossomed apple trees had a higher SLW than fruiting plants. The apparent contradictory observations between lower Pn rates of deblos-

somed plants and higher SLW was attributed to a greater accumulation of assimilates which suppressed Pn in the leaves of deblossomed plants. Leaves of deblossomed citrus (22), eggplant (17), and strawberry plants (17) had higher starch contents than leaves of fruiting plants. Hoffmann and Lenz (17) reported that the content of alcohol soluble carbohydrates in the leaves was not different between fruiting and deblossomed plants. Chloroplasts of non-fruiting strawberry plants had higher starch concentrations than those of fruit-bearing plants (18). It has been postulated that the accumulation of starch in leaves may suppress Pn by interfering with light penetration into the chloroplasts or by increasing mesophyll resistance to CO₂ (29).

Chlorophyll content has been positively correlated with Pn of soybeans (4), but Hesketh (16) reported that chlorophyll content was not related to Pn for several crop species. Therefore the relationship between chlorophyll content and Pn appears variable. Fruiting had no effect on dark respiration of citrus (21), or strawberry (6).

RELATIONSHIP BETWEEN FRUITING AND VEGETATIVE GROWTH OF STRAWBERRY PLANTS

Deblossoming strawberry plants increased total leaf area and leaf dry weight (6, 11, 12, 19, 20, 33). Scott and Marth (33) reported that fruiting strawberry plants had fewer leaves and runners than deblossomed plants. Jahn and Dana (19) observed that bud removal increased leaf size and total leaf area of 'Dunlap', a Junebearer. Total plant dry weight was highly correlated with floral bud number in their study. Guttridge and Anderson (15) found a strong negative correlation between fruit number and plant size. Deblossomed day-neutral plants ('Brighton') had 61, 53, 44, and 36 % more dry weight in the roots, stem, petioles, and leaf blades respectively than fruiting plants (12). Choma, et al. (6) showed that deblossomed day-neutral strawberries (cv. Hecker) had a greater leaf area than fruiting plants during two weeks of a six-week fruiting cycle. Lenz and Bunemann (20) observed that dry matter accumulation in the vegetative organs of strawberry plants decreased with increasing fruit number. They did not discover any differences, however, in total plant dry weight between fruiting and deblossomed plants. Olsen, et al. (31) also observed that a much smaller proportion of dry matter was partitioned to the leaves of strawberry plants during fruiting than during plant establishment.

Fruit have been shown to be the primary sink for carbohydrates in the strawberry plant (9, 31). Long (24) found that carbohydrates were mobilized from the roots and stem to the fruit during fruit maturation. Mann (25) observed that decreased root dry weight of strawberry plants coincided with increased leaf dry weight. Therefore, in the absence of fruit, carbohydrates may be mobilized to the leaves. Sproat et al. (34) found that a greater leaf area in the fall resulted in greater fruit yields the following year for Junebearing strawberry plants. Thus, increased leaf area during plant establishment provided increased photosynthate production to support subsequent increased fruiting.

Studies with ^{14}C have provided valuable information about the pattern of assimilate movement in strawberry plants. Antoszewski and Dzieciol (1) found that fully developed strawberry leaves exported 40-60 % of their labelled assimilates within 2 days after exposure to $^{14}\text{CO}_2$. Udovenko and Goncharova (35) observed that ^{14}C -labelled photosynthates in strawberry leaves were not only transported to the fruit but also into other leaves. Dzieciol (9) reported that fruiting decreased the accumulation of ^{14}C -assimilates in the youngest leaves of strawberry plants. However, the fruiting plants used in that study were not at the same stage of development and were treated with $^{14}\text{CO}_2$ at a different time than the deblossomed plants, making comparisons difficult.

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Chapter II

PARTITIONING OF [^{14}C]-PHOTOSYNTHATE IN FRUITING AND DEBLOSSOMED DAY-NEUTRAL STRAWBERRY PLANTS

ABSTRACT

Deblossomed 'Tribute' strawberry plants had an increased amount of [^{14}C]-photosynthates in untreated leaves 48 hr after treatment with $^{14}\text{CO}_2$. The summed quantity of radioactivity in the untreated leaves and fruit of fruiting plants approximated that in the untreated leaves of deblossomed plants. There was no effect of deblossoming on the amount of ^{14}C in the crown or roots. Autoradiographs showed that the majority of ^{14}C was in the expanding leaves. Therefore, increased leaf area, which often results from deblossoming strawberry plants, may be attributed to an increase in photosynthates partitioned to the expanding leaves.

INTRODUCTION

Deblossomed strawberry plants exhibited increased leaf production rates, thus increasing total leaf area compared to fruiting plants (2, 6, 8, 9, 10). Dzieciol (5) found that fruiting decreased the accumulation of [^{14}C]-assimilates in the youngest leaves of strawberry plants. However, the fruiting plants used in that study

were not at the same stage of development and were treated with $^{14}\text{CO}_2$ at a different time than the deblossomed plants, thereby making comparisons difficult. After treating apple leaves with ^{14}C , Hansen (7) found that ^{14}C -sorbitol was higher in leaves from shoots without fruit than in those from fruit-bearing shoots. Day-neutral strawberry plants are capable of fruiting successively in approximately six week cycles (2), regardless of photoperiod (4). Therefore, they would serve ideally as a model system for testing the effects of fruiting on photosynthate partitioning. The objective of this study was to compare partitioning of [^{14}C]-photosynthates in deblossomed and fruiting plants.

MATERIALS AND METHODS

Day-neutral strawberry plants of the cultivar 'Tribute' (3) were planted in 15 cm diameter plastic pots containing Pro-Mix media and placed in an open ended plastic greenhouse on June 6, 1984. Plants were fertilized weekly with 240 ppm N from a 20N-8.7P-16.6K soluble fertilizer in the irrigation water. Uniform plants were grouped into two treatments: 1) plants with all blossoms removed as they emerged, and 2) plants allowed to flower and fruit normally. Runners were removed from all plants as they emerged. Each treatment consisted of 10 single-plant replications in a randomized complete block design.

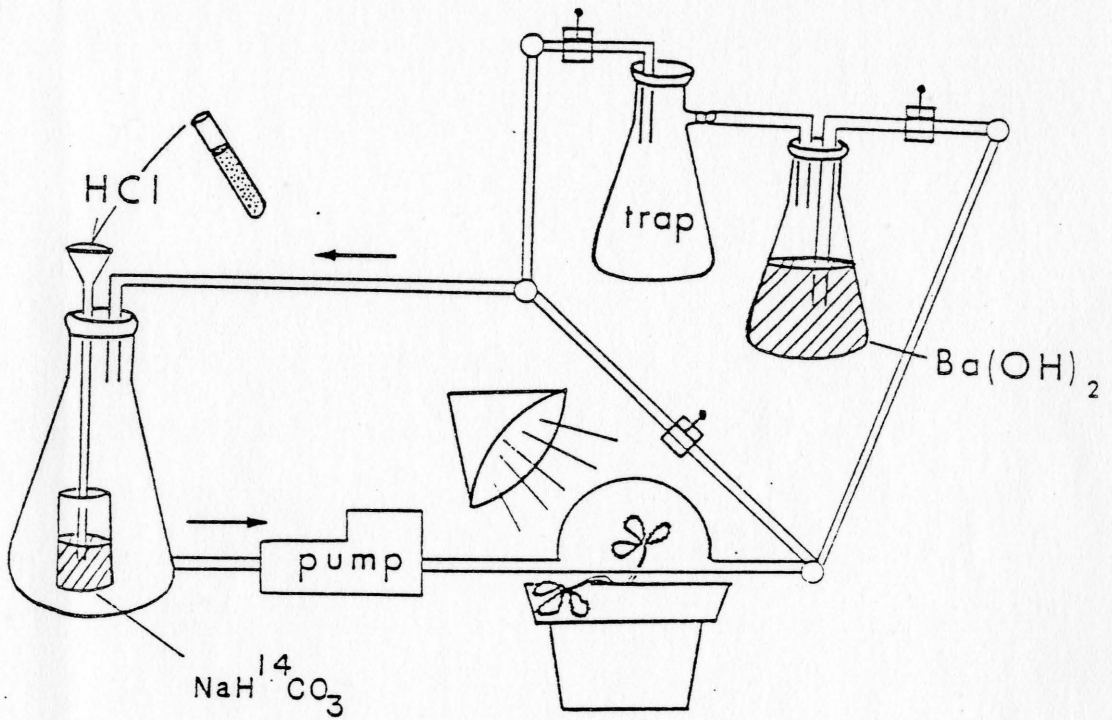


Figure 1. Illustration of apparatus used to treat strawberry leaves with $^{14}\text{CO}_2$.

When the majority of primary flowers were open, one newly emerging leaf was tagged per plant. Twenty eight days later, when the majority of primary fruit were ripe, the leaf area of the tagged leaf (then fully expanded) was determined. Tagged leaves were then exposed to $^{14}\text{CO}_2$ in a sealed plastic chamber attached to a $^{14}\text{CO}_2$ generator (Fig. 1) in a glass greenhouse. The level of photosynthetically active radiation (PAR) from a Sylvania Metalarc lamp was $600 \mu\text{mol s}^{-1}\text{m}^{-2}$ in the leaf chamber as determined by a Licor model LI185 light meter with a quantum sensor. Air temperature in the chamber was $22 \pm 1^\circ\text{C}$. The $^{14}\text{CO}_2$ was produced by adding 5 ml of 1 N HCl to 1 ml of $\text{NaH}^{14}\text{CO}_3$ (2.5 $\mu\text{Ci/ml}$) in an Erlenmeyer flask. The gas was continuously circulated through the leaf chamber for 30 min at a flow rate of 6 liters/min by a pump attached to the flask and chamber with plastic tubing. Excess $^{14}\text{CO}_2$ was then absorbed by bubbling the gas through 1 liter of 1 N $\text{Ba}(\text{OH})_2$ for 5 min. The $^{14}\text{CO}_2$ treated leaves from 5 plants in each treatment were immediately harvested, dried, and weighed. An additional 5 plants of each treatment were placed in an enclosed glass greenhouse for 48 hr. The $^{14}\text{CO}_2$ treated leaf, untreated leaves, crown, roots, and fruits (if present) were harvested, dried, and weighed separately for each plant. A sample of each tissue was pressed and mounted on paper. Autoradiographs were made by

pressing the mounted specimens in contact with Sakura medical-grade x-ray film (Picker Corp, Falls Church, VA) for 14 days in the dark. The film was developed with Kodak Rapid x-ray developer and fixed with Kodak x-ray fixer.

Dried tissue samples from the treated leaves harvested immediately after $^{14}\text{CO}_2$ treatment, and treated leaves, untreated leaves, crown, roots, and fruit harvested 48 hr after treatment were ground separately in a Wiley mill with a 20 mesh screen. Two sub-samples from each tissue were weighed and then oxidized in an Intertechnique model IN 4101 L.S. sample oxidizer, where ^{14}C was collected from each sample in 20 ml of a mixture of Carbosorb II:Permaflor (1:2/v:v) (Packard Instruments Inc., Downersville, IL). The radioactivity of each sample was determined by radioassay with a liquid scintillation spectrometer (Beckman LS-250 series) having a counting efficiency of 90%. The results were calculated for each plant tissue as total disintegrations per minute (dpm) and as the percent of total ^{14}C in each tissue after 48 hr, with reference to the total amount of ^{14}C present in the plant.

RESULTS AND DISCUSSION

There was no difference in the amount of ^{14}C initially fixed by the treated leaf of the fruiting and deblossomed plants. Total radioactivity in the treated leaves of fruiting and deblossomed plants was 946 and 929 dpm g dry wt⁻¹, respectively. Forty eight hours after treatment with $^{14}\text{CO}_2$, radioactivity was detected in the treated leaf, untreated leaves, crown, roots, and fruits (if present) of plants in both treatments. Udovenko and Goncharova (11) also found that ^{14}C -labelled products of photosynthesis in strawberry leaves were not only transported into fruit but also into other leaves. After 48 hr, 60% of the total ^{14}C absorbed by the plants remained in the treated leaf of plants in both treatments (Table 1). This agrees with the results of Antozewski and Dzieciol (1) who found that 40-60% of labelled assimilated remained in the leaves of 'Talisman' strawberry plants 48 hr after exposure to $^{14}\text{CO}_2$. The second highest percentage of total radioactivity was found in untreated leaves of the deblossomed plants. There was no significant difference among the percentage of ^{14}C in the untreated leaves, crown, roots, and fruit of the fruiting plants (Table 1). The summed percentage of radioactivity of the untreated leaves and fruit of the fruiting plants was nearly equivalent to the percentage of radioactivity of only the

untreated leaves of the deblossomed plants. The total percentage of radioactivity in the untreated leaves of the deblossomed plants was higher than the total percentage of radioactivity in the untreated leaves of the fruiting plants (t-test, $p < .05$). There was no difference in the total percentage of radioactivity in the $^{14}\text{CO}_2$ treated leaves, crowns, or roots between treatments ($p < .05$). In the fruiting plants, the treated leaves and fruit had similar amounts of radioactivity (Table 1). The lowest percentage of total radioactivity in plants of both treatments was in the crowns, roots, and fruit. Deblossoming had no observable effect on the partitioning of [^{14}C]-photosynthates to the crown and roots. In agreement with the results of others (6), it was determined that deblossomed plants tended to have a greater total leaf dry weight than fruiting plants at the time of $^{14}\text{CO}_2$ treatment (Table 1).

