

PHYSIOLOGICAL EFFECTS OF SUMMER PRUNING IN APPLE TREES

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Kuo-Tan Li

May 2001

© 2001 Kuo-Tan Li

PHYSIOLOGICAL EFFECTS OF SUMMER PRUNING IN APPLE TREES

Kuo-Tan Li, Ph.D.

Cornell University 2001

Summer pruning has been commonly used in apple (*Malus domestica* Borkh.) orchards to control canopy size and improve fruit color. However, it is expected that the removal of healthy, photosynthetically efficient shoot leaves during the growing season might impair the canopy photosynthetic function and result in shortage of carbohydrate supply for the demand of fruit and vegetative growth. To test this hypothesis, commercial-style summer pruning at various levels of severity was imposed on mature 'Empire' apple trees in Geneva, New York. Summer pruning increased canopy light transmission and light availability for interior leaves. However, photosynthesis of shaded leaves did not recover after re-exposure. Canopy photosynthesis, transpiration, and light interception were reduced in relation to the severity of summer pruning. With commercial ranges of crop load, light to moderate pruning severity did not significantly affect fruit growth. Effects of summer pruning on fruit size, return bloom and root survival were negative-exponentially related to physiological crop load, i.e. canopy photosynthesis per fruit, which represents the carbohydrate availability to fruit after pruning treatments. Results suggested that compared to pruning severity alone, carbon balance provides better explanations on the inconsistency of summer pruning effects.

In addition, the impact of reduced carbohydrate supply after summer pruning on vegetative and reproductive performance may have been

compensated by the simultaneous decrease in canopy transpiration and improved stem water potential. This compensation might be modified by weather conditions.

Simulations with a simplified carbohydrate balance model was tested to integrate the responses of plants to summer pruning. The comparison between field measurements and simulation output generated valuable information to improve the precision of the model and the strategies for summer pruning.

BIOGRAPHICAL SKETCH

Kuo-Tan Li grew up on Hsinchuang in Northern Taiwan. He went to National Chung Hsing University and graduated with the degree of Bachelor of Science from the Department of Horticulture in 1989. During his undergraduate studies, Kuo-Tan worked with Drs. Kuo-Chuan Lee, Yu Sung, and H.L. Lin, and gained experiences on nursery maintenance, hydroponics system management, and element analysis. After graduation he went to National Taiwan University. He was conferred the degree of Master of Science in Agriculture in 1992. His honors project was on the morphology and germination physiology of pollen grains of mango and litchi, advised by Drs. Tzong-Shyan Lin and Ching-Lung Lee. After completion of this degree Kuo-Tan served in the army for two years. In 1994 after fulfilling the citizenship requirements, Kuo-Tan went back to National Taiwan University and worked with Dr. Tzong-Shyan Lin. He was involved in programs related to mango, citrus, and wax apple industries in Central and Southern Taiwan. His interest in whole-tree and environmental physiology was inspired by these experiences. Kuo-Tan enrolled in the Ph.D. program at Cornell University in 1996 and began his studies in Pomology field under the advising of Dr. Alan N. Lakso. While at Cornell, Kuo-Tan enjoyed swimming, biking, hiking, working in the apple orchards, and road traveling around the spacious countryside of spectacular New York. Kuo-Tan hopes to continue his work on fruit crops in the future.

To my parents and family

ACKNOWLEDGMENTS

I would like to thank Dr. Alan Lakso for being the chairman of my committee and for his immense inspiration and patience. I appreciate the assistance of my other committee members, Dr. Terence Robinson, Dr. Tim Setter, Dr. Mark Sorrells, and Dr. Marvin Pritts. The field and laboratory assistance of Rick Piccioni and Steve Denning is gratefully acknowledged. I would also like to thank Dr. Art Agnello and Steve Carpenter for their pest control and orchard management on my test trees, and to Rob Way for developing fish-eye photographic films. Also thanks to Joe Ogrodnick for photo scanning and printing.

I appreciate the help and company of Francesco Sottile, Michael White, Caterina Iannini, and other visiting fellows and graduate students on campus. I would also like to give thanks to Jim Hilbert, Maithreyi Krishnaswami, Michelle Rose, Dee Martin, and Kevin Kless for their summer help, and to Thorsten Manthey and Frank Larsen for translating German and Norwegian reports. I acknowledge the assistance of faculty and administration staff at NYSAES and in the Department of Horticulture Science on Ithaca campus. I am grateful for the constant encouragement of Drs. Kuo-Chuan Lee, Tzong-Shyan Lin, and Ching-Lung Lee over the years. This research was partially funded by the Arthur Boller Apple Research Grants. Red Jacket Orchard is also thanked. I would also like to express my gratitude to the Perrine Scholarship and Mrs. Matthias Prager Homan for their grants support.

TABLE OF CONTENTS

BIOGRAPHICAL SKETCH	iii
DEDICATION	iv
ACKNOWLEDGMENTS	v
TABLE OF CONTENTS	vi
LIST OF TABLES	x
LIST OF FIGURES	xi
CHAPTER ONE: GENERAL INTRODUCTION - LITERATURE REVIEW AND HYPOTHESIS	1
Introduction	1
Adaptation of Apple Leaves to Growth under Different Light Intensities	6
Summer Pruning Effects on Vegetative Growth	8
Summer Pruning Effects on Fruiting and Flowering	11
Summer Pruning Effects on Fruit Quality	14
Hypothesis - Carbohydrate Supply and Demand Balance	16
Potential of Computer Modeling on Summer Pruning Studies	21

Conclusions	22
References	24

**CHAPTER TWO: RE-EXPOSURE OF PRE-SHADED APPLE LEAVES DOES
NOT RECOVER PHOTOSYNTHETIC ABILITY AFTER SUMMER
PRUNING**

	35
Abstract	35
Additional Index Words	36
Introduction	36
Materials and Methods	39
Results and Discussion	42
Conclusions	54
References	56

**CHAPTER THREE: REDUCE CANOPY SIZE BY SUMMER PRUNING
DECREASES WHOLE-CANOPY GAS EXCHANGE AND
TRANSPIRATION IN APPLE TREES**

	62
Abstract	62
Additional Index Words	63
Introduction	63

Materials and Methods	66
Results and Discussion	73
Conclusions	89
References	93

**CHAPTER FOUR: SUMMER PRUNING EFFECTS ON FRUIT
PRODUCTION AND QUALITY, RETURN BLOOM, AND ROOT
GROWTH IN APPLE TREES** **100**

Abstract	100
Additional Index Words	101
Introduction	101
Materials and Methods	104
Results and Discussion	113
Conclusions	143
References	145

**CHAPTER FIVE: COMPUTER MODELING SIMULATION OF SUMMER
PRUNING EFFECTS AND WEATHER PATTERNS ON
CARBOHYDRATE BALANCE IN APPLE TREES** **154**

Abstract	154
-----------------	------------

Additional Index Words	155
Introduction	155
Model Description and Simulation Strategies	156
Results and Discussion	158
Conclusions	171
References	172
CHAPTER SIX: GENERAL CONCLUSIONS AND FUTURE STUDIES	174
APPENDIX A: CLIMATOLOGICAL SUMMARY OF GENEVA, NEW YORK	180
APPENDIX B: THE WHOLE-TREE CARBON BALANCE/DRY MATTER PRODUCTION MODEL FOR APPLE	186

LIST OF TABLES

Table 1.1	References of summer pruning effects on vegetative growth and canopy management in apples.	3
Table 1.2	References of summer pruning effects on apple production	4

LIST OF FIGURES

- Figure 1.1 Relationship between summer pruning and carbohydrate supply/demand balance. 18**
- Figure 1.2 Fruit weight of 'Starkrimson Delicious' apples is exponentially correlated to crop load as in term of whole canopy net carbon exchange rate (NCER) per fruit (Francisconi et al., 1996). 19**
- Figure 1.3 Fruit fresh weight of 'Smoothie'/'Pajam 2' (Giuliani et al., 1997) and 'Crispin'/M.27 (Palmer, 1992) apples is exponentially correlated to crop load as in term of leaf area per fruit. 20**
- Figure 2.1 Light distribution of 14 canopy positions before and after summer pruning treatment on 14-year-old modified central leader 'Empire'/M.26 apple trees. 44**
- Figure 2. 2 Light-saturated net photosynthesis of spur leaves from different canopy positions of 14 year-old modified central leader 'Empire'/M.26 apple trees at five days after summer pruning as a function of prior light environment. 45**
- Figure 2. 3 Seasonal trend of leaf Pn from interior and middle canopy on 14-year-old modified central leader 'Empire/M.26' trees following summer pruning. 47**
- Figure 2. 4 Seasonal trend of photosynthesis system II efficiency (Fv/Fm) of different canopy locations on 14-year-old modified central leader 'Empire'/M.26 trees. 49**
- Figure 2. 5 Correlation between photosynthesis and photosynthesis system II efficiency (Fv/Fm) of spur leaves of 'Empire'/M.26 apple trees on 4 Sept. and 9 Oct. 1999 after summer pruning. 51**

Figure 2. 6 Correlation between specific leaf weight (SLW) and pre summer pruning light exposure on 14-year-old modified central leader 'Empire' /M.26 trees.	53
Figure 2. 7 Leaf net photosynthesis (Pn) as a function of specific leaf weight (SLW) of 14-year-old modified central leader 'Empire' /M.26 trees.	55
Figure 3.1 Photograph of the open-flow "balloon" type gas-exchange chambers on test trees at the experimental site in Geneva, N.Y.	70
Figure 3.2 Photograph of the pipes, blowers, buffer tank, and canopy gas-exchange chambers on test trees at the experimental site in Geneva, N.Y.	71
Figure 3.3 Percentage of leaf area removal by summer pruning treatments on 20-year-old slender spindle 'Empire' /M.9 apple.	75
Figure 3. 4 Correlation between canopy development in 1999 and summer pruning applied on 20-year-old slender spindle 'Empire' /M.9 apple trees in 19983.	76
Figure 3. 5 Correlation between canopy light interception and percentage leaf area removal by summer pruning on 20-year-old slender spindle 'Empire' /M.9 apple trees.	79
Figure 3. 6 Relation between leaf net photosynthesis (Pn) and summer pruning severity in 20-year-old slender spindle 'Empire' /M.9 apple trees.	82
Figure 3. 7 Whole canopy net CO₂ exchange rate (NCER) as a function of summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees.	84
Figure 3.8 Whole canopy transpiration rate as a function of percentage leaf area removal by summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees.	86
Figure 3.9 Correlation between canopy transpiration per unit leaf area and summer pruning severity in 20-year-old slender spindle 'Empire' /M.9 apple trees.	88

Figure 3.10 Correlation between canopy water use efficiency (WUE) and summer pruning severity in 20-year-old slender spindle 'Empire' /M.9 apple.	90
Figure 3.11 Mid-day stem water potential in relation to summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees.	91
Figure 4.1 The controller, monitor, and video cassette recorder (VCR) of the minirhizotron camera-VCR system.	108
Figure 4.2 The camera head module of the minirhizotron camera-VCR system.	109
Figure 4.3 Photograph of three root observation tubes (minirhizotrons) installed around the test tree at the experimental site in Geneva, N.Y.	110
Figure 4.4 The root observation tube (minirhizotron) used in this study.	111
Figure 4.5 Images of apple roots captured from the video tapes recorded with the minirhizotron camera-VCR system showing changes of root status across time.	112
Figure 4.6 Final yield related to summer pruning severity on 20-year-old slender spindle 'Empire' /M.9 apple trees.	114
Figure 4.7 Correlation between the increase in fruit weight from summer pruning to harvest and summer pruning severity on 20-year-old slender spindle 'Empire' /M.9 apple trees.	old 116
Figure 4.8 Relative fruit fresh weight increases of fruits on 20-year-old slender spindle 'Empire' /M.9 apple trees after summer pruning.	117
Figure 4.9 Fruit fresh weight of 'Smoothie'/'Pajam 2' (Giuliani et al., 1997) and 'Crispin' /M.27 (Palmer, 1992) apples is exponentially correlated to crop load as in term of leaf area per fruit.	119

Figure 4.10 Fruit weight of ‘Starkrimson Delicious’ apples is exponentially correlated to crop load as in term of whole canopy net carbon exchange rate (NCER) per fruit (Francisconi et al., 1996).	120
Figure 4.11 Correlation between final fruit weight and physiological crop load ($\mu\text{mol s}^{-1} \text{fruit}^{-1}$) after summer pruning on 20-year-old slender spindle ‘Empire’/M.9 apple trees.	121
Figure 4.12 Return bloom on 20-year-old slender spindle ‘Empire’/M.9 trees related to previous year’s summer pruning severity.	125
Figure 4.13 Return blooming spurs related to summer pruning severity on 20-year-old slender spindle ‘Empire’/M.9 apple trees.	126
Figure 4.14 Correlation between the percentage return bloom on spurs and the previous year’s cropping on 20-year-old slender spindle ‘Empire’/M.9 apple trees.	128
Figure 4.15 Correlation between total flower clusters per tree and physiological crop load following summer pruning on 20-year-old slender spindle ‘Empire’/M.9 apple trees.	129
Figure 4.16 Correlation between return blooming spurs and physiological crop load (NCER fruit ⁻¹) following summer pruning on 20-year-old slender spindle ‘Empire’/M.9 apple trees.	130
Figure 4.17 Summer pruning effect on trunk growth of 20-year-old slender spindle ‘Empire’/M.9 apple trees.	132
Figure 4.18 Root growth pattern of 20-year-old slender spindle ‘Empire’/M.9 apple trees in 1999.	135
Figure 4.19 Root growth pattern of 20-year-old slender spindle ‘Empire’/M.9 apple trees in 2000.	136
Figure 4.20 Time curves of new root remaining white of 20-year-old slender spindle ‘Empire’/M.9 apple trees.	137

Figure 4.21 Root survivorship curves of 20-year-old slender spindle 'Empire' /M.9 apple trees in 1999 and 2000.	138
Figure 4.22 Correlation between early root survivorship in 1999 and physiological crop load (NCER per fruit) of 1998 on 20-year-old slender spindle 'Empire' /M.9 apple trees received summer pruning treatment on 30 July 1998.	140
Figure 4.23 Correlation between final root survivorship and physiological crop load (NCER per fruit) of 1999 on 20-year-old slender spindle 'Empire' /M.9 apple trees received summer pruning treatment on 30 July 1998 and 3 Aug. 1999 respectively.	141
Figure 5.1 Simulation of summer pruning effect on daily canopy photosynthesis (Pn) of mature slender spindle 'Empire' /M.9 apple trees.	159
Figure 5.2 Instant measurements of canopy net gas exchange rate (NCER) and simulation of final photosynthesis accumulations in relation to summer pruning severity in mature slender spindle 'Empire' /M.9 apple trees.	160
Figure 5.3 In situ measurements and computer simulations of canopy light interception in relation to summer pruning severity in mature slender spindle 'Empire' /M.9 apple trees.	162
Figure 5.4 Simulation of summer pruning effect on fruit growth of mature slender spindle 'Empire' /M.9 apple trees with 150 fruit per tree.	164
Figure 5.5 Simulation of carbohydrate availability and demand for fruit growth of mature slender spindle 'Empire' /M.9 apple trees in relation to summer pruning and cropping.	165
Figure 5.6 Seasonal daily total radiations of Geneva, New York (42°52.6'N) of 1999 and average value of 1971-1990.	167
Figure 5.7 Seasonal daily maximum and minimum of Geneva, New York (42°52.6'N) of 1999 and average value of 1971-1990.	168

Figure 5.8 Simulation of total Pn accumulation of mature slender spindle 'Empire' /M.9 apple trees in 1999 and average weather conditions from budbreak until leaf fall.	169
Figure 5.9 Simulation of carbohydrate availability for fruit growth of slender spindle 'Empire' /M.9 apple trees in long-term (1971-1990 average) and annual (1999) weather conditions.	170
Figure 6.1 Fruit demand and final fruit size in relation to canopy carbohydrate supply and transpiration after summer.	176
Figure 6.2 Diagram of canopy carbohydrate supply and transpiration in relation to summer pruning and weather patterns.	177
Figure A.1 Monthly mean temperature of Geneva, N.Y.	180
Figure A.2 Monthly maximum temperature of Geneva, N.Y.	181
Figure A.3 Monthly minimum temperature of Geneva, N.Y.	182
Figure A.4 Monthly daily radiation of Geneva, N.Y.	183
Figure A.5 Monthly precipitation of Geneva, N.Y.	184
Figure A.6 Monthly pan evaporation of Geneva, N.Y.	185
Figure B.1 Structure of the whole-tree carbon balance/dry matter production model– submodel of carbohydrate supply.	189
Figure B.2 Structure of the whole-tree carbon balance/dry matter production model– submodel of leaf area.	190
Figure B.3 Structure of the whole-tree carbon balance/dry matter production model– submodel of fruit growth.	191
Figure B.4 Structure of the whole-tree carbon balance/dry matter production model– submodel of carbohydrate demand.	192

Figure B.5 Structure of the whole-tree carbon balance/dry matter production model– submodels of accumulated respiration, radiation, and leaf dry matter.

CHAPTER ONE

GENERAL INTRODUCTION – LITERATURE REVIEW AND HYPOTHESIS

Introduction

Summer pruning, a cultural practice commonly used in apple orchards, has stimulated the interest of American apple grower as well as scientist since the beginning of last century (Alderman and Auchter, 1916). In a broad sense, summer pruning means selective removal of shoots or branches during the growing season (Flore, 1992; Saure, 1987). It can also be defined more specifically according to timing, tools, and the approaches adopted (Lord et al., 1979a). Although summer pruning can therefore be applied from as early as the beginning of growth season to as late as four weeks before harvest (Morgan et al., 1984) with different severity of thinning cuts, heading, or pinching, based on the vigor of the tree, the variety, the training system, and the most important, the grower's experiences. Belter and Thomas (1980) suggested that summer pruning is good for spur bearing red varieties such as 'Idared', 'Winesap' and others that do not color well. For terminal bearing varieties it is not suitable. Robinson et al. (1991) indicated that summer pruning is required to obtain good fruit color for tree types such as slender spindle trees which canopy has gaps that become filled with shoot growth soon after full bloom. For tree types such as palmette leader (Lakso et al., 1989a) which canopy has larger gaps that remain open for longer in the season, the need for summer pruning is less.

Nevertheless, the major purposes of summer pruning are to control canopy size and improve fruit color. By removing the extension shoots and leaves during the growing season, summer pruning directly reduces the canopy volume at that time. In addition, after a certain amount of leaf area removed by summer pruning, light distribution and penetration within canopies are improved and consequently fruit coloring is enhanced. However, numerous effects on the growth and development of the vegetative part of the tree as well as flowering and fruit production have been reported and comprehensively reviewed by several authors (Ferree et al., 1984; Marini and Barden, 1987; Mika, 1986; Saure, 1987). A significant feature of summer pruning is its highly varied and inconsistent results on either vegetative or reproductive growth and development (Table 1.1 and 1.2). A number of hypotheses, mainly related to endogenous growth control, hormone regulation, and shoot to root ratio (Ferree et al., 1984; Saure, 1992; Stiles, 1980) have been proposed to partially or fully interpret the effects of summer pruning. Yet none successfully explains the inconsistency of summer pruning effects. In this chapter the concept of carbohydrate balance is introduced by searching for the linkage between impact of summer pruning on carbohydrate supply and the demand for tree and fruit growth, and by identifying the potential area in summer pruning where the hypothesis can be applied. Possible approaches to test the hypothesis and the potential of computer modeling on summer pruning are discussed.

Table 1.1 References of summer pruning effects on vegetative growth and canopy management in apples.

	Increased	No effect	Decreased
Shoot growth	Barden and Marini, 1984 Belter and Thomas, 1980 Ellenwood and Fowler, 1944 Marini and Barden, 1982b Myers and Ferree, 1983a Myers and Ferree, 1984 (shoot length) Taylor and Ferree, 1984	Ellenwood and Fowler, 1944 Marini and Barden, 1982a	Alderman and Auchter, 1916 Ferree and Stang, 1980 Maggs, 1965 Marini and Barden, 1982e Mika et al., 1983 Myers and Ferrree, 1984 (shoot number) Platon and Zagrai, 1997 Preston and Perring, 1974 Saure 1985
Post-Pruning regrowth	Elfving, 1976 Kikuchi et al., 1989 Maggs, 1965 Miller, 1982 Ogata et al., 1986 (early pruning) Taylor and Ferree, 1981, 1984	Lord et al., 1979a Morgan et al., 1984	
Trunk	Platon and Zagrai, 1997	Lord and Greene, 1983 Marini and Barden, 1982a Platon and Zagrai, 1997 Taylor and Ferree, 1984	Barden and Marini, 1984 Engel, 1974 Kikuchi et al., 1989 Lord et al., 1979a Marini and Barden, 1982a Marini and Barden, 1982e Mika et al., 1983 Myers and Ferree, 1983c Platon and Zagrai, 1997 Taylor and Ferree, 1981 Upshall and Barkovic, 1963
Root			de Haas and Hein, 1973 Kikuchi et al., 1989 Marini and Barden, 1982e Myers and Ferree, 1983a Taylor and Ferree, 1981
Leaf Pn	Ferree et al., 1984 Marini and Barden 1982c Myer and Ferree, 1983a Taylor and Ferree, 1981	Porpiglia and Barden, 1981	
Leaf transpiration	Marini and Barden 1982c	Myers and Ferree, 1983a Taylor and Ferree, 1981	
Cold hardness	Link, 1984	Brierley, 1919	Blake, 1917 Magness, 1916 Saure, 1985
Light transmission	Marini and Barden 1982b Mika, 1986 Porpiglia and Barden, 1981 Taylor and Ferree, 1984 Warrington et al., 1984		
Canopy NCER			Lakso and Robinson, 1997
Efficiency of pest control	Cooley and Lerner 1994 Lawson et al., 1998 Ocamb-Basu et al., 1988		

Table 1.2 References of summer pruning effects on apple production .

	Increased	No effect	Decreased
Flowering	Link, 1984 Ogata et al., 1986 Utermark, 1977	Chandler, 1923 Ferree, 1979 Greene and Lord, 1983 Lord et al., 1979a, b Marini and Barden, 1982a Morgan et al., 1984	Belter and Thomas, 1980 Ferree and Stang, 1980 Lord et al., 1979a, b Marini and Barden, 1982a Myers and Ferree, 1983c
Fruit set		Belter and Thomas, 1980 Greene and Lord, 1983 Myers and Ferree, 1984 Taylor and Ferree, 1984	
Yield	Link, 1984 Ogata et al., 1986 Platon and Zagrai, 1997	Alderman and Auchter 1916 Autio and Greene, 1990 Ellenwood and Fowler, 1944 Marini and Barden, 1982d Myers and Ferree, 1983b Saure 1985 Stiles, 1980 Struklec, 1994 Ystaas 1989, 1992	Aselage and Carlson, 1977 Redalen, 1992 Säkö and Laurinen, 1982 Stiles, 1980 Taylor and Ferree, 1984 Van der boon 1980
Fruit size/weight	Redalen, 1992 Taylor and Ferree, 1984	Autio and Greene, 1990 Marini and Barden, 1982d Morgan et al, 1984 Myers and Ferree, 1983b, 1984 Ogata et al., 1986 Olszewski and Mika, 1999 Säkö and Laurinen, 1982 Schupp, 1992 Taylor and Ferree, 1984 Upshall and Barkovic, 1963 Warrington et al, 1984 Ystaas, 1989, 1992	Greene and Lord, 1983 Katzler and Wurm, 1998 Lord et al., 1979a Marini and Barden, 1982d Myers and Ferree, 1983b, 1984 Olszewski and Mika, 1999 Redalen, 1992
Constant fruit set	Struklec, 1981		Link 1984 Redalen, 1992
Pre harvest drop	Schupp, 1992		Barden and Marini, 1984 Marini and Barden, 1982d
Fruit color	Autio and Greene, 1990 Barden and Marini, 1984 Belter and Thomas, 1980 Engel, 1974 Lawson et al., 1998 Link, 1984 Lord et al., 1979a Ogata et al., 1986 Stiles, 1980 Struklec, 1981, 1994 Warrington et al., 1984 Ystaas, 1989, 1992	Bardenn and Marini, 1984 Greene and Lord, 1983 Myers and Ferree, 1983b Taylor and Ferree, 1984 Upshall and Barkovic, 1963	
Fruit quality (general)	Preston and Perring, 1974		Katzler and Wurm, 1998 Lord et al., 1979a Marini and Barden, 1982d

Continued

Table 1.2 (continued)

	Increased	No effect	Decreased
Soluble solids		Lawson et al., 1998 Morgan et al., 1984 Taylor and Ferree, 1984	Barden and Marini, 1984 Greene and Lord, 1983 Katzler and Wurm, 1998 Link, 1984 Lord et al., 1979a Marini and Barden, 1982d Myers and Ferree, 1983b Redalen, 1992 Ogata et al., 1986 Taylor and Ferree, 1984
Starch index	Marini and Barden, 1982d Schupp, 1992		
Acidity	Struklec, 1981	Lawson et al., 1998 Ystaas, 1989, 1992	Link, 1984
Firmness	Struklec, 1981	Greene and Lord, 1983 Lawson, et al., 1998 Marini and Barden, 1982d Myers and Ferree, 1983b Schupp, 1992 Taylor and Ferree, 1984	Schupp, 1992
Physiological disorders	Link, 1984 Taylor and Ferree, 1984	Engel, 1974 Ferree et al., 1984 Greene and Lord, 1983 Olszewski and Mika, 1999	Lord et al., 1979a Marini and Barden, 1982d Myers and Ferree, 1983b Struklec, 1981, 1994

Adaptation of Apple Leaves to Growth under Different Light Intensities

Light response of apple leaves usually shows a typical C₃-type hyperbolic curve and saturates at 25% to 50% of full sunlight (Flore and Lakso, 1989; Lakso, 1994). However, physiologically as well as morphologically variances can be found between exposed sun leaves and interior shade leaves. Similar to the adaptation of many other plants to growth under different light intensities (Boardman, 1977; Givnish, 1988), these variances are related to the light environment in where the two types of apple leaf developed (Lakso et al., 1989a). Leaves from the well-exposed canopy locations usually express sun leaf characters. On the other hand, leaves developed in the shaded inner canopy express shade leaf characters. Shade leaves tend to have lower net photosynthesis (P_n) than sun leaves (Barden, 1978; Lakso et al., 1989a; Palmer 1986). Several studies indicated that the differences in P_n were attributed to the morphological and optical properties of leaves. Compared to sun leaves, apple leaves growing in the shade were thinner, have smaller and fewer palisade cells, and have a greater air space within the spongy mesophyll (Ghosh, 1973; Jackson and Beakbane, 1969). Therefore, the specific leaf weight (SLW) of shaded spur leaves was usually much lower than exposed extension shoot leaves (Barden, 1978; Palmer, 1977). Although the reflectance of the two leaf types was similar, greater transmittance and thus lower light absorbing capacity of shade leaves were expected (Palmer, 1977; Ghosh, 1973).

