EFFECTS OF DEFOLIATION ON THE CULTIVATED STRAWBERRY (*Fragaria* X *ananassa* Duch.)

by

Karen Leigh Kerkhoff

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Horticulture

APPROVED:

Jerry M. Williams, Chairman

John A. Barden

John R. Seiler

August, 1987
Blacksburg, Virginia

EFFECTS OF DEFOLIATION ON THE CULTIVATED STRAWBERRY (*Fragaria* X *ananassa* Duch.)

by

Karen Leigh Kerkhoff

Committee Chairman: Jerry M. Williams

Horticulture

(ABSTRACT)

Using 'Redchief' (Junebearer) and 'Tribute' (day-neutral) cultivars, greenhouse and field studies were conducted to determine the effects of defoliation on photosynthesis, growth and yield of the strawberry. From preliminary photosynthesis experiments it was found that both 'Redchief' and 'Tribute' strawberry leaves reached maximum net photosynthesis (Pn) concurrently with full leaf expansion at approximately 8 to 10 days and 4 to 5 days, respectively, after unfolding. By exposing the plants to increasing irradiance it was determined that these cultivars were light saturated at 600 to 700 $\mu mol \cdot m^{-2}s^{-1}$. Neither cultivar showed a consistent diurnal pattern when Pn was monitored hourly over two consecutive days.

In the greenhouse, strawberry plants showed only a slight Pn response to defoliation over 48 hours. The overall defoliation and time effects were significant for both

cultivars, however, analyses at each time Pn was measured showed no real change in Pn that could be attributed to defoliation during the 48 hour period. Pn of both cultivars tended to increase with increasing degree of defoliation over 15 days after treatment. In 'Tribute', the 33 and 66% defoliation treatments increased Pn rates 20 and 35%, respectively, over the control, after 8 days. Pn rates increased after 4 days in defoliated 'Redchief' plants, and were maintained throughout the experimental period. After 12 days, the 66 and 82% defoliation treatment leaves had peak Pn rates 50 and 95% greater than the control, respectively. Specific leaf weight of the new leaves of both cultivars decreased with increasing degree of defoliation.

'Redchief' plants were defoliated in the field during August, September or October. Defoliation reduced total flower number, fruit number, fruit weight and spring vegetative growth the following year. However, reductions were not proportional to degree of defoliation as 100% defoliation reduced flower number by only 35%. Weight per berry increased with increasing degree of defoliation. Plants defoliated in October produced the largest berries, but produced the fewest total flowers, fruit and had the lowest fruit weight and spring vegetative growth.

This thesis is dedicated to my mother

who continues to give freely of herself
for the success of her children.

ACKNOWLEDGEMENTS

Sincere appreciation is expressed to all individuals who made this project a success. I would like first to thank my advisor, Jerry M. Williams for his support and assistance with all aspects of this study. I would also like to thank committee members John R. Seiler, who is an excellent instructor and an exceptional researcher and John A. Barden, who offered not only his expertise on photosynthesis but also his patience, understanding and friendship.

Many thanks go to the greenhouse crew, especially to , who endured the heat of the greenhouse and supplemental lighting for the sake of science. Thanks also to and his rough and ready farm crew. They were helpful beyond the call of duty. Thanks also to all those who helped take Pn measurements and pick strawberries.

Many thanks are extended to and for their help and patience during my stay here. There aren't enough words to truly express my thanks to . I don't know anyone who knows the ins and outs of statistics and computers and who understands the plight of the graduate student as she does.

A very special thanks and appreciation go to my fellow Graduate students; especially to , who always has a kind word and who is going to be a very successfull reseacher, to , who talks as much as

I do and never stops smiling - It's been great!, to

who is one of the most unselfish and kind people I know, and to , who provided motivation with one line - "Just do it!".

But most of all, I thank my best friend and husband

for his emotional support and understanding and because he never stopped believing in me.

TABLE OF CONTENTS

	Page
Introduction	1
Chapter I: Literature Review	3
Effects of Defoliation on Growth and Yield	3
Effects of Defoliation on Photosynthesis	8
Literature Cited	11
Chapter II: Preliminary Photosynthesis Studies on the Strawberry	14
Abstract	14
Introduction	15
Materials and Methods	16
Results and Discussion	19
Literature Cited	25
Chapter III: Effects of Defoliation on Photosynthesis and Growth of Strawberry.	27
Abstract	27
Introduction	29
Materials and Methods	30
Results and Discussion	34
Literature Cited	43

Table of Contents (continued)

Page

Chapter IV: Effects of Defoliation on Growth and Yield of Strawberry 45

Abstract 45

Introduction 47

Materials and Methods 49

Results and Discussion 51

Literature Cited 56

Chapter V: Final Discussion 57

Appendix

Effects of defoliation on net photosynthesis as monitored over six weeks 60

Vita 62

LIST OF FIGURES

Figure Page

Chapter II

1. Net photosynthesis (Pn) (leaf area basis) in response to aging in 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 5 leaves for 'Tribute' and 10 leaves for 'Redchief'. 20

2. Light saturation curves for leaves (approximately 12 days old) of 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 4 plants. 22

3. Net photosynthesis (Pn) (leaf area basis) as measured hourly on leaves (approximately 12 days old) of 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 7 plants 24

Chapter III

1. Defoliation treatments showing leaf surface area removed from each leaf per plant 31

2. Net photosynthesis (Pn) (leaf area basis), as measured on leaves, 12 days after unfolding, over 48 hours after partial defoliation of 'Tribute' and 'Redchief' strawberry plants. Treatment (%) represents surface area removed per leaf. L and Q represent significant linear or quadratic relationships, respectively, at the 1% (***), 5% (**) or 10% (*) level. Each datum is the mean of 7 plants. 35

3. Net photosynthesis (Pn) (leaf area basis), as measured on leaves, 12 days after unfolding, over 15 days after partial defoliation of 'Tribute' and 'Redchief' strawberry plants. Treatment (%) represents surface area removed per leaf. L and Q represent significant linear or quadratic relationships, respectively, at the 1% (**) or 5% (*) level. Each datum is the mean of 7 plants. 36

LIST OF TABLES

Table Page

Chapter III

1. Effects of defoliation on new growth harvested 15 days after treatment of 'Tribute' strawberry plants. Means of total area, area per leaf, total dry weight, dry weight per leaf, new leaves per plant and specific leaf weight. L represents a significant linear relationship at the 10% (*) level and NSR = no significant regression. 38

2. Effects of defoliation on new growth harvested 15 days after treatment of 'Redchief' strawberry plants. Means of total area, area per leaf, total dry weight, dry weight per leaf, new leaves per plant and specific leaf weight. L represents a significant linear relationship at the 1% (***) or 5% (**) level and NSR = no significant regression. 40

Chapter IV

1. Total flower number, fruit number, fruit weight, weight per berry and dry weight of the foliage produced in the spring as affected by degree of defoliation and time of defoliation on 'Redchief' strawberry plants. L represents a significant linear relationship at the 1% (**) or 5% (*) level 52

INTRODUCTION

Insect and disease pests, adverse weather conditions and certain environmental stresses can all contribute to the defoliation of horticultural crops in the field. Loss of leaf area can adversely affect the physiology of the plant. Yet, in some horticultural crops defoliation or defoliation-like practices are an integral part of their commercial production (3,5,8,9,14,16,18,20,25,28). Justifications for these practices include ease of harvest, reduction of water stress, elimination of host plants for pests during non-productive periods, control of plant vigor, increased light penetration, and renovation. Though potentially beneficial, these practices may still prove detrimental to the plant as a whole. The threshold by which certain growth and physiological parameters are affected by leaf area loss have been determined in a broad range of annual and woody perennial plants (11,19,28,29). However, there is little information available on the impact of leaf area loss on herbaceous perennials produced in the horticulture industry.

The cultivated strawberry (Fragaria X ananassa Duch.) is an herbaceous perennial which has wide adaptability to a variety of soil and climatic conditions. As a result, different cultural practices are implemented depending on where the crop is produced. In the eastern United States,

strawberries are generally planted in the spring and allowed to produce runners freely but are not permitted to bear fruit during the first year. Fruiting is prevented by removing inflorescences as they emerge. This practice encourages vegetative growth during the first year which in turn enhances fruiting the following year.

The objective of these studies was to determine the effects of defoliation on strawberry. Firstly, to monitor the responses of photosynthesis and regrowth after defoliation. Secondly, to determine the effects of defoliation imposed during the year of planting during flower bud initiation, on yield and subsequent growth.

Chapter I

LITERATURE REVIEW

EFFECTS OF DEFOLIATION ON GROWTH AND YIELD

As early as 1929, scientists studied the effects of defoliation on horticultural crops. van Graan (23) examined defoliation performed at transplanting to eliminate water stress on tomato, celery and cabbage. He found a reduction in total yield for tomato and cabbage even though cabbage showed an increase in earliness. Celery showed only a slight increase in yield indicating that there was no advantage to topping any of these crops at transplanting.

In 1930, Hoffman (9) defoliated greenhouse-grown tomatoes by removing 0, 50 or 100% of the leaf area. He found yield reductions of up to 35% in the treated plants, manifested by both a loss in fruit number and weight with later treatments showing the greatest reductions. More recently, Aung and Kelly (3) observed different responses to defoliation between determinate and indeterminate type tomatoes. In the determinate cultivar, removal of leaves reduced fruit number and total yield slightly but in the indeterminate type, defoliation induced slightly greater yield. Indeterminate plants produced more flowers with defoliation

resulting in the increased yield, which they speculate was due to more assimilates available for continued growth. Wolk et al. (28) defoliated tomato plants at transplanting or at various stages of flower and fruit development and to varying degrees. Treatment at transplanting reduced yield, but not in proportion to degree of defoliation; only the 80% defoliated plants showed a significant loss in yield. Defoliation did not affect fruit size but decreased fruit number, indicating a reduction in either flower numbers or fruit set. Leaf regrowth varied depending on the stage when treated but generally declined as defoliation was delayed. Stacey (19) defoliated tomato plants to simulate insect damage. He speculated that tomato plants could tolerate up to 25% leaf damage without affecting yield.

Peet and Kramer (15) found that 63% defoliated soybean plants produced 37% less total seed weight per plant, due primarily to a decrease in seed number. When Pimpini (16) defoliated zucchini, he observed a negative effect on all vegetative and reproductive plant characteristics. In geranium, defoliation reduced all parameters measured including inflorescence number, number of leaves per shoot, leaf area per plant and dry weight (27).