Autoradiographs showed that ^{14}C was partitioned to newly developing leaves but not to the fully expanded leaves (Figs. 2 and 3). Udovenko and Goncharova (11) found that a weak exchange of assimilates occurred among mature leaves of strawberry plants. In this study, the autoradiographs may not have been sensitive enough to detect small amounts of radioactivity in the mature leaves. We did not divide the untreated leaves into mature and immature samples for ra-

Table 1. ^{14}C partitioning in fruiting and deblossomed 'Tribute' strawberry plants 4 weeks after flowering.

Plant tissue	Fruiting plants			Deblossomed plants		
	% $^{14}\text{C}^Z$	Dpm x 10^3	Dry wt (g)	% ^{14}C	Dpm x 10^3	Dry wt (g)
$^{14}\text{CO}_2$ treated leaf	60 a ^{YW}	557	1.2	59 a	614	1.0
Untreated leaves	16 b	153	4.6	34 b	362	5.6
Crown	4 b	33	0.8	4 c	40	1.0
Roots	7 b	65	2.0	4 c	35	2.3
Fruit	13 b	120	2.0	-	-	-

^ZPercentage of total radioactivity in the plant.

^YData transformed by arcsine transformation for statistical analysis.

^WMean separation within columns by Tukey's studentized range test (P<0.01).

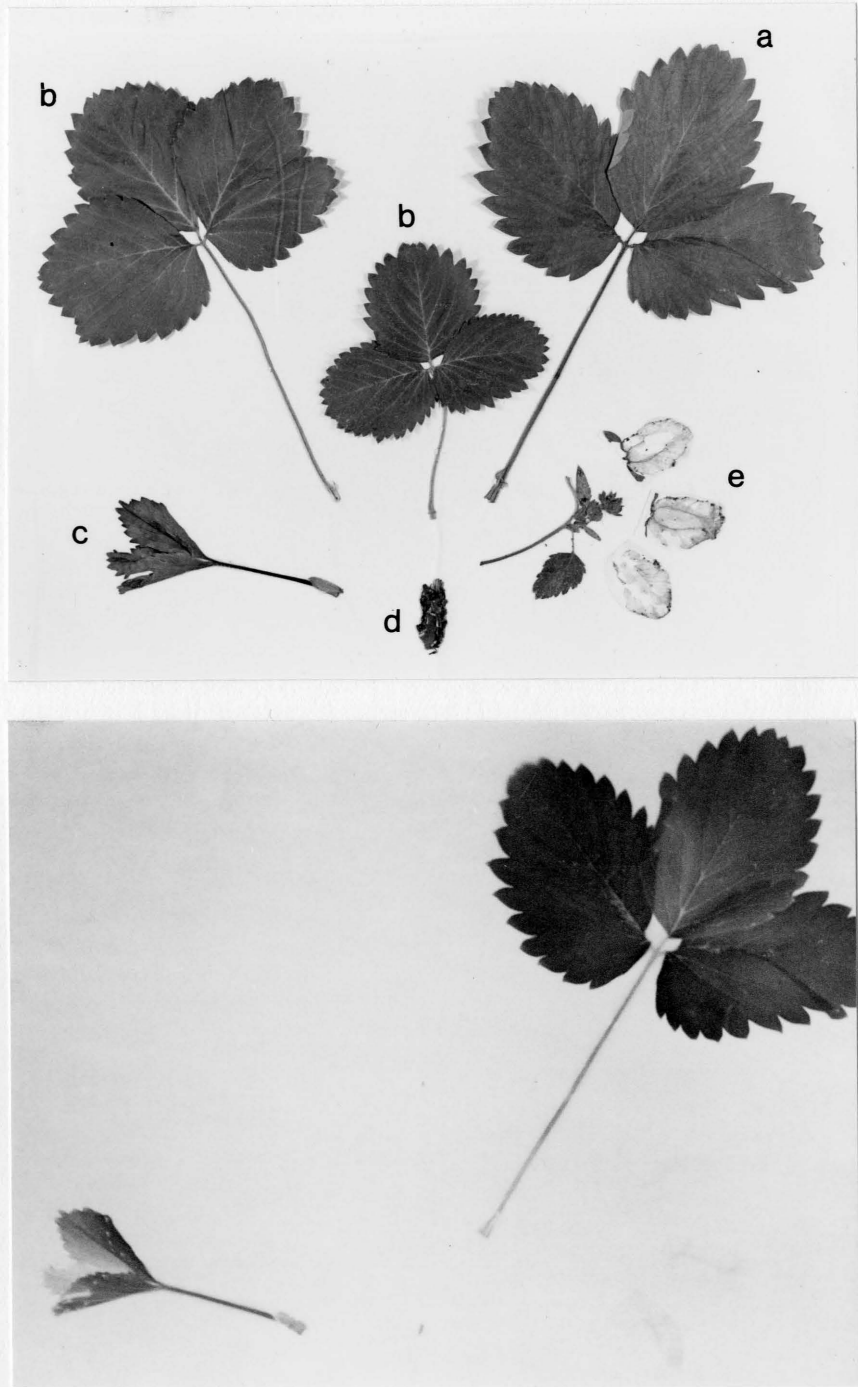


Figure 2. Fruiting strawberry plant specimen and corresponding autoradiograph 48 hr after treatment with $^{14}\text{CO}_2$. a=treated leaf, b=fully expanded leaf, c=young leaf, d=crown, e=fruit.

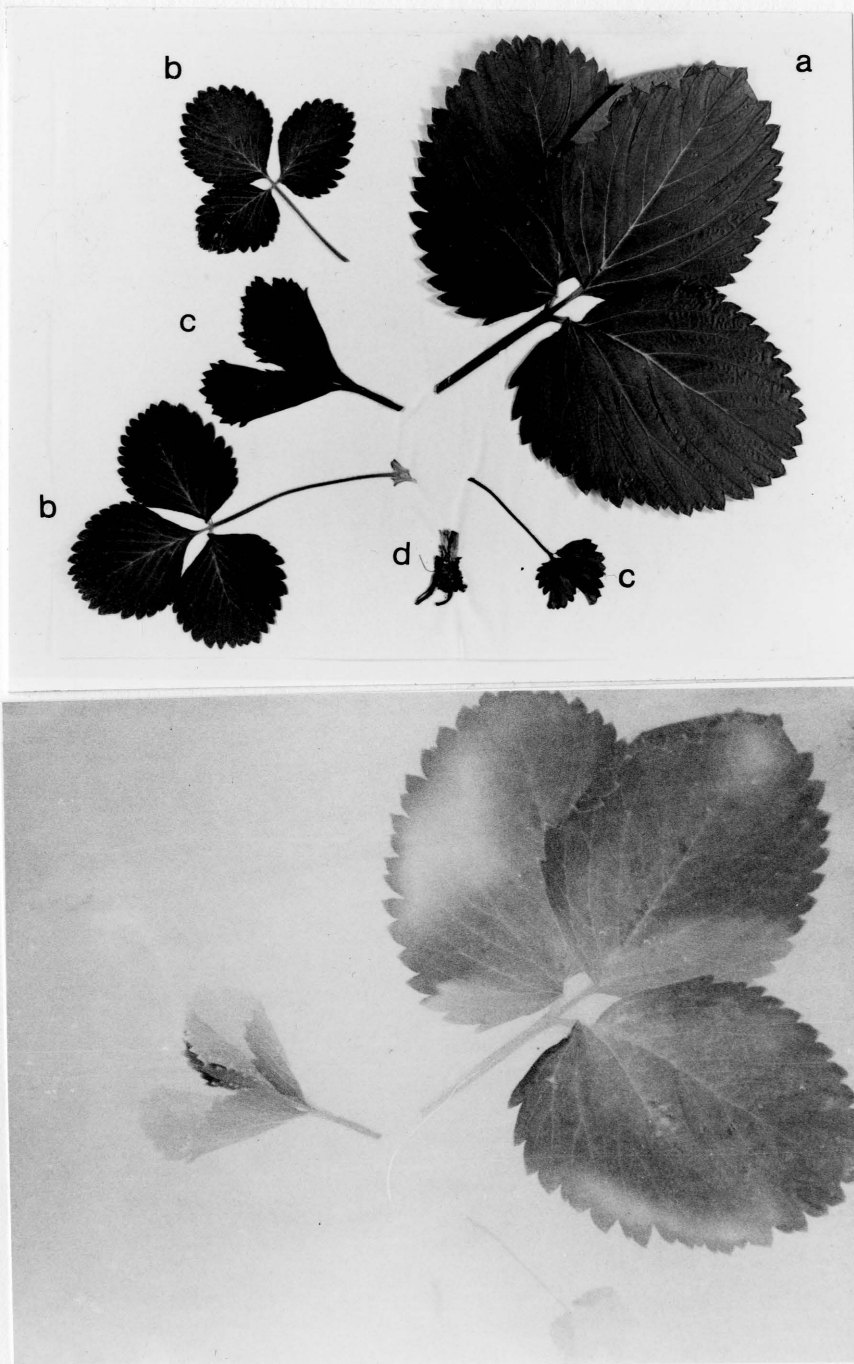


Figure 3. Deblossomed strawberry plant specimen and corresponding autoradiograph 48 hr after treatment with $^{14}\text{CO}_2$. a=treated leaf, b= fully expanded leaf, c=young leaf, d=crown.

radioassay. Therefore, the conclusion that the young leaves absorbed considerably more ^{14}C than the mature leaves is based on qualitative rather than quantitative evidence. Radioactivity levels in the fruit appeared to be low in the autoradiograph (Fig. 2). This is presumably due to the way in which the fruit were sampled. For the autoradiographs, only a thin (1 mm) longitudinal section of fruit was sampled. Therefore, the total fruit contained much more radioactive photosynthate than was evident in the autoradiograph.

It appears that deblossoming 'Tribute' strawberry plants caused [^{14}C]-photosynthate, which normally would have been partitioned to the fruit, to be partitioned to the developing leaves. Thus, in the absence of a fruit sink, the young leaves become the major sink for photosynthates. This may have provided the energy for the increased leaf production rate and subsequent greater leaf area of deblossomed plants.

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Chapter III

NET PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, AND SPECIFIC LEAF WEIGHT OF STRAWBERRY PLANTS AS INFLUENCED BY FRUITING

ABSTRACT

In an initial experiment, 'Tribute' (day-neutral) and 'Allstar' (Junebearing) strawberry plants were grouped into fruiting, partially deblossomed, and deblossomed treatments. Net photosynthesis (P_n), dark respiration (R_d), and stomatal conductance for CO_2 (g_s) were measured at 14-day intervals during the first fruiting cycle of both cultivars and at 7-day intervals during the second fruiting cycle of 'Tribute'. P_n of recently expanded leaves of fruiting plants was higher than that of deblossomed plants during the second week of the first fruiting cycle, as well as the second and third weeks of the second fruiting cycle. There were no differences in R_d or g_s among treatments. At the end of the fruiting cycles, leaves and roots of deblossomed plants of both cultivars had greater dry weights than those of fruiting plants. At the end of the first fruiting cycle, roots of deblossomed 'Tribute' had a higher percentage of total non-structural carbohydrates (TNSC) than roots of fruiting plants.

In another experiment, 'Tribute' strawberry plants were grouped into fruiting and deblossomed treatments. At 7-day intervals throughout the fruiting cycle, P_n was determined for the same leaf (original) of each plant and for the most recently expanded leaf of each plant. P_n of the newly expanded leaf was higher for fruiting plants than deblossomed plants when the fruit began to ripen, but no difference was observed between original leaves in each treatment. During fruit maturation, SLW was higher for deblossomed plants than fruiting plants for both leaves. Deblossomed plants had a higher chlorophyll content in the leaves than fruiting plants during the first, second, and fourth weeks of the fruiting cycle.

INTRODUCTION

Fruiting has been shown to increase P_n of apple (8), sweet pepper (20), pea (6), soybean (17), eggplant (10), and strawberry (4, 7, 10, 26). Hoffmann and Lenz (10) found that fruiting strawberry plants had slightly higher P_n rates than defruited plants, beginning one day after fruit removal. P_n rates (leaf area basis) of the day-neutral strawberry cultivars 'Hecker' (4) and 'Brighton' (7) were higher for fruiting plants than for deblossomed plants. On a whole plant basis, however, P_n of 'Hecker', was not different bet-

ween treatments, due to a greater leaf area of the deblossomed plants (4). Explanations for reduced Pn of deblossomed plants have included: a) interference with light reception caused by an accumulation of starch in the chloroplasts of deblossomed plants and b) reduced stomatal conductance caused by an accumulation of assimilates in the leaves of deblossomed plants (19). Fruiting had no effect on Rd of citrus (12) and strawberry plants (4).

Day-neutral strawberry plants fruit in approximately six week cycles, regardless of photoperiod (5). Therefore, they are an ideal model system for studying the effects of fruiting on Pn and Rd. The objective of this study was to determine the effects of fruiting on Pn, Rd, g_s , SLW, and chlorophyll content of June bearing and day-neutral strawberry plants.