Light absorption of leaves is also determined by pigment content (Woolly, 1971) that is usually correlated with leaf thickness and leaf P_n in apples (Flore and Lakso, 1989), although Ghosh (1973) reported that there was no direct correlation between chlorophyll content and photosynthetic rates. Boardman (1977) pointed out that leaves of many species developed in low light intensity

usually have larger chloroplast and greater amount of chlorophyll per chloroplast. However, fewer chloroplasts per unit of leaf have also been observed.

Similar to many other plants (Charles-Edwards and Ludwig, 1975), the chloroplasts of apple leaves grown in shade condition have thicker grana structure (Skene, 1974). Skene also found that grana thickness changed in response to decreased but not increased light intensity. The irreversible grana structure of chloroplasts of shade leaves after re-exposure might explain the absence of recovery of photosynthesis ability after summer pruning (Lakso et al. 1989a; Porpiglia and Barden, 1981).

Although further evidence has yet to be provided from apples, studies from *Atriplex patula* L. and some other plants indicated that chloroplasts with thin grana had high photosynthetic electron transport capacity and the light saturation of photosynthesis occurred at a relatively high light intensity (Björkman et al., 1972). On the other hand, chloroplasts with thick grana had low photosynthetic electron transport capacity and were saturated at a relatively low light intensity, but the correspondingly low respiration rate allowed more efficient use of light at low intensities.

Evidence also suggested that photosystems and many photosynthetic related enzymes and proteins of sun leaves show greater activity and efficiency than shade leaves (Boardman, 1977; Larcher, 1995). It is unclear if apple leaves behave in the same way.

In addition to the adaptation of developing leaves under different light intensities, morphological adaptation of mature apple leaves have also been observed. Lakso and Johnson (1982) indicated that leaf thickness, SLW, and leaf folding of mature apple leaf can be altered by exposing leaves in different

light intensities. This might play an important role in physiological adaptation. However, photosynthetically modification in relation to light environment is less significant in mature leaves. Evidence suggests that mature healthy apple leaves maintained high Pn ability even after several weeks in shade conditions. (Lakso, personal communication).

Summer Pruning Effects on Vegetative Growth

Shoot Growth and Post-pruning Regrowth

Reductions in vegetative growth by summer pruning have been reported on rootstock, young, and mature apple trees. (Alderman and Auchter, 1916; Ferree and Stang, 1980; Maggs, 1965; Preston and Perring, 1974; Saure 1985). Alderman and Auchter (1916) indicated that summer pruning reduced annual growth, leaf area, and repeated pruning had more severe effects. Platon and Zagrai (1997) indicated that shoot growth of 'Jonathan' and 'Golden Delicious' trees was reduced by summer pruning. In contrast, a similar amount of literature reported that shoot growth was increased following summer pruning (Table 1.1). Marini and Barden (1982a) indicated that shoot growth on trees after summer pruning was increased or showed no effect. However, in a later report they recorded significant reduction in shoot growth following summer pruning (Marini and Barden, 1982e). Myers and Ferree (1984) reported that summer pruning reduced shoot number but increased shoot length. The varied results are most likely simply related to the pruning style used in the experiments. Usually heading cut tends to stimulate more vegetative growth from the remaining part of the shoot following summer

pruning. On the other hand, thinning cut has better canopy control due to the removal of long extension shoot from the base.

Vegetative regrowth in the same year of summer pruning treatment was commonly observed in many studies. Ogata et al. (1986) reported that vegetative regrowth produced more leaf area than was removed by summer pruning on young 'Fuji' trees. The significant post-pruning regrowth was usually reported from young trees with early season heading cut pruning process. Therefore, to avoid vigorous vegetative regrowth in the same season and next year, thinning cut and late pruning are usually recommended.

Leaf and Canopy Performance

Although fruit color may be improved by summer pruning, after the cessation of shoot growth, reductions in canopy photosynthesis due to the removal of a large amount of healthy leaves is also expected. Several studies recorded that leaf photosynthesis and transpiration changed after summer pruning (Table 1.1). The increase in leaf Pn might be due to the improvement of canopy light transmission and distribution. However, Lakso et al. (1989a) pointed out that leaf photosynthesis ability is mainly determined by the light environment during leaf development. It is also possible that severe pruning of young trees may 1) improve tree water status, e.g. improve the relative xylem conductance for the remaining leaves, or 2) provide the remaining leaves with more root-produced cytokinins that may improve leaf photosynthesis (Saure, 1987). Decreased canopy gas exchange rate and transpiration after summer pruning are expected due to the reduced canopy leaf area. Lakso and Robinson (1997) reported 20% to 25% less canopy gas exchange rate following a moderate summer pruning, suggesting a significant

impact on carbohydrate supply. However, the decreased canopy transpiration might provide a potential buffering mechanism if tree function is reduced by drought stress.

Trunk Growth

Reductions in stem cross-section of both young and mature trees by summer pruning treatments have been reported (Engel, 1974; Lord et al., 1979a; Mika et al., 1983; Taylor and Ferree, 1981). On the other hand, Taylor and Ferree (1984) also indicated no influence on trunk cross section by summer pruning. In Platon and Zagrai's study (1997), the increment of trunk cross-section area (TCSA) of 'Jonathan' trees was significantly reduced by summer pruning. However, in 'Golden Delicious' trees, TCSA was either increased in slender spindle type trees or not affected in free palmette trees by summer pruning. Marini and Barden (1982a) indicated that summer pruning reduced trunk growth in 'Golden Delicious' but not in 'Stayman' or 'Delicious' in the same experiment. Noticeably, in the later report (Marini and Barden, 1982d) showed a higher crop load of 'Golden Delicious' than the other two varieties. Mika et al. (1983) also pointed out that the effect of pruning on trunk size is very often affected by fruiting.

These reports suggest that competition among sinks for carbohydrates might occur when the supply is reduced after summer pruning. Therefore, considering summer pruning alone might not be able to explain its effect on trunk growth. Interaction between other carbohydrate sinks should be involved as well.

Root Growth

Decreased root growth and weight either by summer pruning (Table 1.1) or defoliation (Head, 1969; Heinicke, 1935) have been reported. However, all the reports were measured from potted or young apple trees. It is unclear if similar results would occur in mature apple trees. However, root systems of mature fruit trees are believed to be very sensitive to carbohydrate shortage (Buwalda, 1993). In addition, studies from potted trees also indicated that root growth was significantly affected by fruiting (Ebert, 1991; Ebert and Lenz, 1991). These results suggested that similar to trunk growth, root growth of mature apple trees may also be regulated by the supply and demand of carbohydrate, although this has not been confirmed in mature trees where summer pruning is actually used.

Cold Hardiness

A few early observations noticed the influence of summer pruning on tree hardiness and frost damage (Blake, 1917; Magness, 1916; Brierley 1919). On the other hand, Link (1984) reported that summer pruning increased tree hardiness. Carbon reserves might involve in cold hardiness. However, without further evidence it is unclear if tree hardiness following summer pruning also related to carbohydrate balance.

Summer Pruning Effects on Fruiting and Flowering

Flowering and Fruit Set

Similar to the effects on vegetative growth, summer pruning effects on apple flowering and fruiting are also highly varied (Table 1.2). There is no

agreement on summer pruning effect on apple flowering. Morgan et al. (1984) reported no significant effect of summer pruning on bloom, spur number, or time of full bloom following summer pruning. Lord et al. (1979a, b) reported that summer pruning did not improve flower bud formation but actually decreased flowers due to the removal of terminal buds. They also noticed that the increasing flower bud formation in some varieties after summer pruning might be due to the weather conditions favorable to flower formation rather than the pruning itself. Myers and Ferree (1983c) reported that summer pruning improved spur vigor and increased the flower number per spur. However, total blooms per limb were reduced. This suggested that at least part of the variation of summer pruning effect on flowering is due to the variation of canopy structure after different pruning treatments and the variation of counting approaches. In addition, similar to root systems, flower development might also be affected by the supply of carbohydrate and might compete for limited resources with other sinks.

No significant summer pruning effect on final fruit set has been reported (Table 1.2). Myers and Ferree (1983b) found that summer pruning increased the quality and quantity of spurs and the number of flower per cluster, and increased fruit number on the interior spurs. However, the unpruned trees had more fruits on the 2 year-old shoots that were removed on the pruned trees. Therefore, the fruit number per tree was similar. Belter and Thomas (1980) noticed that fewer fruit number after summer pruning is usually due to a percentage of fruit lost during pruning process.

A limited number of studies reported either negative or positive summer pruning effects on pre-harvest fruit drop and biannual bearing control (Table 1.2).

Yield

Apple yield potential is linearly related to canopy light interception (Lakso and Robinson, 1997) and especially the light intercepted by the spur canopy early in the season (Wünsche and Lakso, 2000). Although summer pruning increased light transmission into the spur canopy (Table 1.1), increases in yield in the current season or in the long-term have not always been observed (Table 1.2). Most studies reported decreased or insignificant change in yield after summer pruning. In addition, total yield is also related to the number and growth rate of fruit per tree.

Fruit Size

Early studies suggested that increasing the light environment significantly increased final fruit size (Heinicke, 1963; Jackson, 1968; Jackson and Palmer, 1977; Robinson et al., 1983; Seeley et al., 1980). However, Lakso et al. (1989b) demonstrated that the effect of light on fruit size occurred early in the season. Most studies reported summer pruning either reduced or had no effect on fruit size (Table 1.2). Taylor and Ferree (1984) reported increasing in fruit size in one year and reduction in the other year on 'Jonathan' apples. They indicated that summer pruning might alter the fruit distribution on the canopy following the first year of summer pruning. However, their result suggests significantly lower yields of trees that received summer pruning than control trees. Therefore, the increase in fruit size might be the result of lower fruit number per tree. Upshall and Barkovic (1963) found that yield was reduced but the fruit size was little affected. Myers and Ferree (1983b) reported no effect on yield and fruit weight. However, their data showed the fruit number per tree was relatively low for a 5-year-old tree used in their

experiment. Engel's (1974) study suggested that fruit size was also related to the yield of the trees after summer pruning. Redalen (1992) also indicated that summer pruned trees produced lower yields but better fruit size comparing to unpruned trees. These results suggested a close linkage between fruit size, fruit number per tree, and the final fruit yield. These are generally related to the carbohydrate demand for fruit growth.

Summer Pruning Effects on Fruit Quality

Fruit Color

Fruit color is positively related to light exposure (Jackson et al., 1971; Seeley et al., 1980; Warrington, 1984), especially in some red color varieties (Belter and Thomas, 1980). In general, summer pruning increased fruit color (Table 1.2), especially for fruit from the interior part of the canopy (Warrington et al., 1984; Ystaas, 1989, 1992; Lawson et al., 1998). However, some exceptions have been recorded in which either high color strains (Taylor and Ferree, 1984; Barden and Marini, 1984) or young trees (Myers and Ferree, 1983b; Upshall and Barkovic, 1963) were used in the studies. Robinson et al. (1983) and Seeley et al. (1980) indicated that fruit color of high colored 'Delicious' strains was not affected by light improvement light exposure.

Morgan et al. (1984) and Warrington et al. (1984) indicated that significant color improvement only occurred in low light conditions. Therefore the open canopy structure and the open space between rows of a young or well managed apple orchards could provide enough light for fruit coloring, hence diminishing the summer pruning effect.

Fruit Internal Quality

The relationship between canopy light environment and fruit quality has also been reported. Robinson et al. (1983) indicated that increasing light exposure on 'Delicious' limb canopy improved fruit size, soluble solids, starch content, and total solids but reduced firmness and total acidity. Seeley et al. (1980) also reported similar results without effects on firmness and acidity. Although summer pruning increased light exposure on fruit, inconsistent or negative summer pruning effect on fruit quality have been reported (Table 1.2). Especially in soluble solids, negative influences were often observed. This might be due to the removal of leaf area after summer pruning leading to less photosynthetic assimilates supply. Myers and Ferree (1983b) found that soluble solids were decreased in relation to pruning time. In addition, Taylor and Ferree (1984) suggested that summer pruning affects on soluble solids only happened on fruit on the middle level canopy where a combination of both light reduction and leaf area reduction occurred. Redalen (1992) reported that although summer pruning lowered soluble solids content, the soluble solids content was more significantly affected by fruit number. This suggested that summer pruning effects on soluble solids content of apple fruit might be better interpreted with the carbohydrate supply and fruit demand balance hypothesis.

Summer pruning results on other parameters of fruit internal quality such as starch, firmness and acidity are also inconsistent (Table 1.2). Stiles (1980) indicated that effect of pruning on fruit firmness was related to fruit maturity. Schupp (1992) also suggested that summer pruning might advance fruit maturity based on the result of softer fruit and earlier onset of preharvest

fruit drop. However, fruit firmness and starch did not often coincide with each other.

Inconsistent summer pruning effects on fruit physiological disorders have also been noticed (Table 1.2). Lord et al. (1979a) found increased fruit Ca and improved fruit quality after storage, and eliminated the fruit disorder problems. Struklec (1981; 1994) indicated that the lower incident fruit physiological disorders by early summer pruning is due to the increased calcium content or lowered the ratio of K to Ca on both leaves and fruits. In contrast, Link (1984) reported severe pruning increase K:Ca ratio and incidence of bitter pit. In some studies the incident physiological disorders were believed related better to fruit size or weather condition, rather than to summer pruning (Ferree et al., 1984; Olszewski and Mika, 1999). Similarly, Francesconi et al. (1996b) found that late-season mite infestations reduced postharvest disorders due to reduction in final size that caused less dilution of fruit Ca.

Hypothesis - Carbohydrate Demand and Supply Balance

The highly varied results of summer pruning influences on the plant vegetative and reproductive growth indicated that multiple factors are involved. Therefore, it might be less possible to interpret all the results with a simple hypothesis. Several theories, mainly related to endogeneous control, e.g. hormone regulation, have been proposed to explain the result of summer pruning (Ferree et al., 1984; Saure, 1992; Stiles, 1980). However, no further evidence has been provided to support these hypotheses.

Noticeably, these hypotheses were usually directly or indirectly related to the regulation of carbohydrate supply and demand. A few researchers have noticed the relationship between reduced leaf area and the fruit growth after summer pruning. Ferree et al. (1984) suggested that the reduction in fruit interior quality by summer pruning might be due to the reduction in leaf to fruit ratio and the related reduced carbohydrate supply. Palmer et al. (1992) also pointed out the interaction of light interception, summer pruning, carbon uptake and fruit size.

Whole canopy photosynthesis is generally limited by the amount of canopy leaf area and light interception (Lakso, 1980). Therefore, reduction in canopy photosynthesis following the removal of leaf area by summer pruning would be expected. A preliminary study showed a moderate commercial style summer pruning might reduce canopy net carbon exchange rate (NCER) by 20% to 25% (Lakso and Robinson, 1997), indicating a potentially significant impact on carbohydrate supply after summer pruning. However, the final result will also depend on the amount of the carbohydrate demand for individual sinks or the competition between sinks (Figure 1.1). According to this hypothesis, fruit size, for example, would not be affected as long as the canopy is still able to supply sufficient carbohydrate after summer pruning to fulfill the demand for fruit growth, which is determined by the number of the fruit per tree (Giuliani et al., 1997; Lakso and Robinson, 1997; Plamer, 1992; Wibbe et al., 1993). This may explain many of the inconsistencies of summer pruning effects.

The carbohydrate balance model has been tested in relation to the fruit growth after European red mite (*Panonychus ulmi*) injury (Francesconi et al., 1996a; Lakso et al., 1996). When the range of crop load, either by whole canopy

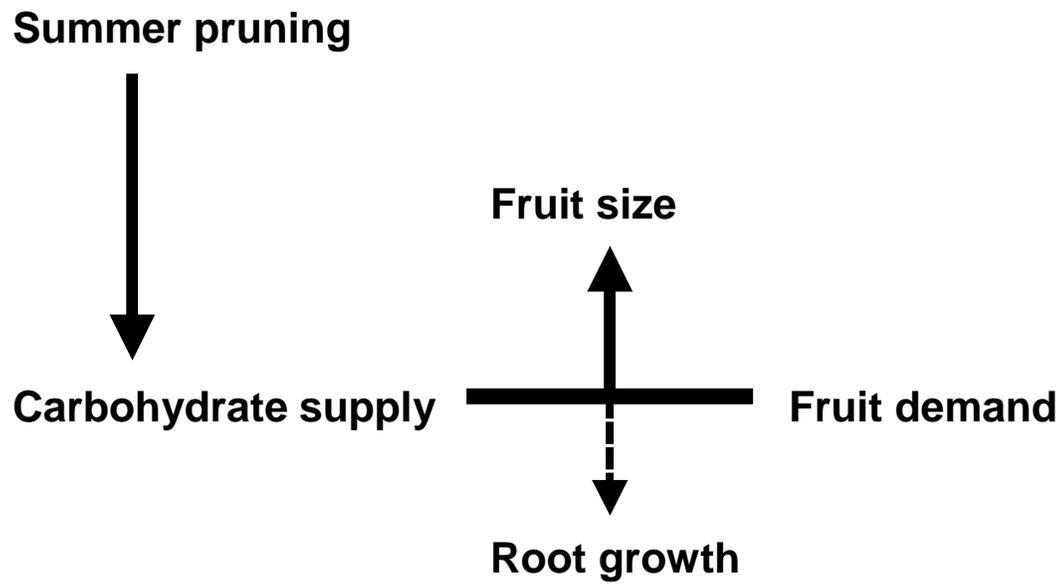


Figure 1.1 Relationship between summer pruning and carbohydrate supply/demand balance.

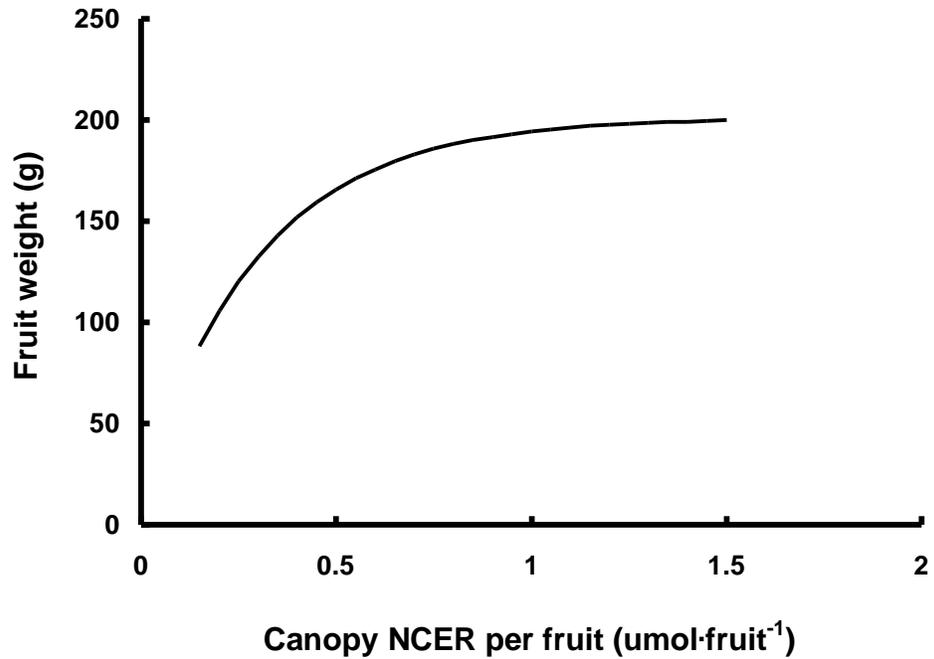


Figure 1.2 Fruit weight of 'Starkrimson Delicious' apples is exponentially correlated to crop load as in term of whole canopy net carbon exchange rate (NCER) per fruit (Francisconi et al., 1996).

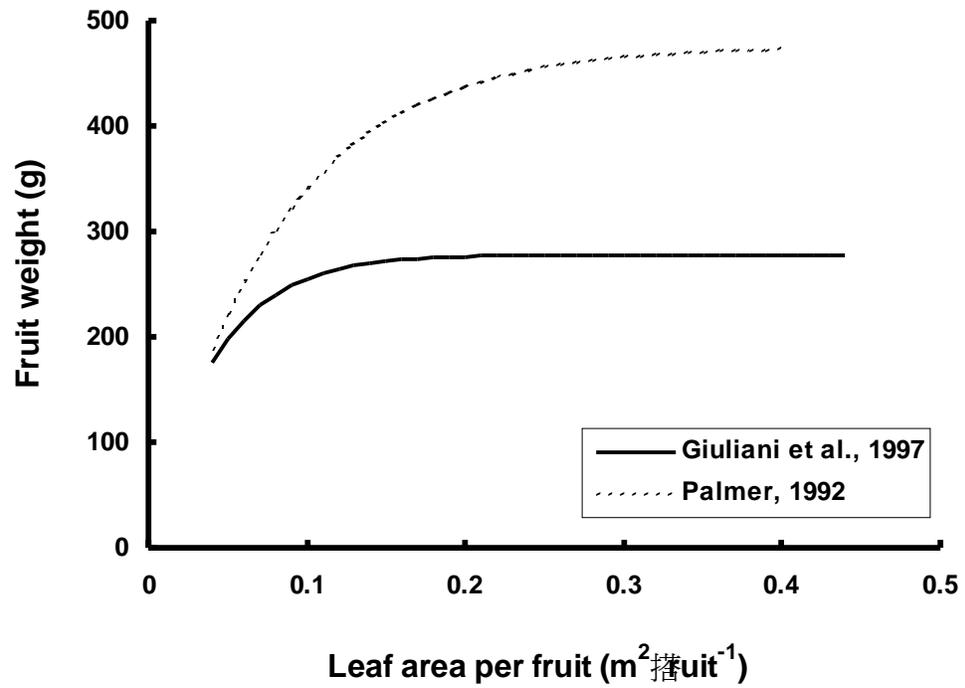


Figure 1.3 Fruit fresh weight of 'Smoothie'/'Pajam 2' (Giuliani et al., 1997) and 'Crispin'/'M.27' (Palmer, 1992) apples is exponentially correlated to crop load as in term of leaf area per fruit.

NCER per fruit or by canopy leaf are per fruit, was well managed, exponential curves are expected (Hansen, 1977; Figure 1.2 and 1.3).

Potential of Computer Modeling on Summer Pruning Studies

Progress on computer modeling techniques has led to a rising interest in research with modeling approaches. Using computer modeling has shown many advantages (Atkins, 1999) in different fields of research depending on the modeling strategies and purpose (Murase, 2000). A number of computer models specific for apple trees have been developed for educational or research purposes. Atkins et al. (1996) proposed the potential of using digitized apple tree structure and computer generated virtual environment on the training and education in the art and science of pruning. Costes et al. (1999) developed a topological database and demonstrated the potential of using the 3D computer reconstruction on the studies on factors affecting fruit quality.

There are also several computer models been developed for the simulation purpose and for improving estimations the eco-physiology and fruit production of apple orchard and orchard managements (Baumgartner et al., 1990; Elfving et al., 1983; Johnson and Lakso, 1991; Lakso and Corelli-Grappadelli 1992; Seem et al., 1986; Thorpe et al., 1978; Wagenmakers, 1996; Wagenmakers and Callesen, 1995).

In addition, there are several models that have been developed to study the canopy architecture of single trees or large scale apple orchards (Godin and Caraglio, 1998; Sinoquet and Rivet, 1997; Smith et al., 1992; Smith and Curtis, 1995).

These models have shown their values in documenting the relationship between light interception, canopy structure, vegetative growth, and fruit production. However, There are a number of assumptions and limitations that reduce the ability of these models to precisely represent the selective removal of leaves by summer pruning. With some modifications, it may be possible to take the advantages of the present models to improve our understanding on summer pruning. Alternatively, model developers might also benefit from the information from summer pruning studies on assumption modification and programming improvement.

Conclusions

Warrington et al. (1984) pointed out that if summer pruning is done correctly, fruit color development could be significantly improved without any other losses of yield or quality. However, it is rather impossible to define a standard summer pruning procedure and it certainly requires great experiences to perceive an appropriate summer pruning practice in the ever changing tree and orchard conditions. The concept of carbohydrate supply and demand balance offers a basic principle for interpreting summer pruning effects. The major objective in this present study is therefore to identify the feasibility of carbohydrate balance hypothesis by general summer pruning approaches used nowadays. Firstly, canopy light environment and leaf photosynthetic performance in relation to summer pruning is documented in chapter two. In chapter three the effects of summer pruning on canopy vigor and function was quantified to illustrate the impact of different summer pruning severity on canopy carbohydrate supply. With this baseline, the

relationship between carbohydrate supply after summer pruning and the demand for growth and development of fruit, flower, trunk, and root were determined in chapter four. In addition, variances such as canopy transpiration and annual weather variations that might modify the output of carbon balance were discussed in chapter four. Attempts to document these variances and to simulate the plant responses to summer pruning were made with a computer modeling approach in chapter five. Hopefully the results would clarify the inconsistency of summer pruning effects and provide a background when developing good summer pruning strategies.