Research on root crops has been undertaken to simulate damage from insect pests and water stress. In sugar beet experiments carried out by Jones, Dunning and Humphries (11), little loss of crop resulted until 50% of the leaf

area had been removed, regardless of time of defoliation. In general, only complete defoliation significantly reduced yield with 30% less roots harvested (11). Similar results were seen by French and Humphries (7) and by Taylor and Bardner (21) in both sugar beet and turnip. The radish plant, on the other hand, was not as resilient as sugar beet and turnip, probably due to its relatively short growing season. At 16, 21, 26 or 31 days after sowing, Jackson (10) defoliated radish plants by 0, 25, 50 or 100%. He found that as degree of defoliation increased, final yield decreased with the greatest losses following the earliest treatment. These results substantiate work done by Taylor and Bardner in 1968 (21). The radish, produced in 4-6 weeks in summer conditions, apparently does not compensate for leaf area lost and therefore, leaf area duration plays an important role in the success of the harvest (10).

The effects of defoliation on tree fruit crops offers another area of interest. Their perennial nature and, in general, their process of flower bud initiation during the year prior to bloom parallels that of the Junebearing strawberry plant. Several studies have focused on the effects of defoliation on yield during the year of treatment, as well as the carry-over effects the following year. Avery et al. (4) partially defoliated apple trees continuously from fruit set to harvest. Though they saw an increase in photosynthesis of the remaining leaf area dur-

ing the year of treatment, the following year there was a marked reduction in yield. They speculated that this was due to defoliation effects on flower-bud formation during the previous season. In a study by Ferree and Palmer (5) on 'Golden Delicious' apple trees, 50% defoliation reduced yield by 30% and complete defoliation reduced yield by 80%. Studies on peach and pecan (13,18,29) have shown reductions in flower number, normal flower number, and regrowth with treatment at or near the time of flower bud initiation. In pecan, Worley (29) found that defoliation prior to October 1 resulted in no yield at all during the next two seasons. He speculated that the regrowth utilized the reserves that could have been used in the production of vigorous fruiting shoots the following year.

There is limited information available on the effects of defoliation on subsequent growth and yield of strawberry. The majority of studies have focused on post-harvest defoliation, which is a common commercial cultural practice in the eastern United States. It is used for sanitation and renovation purposes. Such leaf removal resulted in no detrimental effects but rather enhanced vigor of the plants and increased yield the following year (6,8,12,22,25). Moreover, top removal reduces water stress and decreases pest populations by temporarily eliminating the foliage.

There have been a few pre-harvest defoliation studies

on strawberries, to date. In Florida, Albregts and Howard (1) used defoliation to simulate desiccation at transplanting. In their study, defoliation retarded growth and reduced yield. During the first year, controls were always larger than treated plants, but in the second year differences were not as apparent. The controls produced more marketable fruit earlier than treated plants. Puffer et al. (17), defoliated strawberry plants at digging from the nursery and before transplanting into a production system. They found that the defoliated plants produced more fruit than plants with their leaves intact. Their study took place in California using a cultivar recommended for the area. The different response to defoliation in the two studies was explained by Albregts and Howard (1) as the result of the presence or absence of starch reserves. Strawberries propagated in California have starch reserves and those grown in Florida do not (1).

EFFECTS OF DEFOLIATION ON PHOTOSYNTHESIS

Reports on several crops, ranging from herbaceous annuals and perennials to tree fruits, indicate that partial defoliation stimulates the photosynthetic rate of the remaining leaves, thereby compensating somewhat for those leaves lost (2,3,4,14,15,18,20,26,28).

In greenhouse grown tomatoes, defoliation was used originally to reduce disease incidence and thereby increase yield (9), but the effects of defoliation are more varied. Aung and Kelly (3) found that defoliation increased the net assimilation rate in the remaining leaves in both determinate and indeterminate type tomatoes, indicating a possible increase in net photosynthesis (Pn). Wolk et al. (28) defoliated tomato plants by 25, 50 or 80% and measured Pn on the remaining leaves. They found that Pn increased as the degree of defoliation increased. This response was apparent at 4 days after treatment with a 40% increase in Pn. The higher Pn rates persisted in varying degrees through 14 days when the 80% defoliated plants had a 54% greater Pn per leaf area than comparable leaves on the controls.

Wareing et al. (26), performed a series of partial defoliation experiments with *Phaseolus vulgaris* L., *Zea mays*, and *Salix* spp. In all cases there was an increase in Pn with defoliation alone, but when the tops and the roots

were pruned simultaneously, there was no change in Pn. A more drastic form of defoliation was inflicted on P. vulgaris L. 'Canadian Wonder' when Alderfer and Eagles (2) removed all leaves as they emerged except the first trifoliate leaf. The remaining leaf responded with increased Pn rates sustained throughout the 46 day study accompanied by a larger final leaflet area, when compared to the controls. These results were substantiated by von Caemmerer and Farquhar (24) with a similar defoliation treatment which led to an increase in Pn within 2-3 days along with a slower decline in Pn with aging.

With a determinate-type soybean, Peet and Kramer (15) found that shading side leaflets increased Pn rates of the unshaded center leaflet as long as the side leaflets were covered. Pn declined within 2 days after the leaflets were uncovered. The 37% remaining, unshaded leaf area had Pn rates 25% greater than the control for the first 10 days after shading and 56% greater Pn for the second 10 days.

In apple and peach orchards, summer pruning is a practice performed to increase light penetration into the canopy which in turn may improve fruit quality. Rom and Ferree (18) observed that Pn increased in leaves of pruned peach trees but leaf number, size, area per tree and specific leaf weight were reduced, with effects increasing as pruning was delayed. Marini and Barden (14) studied the effects of time of summer pruning of apple trees. Treat-

ments included early-summer pruning while shoots were actively growing and/or late-summer pruning after shoot extension had ceased. Net photosynthesis (leaf area basis) of the early pruned plants was generally greater than the controls for approximately 6 weeks after treatment. Late-summer pruning seemed to slow the natural decline of Pn that occurred with leaf aging though there was no direct increase in Pn. Other studies support these findings even though there were variations in the actual method of defoliation or damage (4,5,20). In general, when observing Pn on a leaf area basis, there was an increase over the controls. When Pn was expressed on a whole plant basis the decrease in Pn was never as great as the percent leaf area lost. This suggests an increase in Pn of the remaining leaf area.

Wareing et al. (26) suggested that the increased Pn rates are due to increased chlorophyll or plastid protein content, or increased relative demand on the remaining leaves. Marini and Barden (14) suggested that modification of the source-sink ratio and/or altered levels of growth regulators may be responsible for the increased Pn. Avery et al. (4) suggested that the response is due to reduced competition for metabolites supplied by the roots creating an imbalance which is manifested, at least in part, in the remaining leaf area.

LITERATURE CITED

1. Albregts, E.E. and C.M. Howard. 1972. Influence of defoliation at transplanting on strawberry growth and fruiting response. HortScience 7:569-570.

2. Alderfer, R.G. and C.F. Eagles. 1976. The effect of partial defoliation on the growth and photosynthetic efficiency of bean leaves. Bot. Gaz. 137:351-355.

3. Aung, L.H. and W.C. Kelly. 1966. Influence of defoliation on vegetative, floral and fruit development in tomatoes (Lycopersicon esculentum Mill.). J. Amer. Soc. Hort. Sci. 89:563-570.

4. Avery, D.J., C.A. Priestley, and K.J. Treharne. 1979. Integration of assimilation and carbohydrate utilization in apple. In: R. Marcelle, H. Clijsters, and M. Van Poucke (eds.) Photosynthesis and plant development. Junk, The Hague. The Netherlands. p.221-231.

5. Ferree, D.C. and J.W. Palmer. 1982. Effect of spur defoliation and ringing during bloom on fruiting, fruit mineral level, and net photosynthesis of 'Golden Delicious' apple. J. Amer. Soc. Hort. Sci. 107:1182-1186.

6. Fiedler, W. 1979. EinfluB der defoliation unmittelbar zur Ernte auf verschiedene vegetative und generative Merkmale von Erdbeerpflanzen. (Influence of defoliation immediately during harvest time on different vegetative and generative characteristics of strawberry plants.) Archiv fur Gartenbau 27:369-375.

7. French, S.A.W. and E.C. Humphries. 1977. The effect of partial defoliation on yield of sugar beet. Ann. Applied Biol. 87:201-212.

8. Guttridge, C.G. and C.A. Wood. 1961. Defoliation of strawberry plants. Scott. Agr. 41:39-42.

9. Hoffman, I.C. 1930. The effect of leaf pruning upon the yield of greenhouse tomatoes. Proc. Amer. Soc. Hort. Sci. 27:360-362.

10. Jackson, T.A. 1980. The effect of defoliation on yield of radish. Ann. Applied Biol. 94:415-419.

11. Jones, F.G.W., R.A. Dunning and K.P. Humphries. 1955. The effects of defoliation and loss of stand upon yield of sugar beet. Ann. Applied Biol. 43:63-70.

12. Kramer, S., G. Thomas, and R. Benne. 1977. Untersuchungen zur Defoliation bei Erdbeeren. II. EinfluB der Defoliation in Abhangigkeit vom Alter der Bestande auf Ertrag und mittlere Einzelfruchtmasse. (Investigations into the defoliation of strawberry. II. The effect of defoliation on crop yields and average single fruit weight in dependence on the age of the stand.) Archiv fur Gartenbau 25:135-139.

13. Lloyd, D.A. and G.A. Couvillon. 1974. Effects of date of defoliation on flower and leaf bud development in the peach (Prunus persica (L.)). J. Amer. Soc. Hort. Sci. 99:514-517.

14. Marini, R.P. and J.A. Barden. 1982. Net photosynthesis, dark respiration, transpiration, and stomatal resistance of young and mature apple trees as influenced by summer or dormant pruning. J. Amer. Soc. Hort. Sci. 107:170-174.

15. Peet, M.M. and P.J. Kramer. 1980. Effects of decreasing source/sink ratio in soybeans on photosynthesis, photorespiration, transpiration and yield. Plant, Cell and Env. 3:201-206.

16. Pimpini, F. 1983. Effects of variety, plant density and defoliation on zucchini (Cucurbita pepo L.) grown under tunnel for delayed production. Gartenbauwissenschaft 48:5-8.

17. Puffer, R.E., V. Voth, H.J. Bowen, Jr. and R.H. Gupp. 1968. Effects of alar and top removal on yield of Fresno strawberries at three digging dates. Calif. Agr. 22:11-13.

18. Rom, C.R. and D.C. Ferree. 1985. Time and severity of summer pruning influences on young peach tree net photosynthesis, transpiration, and dry weight distribution. J. Amer. Soc. Hort. Sci. 110:455-461.

19. Stacey, D.L. 1983. The effect of artificial defoliation on the yield of tomato plants and its relevance to pest damage. J. Hort. Sci. 58:117-120.

20. Taylor, B.H. and D.C. Ferree. 1981. The influence of summer pruning on photosynthesis, transpiration, leaf abscission, and dry weight accumulation of young apple trees. J. Amer. Soc. Hort. Sci. 106:389-393.