MATERIALS AND METHODS

Expt. 1: Plants of 'Tribute' (day-neutral) and 'Allstar' (Junebearing) cultivars were potted in peat:perlite:vermiculite (1:1:1/v:v:v) in 15 cm plastic pots on May 30, 1983. Plants were placed on benches in an open-ended plastic greenhouse and fertilized with a slow-release fertilizer (18N-2.6P-10K) at 3 g/pot. Uniform plants of both cultivars were grouped into 4 treatments: 1) all blos-

soms and runners removed as they appeared, 2) all but the first inflorescence removed during the only fruiting cycle for 'Allstar' and each of the 2 fruiting cycles for 'Tribute', and runners removed as they appeared, 3) only runners removed, and 4) plants left intact. Each treatment consisted of 6 single-plant replications for each cultivar in a split plot design where main plots were treatments and subplots were cultivars. P_n , R_d , and g_s were determined when the majority of primary flowers were open, and at 14-day intervals throughout the first fruiting cycle of both cultivars. In addition, these determinations were made at 7-day intervals throughout the second fruiting cycle of 'Tribute'. The most recently expanded leaf of each plant was used for each determination. Thus a different leaf on each plant was measured each week.

P_n , R_d , and g_s were determined by enclosing a single leaf in a modification of the chamber described by Syvertsen and Smith (25). The chamber contained a fan, but the bottom was plexiglas instead of copper, and a heat exchanger was not used. Air flow rate into the chamber was maintained at 5 liters min^{-1} and photosynthetic photon flux density was 900 $\mu\text{mol s}^{-1} \text{m}^{-2}$ as determined by a Licor model LI 185 light meter with a quantum sensor. Air temperature in the chamber was $28 \pm 1^\circ\text{C}$ and relative humidity was $50 \pm 5\%$. P_n and R_d

were determined with a Beckman model 865 infrared gas analyzer. For Rd determinations, a black cloth was placed over the plant. Stomatal conductance was calculated by dividing the transpiration rate (determined with a General Eastern model 1100 AP dew point hygrometer) by the water vapor pressure gradient between the leaf and the air and multiplying the resulting quotient by 0.69 (diffusivity of CO₂ in air/diffusivity of H₂O in air) (24). Throughout both fruiting cycles, ripe fruit were harvested, dried, and weighed. After the first fruiting cycle of both cultivars, and the second fruiting cycle of 'Tribute', plants were harvested and dry weights were determined separately for leaves, crowns, and roots of each plant. Total non-structural carbohydrates were extracted from each of these tissues using the technique described by Wolf and Elmore (27). The percentage of TNSC in each tissue was determined colorometrically by reacting free reducing sugars with para-hydroxy benzoic acid hydrazide and measuring the absorbance at 410 nm (15).

Expt. 2: Procedures were modified for this experiment based on results obtained in expt. 1. On June 6, 1984, 'Tribute' plants were potted as in expt. 1. Plants were placed in an open-ended plastic greenhouse and fertilized weekly with 240 ppm N from a 20N-8.7P-16K soluble fertilizer in the irrigation water. Uniform plants were grouped into 2 treatments:

1) plants with all blossoms removed as they appeared, and 2) plants allowed to fruit normally. Runners were removed from all plants in both treatments as they emerged. Each treatment consisted of 10 single-plant replications in a randomized complete block design.

When the majority of primary flowers were open, the most recently emerged leaf on each plant was tagged and its area determined after it was fully expanded. Throughout the 6-week fruiting cycle, P_n was determined for this same leaf ("old leaf") at 7-day intervals. SLW and chlorophyll content were determined weekly for a similar-aged leaf of comparable plants throughout the fruiting cycle. P_n , SLW, and chlorophyll content were also determined for a newly selected, recently expanded leaf ("young leaf") each week throughout the fruiting cycle. P_n was determined as in expt. 1. SLW was determined by drying and weighing 10 leaf disks each with an area of 0.34 cm^2 . Chlorophyll was extracted by placing leaf discs in 10 ml of 85 % methanol in the dark for 48 hr. Two ml of extract were diluted with 25 ml of distilled H_2O and chlorophyll content was determined colorometrically according to Casio, et al. (2).

Lines on all graphs were smoothed using spline functions described by Reinsch (22).

RESULTS

Expt. 1: During the first fruiting cycle, there was no significant interaction ($p > .05$) between cultivar and treatment for P_n , R_d , g_s , or dry weight; therefore, data from both cultivars were combined for analysis. R_d and g_s were not significantly different among treatments during either fruiting cycle. R_d averaged 1.4 and 1.5 mg CO_2 dm^{-2} hr^{-1} during the first and second fruiting cycles respectively. Stomatal conductance averaged 0.26 and 0.25 cm s^{-1} during the first and the second fruiting cycles respectively. During the second week of the first fruiting cycle, as well as the second and third weeks of the second fruiting cycle, P_n was significantly lower for completely deblossomed plants than plants in the other treatments (Table 1). Since both cultivars responded similarly for root dry weights and TNSC, data are reported only for 'Tribute' to facilitate comparisons between the two fruiting cycles. At the end of the first fruiting cycle, partially deblossomed and deblossomed plants had a greater leaf dry weight than fruiting plants with runners (Table 2). Partially deblossomed plants had higher crown dry weights than fruiting plants; completely deblossomed plants had the highest root dry weights.

After the first fruiting cycle, there was no effect of treatment on the percentages of TNSC in the leaves and

Table 1. Net photosynthesis (Pn) of strawberry plants as influenced by fruit and runner removal (Expt. 1).

Treatment ^x	First fruiting cycle ^z			Second fruiting cycle ^y					
	Week			Week					
	<u>2</u>	<u>4</u>	<u>6</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Frt, +R	26.2a ^w	21.2a	16.7a	22.3a	23.6a	18.3a	23.6a	21.8a	14.0a
Frt, -R	27.8a	23.1a	17.2a	17.8a	23.3a	22.5a	19.4a	19.4a	19.0a
Pd, -R	26.7a	22.1a	18.3a	16.1a	24.4a	23.0a	17.5a	17.5a	17.3a
D, -R	24.0b	18.7a	15.9a	21.5a	21.5b	16.1b	18.6a	18.6a	19.0a

^z'Tribute' and 'Allstar'.

^y'Tribute' only.

^xFrt = fruiting; Pd = all but the first inflorescence removed; D = completely deblossomed; +R, -R = runners intact and removed, respectively.

^wMean separation within columns by single degree of freedom F-test, 5% level.

crowns of either cultivar. These averaged 14.0 and 9.4 % respectively for both cultivars combined. There was a significant interaction ($p > .05$) between cultivar and treatment for the percentage of TNSC in the roots. There was no treatment effect on TNSC in roots of 'Allstar'; however, completely deblossomed 'Tribute' plants had a higher percentage of TNSC in the roots than fruiting plants with runners.

After the second fruiting cycle of 'Tribute', the deblossomed plants had higher leaf and root dry weights than fruiting plants (Table 2). There was no significant difference in crown or total plant dry weights among treatments. Average TNSC in the leaves, crowns, and roots of 'Tribute' after the second fruiting cycle were 6.0, 6.2, and 3.8 %, respectively, and were not affected by treatment.

Expt 2.: During the fourth week of the fruiting cycle, the majority of fruit began to ripen as indicated by the onset of red color. Pn of the same leaf followed through the experiment (old leaf) was not different between treatments during any week of the fruiting cycle (Fig. 1). Pn of the most recently expanded leaf (young leaf) was higher for fruiting plants than deblossomed plants during the fifth and sixth weeks of the fruiting cycle (Fig. 2). The SLW of the old leaf was higher for fruiting plants than deblossomed plants during the third through sixth week of the fruiting

Table 2. Tissue dry weights and total non-structural carbohydrates (TNSC) of 'Tribute' strawberry plants as influenced by fruit and runner removal (Expt. 1).

Treatment ^z	Dry weight (g)			Plant ^y	TNSC (%) Root
	Leaves	Crown	Roots		
<u>First fruiting cycle</u>					
Frt, +R	6.2b ^x	1.7b	2.6b	15.7a	2.9b
Frt, -R	7.8ab	1.9b	3.1b	17.7a	4.3ab
Pd, -R	8.8a	2.8a	4.0ab	17.8a	4.5ab
D, -R	9.9a	2.0ab	4.9a	16.8a	6.1a
<u>Second fruiting cycle</u>					
Frt, +R	5.2c	2.4a	5.2b	21.4a	3.2a
Frt, -R	6.0bc	2.1a	4.7b	20.0a	3.6a
Pd, -R	8.3ab	2.9a	7.2ab	20.7a	4.4a
D, -R	9.1a	2.9a	10.4a	22.4a	4.0a

^zFrt = fruiting; Pd = all but the first inflorescence removed;
D = completely deblossomed; +R, -R = runners intact and removed,
respectively.

^yIncludes fruit dry weight.

^xMean separation within columns and fruiting cycles by single
degree of freedom F-test, 5% level.

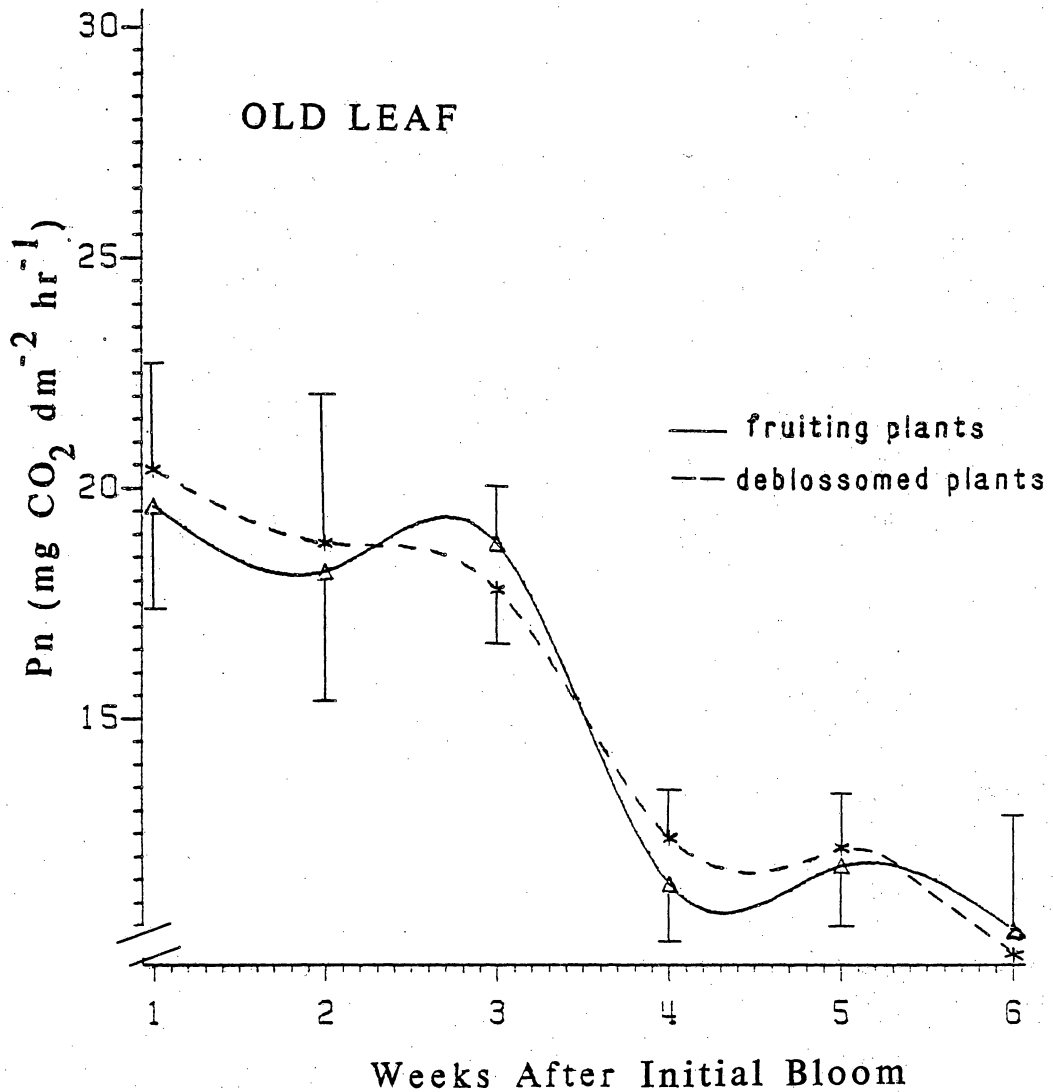


Figure 1. Net photosynthesis (Pn) (leaf area basis) of same leaf (old leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