References

- Alderman, W.H. and E.C. Auchter. 1916. The apple as affected by varying degrees of dormant and seasonal pruning. *W. Va. Agr. Exp. Sta. Bul.* 158:3-56.
- Aselage, J. and R.F. Carlson. 1977. Summer pruning as related to growth control of four apple cultivars. *Compact Fruit Tree* 10:77-85.
- Atkins, T.A. 1999. Directions in modelling fruit growth and orchard processes. *Acta Hort.* 499:31-36.
- Atkins, T.A., R.O. O'Hagan, W.J. Rogers, M.W. Pearson, and E.A. Cameron. 1996. Virtual reality in horticultural education: Pruning simulated fruit trees in a virtual environment. *Acta Hort.* 416:243-245.
- Autio, W.R., and D.W. Green. 1990. Summer pruning affects yield and improves fruit quality of 'McIntosh' apples. *J. Amer. Soc. Hort. Sci.* 115(3):356-359.
- Barden, J.A. 1978. Apple leaves, their morphology and photosynthetic potential. *HortScience* 13(6):644-646.
- Barden J.A. and R.P. Marini. 1984. Summer and dormant pruning of apple: A four year summary. *Acta Hort.* 146:263-268.
- Baumgartner, J., B. Wermelinger, U. Hugentobler, V. Delucchi, P. Baronio, B.E.de, J.J. Oertli, and C. Gessler. 1990. Use of a dynamic model on dry matter production and allocation in apple orchard ecosystem research. *Acta Hort.* 276:123-139.
- Belter, H. and T.M. Thomas. 1980. Preliminary experiences in summer pruning of apples in Michigan. *Compact Fruit Tree* 13:100-101.
- Björkman, O., N.K. Boardman, J.M. Anderson, S.W. Thorne, D.J. Goodchild, and N.A. Pyliotis. 1972. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Inst. Washington Year Book* 71:115-135.

- Blake, M.A. 1917. Observation upon summer pruning of the apple and peach. Proc. Amer. Soc. Hort. Sci. 14:14-23.
- Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants Ann. Rev. Plant Physiol. 28:355-377.
- Brierley, W.G. 1919. Comparison of fall, winter, and spring pruning of apple trees in Minnesota. Proc. Amer. Soc. Hort. Sci. 16:102-104.
- Buwalda, J.G. 1993. The carbon costs of root systems of perennial fruit crops. Environ. & Exp. Bot. 33:131-140.
- Charles-Edwards, D.A. and L.J. Ludwig. 1975. The basis of expression of leaf photosynthetic activities, p. 37-43. In: R. Marcelle (ed.). Environmental and biological control of photosynthesis. Nijhoff/Junk, The Hague, The Netherlands.
- Chandler, W.H. 1923. Results of some experiments in pruning fruit trees. Cornell Univ. Agr. Exp. Sta. Bul. 415
- Cooley, D.R. and S. Lerner. 1994. Summer pruning increases pesticide coverage in apple canopies. Phytopathology 84(11):1370.
- Costes, E., H. Sinoquet, C. Godin, and J.J. Kelner. 1999. 3D digitizing based on tree topology: Application to study the variability of apple quality within the canopy. Acta Hort. 499:271-280.
- Ebert, G. 1991. Die Wurzelatmung von Apfelbäumen II. Einfluß von innerpflanzlichen Faktoren. Erwerbsobstbau 34:165-168.
- Ebert, G. and F. Lenz. 1991. Jahresverlauf der Wurzelatmung von Apfelbäumen und ihr Beitrag zur CO₂-Bilanz. Gartenbauwissenschaft 56(3):130-133.
- Elfving, D.C. 1976. Growth control in young apple trees. Proc. N.Y. Stat. Hort. Soc. 121:107-109.
- Elfving, D.C., S.M. Welch, and G.P. Kroh. 1983. Apple tree modeling and IPM, p. 271-307. In: B.A. Croft and S.C. Hoyt (eds.). Integrated pest management of insect pests of pome and stone Fruits. Wiley-Interscience, New York.

- Ellenwood, C.W. and T.E. Fowler. 1944. Light and heavy pruning compared with no pruning of apples. *Ohio Agr. Exp. Sta. Bul.* 29:219-277.
- Engel, G. 1974. Einfluß des Sommerschnittes auf den Wuchs und Ertrag von Äpfeln auf Sämling. *Erwerbsobstbau* 16:47-48.
- Ferree, D.C. 1979. Current experiences with summer pruning. *Proc. N.Y. Stat. Hort. Soc.* 124:77-79.
- Ferree, D.C., S.C. Myers, C.R. Rom, and B.H. Taylor. 1984. Physiological aspects of summer pruning. *Acta Hort.* 146:243-251.
- Ferree, D.C. and E.J. Stang. 1980. Influence of summer pruning and Alar on growth, flowering, fruit set of 'Jerseymac' apple trees. *Ohio Agr. Res. & Dev. Center Res. Cir.* 259.
- Flore, J.A. 1992. The influence of summer pruning on the physiology and morphology of stone fruit trees. *Acta Hort.* 322:257-264.
- Flore, J.A. and A.N. Lakso. 1989. Environmental and physiological regulation of photosynthesis in fruit crops. *Hort. Rev.* 11:111-157.
- Francesconi, A.H.D., A.N. Lakso, J.P. Nyrop, J. Barnard, and S.S. Denning. 1996a. Carbon balance as a physiological basis for the interactions of European red mite and crop load on 'Starkrimson Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 121(5):959-966.
- Francesconi, A.H.D., C.B. Watkins, A.N. Lakso, J.P. Nyrop, J. Barnard, and S.S. Denning. 1996b. Interaction of European red mite and crop load on maturity and quality, mineral concentrations, and economic value of 'Starkrimson Delicious' apples. *J. Amer. Soc. Hort. Sci.* 121(5):967-972.
- Ghosh, S.P. 1973. Internal structure and photosynthetic activity of different leaves of apple. *J. Hort. Sci.* 48:1-9.
- Giuliani, R., L. Corelli-Grappadelli, and E. Magnaini. 1997. Effects of crop load on apple photosynthetic responses and yield. *Acta Hort.* 451:303-311.
- Givnish, T.J. 1988. Adaptation to sun and shade: A whole-plant perspective. *Aust. J. Plant Physiol.* 15:63-92.

- Godin, C. and Y. Caraglio. 1998. A multiscale model of plant topological structure. *J. Theor. Biol.* 191:1-46.
- Greene, D.W. and W.J. Lord. 1983. Effects of dormant pruning, summer pruning, scoring, and growth regulators on growth, yield, and fruit quality of 'Delicious' and 'Cortland' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):590-595.
- Haas, P.G.D., and K. Hein. 1973. Über die Beeinflussung des Wachstumsverlaufs von Apfelwurzeln durch verschiedene Baumschnittmaßnahmen und durch Entblätterung. *Erwerbsobstbau* 15:137-141.
- Hansen, P. 1977. Carbohydrate allocation, p. 247-258. In: J.J. Landsberg and V. Cutting (eds.). *Environmental effects on crop physiology*. Academic Press, London.
- Head, G.C. 1969. The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. *J. Hort. Sci.* 44:175-181.
- Heinicke, A.J. 1935. Root growth in young apple trees made shortly before and after defoliation. *Proc. Amer. Soc. Hort. Sci.* 33:164-165.
- Heinicke, D.R. 1963. The micro-climate of fruit trees. II. Foliage and light distribution patterns in apple trees. *Proc. Amer. Soc. Hort. Sci.* 83:1-11.
- Jackson, J.E. 1968. Effects of shading on apple fruits. *Ann Rep. East Malling Res. Sta.* 1968:69-73.
- Jackson, J.E. and A.B. Beakbane. 1969. Structure of leaves growing at different light intensities within mature apple trees. *Ann. Rep. East Malling Res. Sta.* 1970:87-89.
- Jackson, J.E., and J.W. Palmer. 1977. Effects of shade on the growth and cropping of apple trees. II. Effects on components of yield. *J. Hort. Sci.* 52:267-287.
- Jackson, J.E., R.O. Sharples, and J.W. Palmer. 1971. The influence of shade and within-tree position on apple fruit size, colour and storage quality. *J. Hort. Sci.* 46:277-286.

- Johnson, R.S. and A.N. Lakso. 1991. Approaches to modeling light interception in orchards. *HortScience* 26(8):1002-1004.
- Katzler, H. and L. Wurm. 1998. Auswirkungen verschiedener Schnittvarianten auf Ertrag sowie äußere und innere Fruchtqualität bei den Apfelsorten Jonagold und Golden Delicious. *Mitteilungen Klosterneuburg* 48:137-144.
- Kikuchi, T., T. Asada, and Y. Shiozaki. 1989. Effect of summer pruning on the next season's shoot growth of young apple trees. *J. Japan. Soc. Hort. Sci.* 58(3):491-497.
- Lakso, A.N. 1980. Aspects of canopy photosynthesis and productivity in the apple tree. *Acta Hort.* 114:100-109.
- Lakso, A. N. 1994. Apple, p. 1-42. In: B. Schaffer and P.C. Andersen (eds.). *Handbook of environmental physiology of fruit crops. Vol. I. Temperate crops.* CRC Press, Boca Raton, Fla.
- Lakso, A.N. and L. Corelli-Grappadelli. 1992. Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Hort.* 322:231-239.
- Lakso, A.N. and R.S. Johnson, 1982. Apple leaf morphology in relation to light exposure and its physiological significance. *Abst. Vol. 1. 21st Int. Hort. Cong.* 1293.
- Lakso, A.N., G.B. Mattii, J.P. Nyrop, and S.S. Denning. 1996. Influence of European red mite on leaf and whole-canopy carbon dioxide exchange, yield, fruit size, quality, and return cropping in 'Starkrimson Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 121(5):954-958.
- Lakso, A.N. and T.L. Robinson. 1997. Principles of orchard systems management optimizing supply, demand and partitioning in apple trees. *Acta Hort.* 451:405-415.
- Lakso, A.N., T.L. Robinson, and S.G. Carpenter. 1989a. The palmette leader: A tree design for improved light distribution. *HortScience* 24(2):271-275.
- Lakso, A.N., T.L. Robinson, and R.M. Pool. 1989b. Canopy microclimate effects on patterns of fruiting and fruit development in apples and

grapes, p. 263-274. In: C.J. Wright (ed.). Manipulation of fruiting. Butterworths, London.

Larcher, W. 1995. Physiological plant ecology. 3rd ed. Springer, Berlin.

Lawson, D.S., W.H. Reissig, and A.M. Agnello. 1998. Effects of summer pruning and hand fruit thinning on obliquebanded leafroller (Lepidoptera: Tortricidae) fruit damage in New York State apple orchards. *J. Agric. Entomol.* 15(2):113-123.

Link, H. 1984. Auswirkungen verschiedener Schnittmaßnahmen auf das Wachsen und Fruchten von Apfelbäumen. *Erwerbsobstbau* 26:28-34.

Lord, W.J. and D.W. Greene. 1983. Effect of summer pruning on flowering growth yield and fruit quality of apple trees. *Proc. Ont. Hort. Conf. Ontario Min. Agric. Food. For* 1983:174-179.

Lord, W.J., D.W. Greene, W.S. Bramlage, and M. Drake. 1979a. Inducing flowering of apple trees and increasing fruit quality by summer pruning. *Compact Fruit Tree* 12:23-29.

Lord, W.J., D.W. Greene, and R.A. Damon, Jr. 1979b. Flowering of young apple trees following summer pruning. *J. Amer. Soc. Hort. Sci.* 104(4):540-544.

Maggs, D.H. 1965. Dormant and summer pruning compared by pruning young apple trees once on a succession of dates. *J. Hort. Sci.* 40:249-265.

Magness, J.R. 1916. The influence of summer pruning on bud development in the apple. *Oregon Agr. Exp. Sta. Bul.* 139:46-77.

Marini, R.P. and J.A. Barden. 1982a. Growth and flowering of vigorous apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):34-39.

Marini, R.P. and J.A. Barden. 1982b. Light penetration on overcast and clear days, and specific leaf weight in apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):39-43.

Marini R.P. and J. A. Barden. 1982c. 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(1):170-174.
- Marini, R.P. and J.A. Barden. 1982d. Yield, fruit size, and quality of three apple cultivars as influenced by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(3):474-479.
- Marini, R.P. and J.A. Barden. 1982e. Effect of summer pruning vs. dormant pruning and NAA treatment on growth of one- and two-year-old apple trees. *J. Amer. Soc. Hort. Sci.* 107(4):604-607.
- Marini, R.P. and J.A. Barden. 1987. Summer pruning of apple and peach trees. *Hort. Rev.* 9:351-375.
- Mika, A. 1986. Physiological responses of fruit trees to pruning. *Hort. Rev.* 8:337-378.
- Mika, A., M.J. Grochowska, and A. Karaszewska, and M.W. Williams. 1983. Effects of dormant and summer pruning, disbudding, and growth retardants on growth, flower bud formation, and fruiting of young apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):655-660.
- Miller, S.S. 1982. Regrowth, flowering, and fruit quality of 'Delicious' apple trees as influenced by summer pruning. *J. Amer. Soc. Hort. Sci.* 107(6):975-978.
- Morgan, D.C., C.J. Stanley, R. Volz, and I.J. Warrington. 1984. Summer pruning of 'Gala' apple: The relationships between pruning time, radiation penetration, and fruit quality. *J. Amer. Soc. Hort. Sci.* 109(5):637-642.
- Murase, H. 2000. Computer applications and "phytotechnology" horticulture. *Acta Hort.* 519:19-36.
- Myers, S.C. and D.C. Ferree. 1983a. Influence of summer pruning and tree orientation on net photosynthesis, transpiration, shoot growth, and dry-weight distribution in young apple trees. *J. Amer. Soc. Hort. Sci.* 108(1):4-9.
- Myers, S.C. and D.C. Ferree. 1983b. Influence of time of summer pruning and limb orientation on yield, fruit size, and quality of vigorous 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):630-633.

- Myers, S.C. and D.C. Ferree. 1983c. Influence of time of summer pruning and limb orientation on growth and flowering of vigorous 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):634-638.
- Myers, S.C. and D.C. Ferree. 1984. Summer pruning for size control in a high density 'Delicious' /M9 system. *Acta Hort.* 146:253-261.
- Ocamb-Basu, C.M., T.B. Sutton, and L.A. Nelson. 1988. The effects of pruning on incidence and severity of *Zygothiala jamaicensis* and *Gloeodes pomigena* infections of apple fruit. *Photopathology* 78(7):1004-1008.
- Ogata, R., H. Kikuchi, T. Hatayama, and H. Komatsu. 1986. Growth and productivity of vigorous 'Fuji' apple trees on M.26 as affected by summer pruning. *Acta Hort.* 160:157-165.
- Olszewski, T. and A. Mika. 1999. The effect of summer pruning and calcium foliar spraying of 'Jonagold' and 'Šampion' apple trees on fruit storage quality. *Acta Hort.* 485:287-291.
- Palmer, J.W. 1986. Seasonal variation of light saturated photosynthetic rate of Golden Delicious apple leaves as influenced by leaf type and crop load, p. 30-33. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta. Geneva, New York.*
- Palmer, J.W. 1992. Effects of varying crop load on photosynthesis, dry matter production and partitioning of Crispin/M.27 apple trees. *Tree Physiol.* 11:19-33.
- Palmer, J.W. 1977. Light transmittance by apple leaves and canopies. *J. Appl. Ecol.* 14:505-513.
- Palmer, J.W., D.J. Avery, and S.J. Wertheim. 1992. Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Sci. Hort.* 52:303-312.
- Platon, I. and L. Zagrai. 1997. The influence of training system and pruning time on growth and apple fruiting. *Acta Hort.* 451:513-518.

- Porpiglia, P.J. and J.A. Barden. 1981. Effects of pruning on penetration of photosynthetically active radiation and leaf physiology in apple trees. *J. Amer. Soc. Hort. Sci.* 106(6):752-754.
- Preston, A.P. and M.A. Perring. 1974. The effect of summer pruning and nitrogen on growth, cropping and storage quality of Cox's Orange Pippin apple. *J. Hort. Sci.* 49:77-83.
- Redalen, G. 1992. Yield and grading result of 'Aroma' apples as influenced by pruning treatments. *Acta Hort.* 322: 299-304.
- Robinson, T.L., A.N. Lasko, and Z. Ren. 1991. Modifying apple tree canopies for improved production efficiency. *HortScience* 26(8):1005-1012.
- Robinson, T.L., E. J. Seeley, and B.H. Barritt. 1983. Effect of light environment and spur age on 'Delicious' apple fruit size and quality. *J. Amer. Soc. Hort. Sci.* 108(5):855-861.
- Säkö, J. and E. Laurinen. 1982. Effect of summer pruning on the growth and yield of apple trees. *Ann. Agr. Fennia* 21:8-12.
- Saure, M. 1985. Der Einfluss von Schnittzeitpunkt und Schnittintensität auf Wachstum und Wuchsleistung junger Apfelbäume. *Erwerbsobstbau* 27:169-173.
- Saure, M.C. 1987. Summer pruning effects in apple: A review. *Sci. Hort.* 30:253-282.
- Saure, M.C. 1992. Interference of pruning with endogenous growth control. *Acta Hort.* 322:241-247.
- Schupp, J.R. 1992. Effect of root pruning and summer pruning on growth, yield, quality, and fruit maturity of McIntosh apple trees. *Acta Hort.* 322:173-175.
- Seeley, E.J., W.C. Micke, and R. Kammereck. 1980. 'Delicious' apple fruit size and quality as influenced by radiant flux density in the immediate growing environment. *J. Amer. Soc. Hort. Sci.* 105(5):645-647.
- Seem, R.C., D.C. Elfving, T.R. Oren, and S.P. Eisensmith. 1986. A carbon balance model for apple tree growth and production. *Acta Hort.* 184:129-37.

- Sinoquet H. and P. Rivet. 1997. Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitizing device. *Trees* 11:265-270.
- Skene, D.S. 1974. Chloroplast structure in mature apple leaves grown under different levels of illumination and their response to changed illumination. *Proc. R. Soc. London B.* 186:75-78.
- Smith G.S., J.P. Curtis, and C.M. Edwards. 1992. A method for analysis plant architecture as it relates to fruit quality using three-dimensional computer graphics. *Ann. Bot.* 70:265-269.
- Smith G.S. and J.P. Curtis. 1995. A fast and effective method of measuring tree structure in 3 dimensions. *Acta Hort.* 416:15-20.
- Stiles, W.C. 1980. Pruning, growth regulator, and nutrition studies with apples. *Maine State Pomo. Soc. Ann. Rep.* 1980:25-34.
- Struklec, A. 1981. Einfluß des Schnittermins beim Sommerschnitt auf Blatt und Frucht beim Apfel. *Gartenbauwissenschaft* 46(6):S. 268-276.
- Struklec, A. 1994. Kann Sommerschnitt die Kalziumkonzentration der Apfelfrucht erhöhen und damit das Auftreten physiologischer Krankheiten verringern? *Erwerbsobstbau* 36:158-160.
- 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(3):389-393.
- Taylor, B.H. and D.C. Ferree. 1984. The influence of summer pruning and cropping on growth and fruiting of apple. *J. Amer. Soc. Hort. Sci.* 109(1):19-24.
- Thorpe, M.R., B. Saugier, S. Auger, A. Berger, and M. Methy. 1978. Photosynthesis and transpiration of an isolated tree: Model and validation. *Plant Cell & Environ.* 1:269-277.
- Upshall, W.H. and J. Barkovic. 1963. Summer pruning of dwarf apple and pear trees. *Ontario Hort. Exp. Sta. & Prod. Lab. Ann. Rep.* 1963:16-19.

- Utermark, H. 1977. Summer pruning to control growth and maintain fruiting in mature apple trees. *Compact Fruit Tree* 10:86-90.
- Van Der Boon, J. 1980. Prediction and control of bitter pit in apples. II. Control by summer pruning, fruit thinning, delayed harvesting and soil calcium dressings. *J. Hort. Sci.* 55:313-321.
- Wagenmakers, P.S. 1996. Effects of light and temperature on potential apple production. *Acta Hort.* 416:191-197.
- Wagenmakers, P.S. and O. Callesen. 1995. Light distribution in apple orchard systems in relation to production and fruit quality. *J. Hort. Sci.* 70(6):935-948.
- Warrington, I.J., C.J. Stanley, R. Volz, and D.C. Morgan. 1984. Effects of summer pruning on Gala apple quality. *The Orchardist of New Zealand.* 12:518-522.
- Wibbe, M.L., M.M. Blanke, and F. Lenz. 1993. Effect of fruiting on carbon budgets of apple tree canopies. *Trees* 8:56-60.
- Wooley, J.T. 1971. Reflectance and transmittance of light by leaves. *Plant Physiol.* 47:656-662.
- Wünsche, J.N. and A.N. Lakso. 2000. The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *HortScience* 35(7):1202-1206.
- Ystaas, J. 1989. Yield, fruit size and fruit quality of two apple cultivars as influenced by summer pruning. *Norsk Landbruksforskning* 3:195-204.
- Ystaas, J. 1992. Effects of summer pruning on yield, fruit size, and fruit quality of the apple cultivar 'Summerred'. *Acta Hort.* 322:277-282.

CHAPTER TWO

RE-EXPOSURE OF PRE-SHADED APPLE LEAVES DOES NOT RECOVER PHOTOSYNTHETIC ABILITY AFTER SUMMER PRUNING

Abstract

Summer pruning increases canopy light penetration and re-exposes spur leaves at interior canopy of apple trees (*Malus domestica* Borkh.) . However, we hypothesized that leaf photosynthesis ability is determined by the pre-pruning light environment, and the re-exposure after summer pruning would be unable to recover the photosynthesis efficiency rate of pre-shaded leaves. To test the hypothesis, a commercial intensity, thinning-cut pruning was applied on 14-year-old modified central leader 'Empire' /M.26 apple trees on 7 Aug. 1997. Changes in light availability, leaf net photosynthesis (Pn), photosystem II efficiency, and specific leaf weight (SLW) were recorded periodically before and after pruning treatment. Pn slightly declined through the growing season and was well correlated with pre-pruning light availability until late September. Although decreases in Pn were more substantial on exterior leaves than interior leaves, Pn of leaves at inner and middle canopy sites was lower than exterior leaves until late October. Efficiency of photosystem II measured by chlorophyll fluorescence slightly declined after pruning and recovered before harvest. No significant difference between canopy locations was found. SLW was well correlated with pre-pruning light availability and a linear relationship with leaf Pn was obtained on August but not on October. Results suggested a commercial summer

pruning significantly increases light environment at inner and middle canopy. However, light availability of interior and middle canopy sites was still much lower than exterior canopy and consequently leaf photosynthetic ability did not increase after pruning.

Addition Index Words

Malus domestica, canopy light interception, photosynthesis, chlorophyll fluorescence, specific leaf weight

Introduction

Canopy light interception¹ has been considered as a major yield-limiting factor not only for agronomic crops (Duncan et al., 1973; Gallagher and Biscoe, 1978) but also for fruit trees (Barritt et al., 1991; Hutton et al., 1987; Jackson, 1978). Comprehensive reviews on light penetration and distribution at the orchard scale as well as within tree canopies have been given by Lakso (1980a) and Jackson (1980). Moreover, recent studies suggested that apple (*Malus domestica* Borkh.) yield is most closely correlated with total light interception by the spur canopy (Wünsche et al., 1994; Wünsche et al., 1996; Wünsche and Lakso, 2000). Therefore, maintaining a maximum light exposure for spur leaf by proper tree design and pruning techniques is the principle for obtaining good potential apple yield (Lakso, 1980a; Lakso et al., 1997; Lakso and Robinson, 1997).

¹ In this paper the term “light” will refer to photosynthetically active radiation (PAR) or photosynthetic photon flux density (PPFD) as typically measured with quantum sensors.

However, light exposure of spur leaves can be limited by the shade cast by extension shoots, which are on the periphery of the canopy (Barritt et al., 1991; Rom, 1991). The negative effects of natural and artificial shading on canopy and leaf photosynthesis efficiency as well as morphology have been investigated in various apple varieties and orchard systems (Asada and Ogasawara, 1998; Barden, 1977; Campbell et al., 1992; Chen et al., 1998; Francesconi et al., 1997; Mika and Antoszewski, 1972; Porpiglia and Barden, 1980, Rom and Ferree, 1986; Tustin et al., 1992). Some alternative canopy architecture designs and management strategies have been proposed to improve canopy composition and enhance light penetration to minimize the shading effect (Corelli and Sansavini, 1989; Ferree et al., 1989; Green et al., 1995; Lakso et al., 1989; Palmer and Warrington, 2000; Robinson, 2000; Robinson et al., 1991).

Summer pruning, a traditional orchard practice to enhance fruit color and control tree size, is one of the most direct and effective approaches to achieve the goal. Numerous studies related to summer pruning were mainly focused on its effect on canopy control as well as fruit color and quality. However, only a limited number of studies on light environment changes due to summer pruning have been reported. Porpiglia and Barden (1981) indicated summer pruning immediately increased PAR inside the canopy. Morgan et al. (1984) and Mika (1986) reported a significantly higher transmission of PPF on trees after summer pruning.

However, removing the well-exposed leaves on the outer canopy did not have a clear effect on photosynthesis of previously-shaded leaves. Some earlier studies on young container-grown and mature apple trees suggested summer pruning increased net photosynthesis (Pn) of shoot leaves close to the

heading cut sites (Ferree et al., 1984; Myers and Ferree, 1983; Marini and Barden, 1982b; Taylor and Ferree, 1981). On the other hand, Porpiglia and Barden's (1981) research indicated no effect on photosynthetic performance of spur leaves. Lakso et al. (1989) suggested Pn of interior spur leaves after summer pruning was determined by the pre-pruning light exposure.