21. Taylor, W.E. and R. Bardner. 1968. Effects of feeding by larvae of Phaedon cochleariae (F.) and Plutella maculipennis (Curt.) on the yield of radish and turnip plants. Ann. Applied Biol. 62:249-254.

22. Thomas, G., R. Benne, and S. Kramer. 1977. Untersuchungen zur Defoliation bei Erdbeeren. III. EinfluB von Defoliation und Wurzelschnitt auf Ertrag und mittlere Einzelfruchtmasse. (Investigations on the defoliation of strawberry. III. The effect of defoliation and root pruning on crop yields and average single fruit weight) Archiv fur Gartenbau 25:147-158.

23. van Graan, L. R. 1929. The effect of early defoliation of vegetable plants on subsequent growth and production. Proc. Amer. Soc. Hort. Sci. 26:109-113.

24. von Caemmerer, S. and G.D. Farquhar. 1984. Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of Phaseolus vulgaris L. Planta 160:320-329.

25. Waldo, G.F. 1939. Effect of leaf removal and crown covering on the strawberry plant. Proc. Amer. Soc. Hort. Sci. 37:548-552.

26. Wareing, P.F., M.M. Khalifa and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.

27. Welander, N.T. 1984. Effect of GA_3, CCC, defoliation and quantum flux density on growth and flowering in Pelargonium x hortorum. Scientia Hort. 23:371-377.

28. Wolk, J.O., D.W. Kretchman and D.G. Ortega, Jr. 1983. Response of tomato to defoliation. J. Amer. Soc. Hort. Sci. 108:536-540.

29. Worley, R.E. 1979. Pecan yield, quality, nutlet set and spring growth as a response to time of fall defoliation. J. Amer. Soc. Hort. Sci. 104:192-194.

Chapter II

PRELIMINARY PHOTOSYNTHESIS STUDIES ON THE STRAWBERRY

ABSTRACT

The effects of leaf aging, irradiance, and time of day on net photosynthesis (Pn) of 'Tribute' (day-neutral) and 'Redchief' (Junebearer) strawberries were examined in greenhouse experiments. In both cultivars, maximum Pn coincided with full leaf expansion. In 'Tribute' and 'Redchief' this occurred at 4 to 5 days and 8 to 10 days, respectively, after the leaves were unfolded. Pn gradually decreased for 5 weeks thereafter. Light saturation curves showed both cultivars attaining maximum Pn at 600-700 μmol $m^{-2}s^{-1}$. There was no significant difference in area or Pn between leaflets of a single leaf. Hourly Pn measurements taken from 8:00 a.m. to 5:00 p.m. on two consecutive days showed no obvious diurnal pattern nor direct response to the environmental parameters monitored, including temperature, relative humidity or the combination of the two.

INTRODUCTION

In 1935, Singh and Lal (12) stated that "as morphological and physiological changes take place with the development of the plant, so parallel changes in the internal complex of the photosynthetic machinery are but to be expected ...". This was the premise of their study on age-assimilation relationships in which they found that photosynthetic efficiency increased up to a certain leaf age after which time photosynthetic rates declined.

Junebearing and day-neutral strawberry cultivars were chosen for these studies. Junebearing plants require short-day conditions to initiate flower buds, whereas day-neutral plants can initiate and develop flower buds under any daylength (2). Under appropriate environmental conditions, day-neutral plants can produce fruit approximately 3 months after planting (2).

Because there is limited information available on the photosynthetic behavior of the cultivated strawberry (*Fragaria* X *ananassa* Duch.), a series of experiments was carried out to provide a basic working knowledge of the photosynthetic peculiarities of this plant. In particular, the pattern of leaf aging, light saturation curves, the amount of variability between leaflets in terms of area and net photosynthesis (Pn) and the Pn pattern throughout the course of a day were examined.

MATERIALS AND METHODS

General. Dormant plants of 'Tribute' (day-neutral) were planted on April 2, 1986 in 15 cm plastic pots containing Promix BX artificial soil mix. Dormant plants of 'Redchief' (Junebearer) were treated in the same manner on May 24, 1986. All plants were placed in a fan-and-pad cooled glasshouse under natural light conditions and fertilized weekly with 240 ppm N from a 20N-8.7P-16.6K soluble fertilizer in the irrigation water. To reduce confounding factors, runners and flowers were pinched off as they emerged. Pn was monitored using an Infrared Carbon Dioxide Analyzer LCA-2 equipped with a Parkinson Leaf Chamber (The Analytical Developmental Co. Ltd.; Herts, England), and was reported on a per unit leaf area basis. The air flow rate through the leaf chamber was approximately 400 ml min^{-1}. All studies, except Pn response to changing irradiance, were carried out in the glasshouse. Temperature in the leaf chamber and photosynthetic photon flux density (PPFD) were also measured. Supplemental lighting was provided by 1000 Watt High Pressure Sodium Vapor lamps.

Pn response to leaf aging. Five plants of each cultivar were chosen at random. To insure uniform age, the most recently emerged leaf on each plant was tagged and was subsequently used for all Pn measurements. Pn measurements began when the leaf was unfolded and were continued every

third day for 7 weeks. The tagged leaves on 'Redchief' plants began to senesce before the end of the experiment, therefore a new leaf on each of these plants was tagged as needed and the Pn of this new leaf was measured over an equal amount of time. PPFD during the Pn measurements averaged 605 μmol $m^{-2}s^{-1}$ $\pm$10.2 and temperatures in the leaf chamber averaged 27.7 °C $\pm$ 0.14. The area of each leaflet was also recorded at each Pn reading by multiplying the length-width product by 0.7 (15).

Pn response to changes in irradiance. Plants were grown in a glasshouse (covered with a shading compound), with PPFD averaging 1100 μmol $m^{-2}s^{-1}$. Four plants of each cultivar were chosen at random and the most recently emerged leaf per plant was tagged and used for all subsequent Pn measurements. On July 14, 1986, 12 days after unfolding, the plants were taken out of the greenhouse and exposed to clear, sunny conditions. The plants were subjected to various PPFD levels, ranging from 90 to 1680 μmol $m^{-2}s^{-1}$, using an increasing number of neutral screens to gradually decrease PPFD. Plants were allowed to equilibrate for an average of 5 minutes before each Pn determination was made. Temperature in the leaf chamber averaged 31.6 °C $\pm$0.13.

Leaflet variability. To determine leaflet variability, Pn was measured on each of the three leaflets per leaf using 5 leaves per plant and 4 plants per cultivar. The

area of each leaflet was measured using a Li-Cor Portable Area Meter Model LI-3000 (Li-Cor, inc.; Lincoln, Nebraska).

Diurnal Pn pattern. Dormant plants of 'Redchief' and 'Tribute' were potted on February 28, 1987 in 15 cm plastic pots containing Promix BX artificial soil mix. They were placed in a glasshouse under 4-hour-night interruption to simulate long-day conditions for promotion of vegetative growth (6). Seven plants of each cultivar were chosen at random and the most recently emerged leaf per plant was tagged and used for all subsequent Pn measurements. On April 21, 1987, 12 days after leaf unfolding, Pn was measured hourly from 8:00 a.m. until 5:00 p.m. This experiment was repeated on the same leaves the next day. PPFD ranged from 480 to 1735 μ mol $m^{-2}s^{-1}$ and temperature in the greenhouse ranged from 22.5 to 40.1 °C.

Data analysis. The relationships between leaf aging and Pn and between PPFD and Pn were determined using regression analysis from SAS Institute (11). Leaflet variability was assessed using Analysis of Variance from SAS Institute (11). Regression analysis using time as the regressor was used on the diurnal Pn data. This data was also subjected to forward, backward and stepwise model building procedures. Included in the model were PPFD, temperature, time, relative humidity, $PPFD^2$, and $temperature^2$, as well as log functions of Pn, temperature and PPFD.

RESULTS AND DISCUSSION

Pn response to leaf aging. 'Tribute' and 'Redchief' reached maximum Pn 4 to 5 days and 8 to 10 days, respectively, after the leaves were unfolded (Fig. 1). Full leaf expansion coincided with maximum Pn in both cultivars. 'Tribute then exhibited a gradual linear decline in Pn over the next 38 days. Pn rates of 'Redchief' exhibited a sharp decline after the initial 10 days, continuing over the next 28 days. The differing rates of decline may be due to differences in plant maturity at the onset of the experiment. 'Tribute' plants were approximately 7 weeks older than 'Redchief' plants, allowing them more time to become established. 'Redchief' plants had probably diminished their reserves and therefore, the leaves were supplying the majority of the energy needed for continued growth. All 'Tribute' leaves were tagged on the same day whereas 'Redchief' leaves, due to senescence, were not tagged on the same day. As a result, 'Redchief' leaves of the same age were measured on different days and, unavoidably, environmental conditions varied which possibly added to the differing response. The different responses may also have been due to cultivar effects.

The pattern of aging was similar to that found in Fragaria virginiana by Jurik et al. (7). They found that maximum Pn coincided with the completion of blade expansion