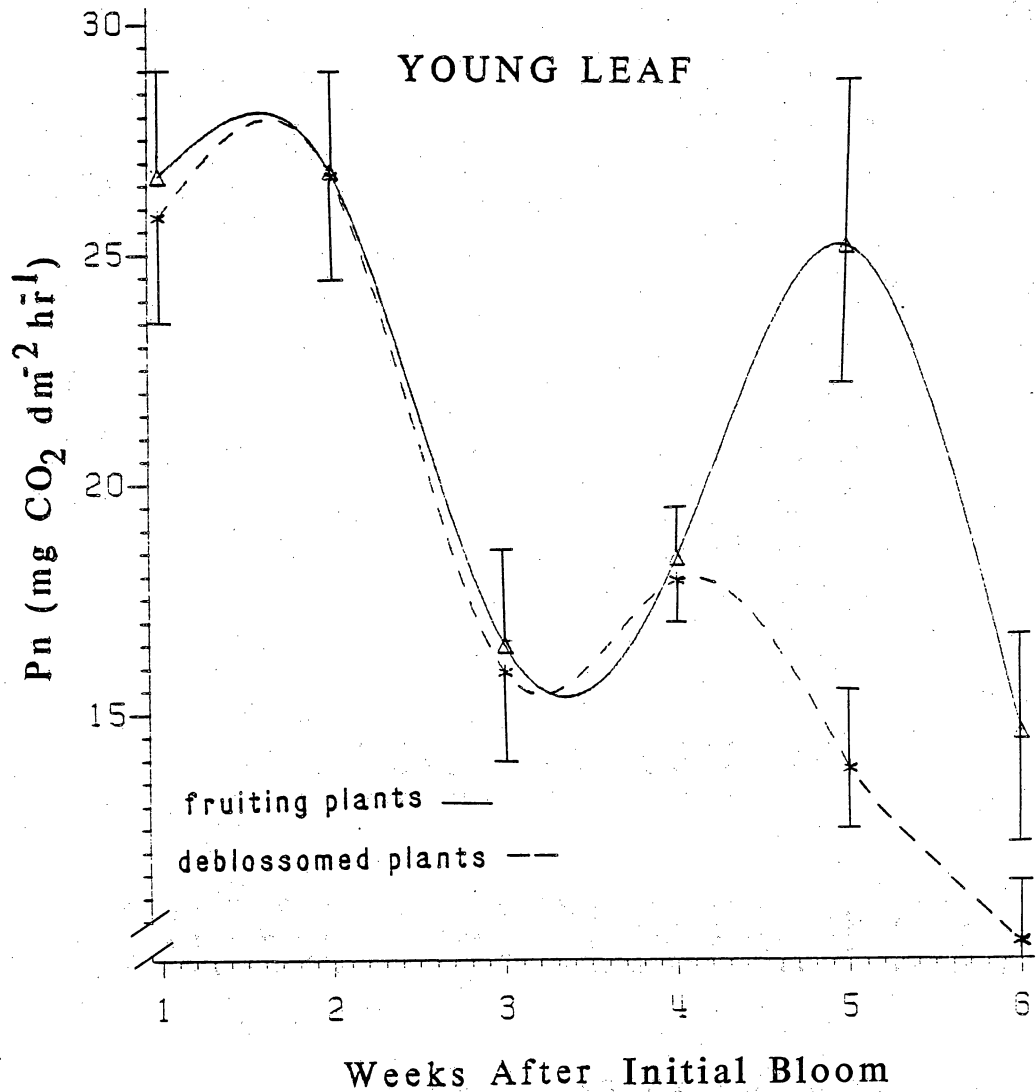


Figure 2. Net photosynthesis (Pn) (leaf area basis) of recently expanded leaf (young leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

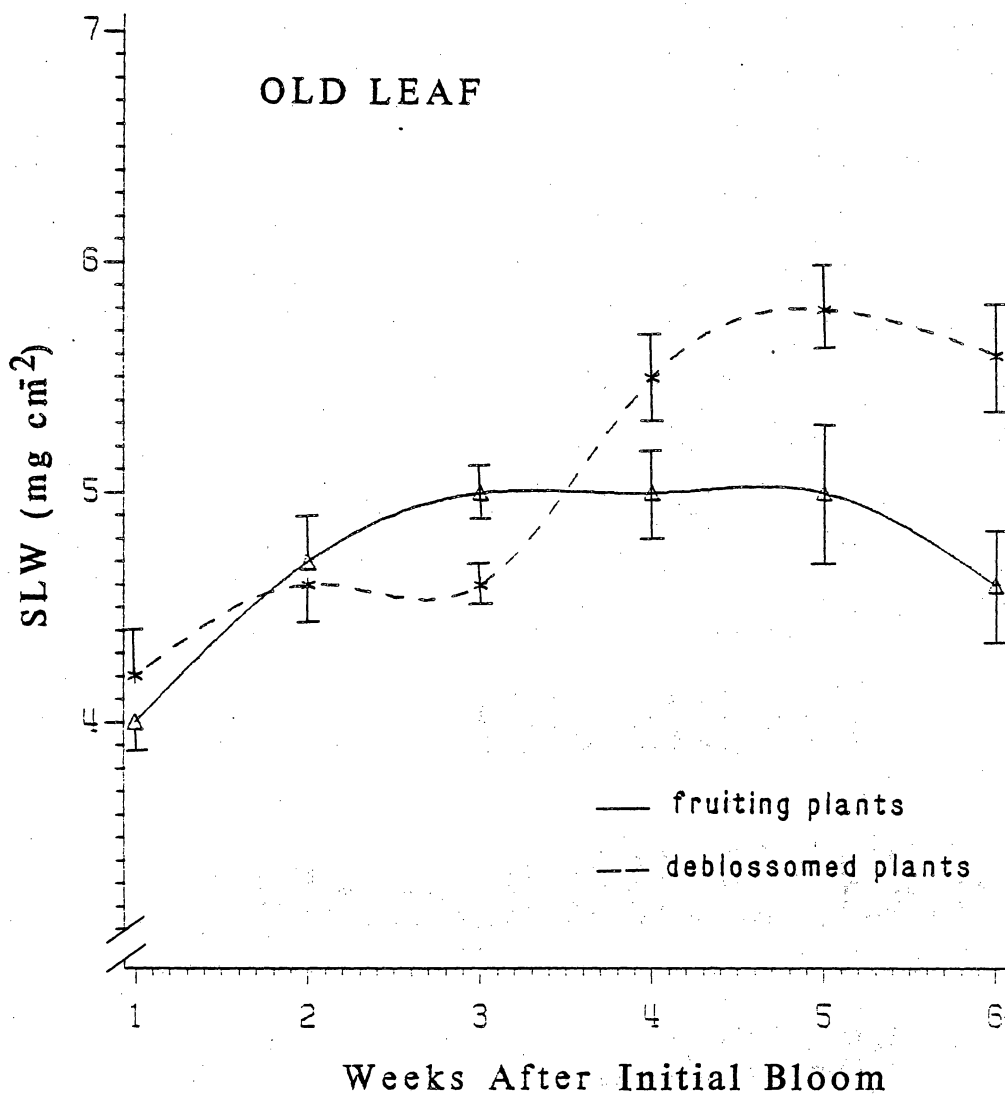


Figure 3. Specific leaf weight (SLW) of same leaf (old leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

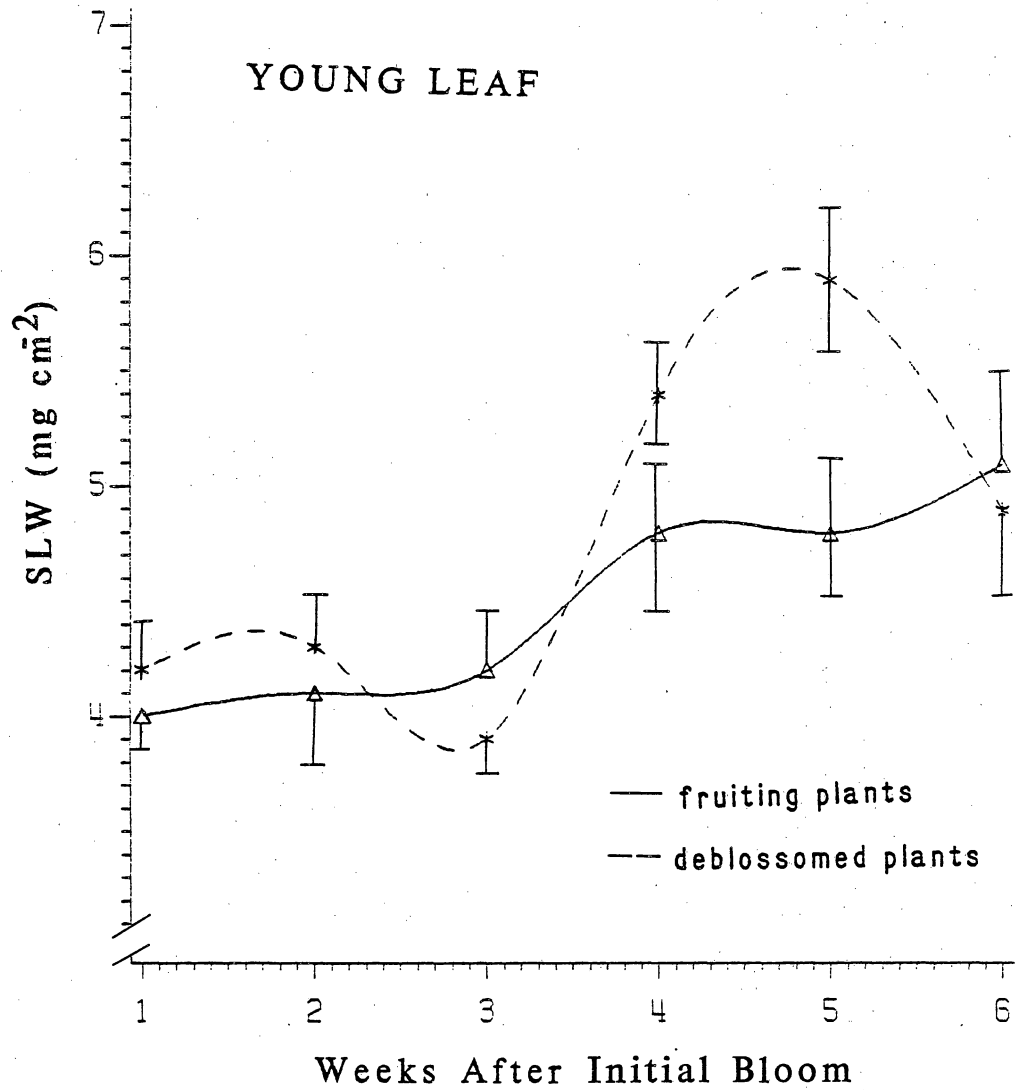


Figure 4. Specific leaf weight (SLW) of recently expanded leaf (young leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

cycle (Fig. 3). The SLW of the young leaf of the deblossomed plants was higher than that of the fruiting plants during the fourth and fifth weeks of the fruiting cycle (Fig. 4). Chlorophyll content in the old leaf was higher for deblossomed than fruiting plants during the first and fourth weeks of the fruiting cycle (Fig. 5). Chlorophyll content in the young leaf was higher for deblossomed plants than fruiting plants during weeks one, two, and four, of the fruiting cycle (Fig. 6).

DISCUSSION

Newly expanded leaves of fruiting strawberry plants had higher Pn rates, on a leaf area basis, during specific weeks of the fruiting cycle than deblossomed plants. The time during the fruiting cycle when Pn was higher for fruiting plants differed between expt. 1 and expt. 2. Choma, et al. (4) found that fruiting 'Hecker' strawberry plants had higher Pn rates (leaf area basis) on five out of six weeks during the fruiting cycle. Since Pn in that study was determined for whole plants, differences between treatments may have been confounded by mutual shading of leaves in the chamber or by different leaf aging patterns between treatments. Deblossomed strawberry plants have been shown to have a greater leaf production rate than fruiting plants