According to these results, we hypothesized that after the re-exposure of the pre-shaded spur leaves, the loss of leaf Pn due to prior shade does not allow tree leaves to compensate the loss of the well exposed shoot leaves after summer pruning. It is also hypothesized that due to the age of the re-exposed leaves, there will be no significant recovery of photosynthetic ability after summer pruning.

The major objective of this study was to test the hypothesis on 'Empire' apple trees with a commercial pruning approach and severity. The correlation between light availability and light-saturated leaf Pn of different canopy position was recorded before and after summer pruning. In addition to leaf Pn, leaf chlorophyll fluorescence from different canopy positions was also measured in this study. Owing to the improvement on methods and instruments, chlorophyll fluorescence analysis, which is easier than gas exchange measurement, has become a potential strategy for rapid monitoring photosynthetic efficiency in the field (Krause and Weis, 1991; van Kooten and Snel, 1990). Some basic characteristics of fluorescence emission of apple leaf have been documented (Buwalda and Noga, 1994; Curry and Burke, 1995; Demming and Björkman, 1987; Fernandez et al., 1997; Greer et al., 1997; Massacci and Jones, 1990). In this study, we measured dark-adapted fluorescence emission to test the responses of photosystem II efficiency to the changes of light environment after pruning treatments.

We also recorded specific leaf weight (SLW) from the selected canopy position. Positive correlations between SLW and photosynthesis as well as light environment in apple tree canopies have been reported especially during leaf expansion (Barden, 1974; Barritt et al., 1987; Marini and Barden, 1982a; Porpiglia and Barden, 1980; Marini and Barden, 1981; Palmer et al., 1992). Our measurements attempted to document the unlikelihood of a significant improvement on physiological as well as morphological aspect of apple leaves after the increasing in light exposure by applying a commercial summer pruning.

The goal of this research is to obtain a better understanding of the photosynthetic performance of apple leaves under various shading environments and their responses to summer pruning. The data would also provide a basic reference for our further work on quantification of the physiological effect of summer pruning on the whole-canopy basis.

Materials and Methods

Plant Materials

In 1997, five 13-year-old 'Empire' /M.26 central leader apple trees were chosen in two north-south rows in New York State Agricultural Experiment Station in Geneva, New York. Trees were on average of 3 m wide and 4.5 m tall with spacing of 3 m within rows and 4.5 m between rows. Trees were growing in a deep loam soil and well managed with commercial fertilizing and pest control.

To create a diversity of light environments for our experiment, a light pruning treatment was applied on part of the trees in the summer of 1996 to open the canopy while other tree canopies remained dense.

Summer Pruning Treatments

On 7 Aug. 1997, when most of the extension shoots were fully expanded and the terminal buds formed, all trees in the two rows received a moderate pruning treatment to open the canopy and allow interior leaves to receive more sunlight. Pruning was carried out with a thinning-cut approach, that is, removal of entire extension shoot from the base, or back to the first fruiting spur on the 1-year-old wood. About 30% to 40% of the extension shoots were thinned out from the canopy after the pruning treatment.

Light Environment Measurement

On 19 June 1997, fourteen canopy locations representing a range of light exposures were visually selected from the canopies of the chosen trees. Light availability during the early growing season for each selected location was estimated with fisheye photography and image analysis system following the procedure of Lakso (1976) at two to three week intervals until the pruning treatment was applied on the trees. Fisheye photographs (TRI-X PAN400, Kodak, Rochester, N.Y.) were taken with a fisheye lens (fisheye 180 degree, 8 mm auxiliary lens, Samigon, Japan) mounted on a 50 mm lens (Nikkor 50 mm 1:2 lens, Nikon Co., Tokyo) under overcast conditions. Pictures were then digitized with an image analysis system (FD 5000, Gould, Inc., San Jose, Calif.). The percentage of the diffuse light and direct light for a given image were then calculated by simulating the visible sky area and the solar track across the sky,

respectively. Overall light availability for the given location was then estimated according to the monthly values of diffuse to direct light from the Climatological Reference Station at the New York State Agricultural Experiment Station, Geneva, N.Y.

Leaf Performance Measurements

Leaf Pn performance was measured in full sunlight a day before and a day after pruning treatment in August, and then bi-weekly after pruning until mid-October. Two healthy leaves from spurs at each of the 14 selected locations were labeled in early June and used for the experiment over the season. Leaf gas exchange was measured with a portable open-system gas exchange analyzer (CIRAS-I, PP systems, Hitchin, Herts, U.K.) under sunny conditions between 0930_{HR} and 1300_{HR} solar time. Before summer pruning, branches were temporarily re-positioned to allow for one hour at full sunlight on interior leaves before Pn measurement.

PSII chlorophyll efficiency was measured by recording dark-adapted chlorophyll fluorescence emission with a pulse-modulated fluorometer (OS-100, Opti-Science, Inc., Tyngsboro, Mass.). The same leaves were used for Pn and fluorescence measurement. Prior to the measurement, leaves were dark-adapted for at least 15 minutes with dark-adapting leaf clips to ensure all the PSII reaction centers at the leaf area being covered by the clips were in an active, "open" state. Fluorescence was excited by a low intensity (less than 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$) modulated solid-state light source of 655 nm wavelengths with filters blocking radiation longer than 700 nm. Fluorescence emission was detected in the 710 to 760 nm ranges. After the minimal fluorescence (F_0) was recorded, the photosystem was saturated by a high intensity light pulse of 350

to 700 nm for 1 second to induce the maximum fluorescence (F_m). Variable fluorescence (F_v) was calculated from ($F_m - F_0$) and the potential yield of the photochemical reaction, or the photochemical efficiency of PSII, was obtained from F_v/F_m as described by Kraus and Weis (1991) and van Kooten and Snel (1990).

Three leaves close to the labeled leaves from each canopy location were sampled on 12 Aug. and 15 Oct. for SLW measurement. Leaf area was recorded with an image analysis system (AgVision, Decagon Devices, Inc., Pullman, Wash.). Dry weight was determined after oven-drying.

Results and Discussion

Light Environment

Measurement with fisheye photography indicated that apple canopies quickly developed after bud break and were mostly closed by mid-June (Lakso, 1980b). Rom (1990) also suggested that within 30 days after bud break, light became limiting on the inner canopy. Therefore, our estimation of light availability based on the two months period before pruning on August would reasonably represent the light environment for different canopy locations in the early and mid-season. As the tree canopy was fully developed in the early August before the pruning treatment, light availability among each canopy category showed a significant difference. A total solar radiation of 1340 MJ m^{-2} from 5 June to 7 Aug. 1997 was estimated. However, due to the heavy shading effect from the canopy, light availability before summer pruning varied from 2% to 90% (Figure 2.1).

Our measurements indicated that commercial style thinning-cut summer pruning significantly enhanced light environment especially for inner and middle canopies (Figure 2.1). Total light availability for inner canopy sites increased from 17% to 30%, and from 40% to 55% for middle canopy sites. However, compared to leaves on the outer canopy sites, the solar radiation that reached the interior canopy was still much lower even after the pruning treatment (Figure 2.1). During the later growing season, the changes of the branch angle due to the crop and to harvest slightly enhanced the canopy light environment again. Similar to the summer pruning effect, a greater increase in light availability was recorded at the inner and middle canopy site. However, the cropping and harvest effect is much smaller than summer pruning effect. This was also observed by Marini and Barden (1982a). Compared to the results from Morgen et al. (1984) and Warrington et al. (1984) on 'Gala' trees, our pruning treatment had better improvement on canopy light transmission, but slightly lower than the result from Mika (1986). It is possibly due to the pruning severity, canopy openness before summer pruning, the vigor of shoot growth, and the tree types.

Leaf Photosynthesis Response to Pre-pruning Light Exposure

Effect of long-term shading on apple leaf photosynthetic ability has been studied on single leaf measurement (Rom and Ferree, 1986) and whole-canopy gas exchange (Francessoni et al., 1997). A strong correlation was obtained between light-saturated Pn on 12 Aug., five days after the pruning treatment, and the light environment for each canopy location before summer pruning (Figure 2.2). The response was similar to single leaf light response curve.

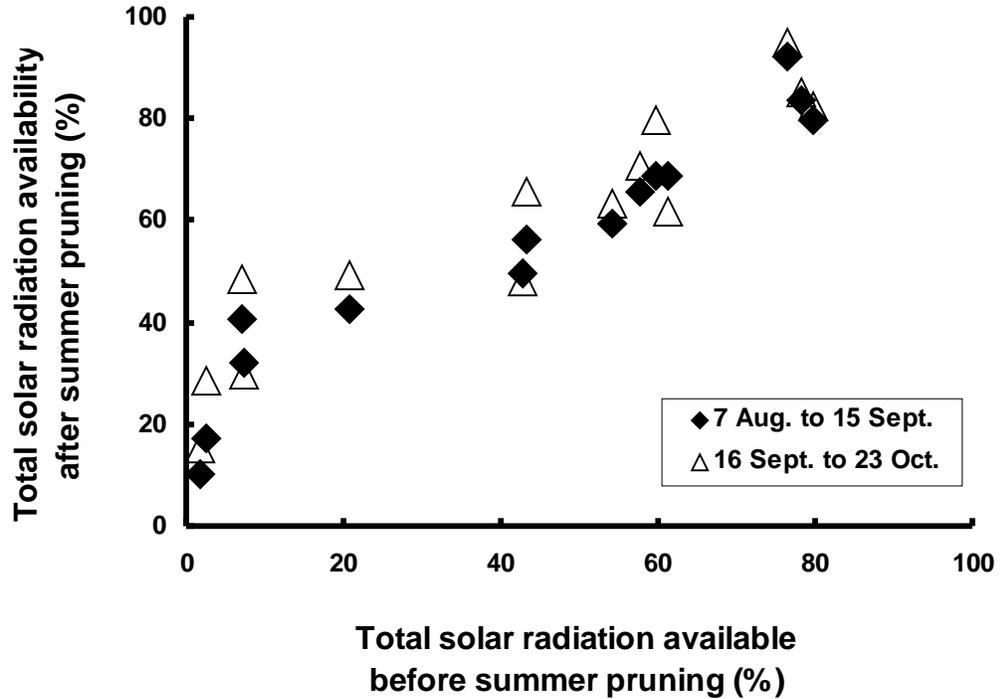


Figure 2.1 Light distribution of 14 canopy positions before and after summer pruning treatment on 14-year-old modified central leader 'Empire' /M.26 apple trees. Summer pruning was applied on 7 Aug. 1997. Estimated total solar radiation from 5 June to 7 Aug. was 1340 MJ·m⁻², 586 and 415 MJ·m⁻² for 8 Aug. to 15 Sept. 1997 and 16 Sept. to 23 Oct. 1997, respectively.

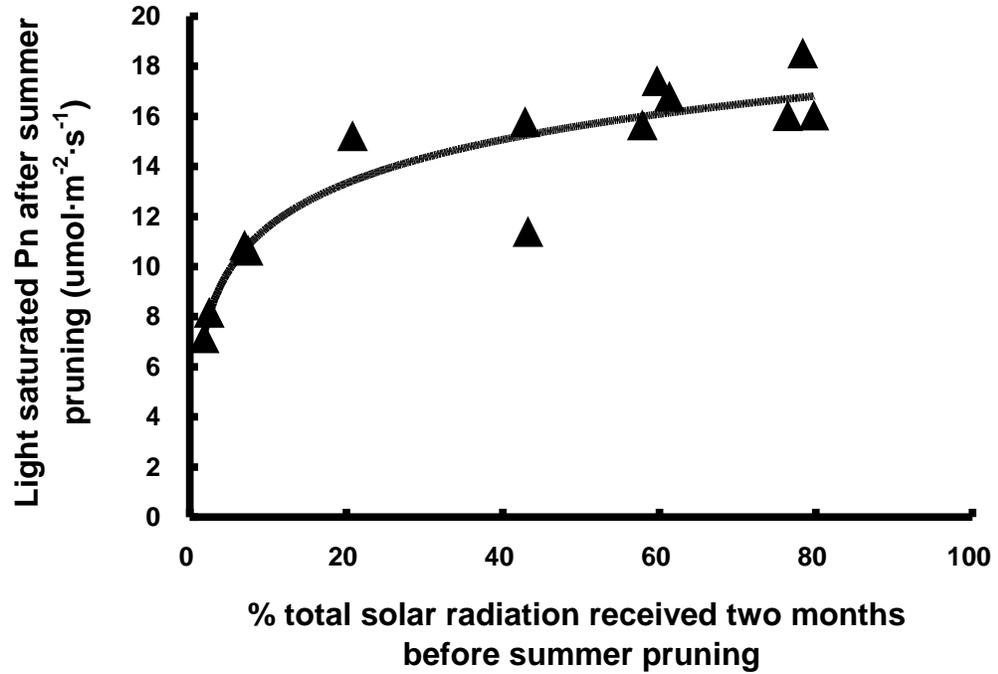


Figure 2.2 Light-saturated net photosynthesis of spur leaves from different canopy positions of 14-year-old modified central leader 'Empire' /M.26 apple trees at five days after summer pruning as a function of prior light environment. Summer pruning was applied on 7 Aug. 1997. Total solar radiation from 5 June to 7 Aug. 1997 was 1340 MJ m⁻². The regression is $y=2.5\ln(x)-8.7$, $r^2=0.8$.

Shading due to the growing extension shoots during the early growing season decreased the total light availability toward the center of the canopy and led to a strong reduction in photosynthetic ability especially for the leaves located in the inner canopy. A similar correlation was reported by Lakso et al.(1989). The present data provides further evidence that post-pruning Pn depends on pre-pruning light exposure. In addition, well-exposed leaves at peripheral canopy not only have higher light-saturated Pn, but also stomatal conductance and dark respiration rate (Campbell et al., 1992).

Although the interior canopy light environment was improved after summer pruning, the improvement at the inner canopy site was unable to induce recovery of the photosynthesis ability of shade leaves. Both leaves on inner and middle canopy sites could only reach 75% photosynthesis efficiency when compared to leaves on outer canopy (Figure 2.3). Gas exchange measurements during September and October indicated a gradual reduction in photosynthetic rate of leaves on all canopy sites regardless the light exposure (data not shown). This might be due to the aging or accumulated environment stress (Kennedy and Fujii, 1986; Marini and Barden, 1982b; Palmer, 1986). The reduction was stronger in leaves exposed to the most sunlight. During the later growing season, however, the photosynthetic rate of shade leaves on inner and middle canopy site maintained 80% of Pn of sun leaves.

Taylor and Ferree (1981) reported a 36% increase in Pn on basal leaves after a severe pruning treatment on potted young apple trees. Marini and Barden (1982b) and Myers and Ferree (1983) also reported increasing Pn of shoot leaves either on potted trees or mature field apple trees. Marini and Barden suggested several possibilities for the higher Pn rate after pruning

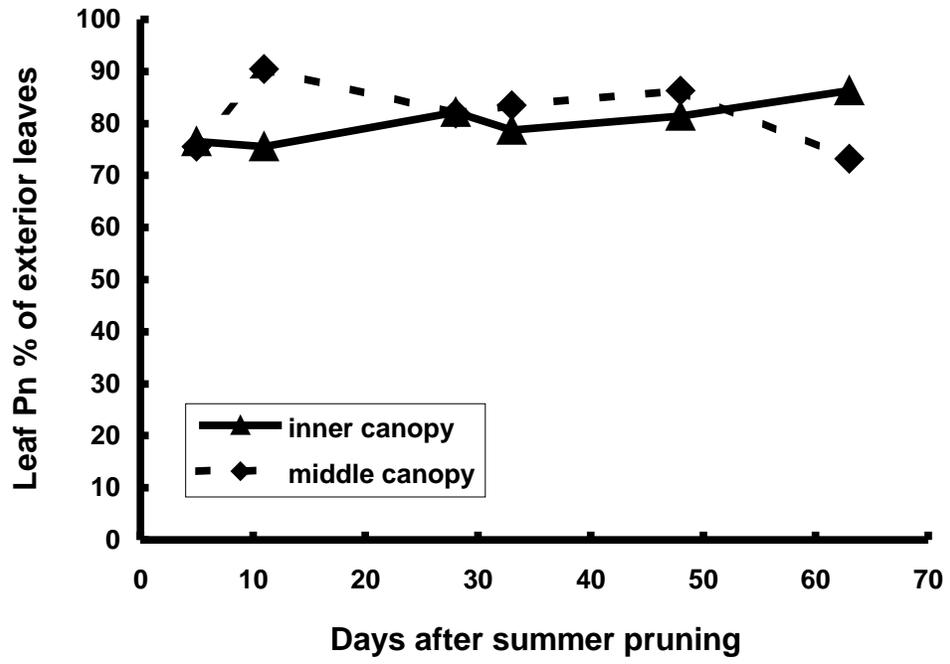


Figure 2.3 Seasonal trend of leaf Pn from interior and middle canopy on 14-year-old modified central leader 'Empire' /M.26 trees following summer pruning on 7 Aug. 1997.

treatment including light adaptation, source-sink modification, and hormone-induced rejuvenation.

However, despite the plant size and pruning severity on their container trials, heading-back pruning cuts, which is less favorable in modern apple orchard management, were used in their studies, and the Pn reading was taken from shoot leaves located at the rest portion of the extension shoot been cut. We pruned the trees with thinning cuts that removed the entire extension shoot when making a cut, and is commonly accepted by growers. Porpiglia and Barden (1981) reported no effect of increasing Pn potential of interior spur leaves after summer pruning. They concluded that the changes in Pn potential as observed by other studies may be a temporary phenomenon and/or only occurred on leaves immediately below the pruning cut. The present results agree with Porpiglia and Barden's conclusions. Also there were no signs of increasing Pn of spur leaves sampled from the exterior canopy close to the pruning cut.

Photosynthesis System II Efficiency

Chlorophyll fluorescence measurements did not show a consistent correlation between canopy light availability and Fv/Fm before and after summer pruning. On 4 Sept. 1997, a positive linear correlation with $r^2=0.7$ was recorded. Leaves showed a higher Fv/Fm value around 0.8 for most exposed leaves, and 0.75 for most shaded leaves. However, the relationship did not appear at other measurement dates through the season. Overall, the result suggested that the PSII efficiency slightly decreased in August and recovered in September and early October (Figure 2.4). The Fv/Fm value reduced again

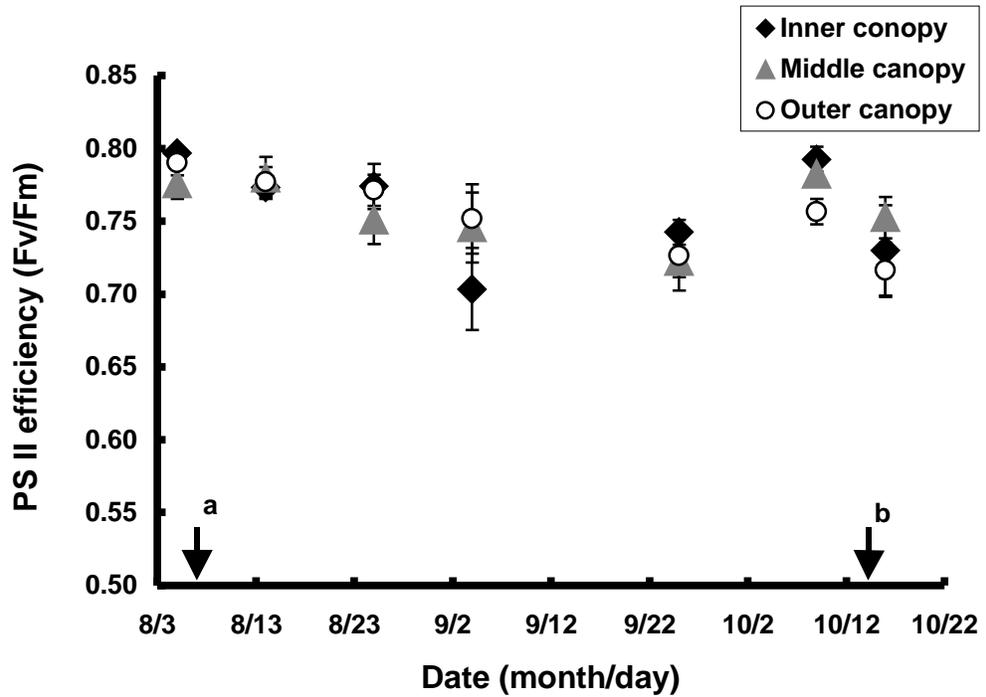


Figure 2.4 Seasonal trend of photosynthesis system II efficiency (Fv/Fm) of different canopy locations on 14-year-old modified central leader 'Empire' /M.26 trees. Summer pruning was carried out on 7 Aug. 1997 (arrow a) and fruits were harvest on 15 Oct. 1997 (arrow b). Vertical bars represent standard errors.

after harvest. Seasonal changes in F_v/F_m from Greer and coworker's (1997) report showed no decline through the growing season.

Results from isolated chloroplasts and detached leaves in controlled environments have shown promise for application of chlorophyll fluorescence as a probe for in situ studies. However, conflicting results due to the incomplete understanding of the fluorescence emission phenomenon and its sensitivity to the environment are not unusual. An example can be found in water stress studies. Measurement in laboratory indicated fluorescence quenching was well correlated with long term water stress on apple leaves (Massaci and Jones, 1990). On the other hand, a field study showed the quenching and other fluorescence parameters were not sensitive to water stress (Fernandez et al., 1997). In a recent study on shading effects in apple trees, Dolega et al. (1997) indicated that chlorophyll fluorescence and leaf P_n quickly responded to the application and removal of artificial shading. Unfortunately they didn't mention which fluorescence parameter had been recorded. However, from their gas exchange result we interpret that their fluorescence readings were the initial fluorescence from leaves without dark-adaptation. Therefore the result might merely represent the light intensity of the shading treatments.

Wünsche et al. (2000) indicated a linear relationship between photochemical yield, represented as $\Delta F/F_m'$, and leaf P_n . However, our study showed the correlation was not clear and inconsistent (Figure 2.5), suggesting the in situ application of chlorophyll fluorescence is still problematic for monitoring leaf photosynthetic performance.

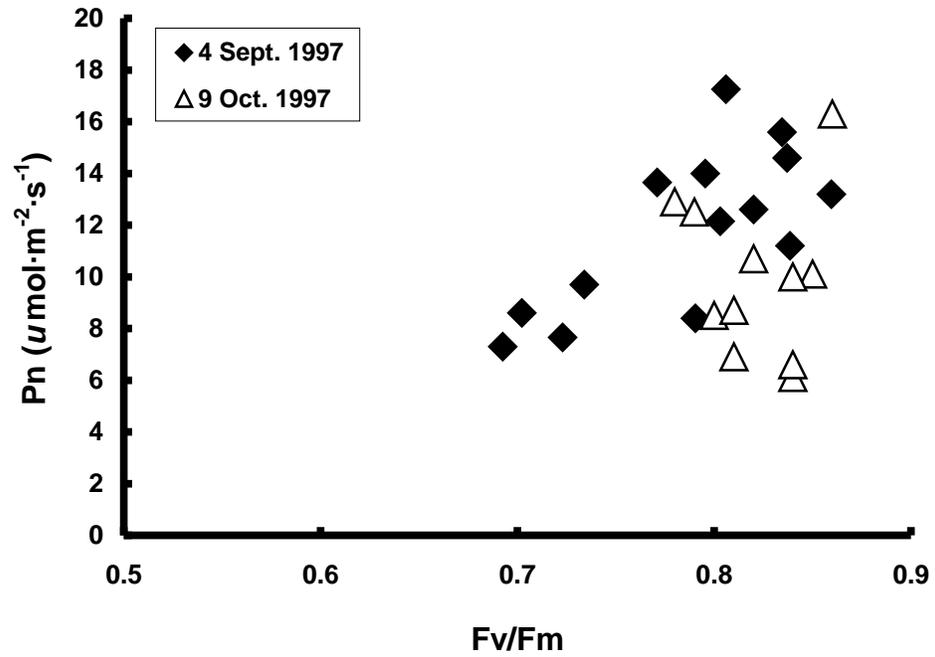


Figure 2.5 Correlation between photosynthesis and photosynthesis system II efficiency (Fv/Fm) of spur leaves of 'Empire'/M.26 apple trees on 4 Sept. and 9 Oct. 1999 after summer pruning.

Noticeably, leaves sampled from the two most exposed canopy sites in the present experiment usually show lower F_v and F_v/F_0 (data not shown). Krause and Weis(1984) mentioned that environmental stress, such as heating or freezing, that cause thylakoid damage usually lowers F_v . Curry and Burke's(1995) experiment indicated that F_v/F_0 value of apple leaves was sensitive to the temperature during the dark-adapting period. Without temperature control in our experiment, temperature of sun leaves might rise faster than of leaves in the inner canopy due to more energy been absorbed by the black shutter of the leaf clip. Therefore, any difference in fluorescence readings could be due to temperature differences, yet the differences were very small.

Specific Leaf Weight, Light and Photosynthesis

Barritt et al.(1987) reported that spur leaves at the top of canopy had greater SLW than leaves at the bottom, and SLW was correlated with the percentage of full sunlight. Barden (1974) also concluded sun leaves have higher SLW than shaded leaves. The study agrees with their conclusions. Right after summer pruning treatment, a good correlation between SLW and canopy light availability before pruning was observed on 12 Aug. (Figure 2.6). Leaves under full sunlight and on outer canopy had an average SLW of 8.5 mg cm^{-2} . Leaves located in the deep shade of inner canopy had SLW about 5.7 mg cm^{-2} .

The relationship between SLW and canopy light exposure on October were similar to which on August. Barden(1974) suggested that light exposure can significantly alter SLW even the leaf was fully mature.