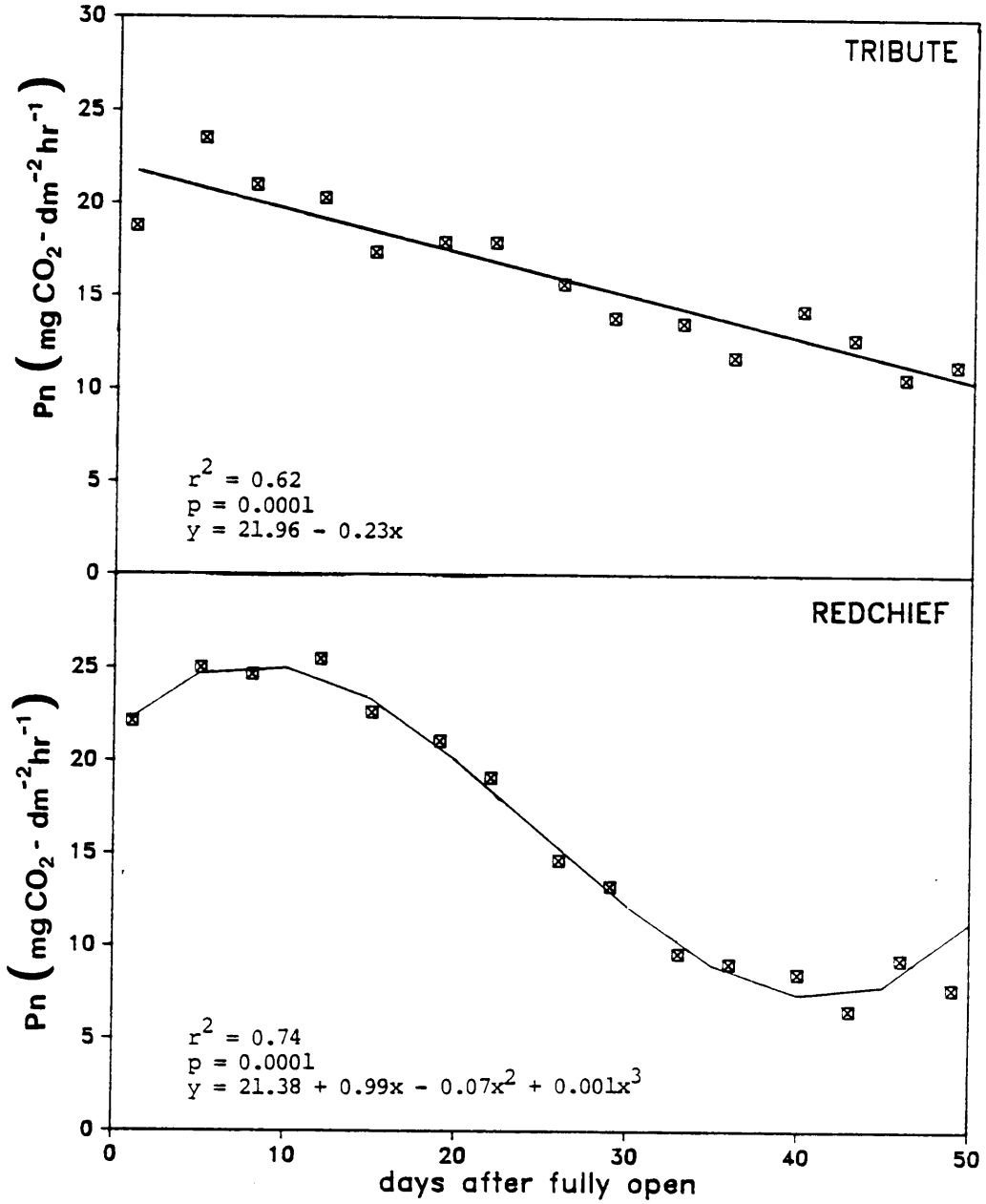

Figure 1. Net photosynthesis (Pn) (leaf area basis) in response to aging in 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 5 leaves for 'Tribute' and 10 leaves for 'Redchief'.

and declined quickly thereafter. This pattern of concurrent full leaf expansion and maximum Pn has also been observed in sour cherry (9), apple (1) and several species of legumes and grasses (3). However, Moss and Peaslee (8) found no differences in Pn of the same maize leaf measured 45 days apart. They attributed the unchanging Pn to adequate nutritional status, especially potassium nutrition.

Pn response to changes in irradiance. Although having different base rates, both cultivars were light saturated at 600-700 μmol $m^{-2}s^{-1}$ (Fig. 2). This is similar to the range seen by Sruamsiri and Lenz (13) using Fragaria X ananassa 'Bogota'. They found light saturation to be at approximately 50 klx (approx. 610 μmol $m^{-2}s^{-1}$ with Halogen-Metallide lamps as the light source) but conversions from photometric to quantum measurements are not equivalent for sources of different spectral content. Therefore such comparisons are not accurate (16). Chabot and Chabot (5) found Fragaria vesca to be saturated in the range of 400-600 μmol $m^{-2}s^{-1}$, regardless of preconditioning under various PPFD levels. They grew the strawberry plants under a maximum of 650 μmol $m^{-2}s^{-1}$, whereas in the present study, the plants were grown under an average of 1100 μmol $m^{-2}s^{-1}$ PPFD levels. Campbell and Young (4) found that, though not the only determining factor, preconditioning at various PPFD levels directly influenced Pn. Strawberry plants preconditioned at 800 μmol $m^{-2}s^{-1}$ approached saturation

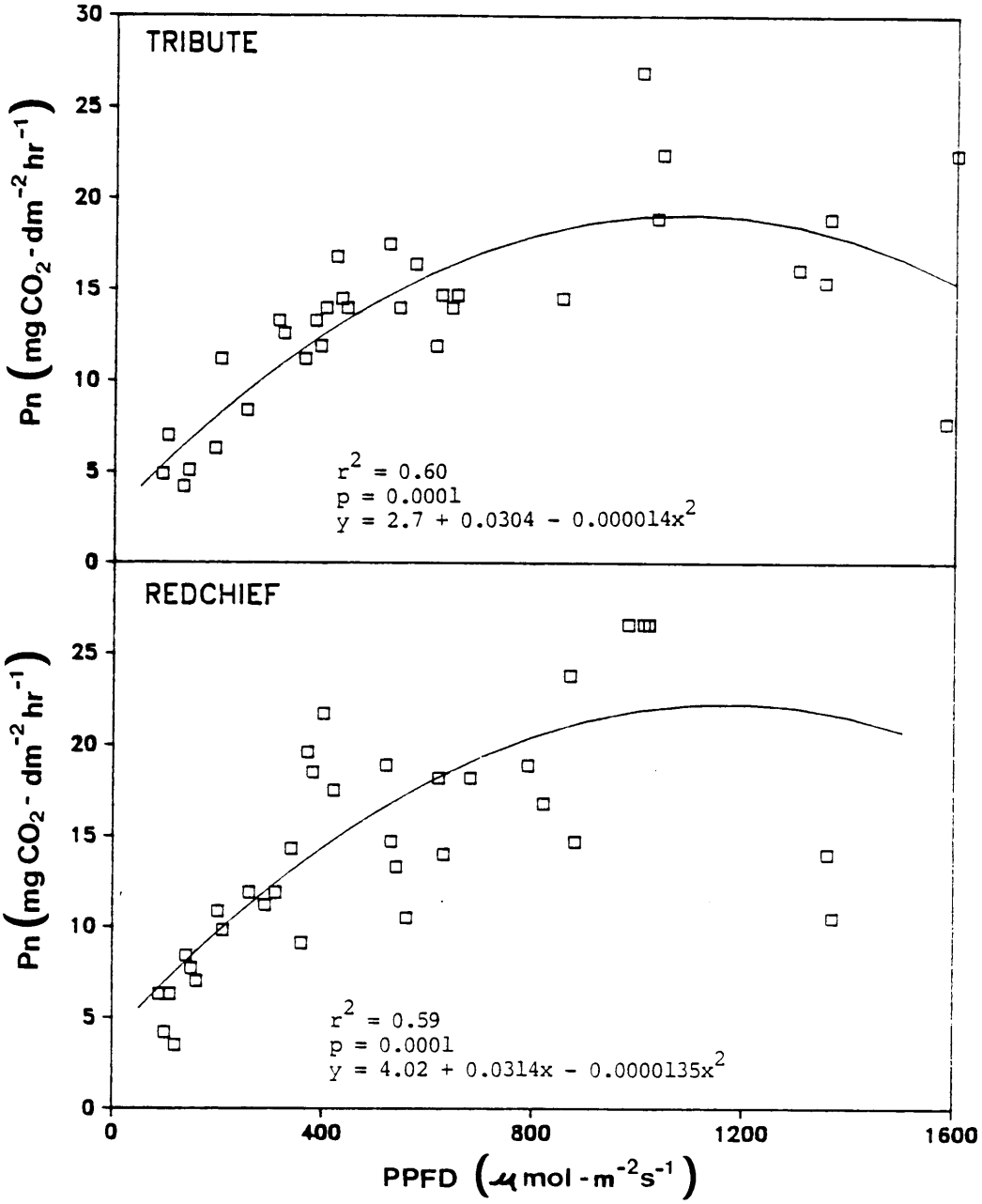

Figure 2. Light saturation curves for leaves (approximately 12 days old) of 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 4 plants.

between 600 and 800 μmol $m^{-2}s^{-1}$ (4).

Leaflet variability. There were no differences in area or Pn rates among individual leaflets of a single leaf. This suggested that Pn response to treatments would not be related to position of the leaflet and that Pn could be measured on any remaining leaflet and give similar results. Leaf area and consequently whole plant leaf area can be calculated from determining only a portion of the area of each leaf per plant.

Diurnal Pn pattern. There was no consistent diurnal Pn pattern apparent in either 'Tribute' or 'Redchief' for the two days (Fig. 3). Hourly responses could not be attributed to any single factor (time, temperature, relative humidity, PPFD) or combination of environmental factors. Some species do exhibit diurnal trends which can generally be attributed to changes in one or more environmental factors (10). Sruamsiri and Lenz (14) reported that the optimum temperature for Pn of strawberries was approximately 15 °C, but no Pn responses could be correlated directly with temperature in this particular study. Conditions on both days were nearly identical with a cloudless sky and temperatures in the greenhouse reaching 40 °C. There may have been too many confounding factors interacting with Pn which resulted in diurnal patterns that were masked or inhibited.