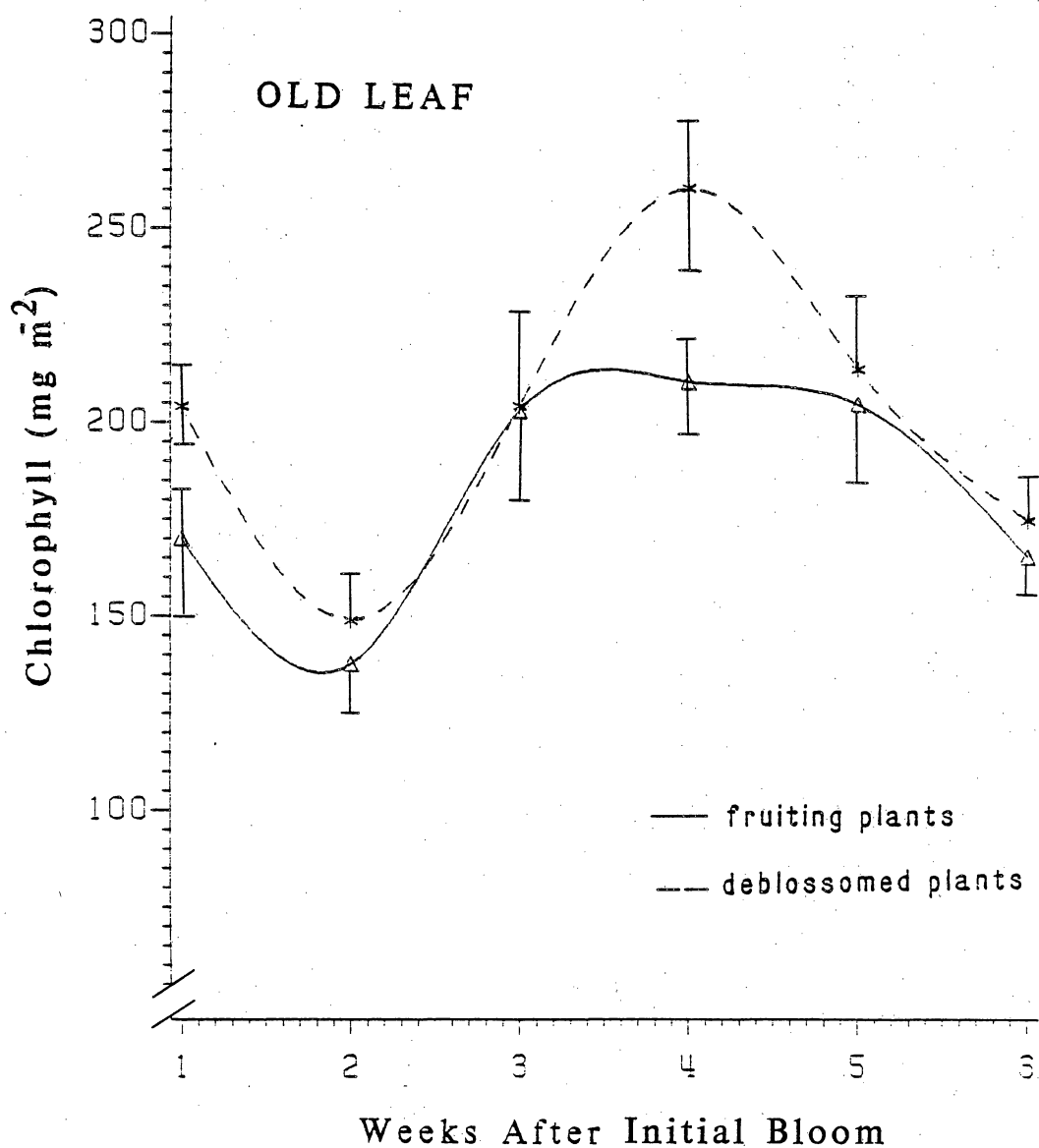


Figure 5. Chlorophyll content of same leaf (old leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

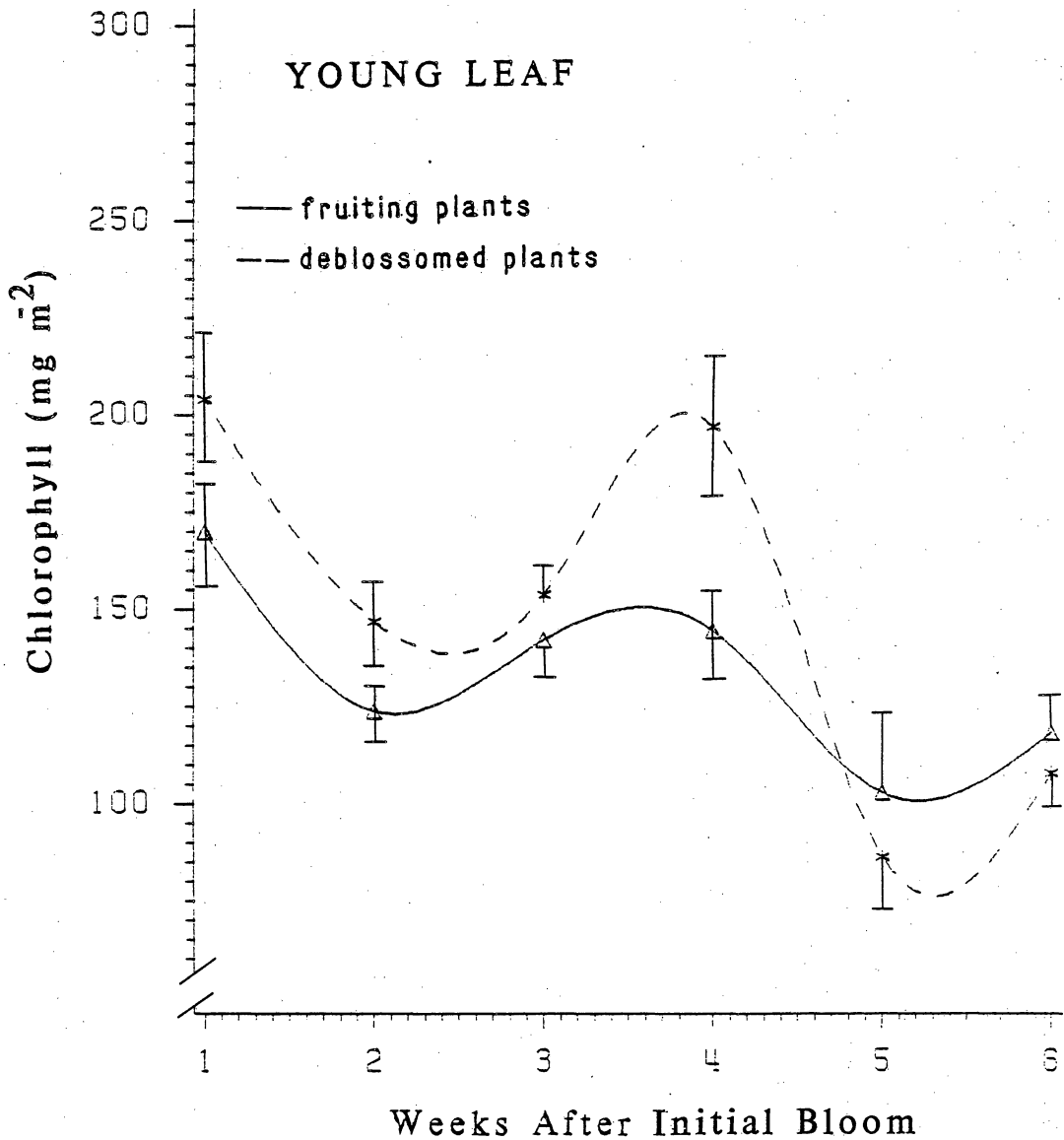


Figure 6. Chlorophyll content of recently expanded leaf (young leaf) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

(4). In our study, deblossoming increased P_n of newly expanded leaves during the fifth week of the fruiting cycle but did not affect the older leaves at that time (Expt. 2, Fig. 1). Forney and Breen (7) found that P_n of fruiting 'Brighton' strawberry plants was 60-80% higher than that of deblossomed plants, 67-79 days after planting. This corresponded to the time the fruit were ripening. In this study, a similar phenomenon was observed with 'Tribute' plants. At the time the fruit began to ripen, P_n of the newly expanded leaf of the fruiting plants was higher than that of the deblossomed plants (Expt. 2, Fig. 1). Thus, leaves produced during the initial stage of fruit maturation may be more photosynthetically efficient. Since no differences in g_s among treatments were observed, increases in P_n in our study could not be attributed to increased g_s of fruiting plants. This conflicts with studies on 'Brighton' strawberries (7), apples (21), and soybeans (14) where the presence of fruit was associated with increased g_s .

Lower P_n rates in deblossomed 'Tribute' strawberries may have resulted from an accumulation of assimilates in the leaves. Both the newly expanded leaves and the older leaves of deblossomed plants had a higher SLW than those of fruiting plants during fruit maturation. SLW has been positively correlated with P_n of apple (16) and strawberry (3). The

positive correlation with strawberry plants was due to an increase of mesophyll cell size and number as SLW increased (3). Monselise and Lenz (18) found that deblossomed apple trees had higher SLW than fruiting plants. The apparent contradictory observations between lower Pn rates of deblossomed plants and higher SLW was attributed to a greater accumulation of assimilates in the leaves of deblossomed plants which suppressed Pn (18). Leaves of deblossomed citrus (13), eggplant (10, 11), and strawberry (10, 11) had higher starch concentrations than leaves of fruiting plants. Chloroplasts of non-fruiting strawberry plants had higher starch concentrations than those of fruit-bearing plants (11). The higher SLW of the deblossomed 'Tribute' plants was presumably due to an accumulation of assimilates in the leaves, since it is unlikely that the amount of structural material in the older leaves would increase.

Chlorophyll content was higher in the leaves of deblossomed 'Tribute' plants than in those of fruiting plants when fruit began to ripen. Chlorophyll content has been positively correlated with Pn of soybean (1). Hesketh (9), however, found that chlorophyll content was not related to Pn rates for several crop species. Strawberry plants may be an additional crop where there is no correlation between chlorophyll content and Pn. The higher chlorophyll content in

leaves of deblossomed plants, may again be due to an accumulation of carbohydrates in the leaves, which act as precursors to chlorophyll synthesis.

Completely deblossomed strawberry plants had greater leaf and root dry weights than fruiting plants with runners at the end of both fruiting cycles. Previous studies with ^{14}C have shown that in the absence of fruit, newly expanding leaves become the dominant sink for photosynthates (23). The resulting greater leaf area and subsequent higher Pn rates (whole-plant basis) resulted in more photosynthates being produced and partitioned to the roots and new leaves. In expt. 1, the percentage of TNSC in the roots of 'Tribute' was higher in completely deblossomed plants than fruiting plants with runners during the first fruiting cycle. In fruiting plants, carbohydrates may have been mobilized from the root to the fruit resulting in lower percentage of TNSC in the roots of fruiting plants.

In summary, fruiting was correlated with increased Pn (leaf area basis) of strawberry plants during specific weeks of the fruiting cycle. The higher Pn rates for the fruiting plants could not be attributed to increases in g_s , but may be due to a depletion of carbohydrates in the leaves at the time of fruit maturation. Deblossoming strawberry plants caused more carbohydrates to be partitioned to the leaves

and roots resulting in greater leaf and root area of deblossomed plants. This observation reinforces the commercial practice in the eastern United States of deblossoming strawberry plants during the year of establishment in order to increase plant vigor prior to flower bud induction.

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Chapter IV

PHOTOSYNTHESIS AND DRY MATTER PARTITIONING IN FRUITING AND DEBLOSSOMED DAY-NEUTRAL STRAWBERRY PLANTS

ABSTRACT

On a whole plant basis, deblossomed 'Tribute' strawberry plants had higher rates of net photosynthesis (P_n) than fruiting plants during the last three weeks of a six week fruiting cycle. Leaves of both fruiting and deblossomed plants had a greater dry weight and total non-structural carbohydrate (TNSC) content than the roots, crown, or fruit. At the end of the fruiting cycle, dry weight and TNSC content of leaves were higher for deblossomed plants than fruiting plants. There was no difference in crown or root dry weights between treatments. P_n was highly correlated with plant dry weight and TNSC during the third, fifth, and sixth weeks of the fruiting cycle.

INTRODUCTION

P_n may be altered by manipulating the growth conditions of the plant (19). Increasing the ratio of the economic 'sink' to the total plant may be the most effective means of improving potential crop yield (6).

Deblossoming strawberry plants increased leaf production rates, resulting in greater leaf area and leaf dry weight (1, 5, 8, 17, 18). In the absence of a fruit sink, the newly developing leaves became the dominant sink for photosynthates (15). Fruiting strawberry plants had higher Pn rates (leaf area basis) than deblossomed plants during certain weeks of the fruiting cycle (1, 16). However, the increased leaf area of the deblossomed plants offset the higher Pn rates of the leaves of the fruiting plants. Therefore, on a whole plant basis, no differences in Pn were detected (1).

The objectives of this study were to determine the effects of fruiting on dry matter and carbohydrate partitioning by day-neutral strawberry plants, and to determine the relationship of this partitioning to Pn on a whole plant basis.

MATERIALS AND METHODS

Day-neutral strawberry plants (cv. Tribute) (3) were potted in peat:perlite:vermiculite (1:1:1/v:v:v) and placed in an open-ended plastic greenhouse on June 3, 1984. Plants were fertilized weekly with 240 ppm N from a 20N-8.7P-16K soluble fertilizer in the irrigation water. Uniform plants were grouped into 2 treatments: 1) plants with all blossoms removed as they emerged, and 2) plants allowed to flower and

fruit normally. Runners were removed from all plants as they emerged. Thirty plants in each treatment were arranged in a randomized complete block design. Each week, during a six-week fruiting cycle, 5 single-plant samples were randomly selected from each treatment.

When the majority of primary flowers were open (16 days after plants were potted), and at 7 day intervals thereafter for 5 weeks, whole-plant P_n was determined by enclosing the entire plant in a 60 liter plexiglass chamber, containing a fan for air circulation. CO_2 depletion of the air stream was determined with a Beckman model 865 infrared gas analyzer. The pot and exposed soil were wrapped in polyvinyl film to reduce the effects of root respiration on CO_2 concentration in the chamber. Air temperature in the chamber was maintained at $30 \pm 2^\circ C$ and relative humidity at $50 \pm 5 \%$. Air flow rate into the chamber was $20 \text{ liters min}^{-1}$ and photosynthetic photon flux density was $900 \mu\text{moles s}^{-1} \text{ m}^{-2}$ as determined by a LiCor model LI 185 light meter with a quantum sensor.