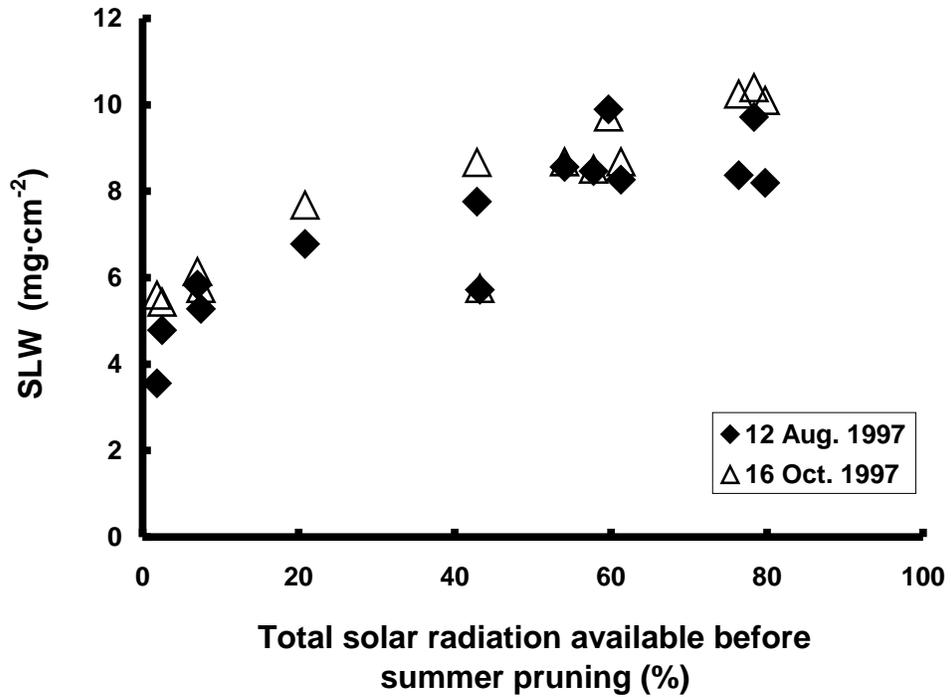


Figure 2.6 Correlation between specific leaf weight (SLW) and pre summer pruning light exposure on 14-year-old modified central leader 'Empire' /M.26 trees. Trees were summer pruned on 7 Aug. 1997 and harvested on 15 Oct. 1997. 1340 MJ m⁻² total solar radiation before summer pruning was estimated from 5 June to 7 Aug. 1997.

Barden (1978) suggested SLW might be a good index of the previous PPFD condition and Pn potential. Our measurements also suggested SLW is a good indicator for leaf photosynthesis. A strong linear correlation between SLW and Pn was observed on August (Figure 2.7). However, possibly due to the difference in senescence rate between well-exposed leaves and shaded leaves, the relationship became unclear on October after harvest, coinciding with Marini and Barden's (1981) and Lakso and Lenz's (1986) results.

Conclusion

Summer pruning has been used by many apple growers to improve canopy light penetration and thus improve fruit color. We found that a commercial intensity summer pruning increased the light exposure of spur leaves at the interior apple canopy. However, the months of canopy shade reduced the photosynthetic ability of the interior leaves. After re-exposure by summer pruning, the leaf photosynthetic ability did not significantly recover. Consequently, loss in photosynthetic function on the whole-canopy level may explain the negative effects of summer pruning such as poor fruit size. The present report is the beginning of our summer pruning studies. Future studies will focus on the quantification of pruning severity and the whole-canopy gas exchange, and the correlation between carbohydrate supply by the canopy and the demand for the fruits to clarify the physiological influence of summer pruning on apple orchard management.

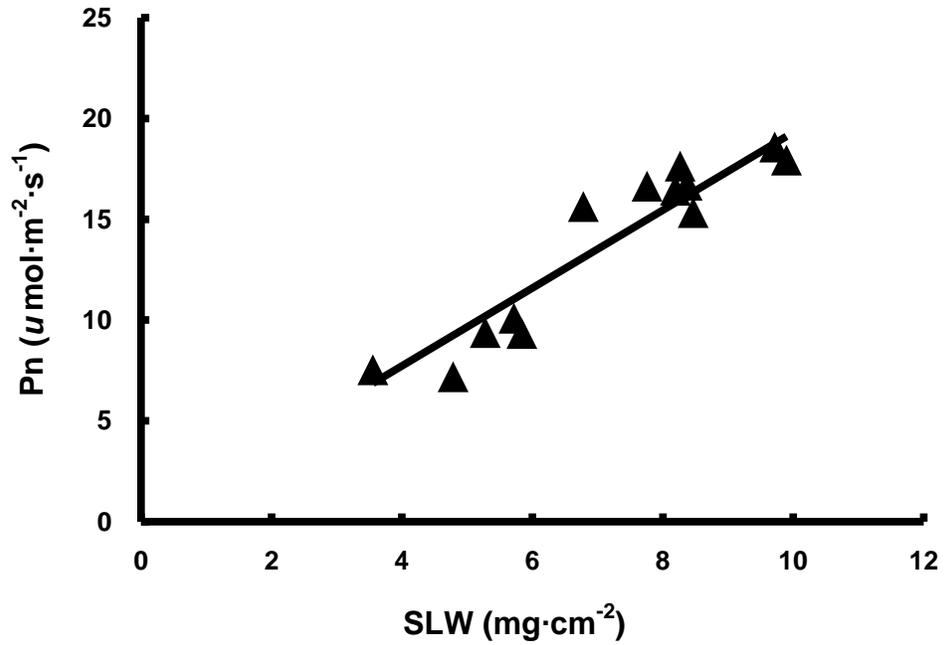


Figure 2.7 Leaf net photosynthesis (Pn) as a function of specific leaf weight (SLW) of 14-year-old modified central leader 'Empire' /M.26 trees summer pruned on 7 Aug. 1997. Leaves were sampled on 12 Aug. 1997. The regression is $y=1.9x$, $r^2=0.89$.

References

- Asada, T. and M. Ogasawara M. 1998. The effects of shading on the growth of young 'Fuji' apple trees. *J. Japan. Soc. Hort. Sci.* 67(5):655-659.
- Barden, J.A. 1974. Net photosynthesis, dark respiration, specific leaf weight and growth of young apple trees as influenced by light regime. *J. Amer. Soc. Hort. Sci.* 99(6):547-551.
- Barden, J.A. 1977. Apple tree growth, net photosynthesis, dark respiration, and specific leaf weight as affected by continuous and intermittent shade. *J. Amer. Soc. Hort. Sci.* 102(4):391-394.
- Barden, J.A. 1978. Apple leaves, their morphology and photosynthetic potential. *HortScience* 13(4):644-646.
- Barritt, B., C.R. Rom, K.R. Guelich, S.R. Drake, and M.A. Dilley. 1987. Canopy position and light effects on spur, leaf, and fruit characteristics of 'Delicious' apple. *HortScience* 22(3):402-405.
- Barritt, B.H., C.R. Rom, B.J Konishi, and M.A. Dilley. 1991. Light level influences spur quality and canopy development and light interception influence fruit production in apple. *HortScience* 26(8):993-999.
- Buwalda, J.G. and G. Noga. 1994. Intra-plant differences in leaf chlorophyll fluorescence parameters in perennial fruiting plants. *New Zealand J. Corp. Hort. Sci.* 22:373-380.
- Campbell, R.J., R.P. Marini, and J.B. Birch. 1992. Canopy position affects light response curves for gas exchange characteristics of apple spur leaves. *J. Amer. Soc. Hort. Sci.* 117(3):467-472.
- Chen, K., G. Hu, and F. Lenz. 1998. apple yield and quality as affected by training and shading. *Acta Hort.* 466:53-57.
- Corelli, L. and S. Sansavini. 1989. Light interception and photosynthesis related to planting density and canopy management in apple. *Acta Hort.* 243:159-174.

- Curry, E.A. and J.J. Burke. 1995. Temperature dependent reappearance of variable PSII fluorescence of apple cultivars and rootstocks. *Sci. Hort.* 63:187-194.
- Demming, B. and O. Björkman. 1987. Comparison of the effect of excessive light on chlorophyll fluorescence (77K) and photon yield of O₂ evolution in leaves of higher plants. *Planta* 171:171-184.
- Dolega, E., W. Stadler, and L. Bertschinger. 1997. Junifruchtfallförderung durch Beschattung: interessante Versuchsergebnisse. 1997. *Obst-Weinbau* 133(23):590-591.
- Duncan, W.G., D.N. Shaver, and W.A. Williams. 1973. Insolation and temperature effects on maize growth and yields. *Crop Sci.* 13:187-190.
- Fernandez, R.T., R.L. Perry, and J.A. Flore. 1997. Drought response of young apple trees on three rootstocks. II. Gas exchange, chlorophyll fluorescence, water relations, and leaf abscisic acid. *J. Amer. Soc. Hort. Sci.* 122(6):841-848.
- Ferree, D.C., S.C. Myers, C.R. Rom, and B.H. Taylor. 1984. Physiological aspects of summer pruning. *Acta Hort.* 146:243-251.
- Ferree, D.C., J.R. Schupp, S.H. Blizzard, T.A. Baugher, and I.J. Warrington. 1989. Influence of five orchard managements on canopy composition, light penetration and photosynthesis of 'Golden Delicious' apple. *Acta Hort.* 243:131-140.
- Francesconi, A.H.D., A.N. Lakso, and S.S. Denning. 1997. The light and temperature effects on whole-canopy net carbon dioxide exchange rates of apple trees. *Acta Hort.* 451:287-294.
- Gallagher, J.H. and P.V. Biscoe. 1978. Radiation absorption, growth and yield of cereals. *J. Agr. Sci., Camb.* 91:47-60.
- Green, S.R., K.G. McNaughton, D.H. Greer, and D.J. McLeod. 1995. Measurement of the increased PAR and net all-wave radiation absorption by an apple tree caused by applying a reflective ground covering. *Agric. For. Meteorol.* 76:163-183.
- Greer, D.H., J.N. Wünsche, and J.W. Palmer. 1997. Effect of fruiting on seasonal apple leaf chlorophyll fluorescence. *Acta Hort.* 451:345-350.

- Hutton, R.J., L.M. McFadyen, and W.J. Lill. 1987. Relative productivity and yield efficiency of canning peach trees in three intensive growing systems. *HortScience* 22:552-560.
- Jackson, J.E. 1978. Utilization of light resources by high density planting systems. *Acta Hort.* 65:61-70.
- Jackson, J.E. 1980. Light interception and utilization by orchard systems. *Hort. Rev.* 2:208-267.
- Kennedy, R.A. and J. Fujii. 1986. Seasonal and developmental changes in apple photosynthesis: enhancement effects due to flowering and fruit maturation, p. 27-29. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.*
- Krause, G.H. and W. Weis. 1984. Chlorophyll fluorescence as a tool in plant physiology II. Interpretation of fluorescence signals. *Photosyn. Res.* 5:139-157.
- Krause, G.H. and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis: the basics. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 42:313-349.
- Lakso, A.N. 1976. Characterizing apple tree canopies by fisheye photography. *HortScience* 11:404-405.
- Lakso, A.N. 1980a. Aspects of canopy photosynthesis and productivity in the apple tree. *Acta Hort.* 114:100-109.
- Lakso, A.N. 1980b. Correlations of fisheye photography to canopy structure, light climate, and biological responses to light in apple trees. *J. Amer. Soc. Hort. Sci.* 105(1):43-46.
- Lakso, A. N., L. Corelli-Grappadelli, J. Wünsche, and T. Robinson. 1997. Understanding apple tree productivity – balancing carbohydrate supply and demand. *Compact Fruit Tree* 30:11-17.
- Lakso, A. N. and F. Lenz. 1986. Regulation of apple tree photosynthesis in the autumn by temperature, p. 34-37. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.*

- Lakso, A.N. and T.L. Robinson. 1997. Principles of orchard systems management optimizing supply, demand and partitioning in apple trees. *Acta Hort.* 451:405-415.
- Lakso, A.N., T.L. Robinson, S.G. Carpenter. 1989. The palmette leader: A tree design for improved light distribution. *HortScience* 24(2):271-275.
- Marini, R.P. and J.A. Barden. 1982a. Light penetration on overcast and clear days, and specific leaf weight in apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):39-43.
- Marini, R.P. and J.A. Barden. 1982b. Net photosynthesis, dark respiration, transpiration, and stomatal resistance of young and mature apple trees as influenced by summer pruning or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):170-174.
- Marini, R.P., and J.A. Barden. 1981. Seasonal correlations of specific leaf weight to net photosynthesis and dark respiration of apple leaves. *Photosyn. Res.* 2:251-258.
- Massacci, A. and H.G. Jones. 1990. Use of simultaneous analysis of gas-exchange and chlorophyll fluorescence quenching for analyzing the effects of water stress on photosynthesis in apple leaves. *Trees: Structure and Function* 4(1):1-8.
- Mika, A. 1986. Treatments improving illumination of the fruit zone of the tree, p. 42-45. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit Trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.*
- Mika, A., and R. Antoszewski. 1972. Effect of leaf position and tree shape on the rate of photosynthesis in the apple tree. *Photosynthetica* 6:381-386.
- Morgen, D.C., C.J. Stanley, R. Volz, and I.J. Warrington. 1984. Summer pruning of 'Gala' apple: the relationships between pruning time, radiation penetration, and fruit quality. *J. Amer. Soc. Hort. Sci.* 109(5):637-642.
- Myers, S.C., and D.C. Ferree. 1983. Influence of summer pruning and tree orientation on net photosynthesis, transpiration, shoot growth, and dry-weight distribution in young apple trees. *J. Amer. Soc. Hort. Sci.* 108(1):4-9.

- Palmer, J.W. 1986. Seasonal variation of light saturated photosynthetic rate of Golden Delicious apple leaves as influenced by leaf type and cropload, p.30-33. In: A.N. Lakso and F. Lenz (eds.). The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.
- Palmer, J.W., D.J. Avery, and S.J. Wertheim. 1992. Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Sci. Hort.* 52:3-3-312.
- Palmer, J.W. and I.J. Warrington. 2000. Underlying principles of successful apple planting systems. *Acta Hort.* 513:357-363.
- Porpiglia, P.J. and J.A. Barden. 1981. Effects of pruning on penetration of photosynthetically active radiation and leaf physiology in apple trees. *J. Amer. Soc. Hort. Sci.* 106(6):752-754.
- Porpiglia, P.J., and J.A. Barden. 1980. Seasonal trends in net photosynthetic potential, dark respiration, and specific leaf weight of apple leaves as affected by canopy position. *J. Amer. Soc. Hort. Sci.* 105(6):920-923.
- Robinson, T.L. 2000. V-shaped apple planting systems. *Acta Hort.* 513:337-343.
- Robinson, T.L., A.N. Lakso, and Z. Ren. 1991. Modifying apple tree canopies for improved production efficiency. *HortScience* 26(8):1005-1012.
- Rom, C.R. 1990. Light distribution in and photosynthesis of apple tree canopies. *Acta Hort.* 279:283-290.
- Rom, C.R. 1991. Light thresholds for apple tree canopy growth and development. *HortScience* 26(8):989-992.
- Rom, C.R., and D.C. Ferree. 1986. The influence of fruiting and shading of spurs and shoots on spur performance. *J. Amer. Soc. Hort. Sci.* 111(3):352-356.
- 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(3):389-393.

- Tustin, S., L. Corelli-Grappadelli, and G. Ravaglia. 1992. Effect of previous-season and current light environments on early-season spur development and assimilate translocation in 'golden Delicious' apple. *J. Hort. Sci.* 67(3):351-360.
- Van Kooten, O. and F. Snel. 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. *Photosyn. Res.* 25:147-150.
- Warrington, I.J., C.J. Stanley, R. Volt, and D.C. Morgen. 1984. Effects of summer pruning on Gala apple quality. *The Orchardist of New Zealand* 12:518-522.
- Wünsche, J.N. and A.N. Lakso. 2000. The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *HortScience* 35(7):1202-1206.
- Wünsche, J.N., A.N. Lakso, and F. Lenz. 1994. Die Grundlage der Ertragsleistung von Apfel-(*Malus domestica* Borkh.) Anbausystemen: Die Rolle der Lichtaufnahme bei Kurz- und Langtriebblättern. *Erwerbsobstbau* 36:188-193.
- Wünsche, J.N., A.N. Lakso, T.L. Robinson, F. Lenz, and S.S. Denning. 1996. The bases of productivity in apple production systems: the role of light interception by different shoot types. *J. Amer. Soc. Hort. Sci.* 121(5):886-893.

CHAPTER THREE

REDUCE CANOPY SIZE BY SUMMER PRUNING DECREASES WHOLE-CANOPY GAS EXCHANGE AND TRANSPIRATION IN APPLE TREES

Abstract

Canopy size control is one of the major purposes of summer pruning. However, reducing canopy size might also result in less light interception, decreasing canopy photosynthetic efficiency and consequently less carbohydrate production, which might lead to the imbalance of carbohydrate supply and fruit demand. To document the effectiveness of summer pruning on canopy control and the impact on canopy performance, pruning treatments at four levels of severity (unpruned, light, moderate, and severe) were carried out on 16 mature 'Empire' / M.9 slender spindle apple trees (*Malus domestica* Borkh.) on 30 July 1998 and 4 Aug. 1999. Changes in leaf area, light interception, leaf and canopy net carbon exchange rate (NCER) as well as transpiration were recorded. The canopy growth was suppressed by summer pruning and the post-pruning regrowth was unremarkable. Total canopy light interception was slightly reduced in relation to pruning severity, while canopy NCER was proportionately reduced in relation to the percentage leaf area removed by summer pruning. The result suggested that commercial pruning severity similar to the moderate to severe treatments in this study could cause a significant reduction in canopy NCER and carbohydrate production. In addition to canopy NCER, canopy transpiration was also reduced in relation to pruning severity, suggesting less water consumption during the growing

season might benefit fruit growth and relieve the impact from carbohydrate shortage.

Additional Index Words

Malus domestica, carbohydrate balance, canopy light interception, whole-canopy gas exchange, canopy transpiration, canopy water use efficiency

Introduction

The application of summer pruning in apple (*Malus domestica* Borkh.) orchards can be traced back to the 17th century, and had scientist's attention since early 1900s (Alderman and Auchter 1916; Saure, 1987). However, a controversy of its effects on vegetative and reproductive growth in apple trees has also been reported since then. Although several theories including endogenous growth control, hormone regulation, and shoot to root ratio have been proposed (Ferree et al., 1984; Saure, 1992; Stiles, 1980), efforts to interpret the unpredictableness of summer pruning are unavailing.

As the knowledge of the importance of light interception and distribution on apple orchard management and fruit production accumulated (Jackson, 1980; Lakso 1980; Palmer, 1989; Wagenmakers and Callesen, 1995; Wünsche and Lakso, 2000), interest in the effects of summer pruning has been revived. On the positive side, by removing part of the extension shoots and leaves, summer pruning improves the light penetration and distribution within the canopy (Chapter two; Lakso et al., 1989; Mika, 1986; Morgan et al., 1984; Porpiglia and Barden, 1981; Warrington et al., 1984). On the negative side, the

great amount of leaf area removal might reduce canopy light interception (Palmer et al, 1992) and weaken the canopy photosynthetic function, causing a potential shortage of carbohydrate supply, and consequently limiting fruit growth and fruit size.

A few scientists were already aware of the risk of reducing in canopy photosynthetic ability by summer pruning (Marini and Barden, 1987). However, the linkage between decreased canopy photosynthetic function by summer pruning and fruit size as well as internal quality has been barely examined. Ferree et al. (1984) suggested that inferior fruit quality by summer pruning might be related to the reduction in leaf to fruit ratio. Palmer et al. (1992) concluded that summer pruning improved the light environment within the canopy but reduced total canopy light interception, which would be expected to reduce total carbon dioxide uptake by the tree and possibly result in smaller fruit size.

A preliminary test of summer pruning effects on canopy net carbon exchange rate (NCER) indicated that a moderate summer pruning could cause 20% to 25% reduction (Lakso and Robinson, 1997). Carbohydrate supply and demand balance has been well defined with computer simulation approaches (Johnson and Lakso, 1991; Lakso and Corelli-Grappadelli, 1992, Lakso et al., 1999). The feasibility of integrating these effects with a carbohydrate supply/demand hypothesis has also been tested on foliar pest injury in apples (Lakso et al., 1996; Francesconi, et al., 1996). The similarity of summer pruning effect and European red mite injury on canopy photosynthetic function and fruit growth therefore encouraged us to hypothesize that carbon balance would best explain the inconsistent results of summer pruning on crop development.

Our objectives were to quantify summer pruning effects on canopy size control, and illustrate the correlations between pruning severity and canopy photosynthesis ability, which is the primary component of the carbohydrate supply module of the carbon balance theory.

In this study we treated mature slender spindle 'Empire' apple trees, a variety and training system that usually require summer pruning to improve fruit coloring and maintain canopy structure (Robinson et al., 1991), with four levels of visual severity of summer pruning. Approaches adopted in early study for quantifying pruning effects on canopies include changes in canopy diameter (Taylor and Ferree, 1984; Upshall and Barkvoic, 1963; Utermark, 1977), height and allotted spacing (Myers and Ferree, 1983b), and leaf area index (Palmer, 1992). In this study canopy size was quantified on leaf area bases to provide a more precise measurement of pruning severity. Canopy light interception and canopy NCER were monitored before and after summer pruning. The results would help us to identify the role of summer pruning in the domain of carbohydrate supply in the carbon balance theory. In addition, while measuring the canopy NCER, the correlation between summer pruning and canopy transpiration caught our attention. Water consumption of apple trees is related to total canopy leaf area (Angelocci and Valancogne, 1993; Lakso, 1994). As water supply and canopy water status is another important factor besides carbohydrate supply that might affect fruit growth (Landsberg and Jones, 1981), smaller canopy size after summer pruning might favor fruit growth due to lower canopy transpiration. The inspiring result from this study indicated that canopy transpiration and water consumption might be one of the major variances in our hypothesis.

Materials and Methods

Plant Materials

In early May 1998, sixteen 20-year-old 'Empire' / M.9 slender spindle apple trees in four north-south rows at New York State Agricultural Experiment Station were selected (four trees from each row) for similar size, vigor, and bloom density. Trees were on average 1.75 m wide and 3.5 m tall, with spacing of 1.6 m between trees and 3.2 m between rows. Trees were well managed and had no nutrient deficiency or pest damage. In 1999 trees were irrigated with a portable irrigation system during a drought period from late July to early August to reduce the impact of drought stress, although some drought stress probably occurred. Trees received a routine winter pruning on 26 Jan. 1998 and 10 Feb. 1999, primarily thinning cuts into older wood to maintain an appropriate training system as in commercial practice. This resulted in the lighter pruning of the trees that received heavier pruning treatments in the summer. Conversely, the trees unpruned in the summer might receive the heaviest dormant pruning.

Summer Pruning Treatments and Leaf Area Estimation

Trees received summer pruning on 30 July 1998 and 4 Aug. 1999 after the cessation of growth of most extension shoots and the formation of terminal buds. Four pruning severities, severe, moderate, light, and control, were used in this experiment to create a range of final targets of leaf area removal. Since the outer of the four rows were adjacent to other training systems, the rows formed blocks.

Each of the four test trees in the same row was randomly assigned to one of the following pruning treatments. All pruning cuts were thinning cuts

to remove entire shoots. No heading cuts were used. The severe pruning removed most extension shoots from the canopy. The moderate pruning treatment thinned out most extension shoots from the middle part of the canopy, and about 50% from the upper and lower part of the canopy, respectively. The light pruning thinned out about 50% of the extension shoots from the middle canopy and 25% from the upper canopy. Trees without summer pruning served as controls. The adjacent trees to the north and south of each test tree received similar pruning treatments to better simulate the pruning of adjacent trees in real orchards. However, the size of the experimental block did not allow all adjacent rows to be pruned the same way. Strong upright branches, water sprouts, and hanging branches were the first priority to be removed.

Leaf area of each test tree was estimated with a detailed shoot sampling approach modified from Lakso (1984) and Wünsche and Palmer (1997b). Shoots were first categorized into five types: I) lateral short shoots on one-year-old woods; II) weak spurs and spurs with fruits; III) terminals, vigorous spurs with or without fruits, and spurs with bourse shoots shorter than 4 cm; IV) spurs with bourse shoots longer than 4 cm; V) spurs with extension shoots. The number of each shoot type on each tree was recorded after the canopy was fully developed before our pruning treatments. Lengths of individual type IV and type V shoots on each tree were also measured. Fifty to 100 of each shoot type were randomly sampled from adjacent trees in the block to estimate the average leaf area per spur of type I, II, and III, and to develop regressions between leaf area and shoot length for type IV and V shoots. Total leaf area of the canopy was then estimated by summing the leaf area of type

IV and V shoots obtained from the regressions and the average respected leaf area multiplied by the number of the type I, II, and III shoots.

Leaf area removed by summer pruning from each tree was measured with a weighted sampling approach. The weight of all leaves collected from pruned shoots from each tree were measured. A sample of 20% to 40% of the leaves in weight was then measured directly for leaf area with an image analysis system (AgVision, Decagon Devices, Inc., Pullman, Wash.) to calculate by the area-to-weight proportionality and the total leaf area removed from each tree.

The percentage of leaf area removal of each test tree after summer pruning was calculated from the ratio of leaf area removal to the pre-pruning canopy total leaf area.

Canopy Light Interception Measurement

Measurements were taken with ceptometer and point grid approaches in 1998 and 1999, respectively following the procedure described by Wünsche et al. (1995) with slight modifications. Canopy light interception was estimated in overcast conditions on 28 July 1998, a day before summer pruning with a linear PAR ceptometer (AccuPAR, Decagon Devices, Inc., Pullman, Wash.) and an above-canopy reference quantum sensor (Li-1000, Li-Cor, Lincoln, Nev.). Light interception was estimated again on 5 Aug. 1998 after treatments. Percentage of light interception was calculated from the ratio of the average value of 16 readings, eight on each tree side recorded with the ceptometer, to one reading for the open-sky above-canopy taken with the quantum sensor for each test tree.