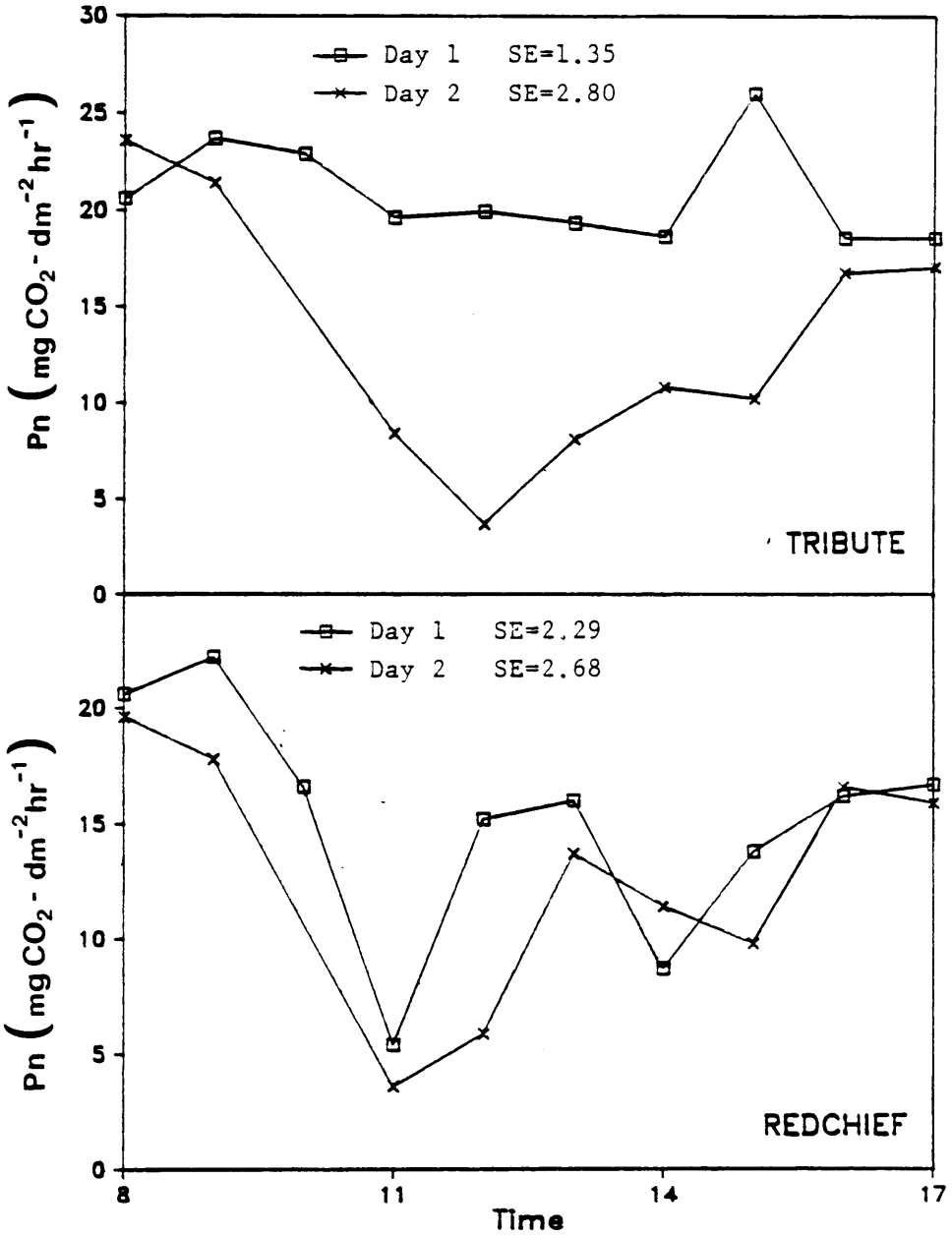

Figure 3. Net photosynthesis (Pn) (leaf area basis) as measured hourly on leaves (approximately 12 days old) of 'Tribute' and 'Redchief' strawberry plants. Each datum is the mean of 7 plants.

LITERATURE CITED

1. Barden, J.A. 1978. Apple leaves, their morphology and photosynthetic potential. HortScience 13:644-646.

2. Bringhurst, R.S. and V. Voth. 1980. Six new strawberry varieties released. Calif. Agr. 34:12-15.

3. Brown, R.H., R.B. Cooper and R.E. Blaser. 1966. Effects of leaf age on efficiency. Crop Sci. 6:206-209.

4. Campbell, D.E. and R. Young. 1986. Short-term CO_2 response to temperature, irradiance, and CO_2 concentration in strawberry. Photosyn. Res. 8:31-40.

5. Chabot, B.F. and J.F. Chabot. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in Fragaria vesca. Oecologia 26:363-377.

6. Durner, E.F., J.A. Barden, D.G. Himelrick, and E.B. Poling. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing, and everbearing strawberries. J. Amer. Soc. Hort. Sci. 109:396-400.

7. Jurik, T.W., J.F. Chabot and B.F. Chabot. 1979. Ontogeny of photosynthetic performance in Fragaria virginiana under changing light regimes. Plant Physiol. 63:542-547.

8. Moss, D.N. and D.E. Peaslee. 1965. Photosynthesis of maize leaves as affected by age and nutrient status. Crop Sci. 5:280-281.

9. Sams, C.E. and J.A. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

10. Sams, C.E. and J.A. Flore. 1983. Net photosynthetic rate of sour cherry (Prunus cerasus L. 'Montmorency') during the growing season with particular reference to fruiting. Photosyn. Res. 4:307-316.

11. SAS User's Guide: Statistics, Version 5. 1985. SAS Institute, Cary, N.C. 27511.

12. Singh, B.N. and K.N. Lal. 1935. Investigation of the effect of age on assimilation of leaves. Ann. Bot. (London) 49:291-306.

13. Sruamsiri, P. and F. Lenz. 1985. Photosynthese und stomatares Verhalten bei Erdbreen (Fragaria X ananassa Duch.). I. EinfluB von Licht. (Photosynthesis and stomatal behaviour of strawberries. I. Effect of light.) Gartenbauwissenschaft 50:78-83.

14. Sruamsiri, P. and F. Lenz. 1985. Photosynthese und stomatares Verhalten bei Erdbreen (Fragaria X ananassa Duch.) II. EinfluB der Temperatur. (Photosynthesis and stomatal behaviour of strawberries. II. Effect of temperature.) Gartenbauwissenschaft 50:84-87.

15. Strik, B.C. and J.T.A. Proctor. 1985. Estimating the area of trifoliolate and unequally imparipinnate leaves of strawberry. HortScience 20:1072-1074.

16. Thimijan, R.W. and R.D. Heins. 1983. Photometric, radiometric, and quantum light units of measure: A review of procedures for interconversion. HortScience 18:818-822.

Chapter III

EFFECTS OF DEFOLIATION ON PHOTOSYNTHESIS AND GROWTH OF STRAWBERRY

ABSTRACT

Greenhouse experiments were conducted to determine the effects of partial defoliation on net photosynthesis (Pn) of Fragaria X ananassa Duch. Nine week old 'Redchief' (Junebearer) and 'Tribute' (day-neutral) plants were defoliated by removing 0, 33, 66, or 82% of each leaf. In separate experiments, Pn was monitored over 48 hours after defoliation and over 15 days after defoliation.

In both cultivars, there were significant overall defoliation and time effects on Pn measured over 48 hours, with no significant interactions. However, regression analyses performed at each time Pn was measured showed no real change in Pn that could be attributed to the defoliation treatments.

Mid-morning Pn measurements taken over 15 days after defoliation showed significant overall defoliation and time effects for both cultivars, with no significant interactions. In 'Tribute', a trend of increased Pn occurred in the 33 and 66% defoliated plants with maximum rise in Pn of 20 and 35%, respectively, evident after 8 days. In 'Red-

chief', the 66 and 82% defoliated plants significantly increased Pn beginning at 4 days and Pn continued to increase for the duration of the study. Maximum increases occurred after 12 days, reflecting a 50 and 95% increase over the control in the 66 and 82% defoliation treatments, respectively. In both cultivars, average area per leaf, average dry weight per leaf and specific leaf weight of the new leaves declined with increasing degrees of defoliation.

INTRODUCTION

Leaf area loss or damage can have various effects on the physiology of the plant. In some plants leaf loss seems to trigger a compensatory response manifested as an increase in net photosynthesis (Pn) or delayed senescence of the remaining leaves (5,7,8,13,14,15). Wolk et al. (15) defoliated tomato plants by 25, 50 or 80% and measured Pn on the remaining leaves; Pn increased as the degree of defoliation increased. Hodgkinson (5) observed a rejuvenation effect as the Pn rates of middle-aged alfalfa leaves returned to rates of recently expanded leaves. In other crops, defoliation has debilitating effects as seen by Jackson when radishes were defoliated (6). He found significant reductions in total yield and new leaf area in all plants treated, regardless of time or degree of defoliation.

The objective of this study was to determine the effects of partial defoliation on strawberry, to be answered in 3 parts. Firstly, do strawberry plants respond to partial defoliation with an increase in Pn, as did many other crops examined? Secondly, if there is an increase in Pn, how soon after defoliation does this increase in Pn occur and to what extent? And, thirdly, what is the relationship between degree of defoliation and the possible change in Pn?

MATERIALS AND METHODS

General. All plants were potted in 15 cm plastic pots with Promix BX artificial soil mix. They were placed in a greenhouse and fertilized weekly with 240 ppm N from a 20N-8.7P-16.6K soluble fertilizer in the irrigation water. To insure uniform leaf age, after 5-6 weeks, the most recently emerged leaf on each plant was tagged and was subsequently used for all Pn measurements. Pn was monitored using an Infrared Carbon Dioxide Analyzer LCA-2 equipped with a Parkinson Leaf Chamber (The Analytical Developmental Co., Inc.; Herts, England), and is reported on a per unit leaf area basis. The air flow rate through the leaf chamber was approximately 400 ml min^{-1}. Also recorded were temperature in the leaf chamber and photosynthetic photon flux density (PPFD). Supplemental light was provided by 1000 Watt High Pressure Sodium Vapor Lamps. The experimental designs were randomized complete blocks with 7 replications.

Pn response over 48 hours. Dormant, bare-root plants of 'Redchief' (Junebearer) and 'Tribute' (day-neutral) were potted on February 28, 1987 and placed in a glasshouse under 4-hour night interruption to simulate long-day conditions (3,4). On April 23, 1987, 12 days after the tagged leaves were unfolded, plants were defoliated by removing 0, 33, 66, or 82% of each leaf (Fig.

Figure 1. Defoliation treatments showing surface area removed from each leaf per plant.

1). Treatments were performed at 7:00 a.m. Pn measurements were begun at 8:00 a.m. and were continued periodically over the next 48 hours. PPFD and temperature in the leaf chamber averaged 574 μmol $m^{-2}s^{-1}$ $\pm$3.46 and 26.2 °C$\pm$0.11.

Pn response over 15 days. 'Tribute' (day-neutral) plants were propagated as runners from mother plants held over in the greenhouse. These runners were rooted while still attached to the mother plants and were transplanted into 15 cm pots on June 7, 1986. 'Tribute' plants were grown in an open-ended plastic greenhouse until 12 days prior to treatment, at which time they were moved to the glass-house. Dormant, bare-root 'Redchief' (Junebearer) plants were potted on June 24, 1986. These plants were placed in a fan-and-pad cooled glasshouse (covered with a shading compound) under natural light conditions. On September 15, 1986, 12 days after the tagged leaves were unfolded, plants were defoliated by removing 0, 33, 66, or 82% of each leaf (Fig. 1). Mid-morning Pn measurements were made one day prior to treatment, on the day of treatment, and every other day for 15 days thereafter. PPFD and temperature in the chamber averaged 810 μmol $m^{-2}s^{-1}$ $\pm$ 7.6 and 28.6 °C $\pm$ 0.17. Leaf area removed was measured using a Licor Portable Area Meter Model LI-3000 (Li-Cor, Inc.; Lincoln, Nebraska); leaves were then oven-dried. Based on these data, initial plant size was esti-

mated. Upon termination of the experiment, new leaves produced after treatment were harvested and their area and dry weight were determined.

Data analysis. Because the photosynthesis measurements were not independent (same leaf per plant used for all measurements), repeated measures analysis of variance (10) was used to analyze the photosynthesis data for defoliation and time effects. Also, regression analysis was performed at each time photosynthesis was measured to determine when response to defoliation occurred. Regression analysis was also used to analyze the data on the new growth harvested in the 15 day study. Initial leaf number, initial leaf area and initial dry weight were used as covariates for this data.