Leaves, crown, roots, and fruit (when present) were then harvested from each plant. Total leaf area was determined with a LiCor model LI-3000 portable area meter. Tissues were dried at $70^\circ C$ and weighed. TNSC were extracted separately from the leaves, crown, and roots using the method

described by Wolf and Elmore (20). Storage carbohydrates were broken down to free reducing sugars with a commercial enzyme mixture (Clarase-900). TNSC were determined colorimetrically after reacting the free reducing sugars with para-hydroxy benzoic acid hydrazide and measuring the absorbance at 410 nm (10).

Lines on all graphs were smoothed using spline functions described by Reinsch (14).

RESULTS

Whole plant Pn was higher for deblossomed plants than fruiting plants during weeks 4-6 of the fruiting cycle (Fig. 1). Leaf area was also higher for the deblossomed plants during that time period (Fig. 2). Total leaf area was highly correlated with whole plant Pn ($r^2=.88$, $p<.01$). Therefore, the higher Pn rates for deblossomed plants can be largely attributed to the greater leaf area. Pn was highly correlated with whole plant dry weight during weeks 3, 5, and 6 and during the fruiting cycle as a whole (Table 1).

Dry weight of leaves increased more rapidly than that of crowns or roots in both treatments. In deblossomed plants, however, leaf dry weight increased more rapidly than for the fruiting plants (Figs. 3 and 4). Deblossomed plants had a significantly greater leaf dry weight than the fruiting

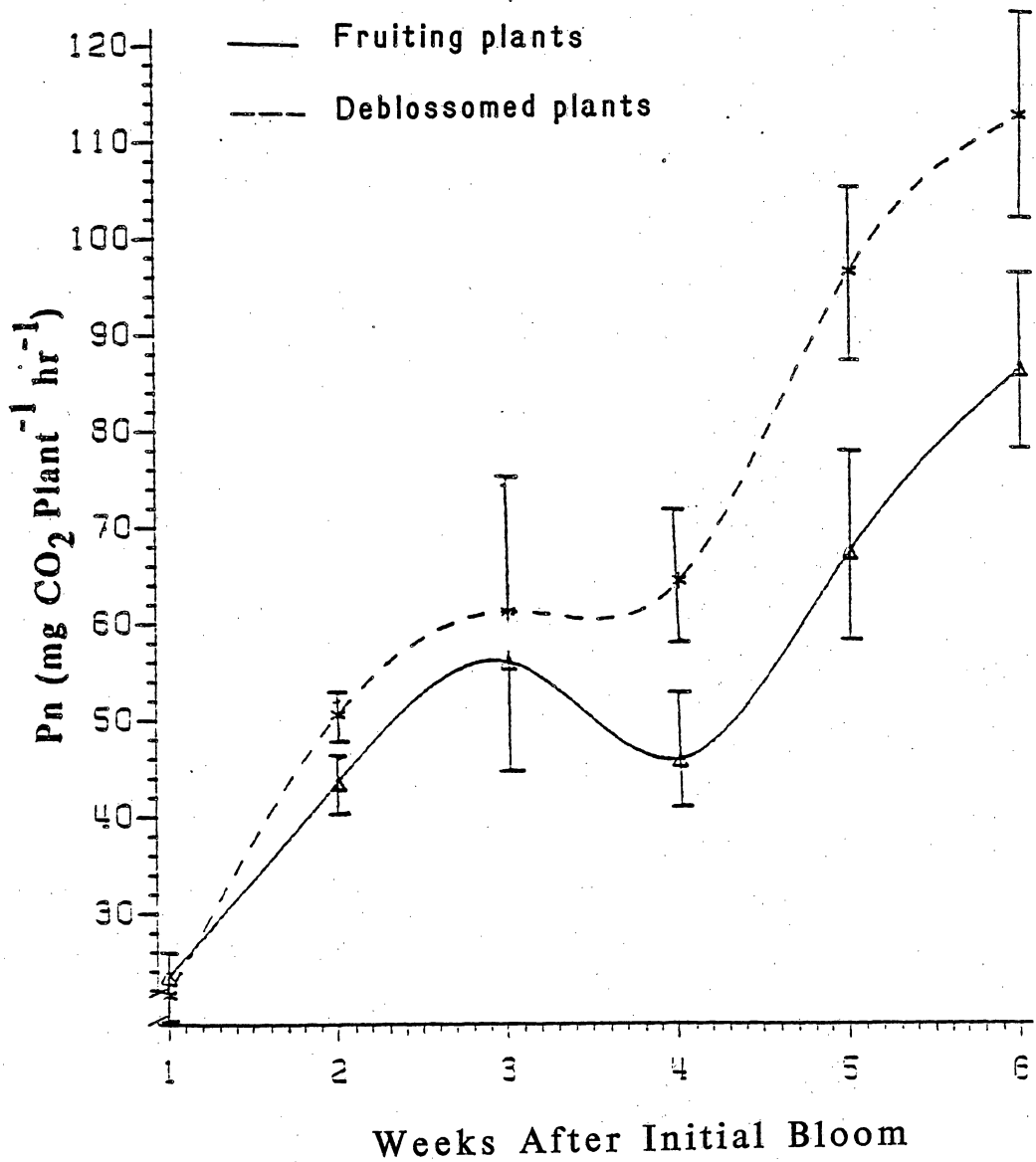


Figure 1. Net photosynthesis (Pn) (whole plant basis) of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

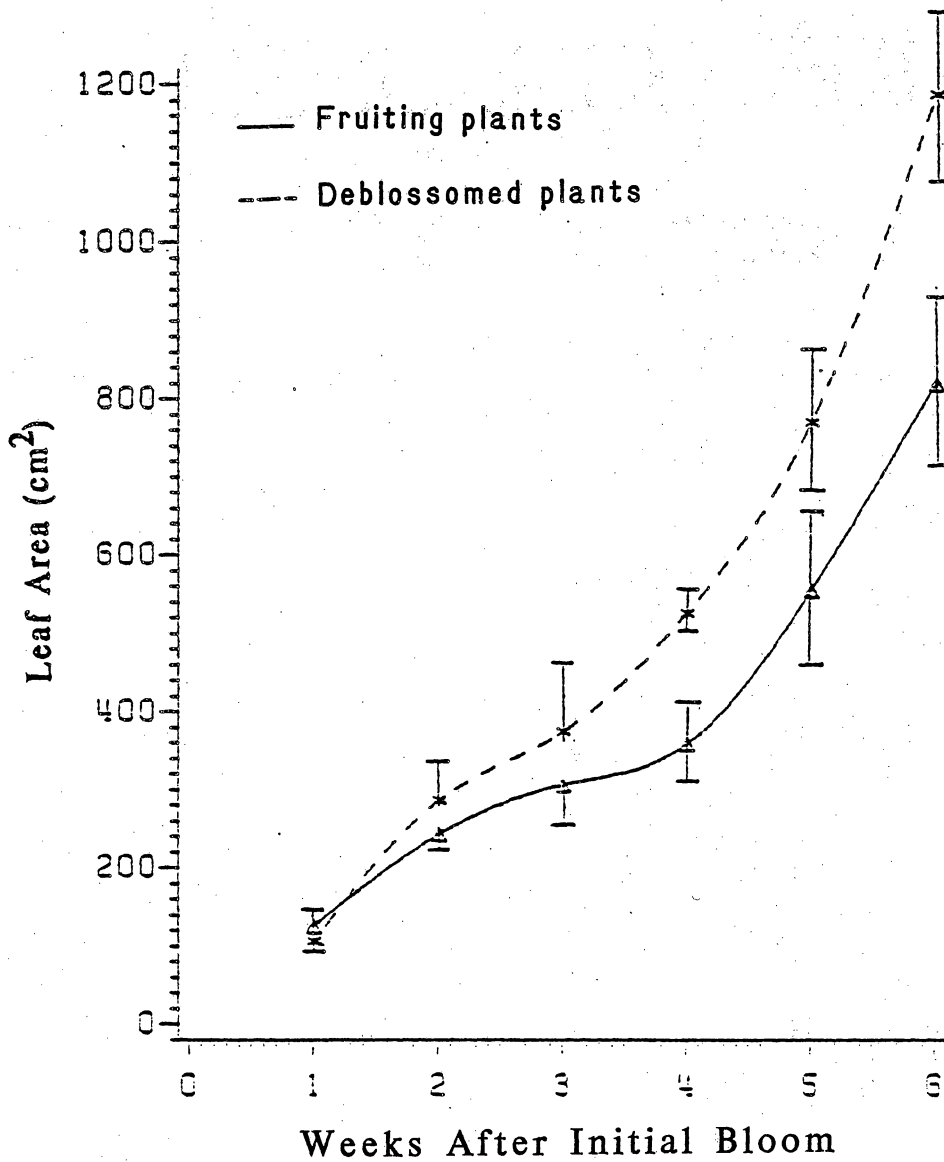


Figure 2. Total leaf area of fruiting and deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical lines represent standard errors.

Table 1. Net photosynthesis (Pn) ($\text{mg CO}_2 \text{ plant}^{-1} \text{ hr}^{-1}$) correlated with plant dry weight (g) and total non-structural carbohydrates (TNSC) (g).

	Weeks after initial bloom						
	1	2	3	4	5	6	Pooled
	<u>Pn x dry wt.</u>						
Correlation coefficient (r)	0.26	0.27	0.90	0.46	0.95	0.83	0.90
Significance level	--	--	** ^Z	--	**	**	**
	<u>Pn x TNSC</u>						
Correlation coefficient (r)	0.03	0.33	0.94	0.68	0.92	0.76	0.86
Significance level	--	--	**	* ^Y	**	*	**

^ZSignificant at 1% level.

^YSignificant at 5% level.

plants during weeks 4 through 6 of the fruiting cycle (t-test, $p < .05$). Crown and root dry weights were similar for fruiting and deblossomed plants throughout the fruiting cycle (Figs. 3 and 4). Accumulated fruit dry weight of the fruiting plants increased steadily throughout the fruiting cycle (Fig. 3).

In both treatments, total leaf TNSC were higher than crown or root TNSC during weeks 3-6 of the fruiting cycle (Figs. 5 and 6). Crown and root TNSC were similar for fruiting and deblossomed plants throughout the fruiting cycle (Figs. 5 and 6). Fruit TNSC were not determined due to the small amount of tissue available.

During weeks 1-3, leaves of both fruiting and deblossomed plants had a higher percentage of TNSC than the crowns or roots (Figs. 7 and 8). The percentage of TNSC in the leaves of plants in both treatments decreased during the fourth week of the fruiting cycle (Figs. 7 and 8). This coincided with an increase in the percentage of TNSC in the crown of the deblossomed plants (Fig. 7). During the fifth week, the percentage of TNSC in the crown of deblossomed plants began to increase. The percentage of TNSC in the roots was similar for fruiting and deblossomed plants throughout the fruiting cycle (Figs. 7 and 8). During the third week, the percentage of TNSC in the roots of plants in both treatments decreased (Figs. 7 and 8).

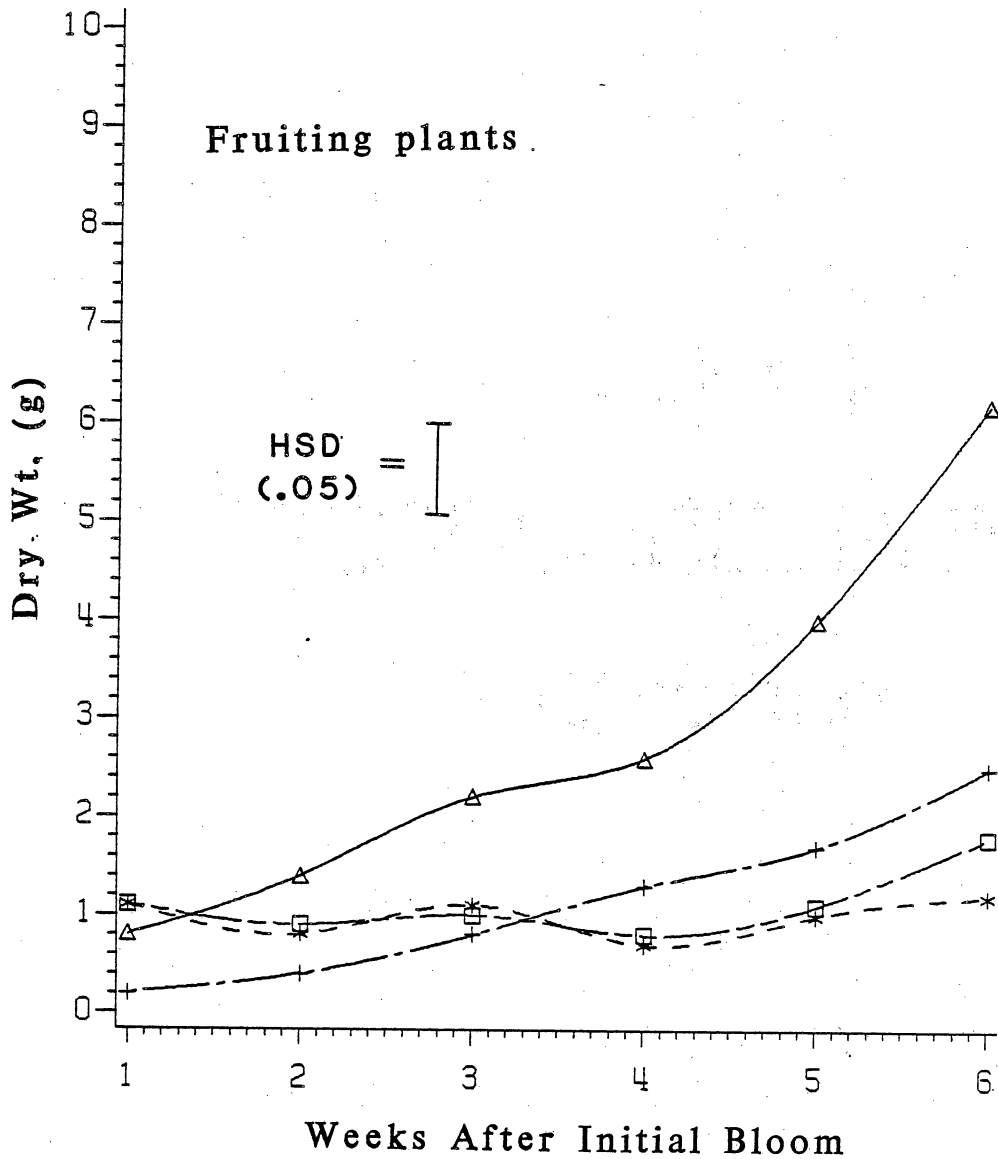


Figure 3. Dry weights of leaves (Δ), crown (\square), roots (*), and fruit (+) of fruiting 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD value at the 5 % significance level.