In 1999, light interception was recorded with a point grid under a clear sunny sky between 1320_{HR} to 1430_{HR} on 4 Aug. right before the trees receiving pruning treatments, and again on 14 Aug. after pruning. A 1.5 m x 1.6 m white plastic sheet with 110 grid points evenly distributed was laid below one side of a test tree. Mid-day readings of direct light were used to reduce the effects of pruning of adjacent trees and rows. Percentage of direct light interception was calculated by the ratio of number of the grid points in the shadow cast by the tree to the total points. Canopy light interception (direct light in this case) was then obtained from the average value of readings from both sides of the test tree.

Leaf Gas Exchange

The photosynthesis rate of two to three well-exposed, healthy bourse leaves from each test tree was periodically measured from June until early September 1998 with a portable open-system gas analyzer (CIRAS-I, PP-systems, Hitchin, Herts, U.K.) under clear sunny conditions between 0830_{HR} to 1530_{HR} solar time. The measurement of different treatments were blocked over time to reduce effects of any diurnal trends.

Whole-Canopy Gas Exchange

Whole-canopy net CO₂ exchange rate was measured with an open-flow clear "balloon" type gas-exchange chamber system following the procedure modified from Corelli-Grappadelli and Magnanini (1993), Francesconi et al. (1996) and Lakso et al. (1996). Four identical Mylar plastic canopy chambers were used in this experiment (Figure 3.1). The chambers were cylinders, 2 m tall, 1.8 m in diameter, with 1 m tall open-end conical tops when inflated. The



Figure 3.1 Photograph of the open-flow "balloon" type gas-exchange chambers on test trees at the experimental site in Geneva, N.Y.



Figure 3.2 Photograph of the pipes, blowers, buffer tank, and canopy gas-exchange chambers on test trees at the experimental site in Geneva, N.Y.

total chamber volume was approximately 6000 L. After trees were enclosed in the chambers, an average 6000 to 7500 L min⁻¹ airflow was pumped into the chamber through a 2 m long 15 cm diameter PVC pipe by a shaded pole blower (1030 rpm and 6.8 amperes, Dayton Electric Mfg. Co., Chicago). Air was introduced from the atmosphere 2.5 m above the ground into a 1600 L (0.9 m x 0.9 m x 2 m) buffer tank before the chamber to reduce any fluctuations in ambient CO₂ concentrations (Figure 3.2).

Inside the chamber, the air flowed through a 15 cm in diameter perforated aluminum manifold surrounding the trunk near the base of the chamber to ensure a well-mixed flow through the canopy. The air velocity in the center of the PVC pipe was measured from an access hole 1 m from the inlet with a hot wire micro-anemometer probe (127MSX Solomat Instruments, Norwalk, Conn.). Three readings of air velocity were taken in the center of the cross-section of the pipe, 2.5 cm, and 5 cm from the center, respectively. Volume flow was obtained from the sum of the velocity readings from three different depths of the pipe multiplied by the respective cross section area of the pipe where they represented. This was also checked by a calibration using the dilution of pure CO₂ injected into the flow system.

Measurements were taken in clear sunny days. The four test trees in the same row were simultaneously enclosed in the four chambers. Once the microclimate inside the chambers was stable, inlet, outlet, and canopy air temperature was recorded with shielded thermocouples in the inlet PVC pipe, inside the chamber near the top, and 1.5 m above ground inside the canopy, respectively. CO₂ and water vapor concentrations were measured with a CIRAS-I portable open-system gas analyzer (PP-systems, Hitchin, Herts, U.K.) by sampling air from the inlet pipe and from the outlet at the top of the

chamber. Light was recorded above canopy with a quantum sensor (Li-100 with Li-185A, Li-Cor, Lincoln, Nebr.). The light transmission of the chambers was estimated at 86% to 88% of PAR.

After readings were recorded, chambers were moved to the next four trees in the next row following the same procedure as described. Readings for 16 test trees were recorded at the same day between 1000_{HR} to 1430_{HR} solar time. Previous measurements suggested relatively stable canopy NCE between 1000_{HR} and 1500_{HR} solar time on clear days (Lakso, unpublished data). Measurements were taken on 30 July 1998, a day before pruning treatment and on 4 Aug. 1999, the same day right before summer pruning. After treatment, whole-canopy gas exchange was monitored again on 31 July, 11 Aug., 12 Aug., 18 Sept. 1998, as well as 6, 9 and 31 Aug. 1999.

Whole canopy NCER was calculated from the ΔCO_2 between the inlet and outlet multiplied by volume flow. Whole canopy transpiration was calculated from $\Delta\text{H}_2\text{O}$ multiplied by volume flow rate. For comparing pruning treatment effects, the influence of temperature fluctuations on vapor pressure and transpiration was reduced by analyzing data with temperature above and below 26 °C separately.

Results and Discussion

Summer Pruning Suppressed Shoot Growth and Controlled Canopy Size

One of the major purposes for growers performing summer pruning is to suppress shoot growth to control the canopy size and maintain the structure of training systems. Upshall and Barkovic (1963) reported 29% less in tree size of 'Northern Spy'/M.9 trees after 10 years summer pruning. Utermark (1977)

indicated after four years summer pruning, canopy diameter of mature 'Ingrid Marie' apple trees was reduced 40% from 5 m to 3 m. Taylor and Ferree (1984) reported 43% less canopy volume of summer pruned mature 'Jonathan' /M.26 trees. After the cessation of shoot growth and the canopy was fully developed in early summer of 1998 before our summer pruning was applied, the average leaf area of our test trees was 9 m². Average leaf area removal by light, moderate, and severe pruning treatments in 1998 was 20%, 37%, and 55%, respectively (Figure 3.3). Canopy leaf area of the same trees before the second year of pruning in 1999 was reduced in relation to the pruning severity of previous year (Figure 3.4). On average, canopy leaf area of control trees increased 33% from 9 m² to 12 m². Leaf area of light and moderate pruned trees slightly increased 10% to 10 m². Severe summer pruning reduced the total canopy leaf area to 8.6 m², suggesting summer pruning effectively controlled the canopy expansion.

In some early studies where heading cuts were used, greater shoot growth in the following year after summer pruning was recorded (Barden and Marini, 1984; Belter and Thomas, 1980; Ellenwood and Fowler, 1944; Ellenwood and Fowler, 1944; Marini and Barden, 1982a, 1982d; Taylor and Ferree, 1984). However, other studies where thinning cuts were used or pruning approaches were not mentioned suggested that summer pruning tended to suppress shoot growth (Mika et al., 1983; Myers and Ferree, 1983b; Platon and Zagrai, 1997; Prestone and Perring, 1974; Saure, 1985). Saure (1985) indicated that number of shoots and total shoot length were reduced with increasing pruning severity while mean shoot length increased.

In our experiment, there was no clear relationship between pruning severity in 1998 and the average extension shoot length for 1999 (data not

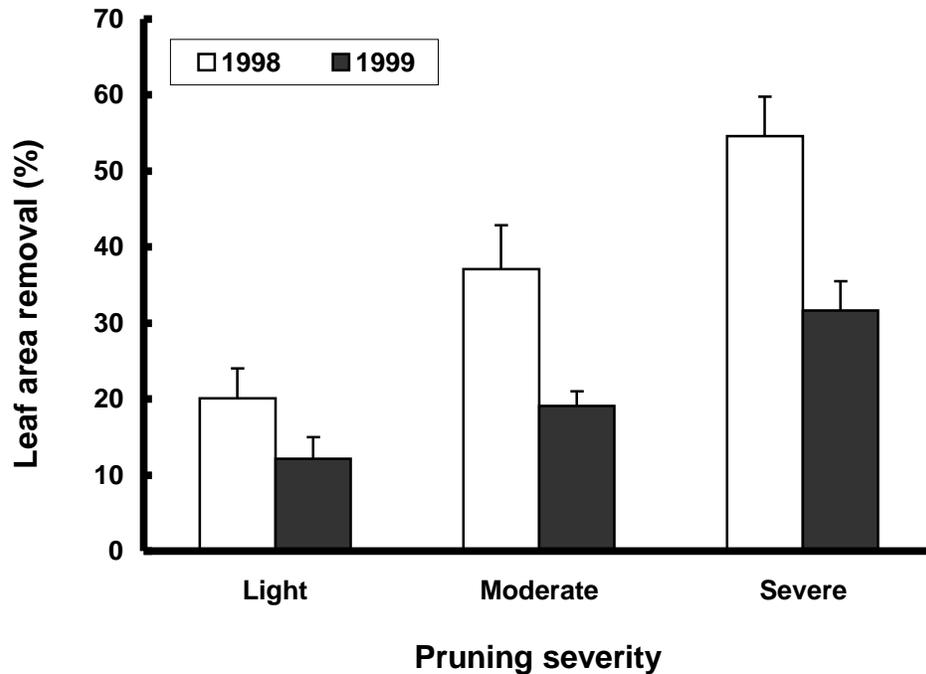


Figure 3.3 Percentage of leaf area removal by summer pruning treatments on 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999, respectively. Each individual tree received similar pruning treatment in both years. Three trees also received a routine winter pruning on 10 Feb. 1999. Vertical bars represent standard errors.

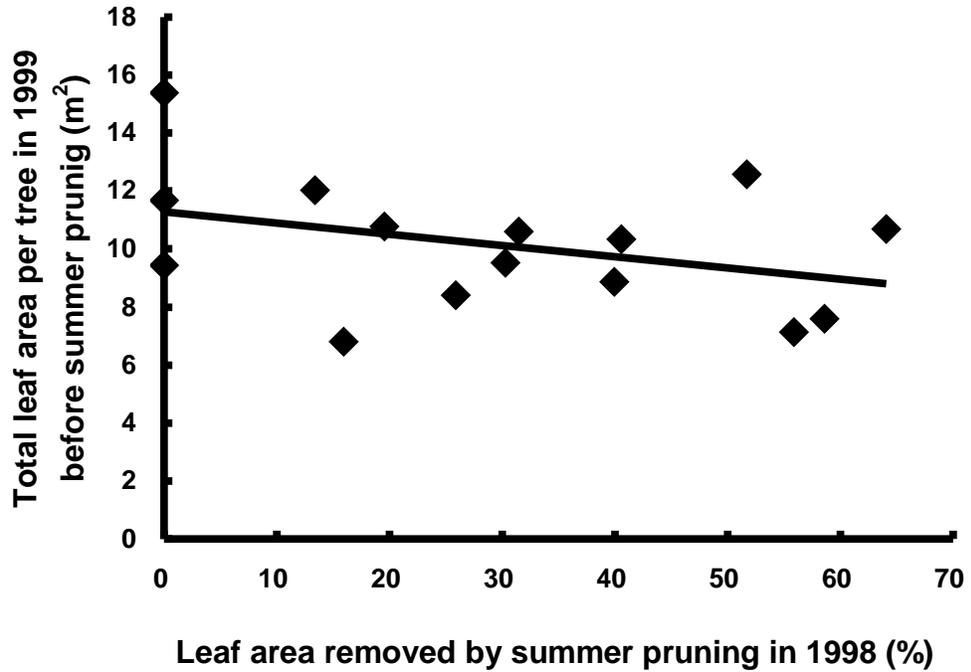


Figure 3.4 Correlation between canopy development in 1999 and summer pruning applied on 20-year-old slender spindle 'Empire' /M.9 apple trees in 1998. Sixteen test trees were pruned on 30 July 1998. Canopy leaf area was measured after the cessation of shoot growth on late July 1999. Threes also received a routine winter pruning on 10 Feb. 1999. The regression is $y = -0.0386x + 11.275$, $r^2 = 0.14$.

shown). Instead, all test trees tended to grow a larger number but shorter extension shoots. Consequently, less leaf area from each test tree was removed in 1999 by the similar pruning severity of 1998. 12%, 19%, and 32% leaf area were removed by light, moderate, and severe pruning, respectively (Figure 3.3). Saure (1985) concluded that forecasts of growth behavior of apple trees following pruning are unreliable. Our experiences suggested that it is likely due to the growth pattern which is not only related to pruning treatment but also the varieties, weather condition, cropping, and blooming of previous and current years. The season of 1999 was hotter and drier than in 1998. Combined with the heavier crop in 1999, the drier conditions likely caused the generally reduced growth.

Regrowth of shoots shortly after summer pruning has been reported in many studies (Miller, 1982; Taylor and Ferree, 1981; Taylor and Ferree, 1984). From a potted young apple tree trial, Taylor and Ferree (1981) suggested that the loss of leaf area by summer pruning could be partially compensated by leaves from the subsequent regrowth. Report from Ogata et al. (1986) on 5 year-old 'Fuji' trees indicated that the regrowth was so vigorous that the leaf area eventually exceeded the original leaf area before summer pruning. However, there was no significant regrowth in our studies except a few new leaves and rarely some off-season flowers around the pruning sites in early September 1998. The off-season blooming was also reported by Ogata et al. (1986).

The post-pruning regrowth and shoot growth in the next growing season following summer pruning occurred more often on young trees and especially when summer pruning was carried out in the early growing season before shoot growth terminated (Elfving, 1976, Kikuchi et al., 1989; Maggs, 1965;

Ogata et al., 1986). Morgan et al. (1984) reported that regrowth was minimal in late summer pruned trees. In addition to the timing of summer pruning, Miller (1982) pointed out the post-pruning regrowth might be affected by seasonal weather patterns. It might also vary among varieties or the pruning styles (Lord et al., 1979b). The studies of Lord et al. (1979a) in 'Cortland' and 'McIntosh' with timing and cutting styles similar to our experiment reported no regrowth after pruning treatment. Together with our observations, this suggests that in the New York and Northeast areas, post-pruning regrowth on these major varieties could be avoided if summer pruning is carried out after the cessation of extension shoot growth and with a thinning cut style of pruning.

Summer Pruning Affected Canopy Light Interception

Another purpose of summer pruning is to improve fruit coloring by opening the canopy and thus increase the canopy light environment, which has been documented by our previous study (Chapter two) and by other scientists (Marini and Barden, 1982b; Taylor and Ferree, 1984; Warrington et al., 1984). However, the removal of shoots and leaves might also result in less total canopy light interception due to the reduction in canopy size. On 28 July 1998, a day before our first pruning trial, the canopy light interception for the test orchard was 64.3%. Canopy light interception was slightly reduced in relation to the summer pruning severity when measurement was taken on 5 Aug. 1998 (Figure 3.5). On average, light and moderate pruning treatments reduced canopy light interception by 21%, and severe pruning reduced light interception by 28%. The smaller reduction in canopy light interception

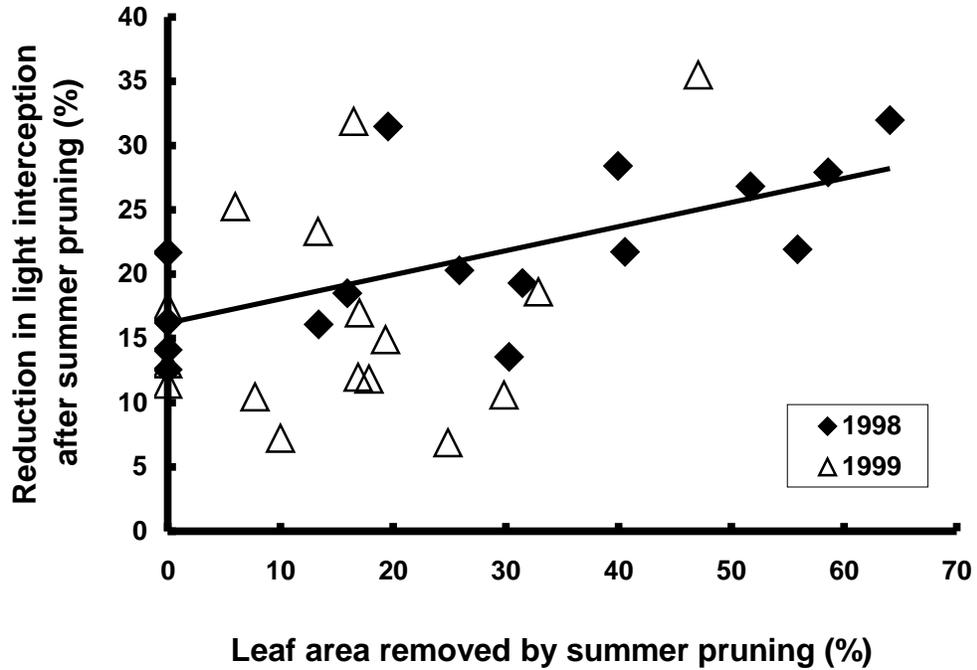


Figure 3.5 Correlation between canopy light interception and percentage leaf area removal by summer pruning on 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999. Canopy light interception was estimated on 28 July and 5 Aug. 1998, and 4 Aug. and 14 Aug. 1999. The regression for 1998 data is $y=0.1881x+16.166$, $r^2 = 0.44$.

compared to leaf area after summer pruning was expected because part of the sunlight originally intercepted by the extension shoots and leaves on the exterior of the canopy was captured by the spur leaves at the interior canopy after the extension shoots were thinned off (Chapter two). Evidence was also provided by Palmer et al. (1992) who reported that LAI was decreased by 10% to 30% after summer pruning, while light interception was only reduced by 6% to 14%.

Palmer (1993) pointed out variances and difficulties of light interception measurement in discontinuous canopies such as apple orchard. These variances might be amplified due to the uninformed canopy size and structure after pruning treatment. Therefore, the reduction in canopy light interception recorded from the unpruned trees was likely an experimental limitation due to the lack of buffer trees on adjacent rows (Figure 3.5). We were unable to provide enough buffer trees in the adjacent rows due to the small orchard size. Therefore, when parts of the tree canopies in the adjacent rows were removed after different severity of summer pruning treatment, the allotted area under the control trees might actually receive more sunlight, resulting in apparent reduction in light interception. A regression with stronger slope would be expected if trees in the adjacent rows also received similar pruning severity.

On 4 Aug. 1999, 49% direct sunlight was intercepted by the orchard canopy. However, to avoid the impact of the lack of buffer trees in the adjacent rows and even less uniformity of canopy size of each trees due to the different treatment in previous year, only mid-day readings were recorded. Therefore, the result might not be able to represent the canopy light interception in 1999 (Figure 3.5).

Summer Pruning Effects on Leaf and Whole Canopy NCER

Results from previous research (Chapter two) indicated that the NCER of the pre-shaded spur leaves was not significantly recovered after re-exposure by summer pruning. In the growing season of 1998, we tested the effect of summer pruning on photosynthetic ability of well-exposed leaves at bourse shoots on the exterior of the canopy. In clear sunny days before summer pruning leaf NCER was 16 to 17 $\mu\text{mol m}^{-2} \text{s}^{-1}$, similar to the photosynthetic efficiency of well-exposed spur leaves recorded about the same time of the year from our previous study. Marini and Barden (1982c) reported that summer pruning increased leaf Pn of potted young apple trees. They also reported that Pn of leaves of the peripheral canopy of mature trees was increased by summer pruning and the higher Pn rate last until early October. However, in our observation, similar to those of mature spur leaves, leaf Pn of mature bourse shoot leaves did not significantly respond to summer pruning, and there is no clear relationship between Pn and pruning severity (Figure 3.6). In general, leaf Pn gradually decreased over the growing season as we observed from spur leaves in previous study (Chapter two) and as reported by other scientists (Marini and Barden, 1982c; Wünsche and Palmer, 1997a). However, we noticed higher leaf Pn rates on 4 Sept. compared to readings from 22 Aug. and other measurement dates (Figure 3.6). Palmer (1992) also observed higher NCER in the late growing season and suggested that it was likely due to alleviation of water stress by rain. Since 1999 was quite dry, the higher reading on 4 Sept. was possibly related to cooler temperatures and rainfall on the previous day.

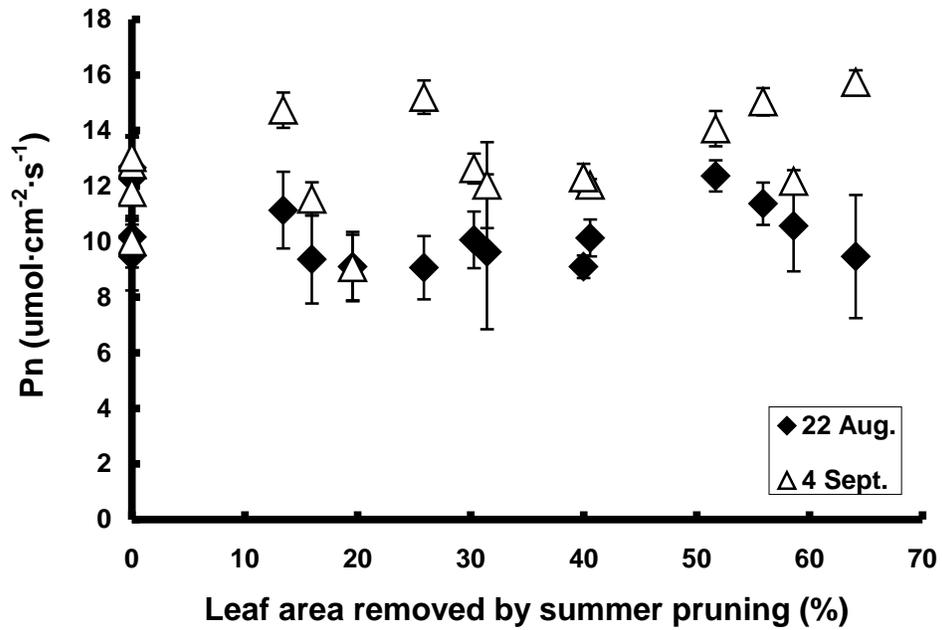


Figure 3.6 Relation between leaf net photosynthesis (Pn) and summer pruning severity in 20-year-old slender spindle 'Empire'/M.9 apple trees. Summer pruning was carried out on 30 July 1998. Data represents the average value of readings from two to three well-exposed bourse leaves. Vertical bars represent standard errors.

Marini and Barden (1982b) suggested that canopy light levels were improved after summer pruning, and the improved light might delay leaf senescence. Consequently, they predicted that summer pruning might not reduce whole-tree photosynthesis as much as would be expected based on leaf surface area of the tree. However, our results suggested that whole-canopy photosynthesis was approximately proportionally reduced by summer pruning in relation to pruning severity in both years (Figure 3.7). Average instant readings from clear sunny conditions before summer pruning in 1998 reached $145 \mu\text{mol s}^{-1}$ ($\cong 15.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). Control trees maintained high NCER after summer pruning, while average readings from test trees received light, moderate, and severe summer pruning reduced to 121, 95, and 66 $\mu\text{mol s}^{-1}$, respectively, which were 16.6%, 34.5%, and 54.5% reduction. The reduction in canopy NECR following summer pruning in 1999 showed a trend similar to which in 1998, up to 43% reduction in canopy NCER was recorded from the most severely pruned test tree from which 47% leaf area was removed (Figure 3.7). The reduced canopy NCER was possibly due to the combination of 1) decreased canopy light interception after summer pruning and 2) increased percentage of pre-shaded spur leaves representing the whole canopy leaf area. Growers tended to apply summer pruning with severity similar to our moderate to severe treatments. Our result shows that a strong impact on canopy carbohydrate supply could happen following summer pruning, indicating the important role of carbon balance in the influence of summer pruning on physiology and productivity in apple trees.

There was no measurable increase in canopy NCER per unit of leaf area in related to summer pruning severity, providing further evidence of the insignificant leaf Pn recovery on the interior canopy.

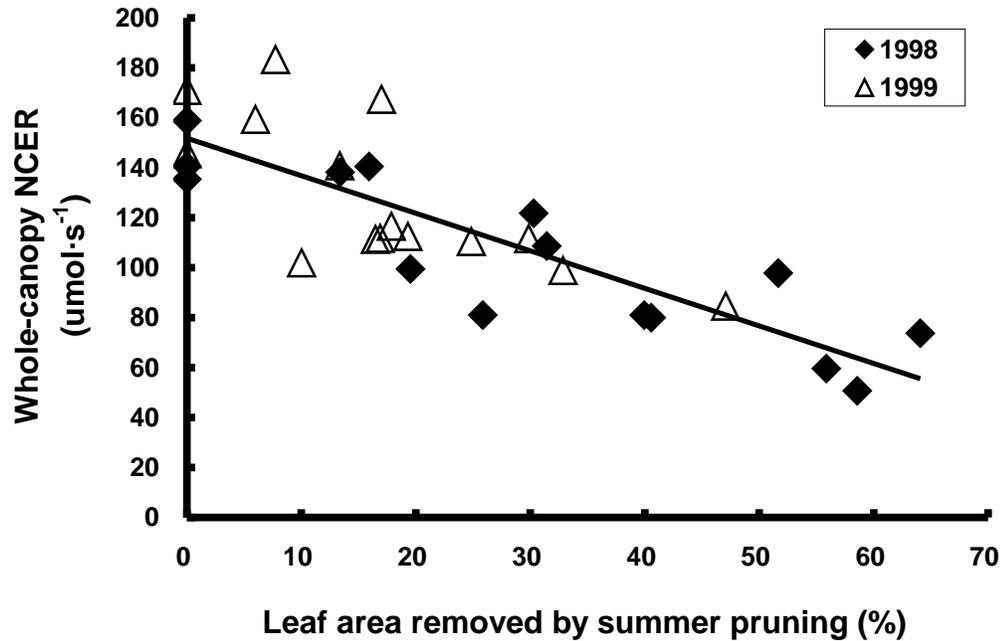


Figure 3.7 Whole canopy net CO₂ exchange rate (NCER) as a function of summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999. Data represents average values of readings recorded on 31 July, 11 and 12 Aug., and 18 Sept. 1998, and 6, 9, and 31 Aug. 1999. The regression is $y = -1.5x + 151.9$, $r^2 = 0.69$.