RESULTS AND DISCUSSION

Pn response over 48 hours. Repeated measures analysis of variance (10) indicated overall significant defoliation and time effects with no significant interactions for both 'Tribute' and 'Redchief' (Fig. 2). However, analyses at each time Pn was measured showed that, in both cultivars, there were significant regressions at the onset of the study which continued throughout the 48 hours. This implied that there was no real change in Pn in response to defoliation during the period that Pn was monitored.

Pn response over 15 days. Repeated measures analysis of variance (10) indicated overall significant defoliation and time effects with no significant interactions for both cultivars. There were significant differences between cultivars, therefore, the two will be discussed separately. In 'Tribute', analyses performed at each time Pn was recorded showed significant quadratic regressions at 6 and 8 days after defoliation (Fig. 3). This translated into a 21% increase in Pn in the 66% defoliation treatment plants when compared to the controls at 6 days and 21 and 32% increase in the 33 and 66% defoliation treatment plants, respectively, at 8 days. The 82% defoliation treatment plants did not differ greatly from the controls for the duration of the study.

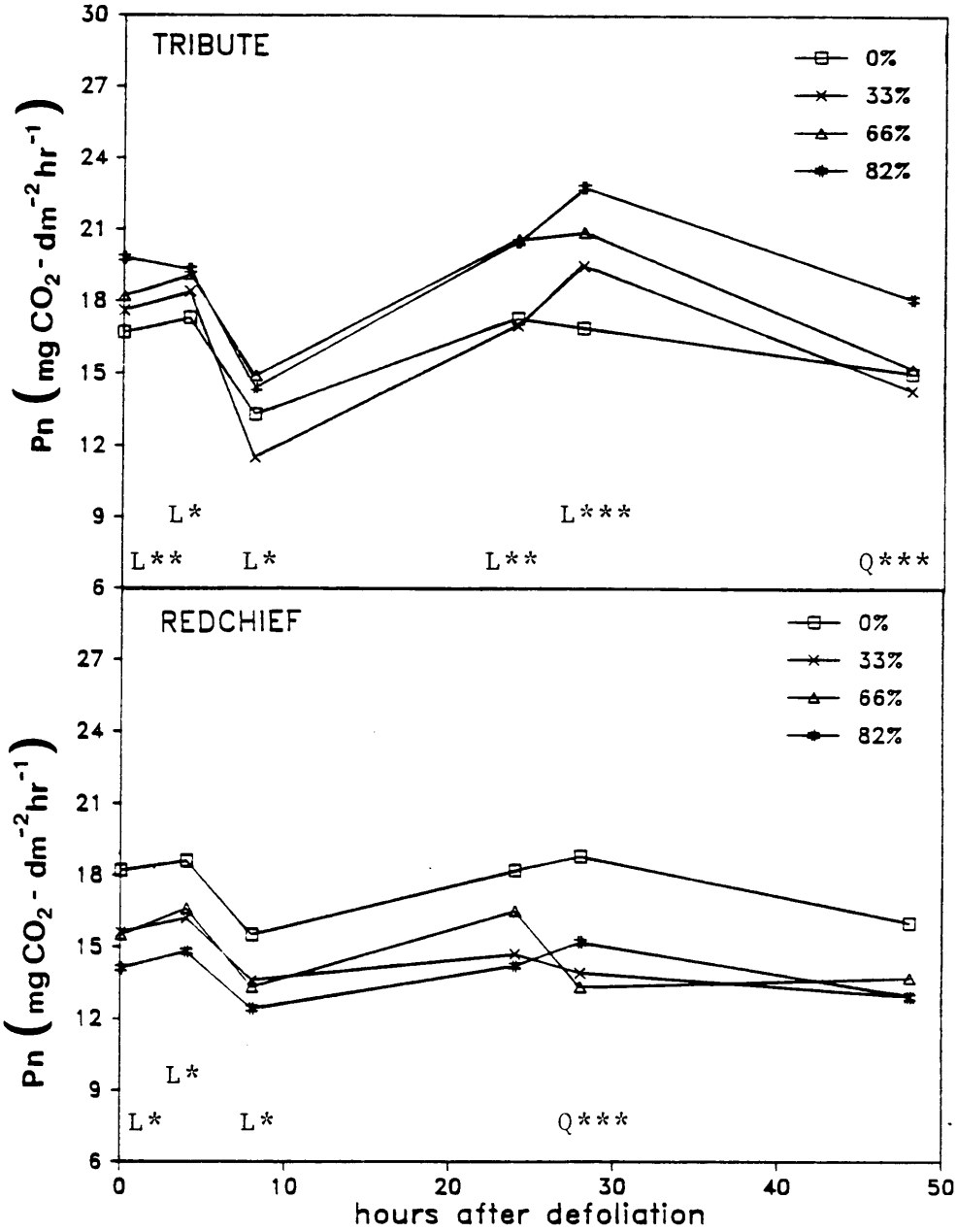

Figure 2. Net photosynthesis (Pn) (leaf area basis) as measured on leaves, 12 days after unfolding, over 48 hours after partial defoliation of 'Tribute' and 'Redchief' strawberry plants. Treatment (%) represents surface area removed per leaf. L and Q represent significant linear or quadratic relationships, respectively, at the 1% (***), 5% (**) or 10% (*) level. Each datum is the mean of 7 plants.

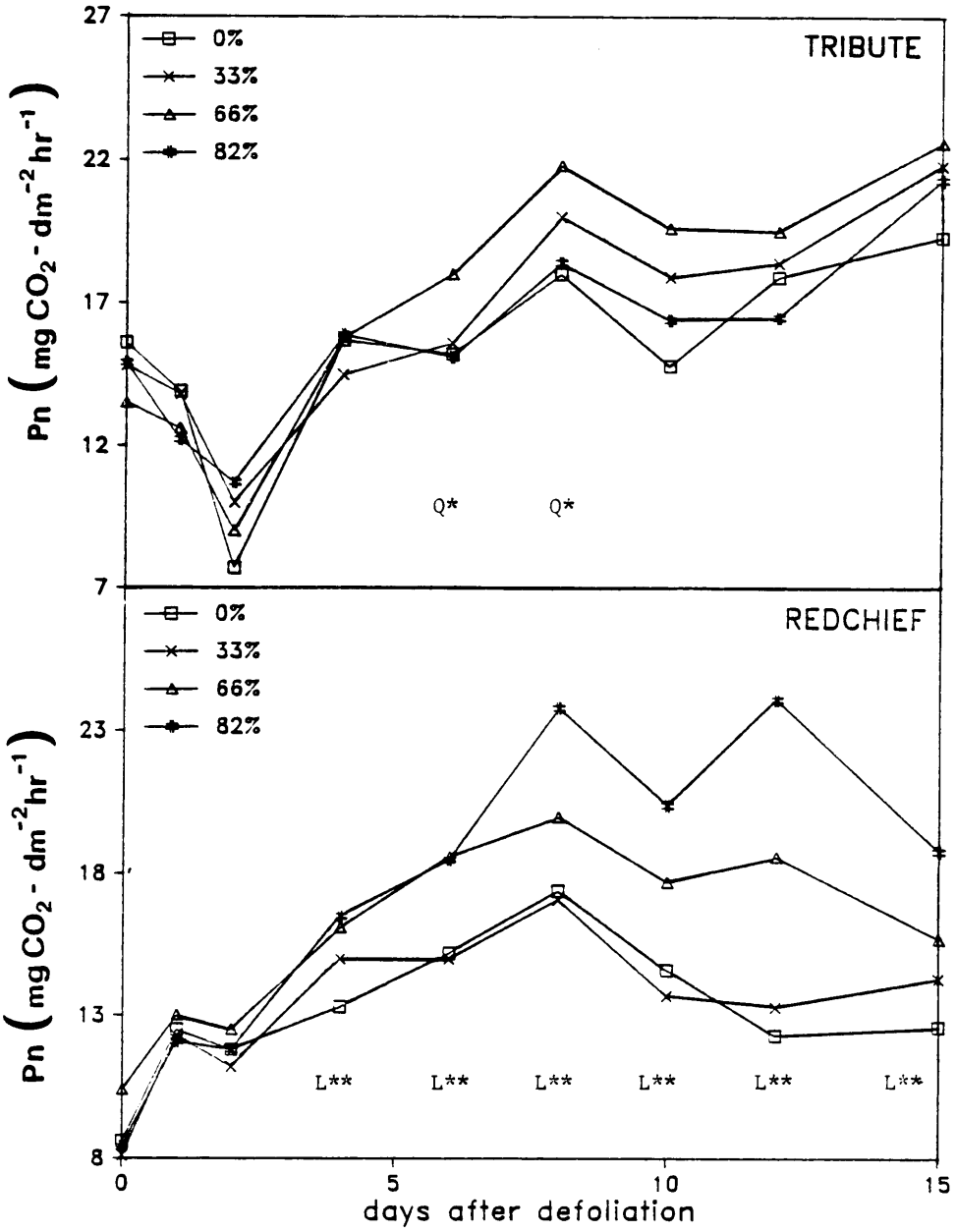

Figure 3. Net photosynthesis (Pn) (leaf area basis) as measured on leaves, 12 days after unfolding, over 15 days after partial defoliation of 'Tribute' and 'Redchief' strawberry plants. Treatment (%) represents surface area removed per leaf. L and Q represent significant linear or quadratic relationships, respectively, at the 1% (**) or 5% (*) level. Each datum is the mean of 7 plants.

In 'Redchief', the treatment effects were more pronounced with increased Pn apparent from 4 days after defoliation throughout the duration of the study (Fig. 3). The increases occurred in the 66 and 82% defoliation treatment plants, while the 33% defoliation treatment plants did not differ greatly from the control until 15 days after treatment. The 82% defoliation treatment leaves showed a more rapid increase over the other treatments until they reached a peak 12 days after leaf removal with Pn rates 95% greater than the control. The 66% defoliation treatment leaves also peaked at 12 days with Pn rates 50% greater than the control. Pn rates in all treatments, appeared to be declining by day 15. The duration of the response seems to be related to the type of plant material studied. In apple, the response was apparent for as long as 6 weeks after pruning (2,7,12) but in alfalfa the peak rates were sustained only 3 to 4 days before declining (5).

The area per leaf and dry weight per leaf of the new leaves produced by 'Tribute' tended to decrease with increasing degree of defoliation (Table 1). The specific leaf weight (SLW) showed a significant negative linear relationship with degree of defoliation. Area and dry weight for the new leaves of the control plants were not determined. In 'Redchief', the response was similar as the area per leaf tended to decrease with increasing

Table 1. Effects of defoliation on new growth harvested 15 days after treatment of 'Tribute' strawberry plants. Means on total area, area per leaf, new leaves per plant, total dry weight, dry weight per leaf and specific leaf weight. L represents a significant linear relationship at the 10% (*) level and NSR = no significant regression.