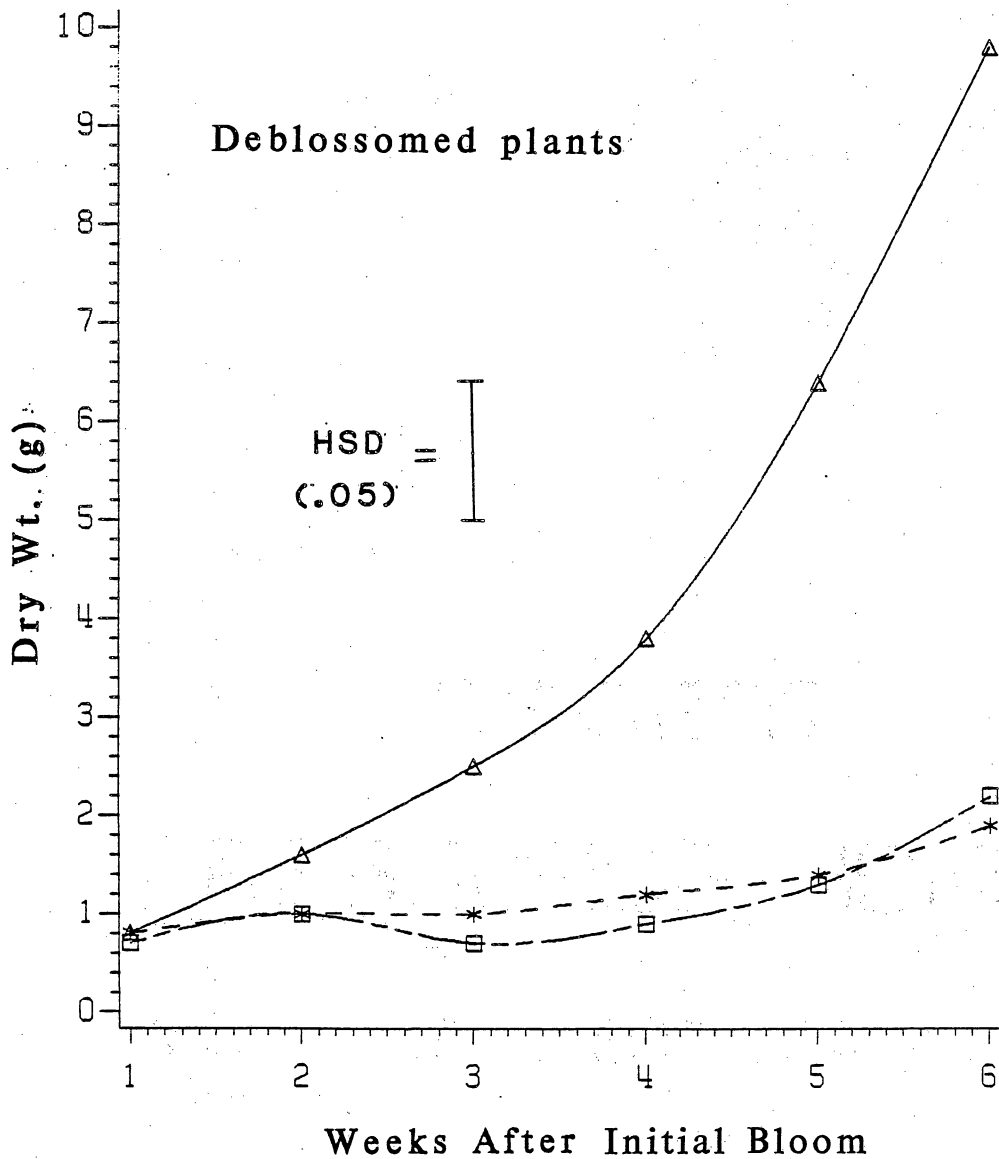


Figure 4. Dry weights of leaves (Δ), crown (\square), and roots (*) of deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD value at the 5 % significance level.

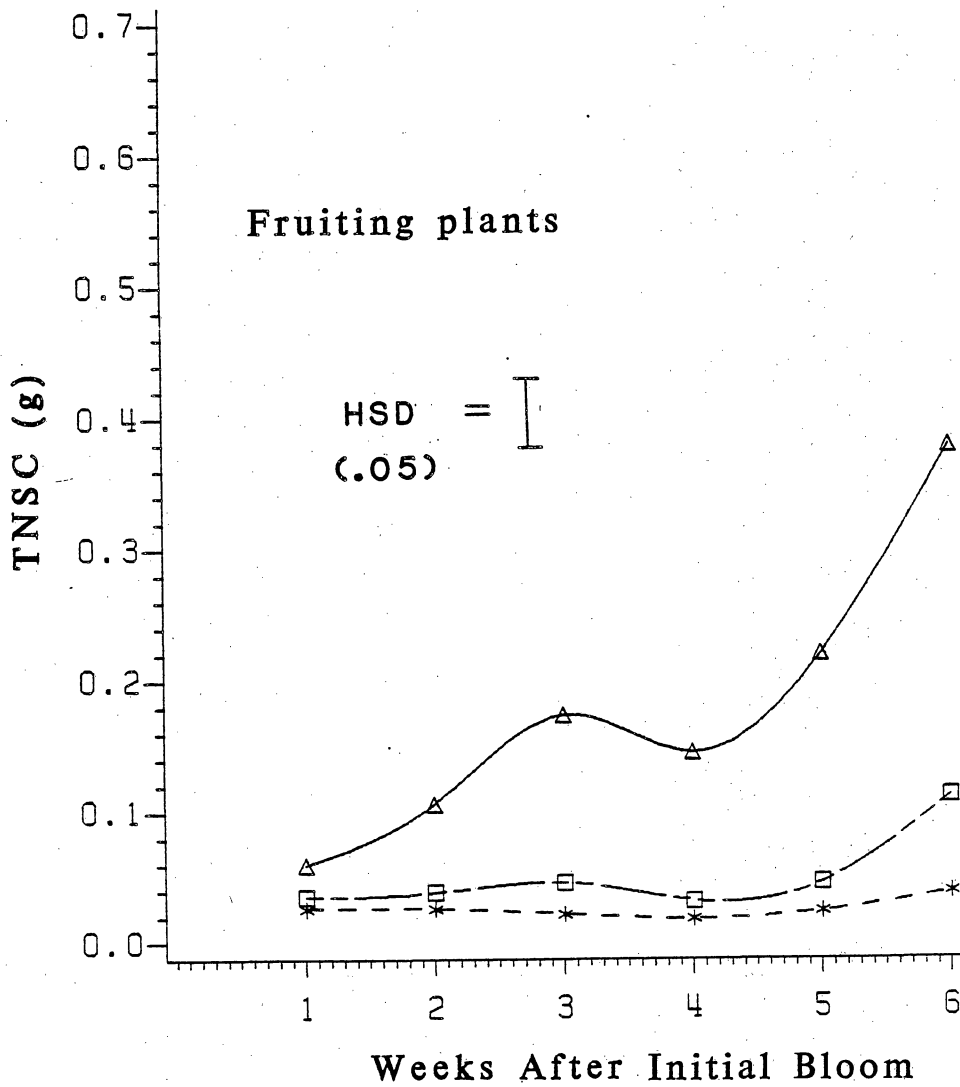


Figure 5. Total non-structural carbohydrates (TNSC) in leaves (Δ), crown (\square), and roots ($*$) of fruiting 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD at the 5 % significance level.

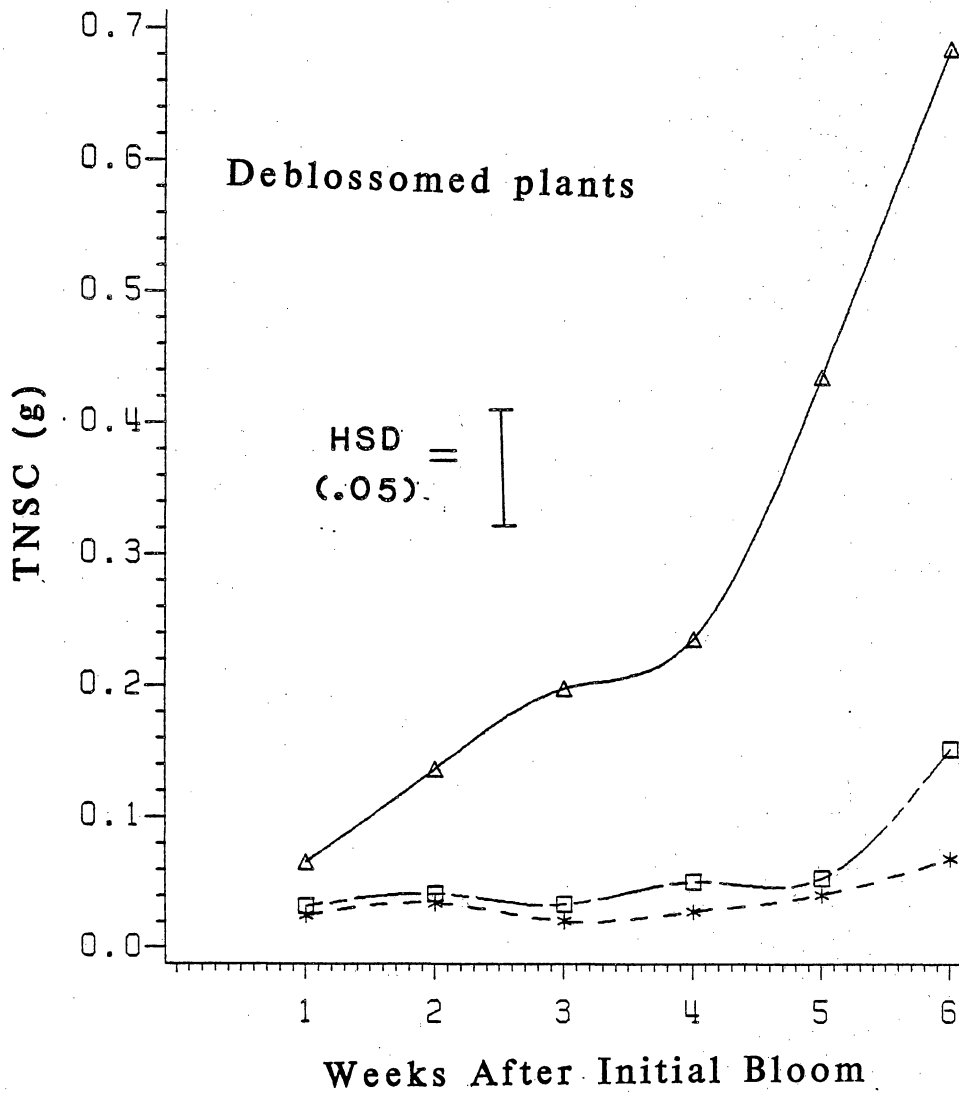


Figure 6. Total non-structural carbohydrates (TNSC) in leaves (Δ), crown (□), and roots (*) of deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD value at the 5 % level of significance.