Summer Pruning Reduced Canopy Transpiration and Water Use Efficiency (WUE)

Whole-canopy transpiration was also reduced by summer pruning in related to pruning severity, especially when the measurement was taken in higher air temperature (Figure 3.8). After summer pruning in 1998, instantaneous readings of the transpiration from control trees above 26 °C maintained high at 15.2 mmol s⁻¹, while the average readings from trees after light, moderate, and severe pruning treatments decreased to 13.1, 12.8, and 9.4 mmol s⁻¹, respectively, which were 13.8%, 15.8%, and 38.2% reduction. In the most severely pruned tree, 58% leaf area was removed and the canopy transpiration was only 7.4 mmol s⁻¹, which was 53.2% less. Similar correlation between canopy transpiration and pruning severity was obtained from 1999. Atkinson (1978) reported that canopy water loss was approximately proportional to leaf area for apples. Landsberg and Jones (1981) indicated that leaf area and its distribution are important factors determining evaporation from orchard. Therefore, smaller leaf areas and light interception of the pruned trees might require less water consumption during the warmer and dryer growing season.

Early studies suggested that leaf transpiration rate after summer pruning did not change in potted tree experiments (Taylor and Ferree, 1981; Myers and Ferree, 1983a). Marini and Barden (1982c) reported summer pruning increased transpiration rate of mature Delicious apple interior leaves due to better exposure but less effect on exterior leaves. Transpiration rate of well-exposed exterior bourse shoot leaves from leaf gas exchange measurement in 1998 was not related to pruning treatment. In addition, transpiration rate of spur leaves from different canopy locations in previous study (Chapter two) showed a

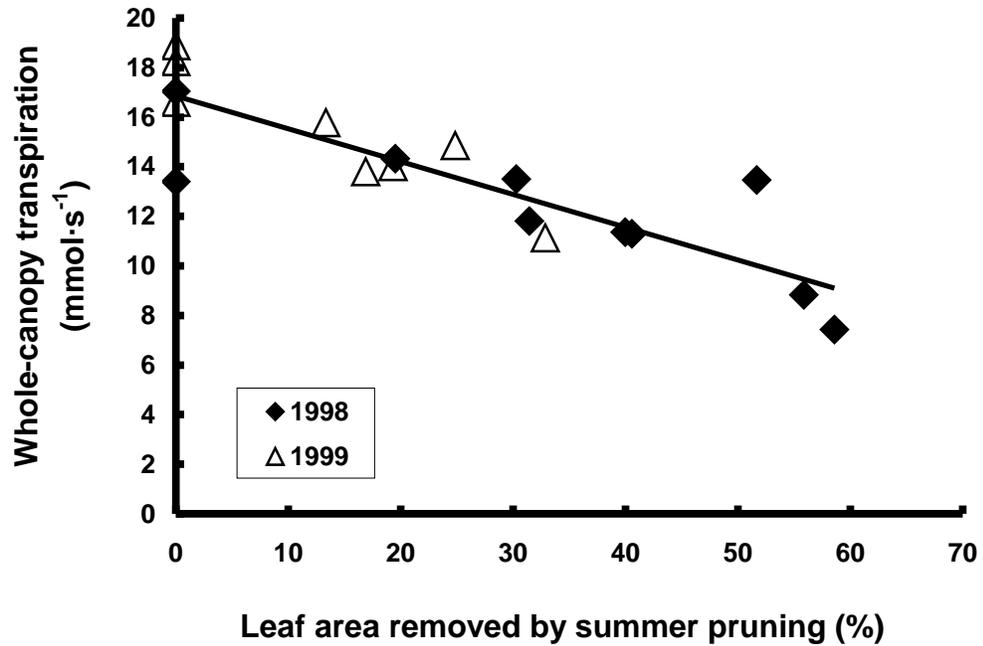


Figure 3.8 Whole canopy transpiration rate as a function of percentage leaf area removal by summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999. Data represents average values of readings recorded on 31 July, 11 and 12 Aug., and 18 Sept. 1998, and 6, 9, and 31 Aug. 1999. The regression is $y = -0.13x + 16.85$, $r^2 = 0.75$.

seasonal trend similar to those of leaf photosynthetic ability under saturated light, gradually decreasing over the season with a higher reduction rate on exterior leaves.

Mean leaf transpiration (canopy transpiration divided by leaf area) increased after summer pruning in relation to pruning severity even though the total canopy transpiration was reduced (Figure 3.9). Transpiration of apple leaves is closely related to photosynthesis and stomatal conductance (g_s) which are regulated by microclimate such as temperature, light, and leaf to air vapor pressure deficits (VPD) (Green and McNaughton, 1997; Lakso, 1983; Landsberg and Butler, 1980; Warritt et al., 1980) and by the presence of crop load (Giuliani et al., 1997; Wünsche and Palmer, 2000). Although g_s of the re-exposed interior leaves might increase in response to the increased light intensity after summer pruning, the possible simultaneously increased leaf to air VPD due to improved canopy ventilation after summer pruning might partly counterbalance the response of stomata to the light. This might diminish the importance of g_s influence in our study. However, Bulter (1976) and Landsberg et al. (1975) indicated that VPD is the driving force in the transpiration process of apple leaves that is increased when the leaves are heated by radiant energy. The rising canopy transpiration per unit of leaf area is possibly related to the energy balance and the dissipation of extra energy due to the increased average light exposure and energy absorption of the canopy after summer pruning. Consequently, water use efficiency was also affected by pruning severity (Figure 3.10). The removal of healthy extension shoot leaves, and the increase in the percent less photosynthetically functional

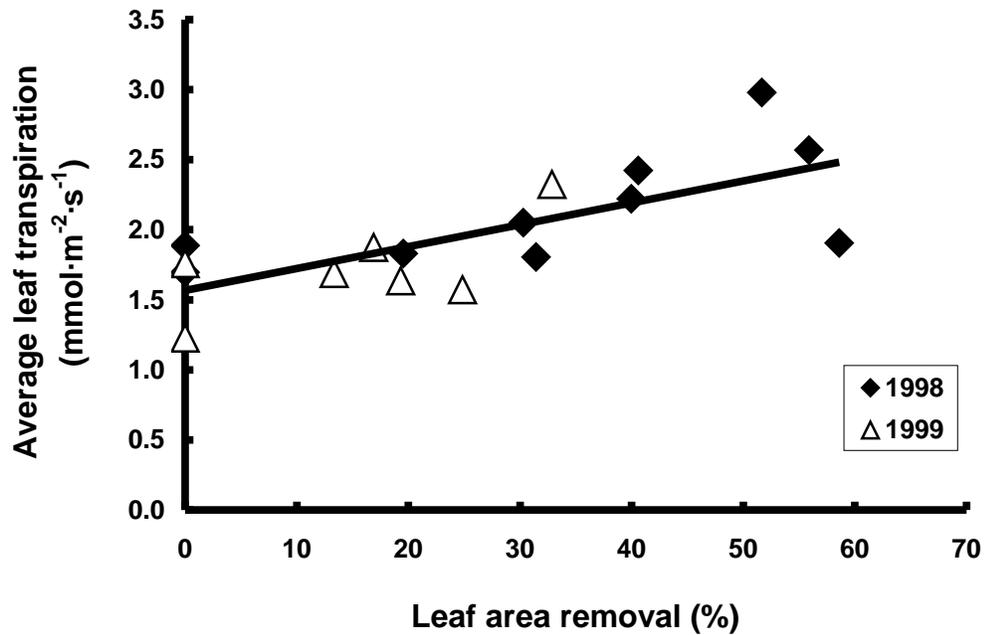


Figure 3.9 Correlation between canopy transpiration per unit leaf area and summer pruning severity in 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999. Data represents average values of readings recorded on 31 July, 11 and 12 Aug., and 18 Sept. 1998, and 6, 9, and 31 Aug. 1999. The regression is $y=0.0156x+1.5677$, $r^2=0.52$.

pre-shaded leaves of the canopy after summer pruning reduced the canopy WUE.

This might be physiologically undesirable, however, the reduced canopy water consumption and improved water status due to decreasing canopy transpiration may possibly be more significant in orchard management and fruit growth. Jones et al. (1985) pointed out that changes in canopy leaf area occurring naturally or artificially by pruning is expected to reduce water loss and decrease the depression of leaf and soil water potentials. A preliminary experiment in summer 2000 indicated that summer pruning immediately increased leaf and stem water potential (Figure 3.11), which was reported to be beneficial to fruit growth and fruit quality (Peretz et al., 1986). In dry years, as in this study, an apple tree after summer pruning might therefore benefit from better water status for fruit growth. This may potentially compensate for the disadvantage of reduced carbohydrate supply. In wet and cool years the water status may not be limiting and therefore the carbohydrate supply/demand effects may be more dominant.

Conclusion

Early studies tended to treat summer pruning as an alternative of dormant pruning. Comparisons were usually made between trees receiving either summer or dormant pruning alone. In contrast, today's growers tended to practice summer pruning in addition to winter pruning. Results from this study are more likely similar to the reality of modern apple orchard management. Clearly, canopy size and training systems can be controlled without undesirable post-pruning regrowth by the summer pruning approach

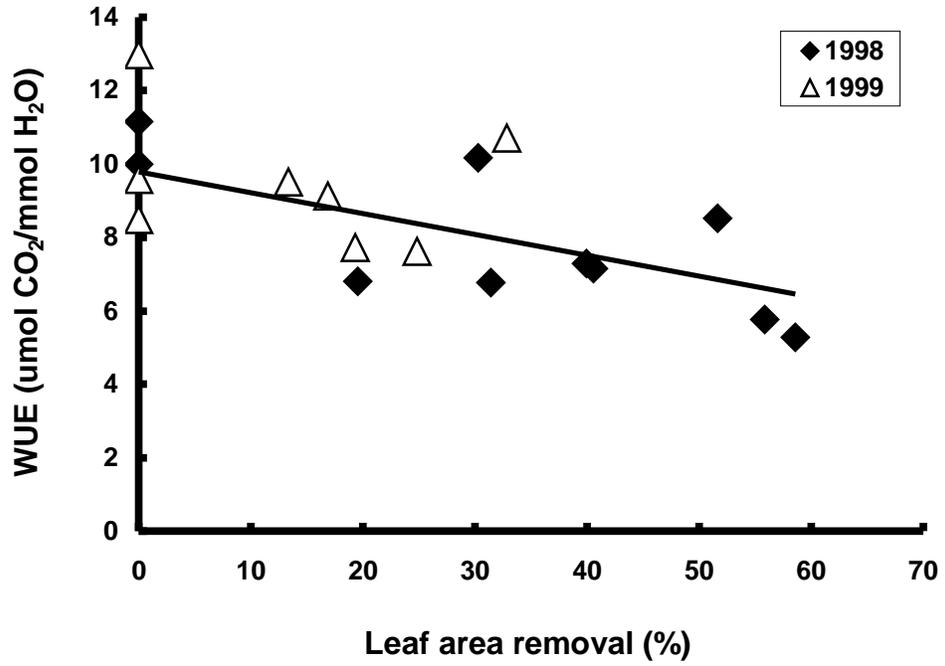


Figure 3.10 Correlation between canopy water use efficiency (WUE) and summer pruning severity in 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 4 Aug. 1999. Data represents average values of readings recorded on 31 July, 11 and 12 Aug., 18 Sept. 1998, and 6, 9, and 31 Aug. 1999. The regression is $y = -0.0565x + 9.783$, $r^2 = 0.42$.

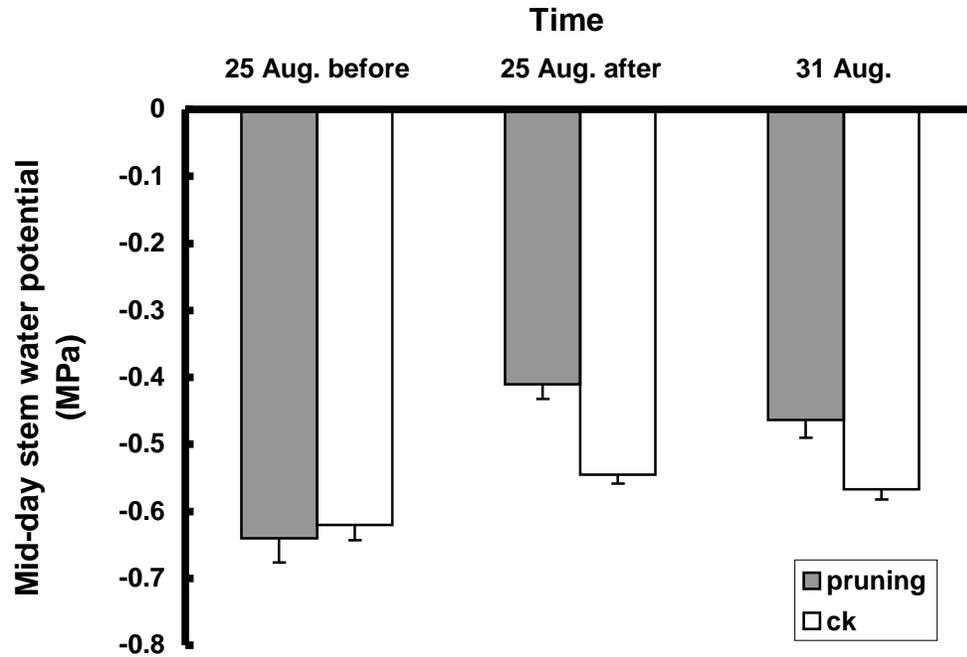


Figure 3.11 Mid-day stem water potential in relation to summer pruning in 20-year-old slender spindle 'Empire' /M.9 apple trees. Moderate summer pruning was carried out at 1400 HR, 25 Aug. 2000. Stem water potential was measured at 1340 HR to 1400 HR before pruning, and at 1420 HR to 1430 HR after pruning. Measurements were repeat at 1340 HR to 1430 HR, 31 Aug. 2000. Data represents average values of four leaves from one unpruned tree and 12 leaves from three pruned trees. Vertical bars represents standard errors.

we used. However, a strong reduction in canopy NCER was found due to the removal of leaf area, resulting in less photosynthetic assimilate supply, which might lead to smaller fruit size and yield, depending on the sink demand. This result provides a baseline for our next step to determine the impact of shortage of carbohydrate supply on fruit growth. In addition, the reduced canopy transpiration might be a potentially positive effect of summer pruning on fruit growth under dry conditions. Efforts to strengthen the relationship between carbohydrate and water regulation is of importance in the future studies.

References

- Alderman, W.H. and E.C. Auchter. 1916. The apple as affected by varying degrees of dormant and seasonal pruning. *W. Va. Agr. Exp. Sta. Bul.* 158:3-56.
- Angelocci, L.R. and C. Valancogne. 1993. Leaf area and water flux in apple trees. *J. Hort. Sci.* 68(2):299-307.
- Atkinson, D. 1978. Use of soil resources in high density planting systems. *Acta Hort.* 65:79-89.
- Barden, J.A. and R.P. Marini. 1984. Summer and dormant pruning of apple: A four year summary. *Acta Hort.* 146:263-268.
- Belter, H. and T.M. Thomas. 1980. Preliminary experiences in summer pruning of apples in Michigan. *Compact Fruit Tree* 13:100-101.
- Butler, D.R. 1976. Estimation of the transpiration rate in an apple orchard from net radiation and vapour pressure deficit measurements. *Agric. Meteorol.* 16:277-289.
- Corelli-Grappadelli, L. and E. Magnanini. 1993. A whole tree system for gas-exchange studies. *HortScience* 28(1):365-368.
- Elfving, D.C. 1976. Growth control in young apple trees. *Proc. New York State Hort. Soc.* 121:107-109.
- Ellenwood, C.W. and T.E. Fowler. 1944. Light and heavy pruning compared with no pruning of apples. *Ohio Agr. Exp. Sta. Bul.* 29:219-277.
- Ferree, D.C., S.C. Myers, C.R. Rom, and B.H. Taylor. 1984. Physiological aspects of summer pruning. *Acta Hort.* 146:243-251.
- Francesconi, A.H.D., A.N. Lakso, J.P. Nyrop, J. Barnard, and S.S. Denning. 1996. Carbon balance as a physiological basis for the interactions of European red mite and crop load on 'Starkrimson Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 121(5):959-966.

- Giuliani, R., F. Nerozzi, E. Magnanini, and L. Corelli-Grappadelli. 1997. Influence of environmental and plant factors on canopy photosynthesis and transpiration of apple trees. *Tree Physiol.* 17:637-645.
- Green, S.R. and K.G. McNaughton. 1997. Modelling effective stomatal resistance for calculating transpiration from an apple tree. *Agric. For. Meteorol.* 83:1-26.
- Jackson, J.E. 1980. Light interception and utilization by orchard systems. *Hort. Rev.* 2:208-267.
- Johnson, R.S. and A.N. Lakso. 1991. Approaches to modeling light interception in orchards. *HortScience* 26(8):1002-1004.
- Jones, H.G., A.N. Lakso, and J.P. Syversten. 1985. Physiological control of water status in temperate and subtropical fruit trees. *Hort. Rev.* 7:301-344.
- Kikuchi, T., T. Asada, and Y. Shiozaki. 1989. Effect of summer pruning on the next season's shoot growth of young apple trees. *J. Japan. Soc. Hort. Sci.* 58(3):491-497.
- Lakso, A.N. 1980. Aspects of canopy photosynthesis and productivity in the apple tree. *Acta Hort.* 114:100-109.
- Lakso, A.N. 1983. Morphological and physiological adaptations for maintaining photosynthesis under water stress in apple trees, p. 85-93. In: R. Marcelle, H. Clijsters, and M. van Poucke (eds.). *Effects of stress on photosynthesis*. Nijhoff/Junk, The Hauge, The Netherlands.
- Lakso, A.N. 1984. Leaf area development patterns in young pruned and unpruned apple trees. *J. Amer. Soc. Hort. Sci.* 109(6):861-865.
- Lakso, A.N. 1994. Apple, p.4-42. In: B. Schaffer and P.C. Anderson (eds.). *Handbook of environmental physiology of fruit crops*. Vol. I. Temperate crops. CRC. Press, Boca Raton, Fla.
- Lakso, A.N. and L. Corelli-Grappadelli. 1992. Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Hort.* 322:231-239.

- Lakso, A.N., G.B. Mattii, J.P. Nyrop, and S.S. Denning. 1996. Influence of European red mite on leaf and whole-canopy carbon dioxide exchange, yield, fruit size, quality, and return cropping in 'Starkimson Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 121(5):954-958.
- Lakso, A.N. and T.L. Robinson. 1997. Principles of orchard systems management optimizing supply, demand and partitioning in apple trees. *Acta Hort.* 451:405-415.
- Lakso, A.N., T.L. Robinson, and S.G. Carpenter. 1989. The palmette leader: A tree design for improved light distribution. *HortScience* 24(2):271-275.
- Lakso, A.N., J.N. Wünsche, J.W. Palmer, and L. Corelli-Grpadelli. 1999. Measurement and modeling of carbon balance of the apple tree. *HortScience* 34(6):1041-1047.
- Landsberg, J.J., C.L. Beadle, P.V. Biscoe, D.R. Butler, B. Davidson, L.D. Incoll, G.B. James, P.G. Jarvis, P.J. Martin, R.E. Neilson, D.B.B. Powell, E.M. Slack, M.R. Thorpe, N.C. Turner, B. Warrit, and W.R. Watts. 1975. Diurnal energy, water and CO₂ exchanges in an apple (*Malus pumila*) orchard. *J. Appl. Eco.* 12:659-684.
- Landsberg, J.J. and D.R. Butler. 1980. Stomatal response to humidity: Implications for transpiration. *Plant, Cell & Environ.* 3:29-33.
- Landsberg, J.J. and H.G. Jones. 1981. Apple orchards, p.419-469. In: T.T. Kozlowski (ed.). *Water deficits and plant growth*. Vol. 6. Academic Press, N.Y.
- Lord, W.J., D.W. Greene, W.S. Bramlage, and M. Drake. 1979a. Inducing flowering of apple trees and increasing fruit quality by summer pruning. *Compact Fruit Tree* 12:23-39.
- Lord, W.J., D.W. Greene, and R.A. Damon, Jr. 1979b. Flowering of young apple trees following summer pruning. *J. Amer. Soc. Hort. Sci.* 104(4):540-544.
- Maggs, D.H. 1965. Dormant and summer pruning compared by pruning young apple trees once on a succession of dates. *J. Hort. Sci.* 249-265.

- Marini, R.P. and J.A. Barden. 1982a. Growth and flowering of vigorous apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):34-39.
- Marini, R.P. and J.A. Barden. 1982b. Light penetration on overcast and clear days, and specific leaf weight in apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):39-43.
- Marini R.P. and J. A. Barden. 1982c. 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(1):170-174.
- Marini, R.P. and J.A. Barden. 1982d. Yield, fruit size, and quality of three apple cultivars as influenced by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(3):474-479.
- Marini, R.P. and J.A. Barden. 1987. Summer pruning of apple and peach trees. *Hort. Rev.* 9:351-375.
- Mika, A. 1986. Treatments improving illumination of the fruiting zone of the tree, p. 42-45. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.*
- Mika, A., M.J. Grochowska, and A. Karaszewska, and M.W. Williams. 1983. Effects of dormant and summer pruning, disbudding, and growth retardants on growth, flower bud formation, and fruiting of young apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):655-660.
- Miller, S.S. 1982. Regrowth, flowering, and fruit quality of 'Delicious' apple trees as influenced by summer pruning. *J. Amer. Soc. Hort. Sci.* 107(6):975-985.
- Morgan, D.C., C.J. Stanley, R. Volz, and I.J. Warrington. 1984. Summer pruning of 'Gala' apple: The relationships between pruning time, radiation penetration, and fruit quality. *J. Amer. Soc. Hort. Sci.* 109(5):637-642.
- Myers, S.C. and D.C. Ferree. 1983a. Influence of summer pruning and tree orientation on net photosynthesis, transpiration, shoot growth, and

- dry-weight distribution in young apple trees. *J. Amer. Soc. Hort. Sci.* 108(1):4-9.
- Myers, S.C. and D.C. Ferree. 1983b. Influence of time of summer pruning and limb orientation on growth and flowering of vigorous 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):634-638.
- Ogata, R., H. Kikuchi, T. Hatayama, and H. Komatsu. 1986. Growth and productivity of vigorous 'Fuji' apple trees on M.26 as affected by summer pruning. *Acta Hort.* 160:157-165.
- Palmer, J.W. 1993. Recent developments on light and fruit tree canopies. *Acta Hort.* 349:99-109.
- Palmer, J.W. 1992. Effects of varying crop load on photosynthesis, dry matter production and partitioning of Crispin/M.27 apple trees. *Tree Physiol.* 11:19-33.
- Palmer, J.W. 1989. Canopy manipulation for optimum utilization of light, p. 245-262. In: C.J. Wright (ed.). *Manipulation of fruiting*. Butterworths, London.
- Palmer, J.W., D.J. Avery, and S.J. Wertheim. 1992. Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Sci. Hort.* 52:303-312.
- Peretz, J., E.L. Proebsting, and R.G. Evans. 1986. Effects of managed water deficit on relative fruitfulness, growth and fruit quality of apples, p. 79-84. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees*. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.
- Platon, I. and L. Zagrai. 1997. The influence of training system and pruning time on growth and apple fruiting. *Acta Hort.* 451:513-518.
- Porpiglia, P.J. and J.A. Barden. 1981. Effects of pruning on penetration of photosynthetically active radiation and leaf physiology in apples trees. *J. Amer. Soc. Hort. Sci.* 106(6):752-754.
- Preston, A.P. and M.A. Perring. 1974. The effect of summer pruning and nitrogen on growth, cropping and storage quality of Cox's Orange Pippin apple. *J. Hort. Sci.* 49:77-83.

- Robinson, T.L., A.N. Lakso, and Z. Ren. 1991. Modifying apple tree canopies for improved production efficiency. *HortScience* 26(8):1005-1012.
- Saure, M. 1985. Der Einfluss von Schnittzeitpunkt und Schnittintensität auf Wachstum und Wuchsleistung junger Apfelbäume. *Erwerbsobstbau* 27:169-173.
- Saure, M.C. 1987. Summer pruning effects in apple: A review. *Sci. Hort.* 30:253-282.
- Saure, M.C. 1992. Interference of pruning with endogenous growth control. *Acta Hort.* 322:241-247.
- Stiles, W.C. 1980. Pruning, growth regulator, and nutrition studies with apples. *Maine Sta. Pom. Soc. Ann. Rep. for 1980*:25-34.
- 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(3):389-393.
- Taylor, B.H. and D.C. Ferree. 1984. The influence of summer pruning and cropping on growth and fruiting of apple. *J. Amer. Soc. Hort. Sci.* 109(1):19-24.
- Upshall, W.H. and J. Barkovic. 1963. Summer pruning of dwarf apple and pear trees. *Ontario Hort. Exp. Sta. & Prod. Lab. Ann. Rep.* 1963:16-19.
- Utermark, H. 1977. Summer pruning to control growth and maintain fruiting in mature apple trees. *Compact fruit tree* 10:86-90.
- Wagenmakers, P.S. and Callesen, O. 1995. Light distribution in apple orchard systems in relation to production and fruit quality. *J. Hort. Sci.* 70(6):935-948.
- Warrington, I.J., C.J. Stanley, R. Volz, and D.C. Morgan. 1984. Effects of summer pruning on Gala apple quality. *The Orchardist of New Zealand.* 12:518-522.
- Warrit, B., J.J. Landsberg, and M.R. Thorpe. 1980. Responses of apple leaf stomata to environmental factors. *Plant, Cell & Environ.* 3:13-22.