Percent leaf area removed	Total leaf area (cm^2)	Average area per leaf (cm^2)	Total dry weight (g)	Average dry wt per leaf (g)	Number new leaves	Specific leaf weight ($mg\ cm^{-2}$)
33	497	40.6	3.51	0.29	12.7	7.04
66	435	37.1	2.95	0.26	12.4	6.83
82	308	26.6	2.02	0.18	11.7	6.63
Significance	NSR	NSR	NSR	NSR	NSR	L*

degree of defoliation (Table 2). Dry weight per leaf and SLW decreased significantly with degree of defoliation. Taylor and Ferree (12) found that all apple pruning treatments suppressed the area of individual leaves on regrowth by about 50% when compared to the control. This same response was seen in young peach trees as leaf number, size, area per tree and SLW were all reduced by pruning (9). However, Alderfer and Eagles (1) found that bean plants almost totally defoliated had a larger final leaflet area than the controls due to continued leaf expansion throughout the sampling period. A larger dry weight accompanied the increased leaflet area, with the mean dry weight being 2.5 times greater than the controls (1).

The magnitude of the responses of the regrowth may have differed between the cultivars due to differing propagation methods. 'Tribute' plants were runner propagated and as such when transplanted into 15 cm pots had only to develop more leaves and roots whereas the dormant crowns of 'Redchief' plants needed to develop a complete root system as well as new top growth. This would leave 'Redchief' plants with diminished reserves for continued growth after treatment. In contrast, 'Tribute' plants were probably able to become established using minimal reserves; therefore, defoliation did not stress the plants to the same extent as in 'Redchief'. Differences

Table 2. Effects of defoliation on new growth harvested 15 days after treatment of 'Redchief' strawberry plants. Means on total area, area per leaf, new leaves per plant, total dry weight, dry weight per leaf and specific leaf weight. L represents a significant linear relationship at the 1% (***) or 5% (**) level and NSR = no significant regression.

Percent leaf area removed	Total leaf area (cm^2)	Average area per leaf (cm^2)	Total dry weight (g)	Average dry wt per leaf (g)	Number new leaves	Specific leaf weight (mg cm^{-2})
33	175	63.0	1.69	0.61	2.9	9.68
66	181	60.2	1.57	0.53	3.1	8.71
82	200	56.7	1.55	0.44	3.6	7.80
Significance	NSR	NSR	NSR	L**	NSR	L***

may also be attributed to cultivar effects. These same explanations may apply to the difference in magnitude of the Pn response.

Although there were treatment and time differences over 48 hours, the overall Pn response was slight for both cultivars. This suggests that the possible response to defoliation had not occurred in 48 hours. This is supported by the delayed response observed in the 15 day study. There was no significant response to defoliation until 4 days after treatment in 'Redchief' plants and 6 days after treatment in 'Tribute' plants. Also, PPFD during the 48 hours was not optimal despite supplemental lighting. The cloud cover was very heavy resulting in PPFD ranging from 520 to 800 μmol $m^{-2}s^{-1}$ possibly causing a slower reaction than if the conditions were more conducive for photosynthesis. Temperatures ranged from 22.4 to 28.7 $^{\circ}$C. The response time for other crops studied varied, but most reported reactions within 2 to 3 days of defoliation (2,9,13,14,15).

The increase in Pn, over 15 days, in all treatments of 'Tribute' and the 66 and 82% in 'Redchief' may indicate a possible compensation mechanism in the remaining leaf tissue. Though whole plant Pn may have been affected, the reduction can not have been in proportion to the amount of leaf area lost. It is not clear what causes this phenomenon. Stacey (11) suggested that the

photosynthetic apparatus in the remaining leaf material may function more efficiently when stressed, and Wareing et al. (14) speculated that the increase may be due to reduced competition among the remaining leaves for mineral nutrients or metabolites supplied by the roots. Other explanations for increased Pn include modification of the source-sink ratio or altered levels of growth regulators (7).

LITERATURE CITED

1. Alderfer, R.G. and C.F. Eagles. 1976. The effect of partial defoliation on the growth and photosynthetic efficiency of bean leaves. Bot. Gaz. 137:351-355.

2. Avery, D.J., C.A. Priestley, and K.J. Treharne. 1979. Integration of assimilation and carbohydrate utilization in apple. In: R. Marcelle, H. Clijsters, and M. Van Poucke (eds.) Photosynthesis and plant development. Junk, The Hague. The Netherlands. p.221-231.

3. Darrow, G.M. 1936. Interrelation of temperature and photoperiodism in the production of fruit-buds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.

4. Durner, E.F., J.A. Barden, D.G. Himelrick, and E.B. Poling. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing, and everbearing strawberries. J. Amer. Soc. Hort. Sci. 109:396-400.

5. Hodgkinson, K.C. 1974. Influence of partial defoliation on photosynthesis, photorespiration and transpiration by Lucerne leaves of different ages. Aust. J. of Plant Phys. 1:561-578.

6. Jackson, T.A. 1980. The effect of defoliation on yield of radish. Ann. of Applied Biol. 94:415-419.

7. Marini, R.P. and J.A. Barden. 1982. Net photosynthesis, dark respiration, transpiration, and stomatal resistance of young and mature apple trees as influenced by summer or dormant pruning. J. Amer. Soc. Hort. Sci. 107:170-174.

8. Peet, M.M. and P.J. Kramer. 1980. Effects of decreasing source/sink ratio in soybeans on photosynthesis, photorespiration, transpiration and yield. Plant, Cell and Environ. 3:201-206.

9. Rom, C.R. and D.C. Ferree. 1985. Time and severity of summer pruning influences on young peach tree net photosynthesis, transpiration and dry weight distribution. J. Amer. Soc. Hort. Sci. 110:455-461.

10. SAS User's Guide: Statistics, Version 5. 1985. SAS Institute, Cary, N.C. 27511.

11. Stacey, D.L. 1983. The effect of artificial defoliation on the yield of tomato plants and its relevance to pest damage. J. Hort. Sci. 58:117-120.

12. Taylor, B.H. and D.C. Ferree. 1981. The influence of summer pruning on photosynthesis, transpiration, leaf abscission and dry weight accumulation of young apple trees. J. Amer. Soc. Hort. Sci. 106:389-393.

13. von Caemmerer, S. and G.D. Farquhar. 1984. Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of Phaseolus vulgaris L. Planta 160:320-329.

14. Wareing, P.F., M.M. Khalifa and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.

15. Wolk, J.O., D.W. Kretchman and D.G. Ortega, Jr. 1983. Response of tomato to defoliation. J. Amer. Soc. Hort. Sci. 108:536-540.

Chapter IV

EFFECTS OF DEFOLIATION ON GROWTH AND YIELD OF STRAWBERRY

ABSTRACT

A field study was implemented to determine the effects of defoliation on the growth and yield of cultivated strawberry plants. Defoliation was imposed during the year of planting at times during flower bud initiation. Plants were defoliated to varying degrees (0, 33, 66, 82, or 100%) by removing the respective amount of tissue from each leaf. Defoliations were performed on August 4, September 6, or October 5. There were significant defoliation and time effects but no significant interactions. Total flower number decreased with increasing degree of defoliation as did fruit number, fruit weight and dry weight of the foliage produced in the spring. However, the reductions were not in proportion to the amount of leaf area lost. Total flower number, fruit number, fruit weight and foliage dry weight were decreased by only 35, 27, 18 and 18%, respectively when plants were 100% defoliated. The average weight per berry increased with increasing degree of defoliation as 100% defoliation treatments produced berries 18% larger than the controls. Time of defoliation signifi-

cantly affected the total flower number, fruit number, fruit weight and the foliage dry weight. Treatments made in October produced the fewest flowers and the lowest foliage dry weight. Plants defoliated in October produced the largest berries. Defoliation did not affect the amount of runners produced in the spring, which averaged 4.1 per plant.

INTRODUCTION

In the eastern United States, commercially grown June-bearing strawberries are typically planted in the spring to early summer. To promote maximum yield the second year, plants are normally prevented from fruiting during the year of planting, by removing inflorescences as they emerge. Limited runners are allowed to develop, creating a matted-row where the resulting plantlets ultimately build up reserves needed for the following fruiting season. June-bearing strawberries initiate flower buds under the shortening days of late summer and early fall of the year prior to fruiting (3,4). Therefore, this time is a critical physiological period in determining potential yield.

There are many environmental factors which may damage the leaf area during the year of establishment; these include desiccation and insect and disease pests. Sproat et al. (9) found that leaf area in the fall strongly influenced flower bud formation, which in turn largely determined yield the following spring.

There is limited information available on the effects of strawberry defoliation during the year of planting on vegetative growth and fruiting the following year. In Florida, Albregts and Howard (1) used defoliation to simulate leaf area lost at transplanting due to inadequate irrigation. They found that the controls were always

larger than defoliated plants during the first year with differences not as apparent the following year. The controls produced more marketable fruit earlier than treated plants. Puffer et al. (6) defoliated strawberry plants at digging from the nursery prior to transplanting into a production system. They found that the defoliated strawberry plants produced more fruit than those with the leaves left intact. Their study took place in California using a cultivar recommended for the area. The difference in results between the Florida and California studies was explained by Albregts and Howard (1) as the result of the presence or absence of starch reserves. Strawberry plants grown in California contain starch reserves and Florida grown strawberry plants do not (1).

The objective of this study was to determine the effects of defoliation imposed during the year of planting during flower bud initiation on subsequent vegetative growth and yield.

MATERIALS AND METHODS

Dormant plants of 'Redchief', a Junebearing cultivar commonly grown commercially in Virginia, were planted on June 11, 1986 at the Virginia Tech Horticulture Research Farm. The experimental area (Lodi loam with porous substrata; pH 6.1) was plowed and amended with 9.2 kg N, 14.4 kg P, and 35.0 kg K per hectare prior to planting, as recommended through soil testing. The plants were planted in rows 107 cm apart with in-row spacing of 46 cm. The experimental design was a split plot with degrees of defoliation (0, 33, 66, 82 or 100%) as main plots and time of defoliation (August 5, September 4 or October 6) as subplots. There were 5 replications with each subplot containing 3 plants for a total of 225 plants. Plants were manually defoliated by removing the assigned portion of each leaf on the plant (Fig. 1 Chap. III). Leaf area removed was measured using a Licor Portable Area Meter Model LI-3000 (Li-Cor, Inc.; Lincoln, Nebraska). Based on these data, initial plant size was estimated. The field was weeded and irrigated as necessary. Inflorescences were removed as they emerged to conform with standard commercial practice. To minimize confounding factors, runners were counted and removed, as they developed. The plants were sidedressed with 9 kg ha^{-1} of N, in the form of a 10-10-10 granular fertilizer, thirty days after planting and again

on September 9, 1986. Winter protection was provided in the form of a wheat straw mulch applied on December 18, 1986.