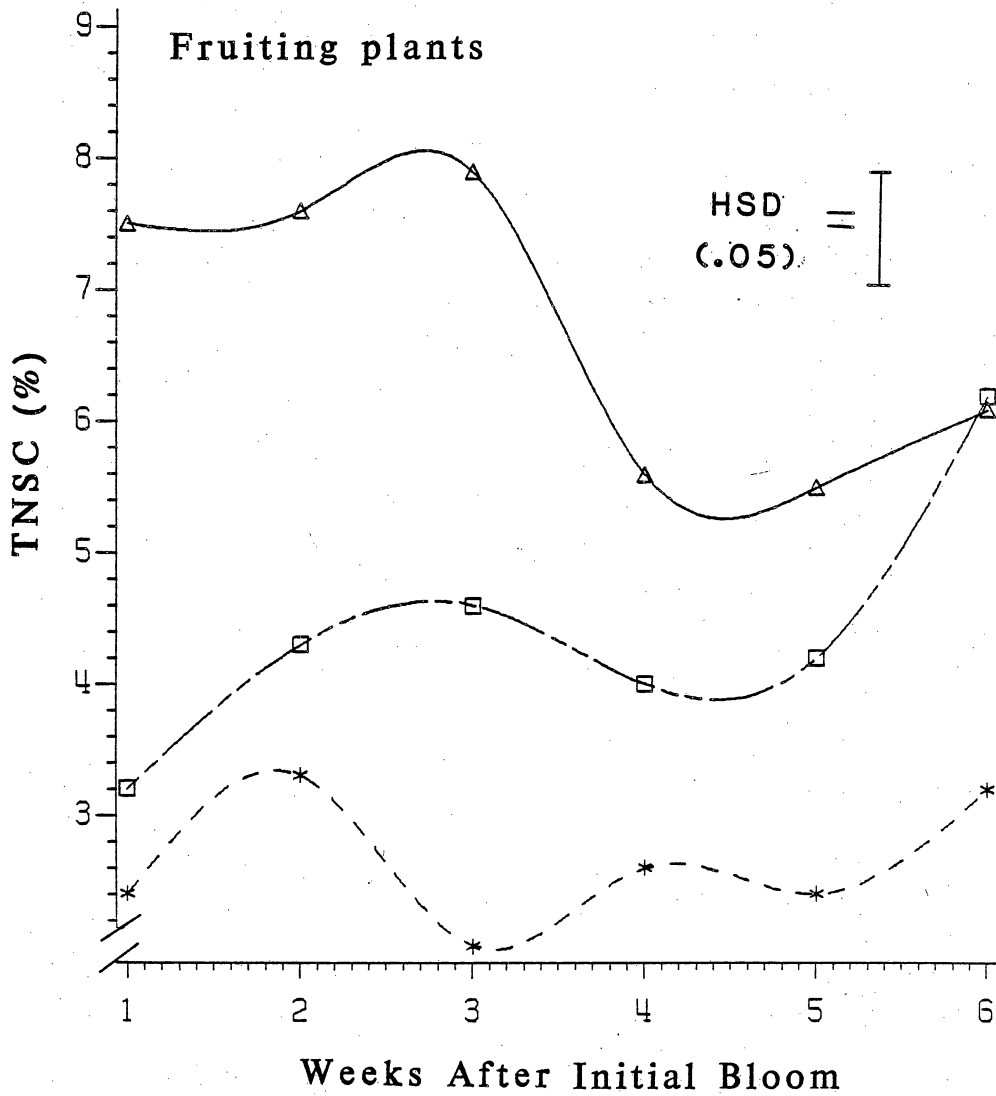


Figure 7. Percentage of total non-structural carbohydrates (TNSC) in leaves (Δ), crown (\square), and roots ($*$) of fruiting 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD at the 5 % significance level.

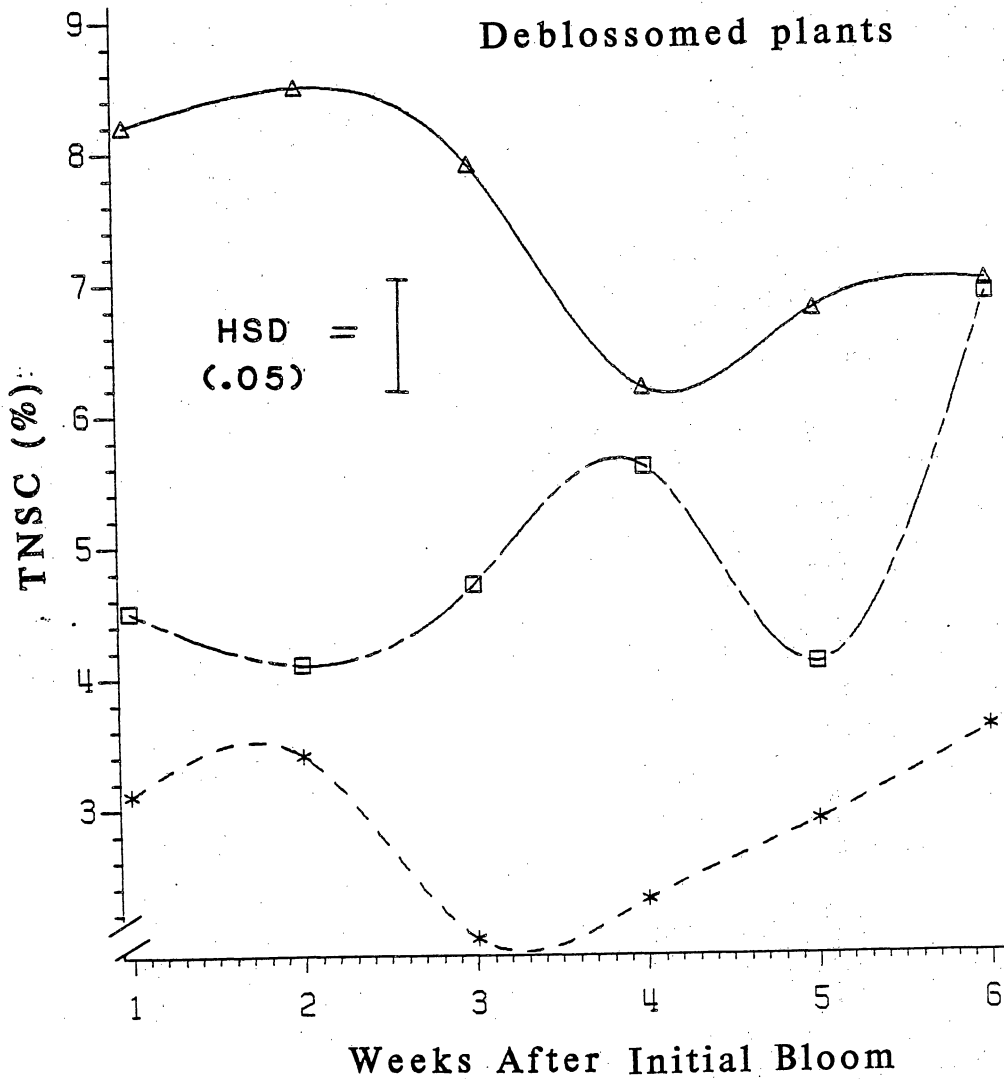


Figure 8. Percentage of total non-structural carbohydrates (TNSC) in leaves (Δ), crown (\square), and roots ($*$) of deblossomed 'Tribute' strawberry plants during a six-week fruiting cycle. Vertical line represents pooled Tukey's HSD at the 5% significance level.

DISCUSSION

Dziencial (4) and Schaffer et al. (15) found that fruiting decreased the accumulation of ^{14}C -assimilates in the youngest leaves of strawberry plants. In this study, deblossomed plants had a greater leaf area, which was in agreement with the observations of others (1, 8, 17, 18). During the last 3 weeks of the fruiting cycle, P_n (whole plant basis) was higher for deblossomed plants than fruiting plants, presumably due to the greater leaf area of the deblossomed plants. Choma et al. (1) found no difference in P_n (whole plant basis) between fruiting and deblossomed 'Hecker' strawberry plants. Their study was conducted under short days of January, whereas this study was conducted under longer days of June. Therefore, discrepancies between studies may be due to cultivar or irradiance differences. During 5 of 6 weeks of a fruiting cycle, P_n (leaf area basis) of 'Hecker' strawberries was higher for fruiting than deblossomed plants (1). P_n (leaf area basis) of 'Tribute' was also higher for fruiting than deblossomed plants during week 5 of a 6-week fruiting cycle (16). Thus, fruiting increased photosynthetic efficiency of leaves of day-neutral strawberry plants during certain weeks of the fruiting cycle. The greater photosynthetic efficiency of the leaves of fruiting plants may have compensated, in part, for the greater leaf area of the deb-

lossomed plants. However, on a whole plant basis, Pn was still higher for deblossomed plants since the increased efficiency was not great enough to offset the greater leaf area of the deblossomed plants.

Hoffmann and Lenz (7) reported that leaves of deblossomed strawberry plants had higher starch and soluble carbohydrate contents than those of fruiting plants. Lenz and Bunemann (9) observed that dry matter accumulation in the vegetative organs of strawberry plants decreased with increasing fruit numbers. They did not find any differences, however, in total plant dry weight between fruiting and deblossomed plants. In this study, no differences were detected in dry matter accumulation or TNSC in the crown and roots between fruiting and deblossomed plants. The leaves of the deblossomed plants, however, accumulated more dry matter and TNSC than leaves of the fruiting plants.

Olsen et al. (13) reported that a much smaller proportion of dry matter was partitioned to the leaves during fruiting than during plant establishment. This indicates that fruit are a strong sink for assimilates. Although TNSC were not extracted from the fruit in this study, strawberry fruit have been shown to be the primary sink for photosynthates (5). In the absence of a fruit sink, additional assimilates accumulated in the leaves, resulting in a greater leaf dry

weight and leaf area for deblossomed plants (13, 15). Pn was not highly correlated with total plant dry weight or TNSC during the first 2 weeks of the fruiting cycle. This was presumably because the plants had sufficient carbohydrates stored at that time to sustain growth.

The leaves of both fruiting and deblossomed plants had the highest percentage of TNSC of any plant tissue. During the fourth week of the fruiting cycle, there was a decline in the percentage of TNSC in the leaves of both fruiting and deblossomed plants. During this same week, the percentage of TNSC in the crown of the deblossomed plants increased, presumably because carbohydrates were mobilized from the leaves to the crown. Leaf primordia originate from the crown of strawberry plants (2). Therefore, carbohydrates translocated from the leaves to the crown of the deblossomed plants, may have provided energy for the formation of new leaves. The greater leaf area of the deblossomed plants, beginning the fourth week supports this hypothesis. In the fruiting plants, the percentage of TNSC in the crown did not increase during the third week of the fruiting cycle, although the percentage of TNSC in the leaves decreased at that time. TNSC in the leaves of the fruiting plants may have been mobilized to the maturing fruit during the third week of the fruiting cycle.

Mann (12) observed that decreased strawberry root dry weight and carbohydrate content coincided with increased leaf growth. Thus, carbohydrates may have been mobilized from the roots to the developing leaves. Long (11), reported that carbohydrate reserves in the roots and stems of strawberry plants are drawn upon heavily by the developing fruit. In this study, the percentage of TNSC in the roots of both fruiting and deblossomed plants decreased during the third week of the fruiting cycle. This may have been due to a mobilization of TNSC from the roots to the crown of the deblossomed plants and to the fruit of the fruiting plants.

In conclusion, fruit removal altered the distribution of assimilates in day-neutral strawberry plants as shown by an increase in leaf area of the deblossomed plants, resulting in higher Pn rates on a whole plant basis. Since Pn was highly correlated with plant dry weight, plant growth and subsequent productivity may be increased by manipulating the ratio of vegetative to reproductive growth during the time of plant establishment.

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Chapter V

FINAL DISCUSSION

Removal of the fruit from day-neutral strawberry plants caused additional photosynthates to be partitioned to the developing leaves. This resulted in a greater leaf area for deblossomed plants than fruiting plants. Due largely to the greater leaf area, deblossomed plants had higher rates of net photosynthesis (Pn) on a whole-plant basis.

For fruiting plants, individual leaves which developed during fruit maturation were more photosynthetically efficient than those of deblossomed plants at the same stage of development. Specific leaf weight (SLW) was higher for deblossomed plants. The higher SLW for deblossomed plants may have been due to structural components such as increased mesophyll cell size or due to non-structural components such as an accumulation of carbohydrates in the leaves. Since SLW in deblossomed plants was higher for both young leaves and old leaves, it appears that the increased SLW of deblossomed plants was due to an accumulation of carbohydrates in the leaves since it is unlikely that older leaves would produce additional structural material. In future studies, it would be beneficial to look at the anatomy of leaves of plants in each treatment as well as the individual carbohy-

drate components since SLW seems to be too inclusive. The accumulation of carbohydrates in the leaves of deblossomed plants may have suppressed P_n by increasing mesophyll resistance or decreasing light penetration into the chloroplast.

The higher photosynthetic efficiency of the leaves of fruiting plants may have compensated, in part, for the greater leaf area of the deblossomed plants, thus allowing additional photosynthates to be produced and partitioned to the fruit. This higher P_n rate (leaf area basis) for fruiting plants was not enough, however, to equal P_n on a whole-plant basis for the deblossomed plants.

Day-neutral strawberry plants were an ideal model system for testing the effects of fruiting on several physiological parameters. Because of their ability to fruit successively in approximately six-week cycles regardless of photoperiod, it was possible to collect a great deal of data in a relatively short period of time. Since day-neutral cultivars have come on the market fairly recently, information from our study may ultimately allow growers to manipulate these plants to obtain higher yields. The additional leaf area and greater P_n rates obtained by deblossoming these plants during the first fruiting cycle may result in increased yields during subsequent fruiting cycle. Therefore, the effect of deblossoming on subsequent yields should be investigated.

Most commercially grown strawberries are Junebearing cultivars. Junebearing plants responded similarly to day-neutral plants for many of the parameters measured. Therefore much of the information obtained for day-neutral strawberries may be applied to Junebearing cultivars.

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