In the spring of 1987, plants were irrigated as needed and routine pest control maintained throughout the season. Berries were harvested as they ripened and number and weight of berries was recorded for each plant. After all primary and secondary berries were harvested, all remaining berries and flowers were collected and counted. Total flower number for the season was derived from total fruit harvested plus flower count at the termination of the study. Number of runners and crown number were also recorded. Top growth was harvested and dry weight recorded. Analysis of covariance and regression analyses as outlined in SAS (8) were used to determine relationships among degree and time of defoliation and total flower number, fruit number and weight, weight per berry, spring vegetative growth and number of runners produced in the spring.

RESULTS AND DISCUSSION

Berry harvest began on May 28, 1987 and continued through June 9 at which time all remaining berries and flowers were removed and counted. The bearing season was shorter than normal due to unseasonably warm temperatures beginning in April and continuing through the end of harvest.

Total flower number was affected by both defoliation treatments and time of defoliation (Table 1). There were no significant interactions between treatment and time for any of the parameters measured. Flower number decreased gradually with increasing degree of defoliation with no apparent leveling off point. However, 100% defoliation reduced flower number by only 35% when compared to the controls. October defoliated plants produced fewer total flowers than treatments made in August or September which did not differ greatly. Lloyd and Couvillon (5) reported that 80% of the flower buds were abnormal when peach trees were defoliated in late July and early August.

Defoliation had a negative effect on both fruit number and weight, which decreased with increasing degree of defoliation, paralleling the response seen in total flower number data (Table 1). The reduction was not proportional to the area removed as 100% defoliation treatment reduced fruit number by 27% and fruit weight by 18%. The extent of

Table 1. Total flower number, fruit number, fruit weight, weight per berry and dry weight of the foliage produced in the spring as affected by degree of defoliation and time of defoliation on 'Redchief' strawberry plants. L represents a significant linear relationship at the 1% (**) or 5% (*) level.

	Total flower number	Fruit number	Fruit weight (g)	Weight per berry (g)	Dry weight spring top growth (g)
Treatment (%)					
0	153	105	808	7.9	57
33	135	101	767	8.0	53
66	123	95	780	8.5	52
82	132	95	736	8.2	49
100	100	77	659	9.3	47
Significance	L**	L*	L*	L**	L*
Date of defoliation					
Aug 4	138	97	776	8.2	54
Sept 6	134	88	762	8.1	53
Oct 5	114	98	712	8.9	48
Significance	L*	L*	L*	L*	L**

damage with defoliation seems to vary with the crop. Worley (10) reported that defoliated pecan trees did not produce a crop the following year when treated prior to October 1. Early September treatments were the most devastating, resulting in delayed bud break and shoot growth the following spring.

The average weight per berry increased with increasing severity of defoliation (Table 1). Interestingly, with 100% defoliation, the average weight per berry was 18% greater than the controls. October defoliated plants produced larger berries than plants defoliated in August or September. Pearson correlation coefficients showed that there was a negative correlation between flower number and berry size which is probably due to the heavier defoliations affecting flower bud initiation resulting in fewer flowers to be supported by the plant.

In the spring, there were no treatment or time of defoliation effects on number of runners produced, which averaged 4.1 per plant. Although the dry weight of the spring vegetative growth decreased with increasing degree of defoliation, the 100% defoliation treated plants produced only 18% less vegetative growth in the spring than did the control plants. October defoliation produced the lowest dry weights. Rom and Ferree (7) found that leaf number, area and dry weight decreased as summer pruning of peach trees was delayed. Dana (2) reported that the embry-

onic strawberry leaves initiated in the fall were the first to elongate and expand with suitable growing conditions in the spring. It is possible that the differences in vegetative growth in this study were partially due to defoliation effects on the leaf initiation process during the previous fall. Also, defoliation obviously decreased whole plant photosynthesis possibly resulting in fewer reserve photosynthates.

As might be expected, there are physiological periods in the plant that are especially sensitive to environmental and physical stresses. Because the flowering process in the strawberry encompasses two seasons, the effects of defoliation during flower bud initiation can be especially harmful. The difference in total flower number may have been due to defoliation effects on flower bud initiation or defoliation may have affected flower bud development. Under the shortening days of late summer and fall, strawberry plants not only initiate and develop next season's flowers, but they also build up reserves to carry them through the winter (2). The effects of a premature disruption of vegetative growth could very well carry over into the next growing season.

Because time of flower bud initiation is not clearly established for this strawberry variety in southwest Virginia, speculation on the responses of these plants to time of defoliation was limited. The mild fall and more than

adequate rainfall in 1986 could have affected the magnitude of the responses. This would allow more recovery time after defoliation to build up reserves or to continue flower bud initiation and development. Nearly all plants were able to produce new leaves directly after defoliation regardless of when defoliation occurred. Also, the mortality rate was approximately 1% of those planted and could not be attributed to defoliation.

The overall response to defoliation was that of a reduction in yield whether it was berries or vegetative growth. There does not seem to be a threshold of tolerance but rather a slight linear response, with increasing degree of defoliation, implying that yield is related to the amount of leaf area remaining on the plant. Sproat et al. (9) found that the larger the leaf area of strawberries during the fall when the flower buds were formed the larger the crop the following spring. They suggested using any means to produce the largest number of leaves per plant before the period when flower bud initiation occurs.

LITERATURE CITED

1. Albregts, E.E. and C.M. Howard. 1972. Influence of defoliation at transplanting on strawberry growth and fruiting response. HortScience 7:569-570.

2. Dana, M.N. 1981. The strawberry plant and its environment. In: The strawberry: cultivars to marketing. Childers, N.F., (ed.) Horticultural Publications, FL. pp. 33-44.

3. Darrow, G.M. 1936. Interrelation of temperature and photoperiodism in the production of fruit-buds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.

4. Durner, E.F., J.A. Barden, D.G. Himelrick, and E.B. Poling. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing, and everbearing strawberries. J. Amer. Soc. Hort. Sci. 109:396-400.

5. Lloyd, D.A. and G.A. Couvillon. 1974. Effects of date of defoliation on flower and leaf bud development in the peach. J. Amer. Soc. Hort. Sci. 99:514-517.

6. Puffer, R.E., V. Voth, H.J. Bowen, Jr. and R.H. Gupp. 1968. Effects of alar and top removal on yield of Fresno strawberries at three digging dates. Calif. Agr. 22:11-13.

7. Rom, C.R. and D.C. Ferree. 1985. Time and severity of summer pruning influences on young peach tree net photosynthesis, transpiration and dry weight distribution. J. Amer. Soc. Hort. Sci. 100:455-461.

8. SAS User's Guide: Statistics, Version 5. 1985. SAS Institute, Cary, N.C. 27511.

9. Sproat, B.B., G.M. Darrow and J.H. Beaumont. 1935. Relation of leaf area to berry production in the strawberry. Proc. Amer. Soc. Hort. Sci. 33:389-392.

10. Worley, R.E. 1979. Pecan yield, quality, nutlet set and spring growth as a response to time of fall defoliation. J. Amer. Soc. Hort. Sci. 104:192-194.

Chapter V

FINAL DISCUSSION

Numerous factors affect the photosynthesis of a strawberry plant at any one time. These include the age of the leaf, age of the plant, growing conditions, physiological stage of the plant, and all the environmental factors acting on the plant at the time of a photosynthesis measurement. These factors make it difficult to attribute a response to any one experimental factor. Photosynthesis studies carried out in the greenhouse, though not perfect, make it possible to create conditions closer to the plant's natural environment than in a growth chamber. Experimentation under controlled environment may help to focus attention on a particular factor but cannot be considered absolute in the knowledge it provides because there is a continuum of interactions that help to create the photosynthetic response.

Both the greenhouse and field experiments indicated that the effects of defoliation on photosynthesis, growth and yield were not in proportion to the amount of leaf area removed. This can be attributed, in part, to an increase in net photosynthesis (Pn) per unit leaf area. The strawberry responds in much the same way as many other species tested, in that there is an increase in Pn with leaf area loss. There must be other factors influencing the plant as

well, with the combination resulting in compensation for the leaf loss.

More insight into the response of strawberry to defoliation could be gathered in further greenhouse and field experiments. The inclusion of a 50% defoliation treatment would help determine the tolerance level of the plant. By monitoring Pn over 72 or 96 hours, the initial changes in Pn could be more clearly defined. Also, monitoring Pn longer than 15 days would help determine the duration of the response. The field study could be improved by shortening the intervals between defoliations and/or beginning earlier and ending later in the season. This would allow us to more accurately determine the effects of time of defoliation on flower bud initiation and development.

There are many applications for the information gathered from these studies. Biostatisticians could use the information to help create models used for prediction purposes, then the reduction in yield following leaf area loss or damage, could be calculated. Entomologists and pathologists may be able to extrapolate from the data for comparison with pest damage and thereby make recommendations for pest control. The bottom line in commercial production is the net return for money invested in production. If the yield reduction caused by leaf damage due to insects or diseases is not any greater in monetary value than the cost of controlling the pest then pest control would not be war-

ranted.

Areas of further research include examining the difference in response among Junebearing, day-neutral and everbearing strawberry plants to defoliation as well as the differences in propagation method or age of the plant at the time of defoliation.

Appendix

EFFECTS OF DEFOLIATION ON NET PHOTOSYNTHESIS AS MONITORED OVER SIX WEEKS

MATERIALS AND METHODS

Dormant plants of 'Tribute' (day-neutral) were potted on April 2, 1986 in 15 cm plastic pots with Promix artificial soil mix, and placed in a greenhouse under natural light conditions. On May 6, an initial net photosynthesis (Pn) measurement was taken on a tagged leaf. On May 8, plants were defoliated by removing 0, 33, 66, 82 or 100% of all leaves except the tagged leaf and Pn was monitored on a weekly basis over the next 6 weeks. Pn was measured using an Infrared Carbon Dioxide Analyzer LCA-2 equipped with a Parkinson leaf chamber (The Analytical Development Co., Ltd.; Herts, England). This instrument also measures temperature and relative humidity in the leaf chamber as well as PPFD. Experimental design was a randomized complete block with 7 replications.

Table 1. Net photosynthesis (Pn) (leaf area basis) as measured on the same leaf over 6 weeks after defoliation on 'Tribute' strawberry plants. Treatment (%) represents surface area removed on all but one leaf. L* represents a significant linear relationship at the 10% level and NSR = no significant regression.

% removed	Date 5/16	5/23	5/31	6/6	6/19
0	21.5	22.3	13.9	14.9	9.4
33	22.9	24.2	12.9	14.4	8.8
66	23.6	27.3	15.2	15.4	7.2
82	24.1	26.0	11.5	13.2	8.0
100	22.7	27.4	15.5	13.5	9.7
Significance	NSR	L*	NSR	NSR	NSR

The vita has been removed from the scanned document