- Wünsche, J.N., and A.N. Lakso. 2000. The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *HortScience* 35(7):1202-1206.
- Wünsche, J.N., and J.W. Palmer. 2000. Effects of crop load on fruiting and gas-exchange characteristics of 'Braeburn'/M.26 apple trees at full canopy. *J. Amer. Soc. Hort. Sci.* 125(1):93-99.
- Wünsche, J.N., A.N. Lakso, and T.L. Robinson. 1995. Comparison of four methods for estimating total light interception by apple trees of varying forms. *HortScience* 30(2):272-276.
- Wünsche, J.N. and J.W. Palmer. 1997a. Effects of fruiting on seasonal leaf and whole-canopy carbon dioxide exchange of apple. *Acta Hort.* 451:295-301.
- Wünsche, J.N. and J.W. Palmer. 1997b. Comparison of non-destructive methods of estimating leaf area in apple tree canopies. *Acta Hort.* 451:701-707.

CHAPTER FOUR

SUMMER PRUNING EFFECTS ON FRUIT PRODUCTION AND QUALITY, RETURN BLOOM, AND ROOT GROWTH IN APPLE TREES

Abstract

While many undesirable effects of summer pruning on apple (*Malus domestica* Borkh.) growth and development have been reported, the results are inconsistent and difficult to interpret. However, our previous study indicated the potential impact of reducing canopy photosynthesis after summer pruning, depending on the balance of carbohydrate supply and demand. To test the hypothesis that summer pruning influences carbohydrate balance, we measured fruit growth, fruit quality, return bloom, trunk growth, and root growth in 20-year-old slender spindle 'Empire' /M.9 apple trees in response to severities of summer pruning. Results were interpreted in relation to pruning severity, cropping, and the integrated physiological crop load. Within commercial cropping ranges, light and moderate summer pruning had slight influences on fruit size and fresh weight. Summer pruning alone did not affect fruit color, soluble solids content, starch, and firmness. No effect on return bloom, trunk growth, and root development were recorded. However, the potential negative effects of summer pruning on fruit growth, return bloom, and root lifespan can be interpreted by their relationships with physiological crop load, i.e. canopy net carbohydrate exchange rate per fruit. This suggests that the carbohydrate supply and demand balance model may explain summer pruning influences. The impact of carbohydrate shortage after

summer pruning might be mediated by the reduction in canopy transpiration, and the annual weather pattern might play an important role on regulating the final output.

Additional Index Words

Malus domestica, carbohydrate supply and demand balance, trunk cross section area, minirhizotron, root lifespan

Introduction

Fruit color and size are the major criteria for commercial grading of red apple (*Malus domestica* Borkh.) varieties. The importance of light on apple fruit coloring has been well documented (Doud and Ferree, 1980; Jackson et al., 1977; Seeley et al., 1980; Saure, 1990). In addition, insufficient light or shading might suppress fruit size and quality (Jackson et al., 1971; Palmer and Warrington, 2000; Robinson et al., 1983), flower bud development (Cain, 1973; Lakso, 1980), fruit set (Jackson and Palmer, 1977) and fruit soluble solids content (Doud and Ferree, 1980; Seeley et al., 1980).

Although there are some theoretical and practical alternatives for fruit color improvement (Andris et al., 1996; Curry, 1997; Iglesias et al., 2000; Mika, 1986b; Moreshet et al., 1975; Smock, 1963, 1964), summer pruning, by removing shoots and leaves during the growing season, has been traditionally used to improve canopy light environment and thus enhance fruit color (Autio and Greene, 1990; Belter and Thomas, 1980; Engel, 1974; Lawson et al., 1998; Lord et al. 1979a; Stiles, 1980; Struklec, 1994; Ystaas, 1989, 1992), except

in some high-coloring strains in which fruit color has been found not affected by increasing light exposure or summer pruning (Barden and Marini, 1984; Robinson et al., 1983).

However, undesirable fruit size, yield, and internal quality have often been reported from tree after summer pruning (Katzler and Wurm, 1998; Myers and Ferree, 1983b; Olszewski and Mika, 1999; Redalen, 1992; Säkö and Laurinen, 1982; Taylor and Ferree, 1984; Upshall and Barkovic, 1963). In addition, changes in the growth and development of many parts of the apple trees, either positively or negatively, has been associated with summer pruning practice (Marini and Barden, 1987; Mika, 1986a; Saure, 1987). The highly varied results of summer pruning effects indicated that many factors such as varieties, orchard management, and environment are involved. Also, the term “summer pruning” is not precise regarding the type or the severity of pruning. It is therefore difficult to interpret summer pruning merely by a simple hypothesis.

However, a number of studies have noticed the importance of canopy carbohydrate supply (Lakso and Corelli-Grappadelli, 1992; Lakso et al., 1998; Lakso and Robinson, 1997; Poll et al., 1996) and the risk of leaf area removal by summer pruning on fruit growth and fruit quality (Ferree et al., 1984). In the previous report we successfully quantified the decreased canopy photosynthesis due to summer pruning (Chapter three). The close relationship between canopy net carbon exchange rate (NCER) and the pruning severity revealed the effects on carbohydrate supply. With the knowledge of crop demand, we can draw an outline of carbon balance in response to summer pruning. According to the hypothesis, the severity of the impact from carbohydrate shortage after summer pruning will depend on the demand and

the strength of individual carbohydrate sinks, such as growth and development of fruits and flower buds.

In addition, the root systems of mature fruit trees are believed to be very sensitive to variations in assimilate supply (Buwalda, 1993). A number of studies suggested that the root systems of young potted apple trees responded quickly to summer pruning or defoliation treatments (Head, 1967; Heinicke, 1935; Taylor and Ferree, 1981). In addition to summer pruning, decreased root growth of young trees with high fruit set has also been reported (Ebert, 1992; Ebert and Lenz, 1991; Forshey and Elfving, 1989; Maggs, 1963; Palmer, 1988). These results suggested that summer pruning should reduce carbohydrate balance and strongly affect root growth. However, due to the difficulties of accessing root system of mature trees, the influence of summer pruning on root systems of mature apple trees remains unclear.

In this report, we first examine the influences of decreasing canopy photosynthesis on fruit growth, fruit quality, return blooming, and trunk growth of 'Empire' /M.9 apple trees that received commercial cropping control and summer pruning treatments. With the recent technology of minirhizotron observation tubes and remote video systems (Cheng et al., 1991; Johnson et al., 2001) we were also able to monitor the in situ growth and lifespan of root of mature apple trees. The objectives of this study were to test the carbohydrate balance concept to explain summer pruning influences on fruit and root growth, and to identify the sensitivity of each to the changes of carbohydrate balance after summer pruning.

Materials and Methods

Plant Material and Summer Pruning Treatment

Sixteen 20-year-old slender spindle 'Empire'/M.9 apple trees in four north-south rows located in New York State Agricultural Experiment Station in Geneva, New York were used in this study. Trees were on average 1.75 m wide and 3.5 m tall, with spacing of 1.6 m between trees and 3.2 m between rows. Trees were well managed and had no nutrient deficiency or pest damage. In 1999 trees were irrigated with a portable irrigation system during a drought period from late July to early August to reduce the impact of drought stress, although some drought stress probably occurred. Trees received a routine winter pruning on 26 Jan. 1998 and 10 Feb. 1999, primarily thinning cuts into older wood to maintain an appropriate training system as in commercial practice. This resulted in the lighter pruning of the trees that received heavier pruning treatments in the summer. Conversely, the trees unpruned in the summer might have received the heaviest dormant pruning.

Test trees on each row were randomly treated with one of the four levels of summer pruning (unpruned, light, moderate, and severe) on 30 July 1998 and 4. Aug 1999. Each test tree received similar pruning severity in two successive years. Details of the pruning treatments, changes in leaf area, light interception, canopy NCER, and transpiration were quantified as described in a previous chapter (Chapter three).

Cropping Regulation

In early June 1998, trees were chemically-thinned with a combination of the synthetic auxin naphthaleneacetic acid (NAA) and the insecticide Sevin® (Carbaryl, that has thinning effects), followed by a light hand thinning to

reduce the fruit number while maintaining a natural variation of fruit set among the chosen trees. Since the crop loads were relatively light in 1998, heavier crops were desired in 1999. Therefore, no chemical thinning was applied in 1999; instead, on 3 June fruit clusters per tree were counted and a final target of 150 to 250 fruits per tree was made by hand thinning.

Fruit Growth and Final Yield

Twenty fruits per tree, 10 located in the inner canopy and the other 10 in the outer canopy, were labeled on 22 June 1998 and 8 July 1999, respectively, for fruit growth monitoring. Fruit diameter was recorded weekly with a digital micrometer (Ultra-cal III, Fowler, Boston) until harvest. Meanwhile, 10 fruits from the buffer trees in the same block were sampled weekly for fresh weight and dry weight estimation. Diameter, fresh weight, and dry weight after oven-drying were recorded. Regression equations of diameter to fresh weight and to dry weight for both growing seasons were then obtained and used for estimating fruit weight of the labeled fruits during the season.

Fruits were harvested on 28 Sept. 1998 and 30 Sept. 1999, respectively. Total fruit number and total fruit weight per tree were recorded at harvest. In addition to the 20 labeled fruits, another 40 fruits were randomly sampled during picking from each tree for fruit color estimation and internal quality tests.

Fruit Color and Internal Quality

Half of the randomly sampled fruits and all the labeled fruit were tested immediately after harvest. Fruit color was visually determined by estimating the percentage of acceptable red color area on the skin. Internal quality tests

included fruit firmness, starch, soluble solids, and internal breakdown after storage. Fruit firmness was recorded with a pressure tester (EPT-1-R, Lake City Technical Products Inc., Canada). Two readings from opposite sides, near the equator of the fruit, were recorded from each fruit. Soluble solids were measured with a portable refractometer (Atago, Japan). Fruit maturity was estimated with the starch-iodine index after staining equatorial cut surfaces of each test fruit with potassium-iodine solution. Maturity was then estimated following the Cornell University Generic Starch-Iodine Index Chart for Apples after the stained pattern was developed. All the measurements were finished within 24 hours after harvest. Data from labeled fruits and random samples were analyzed separately.

The rest of the randomly sampled fruits from each tree harvested in 1998 were stored in a cold room at 0 °C and about 80% relative humidity until Feb. 1999. Ten fruits were removed from the cold room on 7 Feb. 1999 and placed at room temperature for 7 days before internal breakdown was visually inspected through the cross section of the fruit. The other 10 fruits were examined on 21 Feb. 1999.

Return Bloom

Flower clusters were counted on 4 May 1999 and 8 May 2000, respectively. Number of flower clusters and vegetative buds on spurs and on 1-year-old extension shoots were recorded and analyzed separately.

Trunk Growth

Trunk cross section area was estimated from the average readings of trunk circumference recorded at 30 cm above ground and 30 cm above rootstock-scion conjunction on 14 May 1998 and 20 Oct. 1999, respectively.

Root Growth Observations

Nine trees from the 16 test trees were selected for root observation with a minirhizotron camera-video cassette recorder (VCR) system (Figure 4.1 and 4.2) (BTC-2, Bartz Technology, Santa Barbara, Calif.). On May 27 1999, three observation tubes (minirhizotrons) were installed at angle of 30 degrees from the vertical into the ground 75 cm away from the trunk of each selected tree (Figure 4.3). The minirhizotron for this study is made of 5 cm bore, 60 cm long clear butyrate tube with a single vertical row of 1.8 cm x 1.2 cm observation windows engraved which allow the roots in the soil as deep as 35 cm to be recorded (Figure 4.4). The bottom of the minirhizotron was sealed with a quick-seal rubber plug (570-012, Dorman Products, Warsaw, Ky.). Opaque tape, a rubber stopper and a white aluminum covers were used to prevent light from penetrating into the tube through the top.

Images of roots around the minirhizotron were recorded on 8 mm videotapes with the camera-VCR system every 10 to 14 days from 29 June 1999 to 18 Nov. 1999, and from 6 June 2000 to 3 Aug. 2000. The tapes were then reviewed on a videocassette recorder (EV-S7000, Sony Co., Tokyo) connected to a computer (Mac OS 8.6, Apple Computer, Inc., USA). Desirable images were then captured with Apple Video Player and manipulated with an image-editing program (PhotoDeluxe, Adobe Systems, Inc., San Jose, Calif.).



Figure 4.1 The controller, monitor, and video cassette recorder (VCR) of the minirhizotron camera-VCR system (BTC-2, Bartz Technology, Santa Barbara, Calif.).



Figure 4.2 The camera head module of the minirhizotron camera-VCR system (BTC-2, Bartz Technology, Santa Barbara, Calif.).



Figure 4.3 Photograph of three root observation tubes (minirhizotrons) installed around the test tree at the experimental site in Geneva, N.Y.



Figure 4.4 The root observation tube (minirhizotron) used in this study.

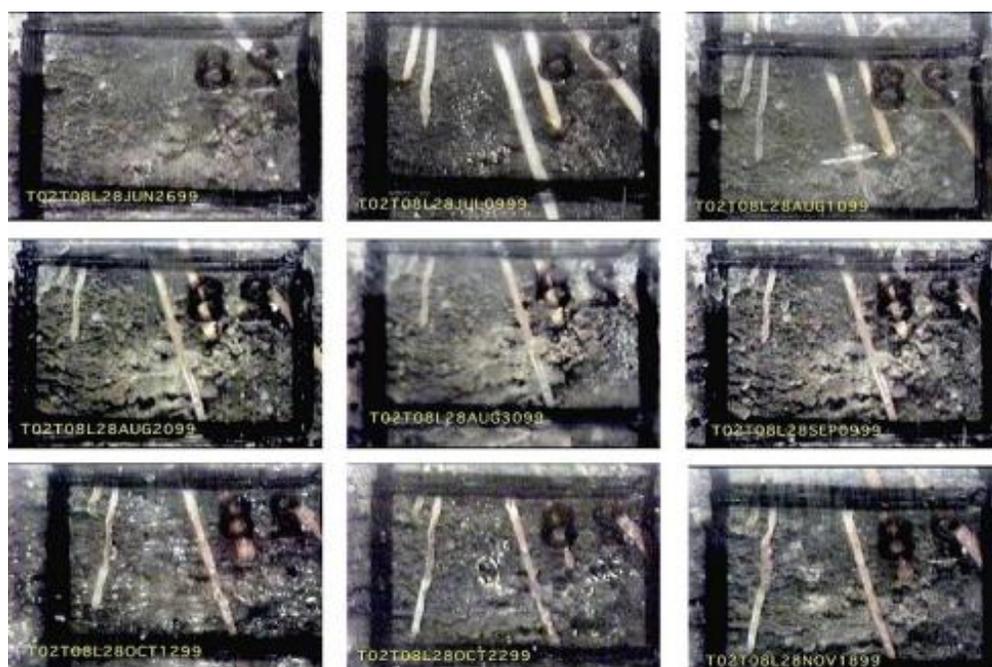


Figure 4.5 Images of apple roots captured from the video tapes recorded with the minirhizotron camera-VCR system showing changes of root status across time.

Each picture was then adjusted to its best quality and marked with an identifying number (Figure 4.5).

The number of new roots at each observation date and the color changes of individual roots were recorded through the growing season. Root growth patterns were identified by recording the number of new roots that emerged at each measurement date. Estimation of root turnover and survival was based on the timing of changes in the color of cortex. Duration of individual roots remaining white and time from emergence to turning black or becoming invisible were analyzed to estimate root survival. Due to the insufficient number of roots recorded in the late growth season and the much slower color changes of fall roots (Rogers, 1939; Head, 1966), only roots recorded before August in both year were sampled for survivorship estimation.

Results and Discussion

Fruit Yield

Total yield from both experiment years was not related to summer pruning severity (Figure 4.6). Unpruned trees and trees receiving light pruning tended to have large variance in yield, while yield of trees receiving moderate and severe pruning tended to be more stable, with a cropping regulation either by hand or chemical thinning.

The absence of significant effect of summer pruning on apple yield has also reported from young 'Golden Delicious' and 'Graham' trees by Saure (1985). On the other hand, Ogata et al.(1986) reported that yield of 5-year-old 'Fuji' /M.26 increased for 3 years following early summer pruning. Platon and Zagrai (1997) also indicated that summer pruning significantly increased fruit

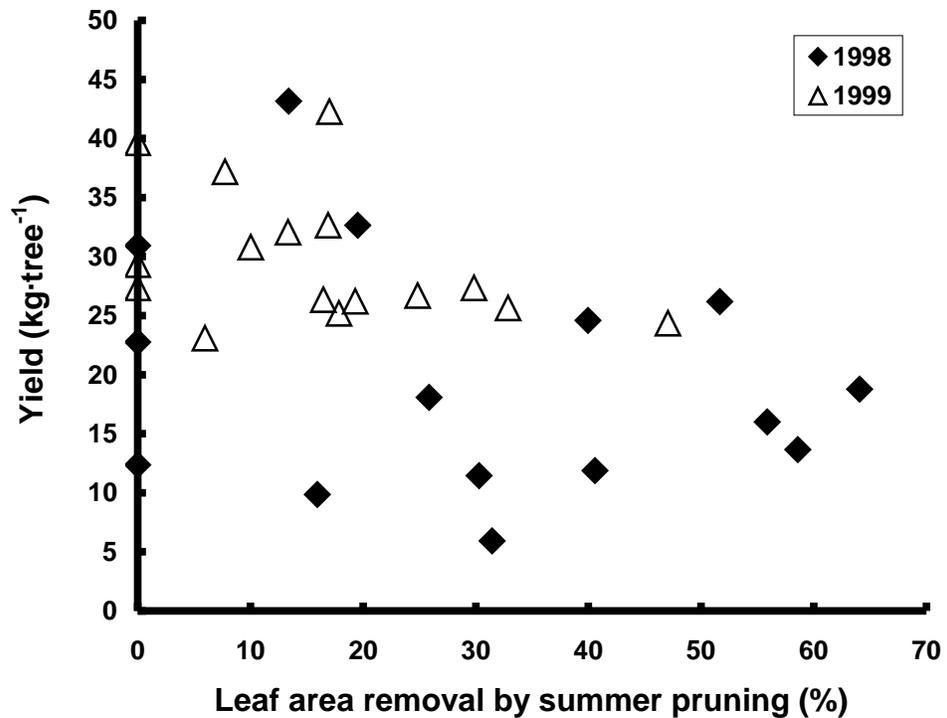


Figure 4.6 Final yield related to summer pruning severity on 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 3 Aug. 1999, respectively. Fruit number per tree was regulated by chemical and hand thinning in 1998 and by hand thinning alone in 1999.

yield of mature slender spindle and free palmette leader 'Golden Delicious' and 'Jonathan' apples by 10% to 20%. In contrast, Katzler and Wurm (1998) reported that 'Jonagold' and 'Golden Delicious' orchard after summer pruning produced lower yield when compared to unpruned trees, while no significant difference were found between summer pruning and winter pruning treatments. Robinson et al. (1993) pointed out factors that affect apple yield including pruning and training strategy, rootstock, and spacing. It is therefore difficult to compare results without clearly identifying every component in each trial. In addition, our results also showed that fruit yield is linearly related to fruit number per tree (data not shown). Consequently, summer pruning may not be expected to affect yield very much. Since yield is primarily controlled by fruit numbers set early in the season, of course, multiple-year effects may occur, but would be very complex.

Fruit Size

Our results showed that percent fruit growth after summer pruning was slightly reduced in relation to the severity of summer pruning (Figure 4.7). However, similar to yield, it is less reliable to make a conclusion merely based on the summer pruning. As our hypothesis suggested, the degree of impact of summer pruning on fruit growth and final fruit size also depends on the carbohydrate demand for fruit growth (fruit number per tree). In 1998, the different fruit numbers and pruning severities made separation of crop and pruning effects difficult. To minimize the variations in cropping effect, hand thinning was applied in 1999 to maintain a more uniform cropping among test trees. Results suggested that with a general commercial crop range, only severe pruning treatments showed reductions in the fruit growth in the late

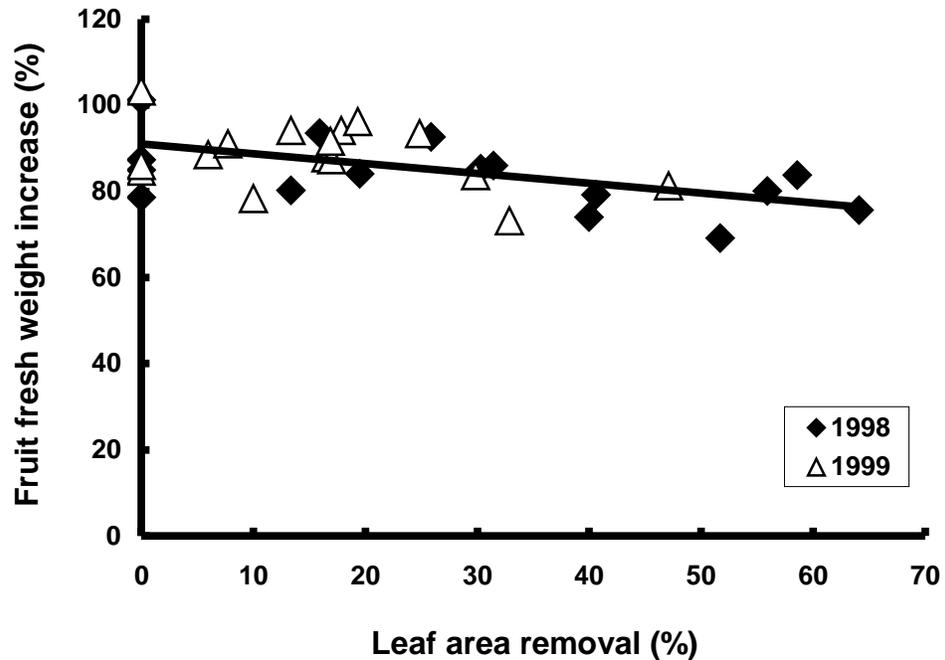


Figure 4.7 Correlation between the increase in fruit weight from summer pruning to harvest and summer pruning severity on 20-year-old slender spindle 'Empire' /M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 3 Aug. 1999, respectively. A pooled regression was used since the regression for each year were not significant different. The regression is $y = -0.227x + 90.96$, $r^2 = 0.29$.

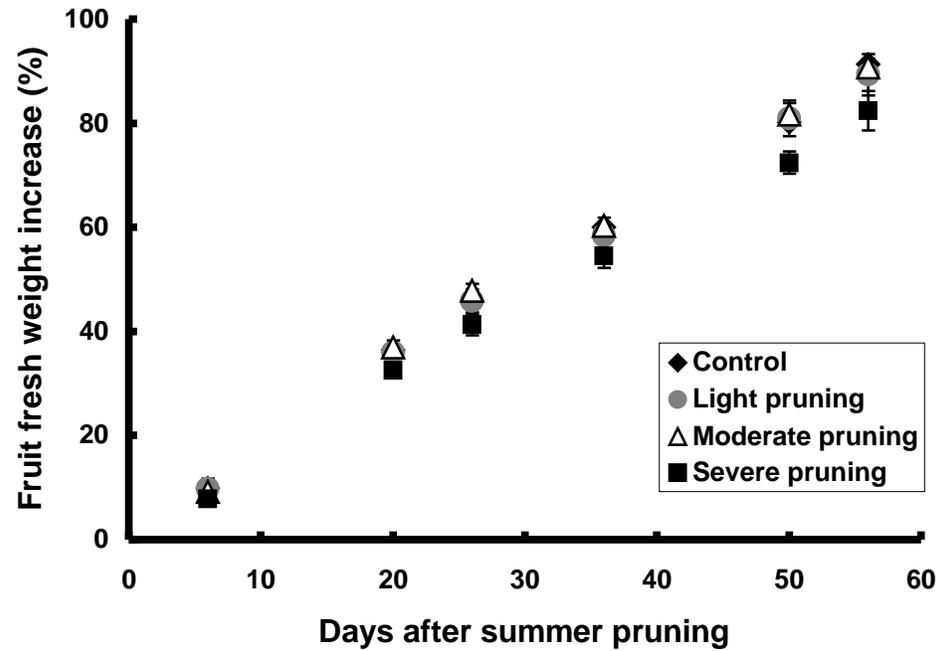


Figure 4.8 Relative fruit fresh weight increases of fruits on 20-year-old slender spindle 'Empire' /M.9 apple trees after summer pruning. Summer pruning was carried out on 3 Aug. 1999. Data represents the average values of four replicates with 20 fruits on each test tree. Vertical bars represent standard errors.

summer after pruning (Figure 4.8).

Taylor and Ferree (1984) found that fruit size was reduced in the first year of pruning treatment while increased in the second year. They point out that summer pruning might alter the distribution of fruit set on the canopy resulting in more fruit were set on the top of the canopy. This might lead to bigger fruit size. However, their data also showed that trees receiving summer pruning produce significantly lower yield than unpruned control trees. Therefore, the bigger fruit size might be possibly due to the lower fruit number and yield. In general, summer pruning does not affect fruit size on low cropping or low yield trees. Engel (1974) indicated that the increasing fruit size in two varieties is related to the decrease in yield after summer pruning, while fruit size was unaffected on other varieties in which the yield was also relatively constant. Redalen (1992) reported that summer pruning reduced fruit yield but produced better fruit size. The close linkage between fruit size and yield can be traced from many other reports (Autio and Greene, 1990; Barden and Marini 1984; Morgan et al., 1984; Myers and Ferree, 1983b; Säkö and Laurinen. 1982; Ystaas, 1989, 1992). This makes interpretation of pruning effects on fruit growth difficult.

To integrate the interaction between summer pruning severity and cropping, an exponential relationship is assumed between fruit growth or final weight and the carbohydrate supply to fruit demand. The supply/demand balance has been expressed as leaf area per fruit (Figure 4.9) (Giuliani et al., 1997; Palmer, 1992), light interception per fruit (Palmer, 1992), or canopy NCER per fruit (Figure 4.10; Francesconi et al., 1996). Our results expressed in this way indicated that within a commercial range of crops, the reduction in carbohydrate supply after summer pruning treatment did not

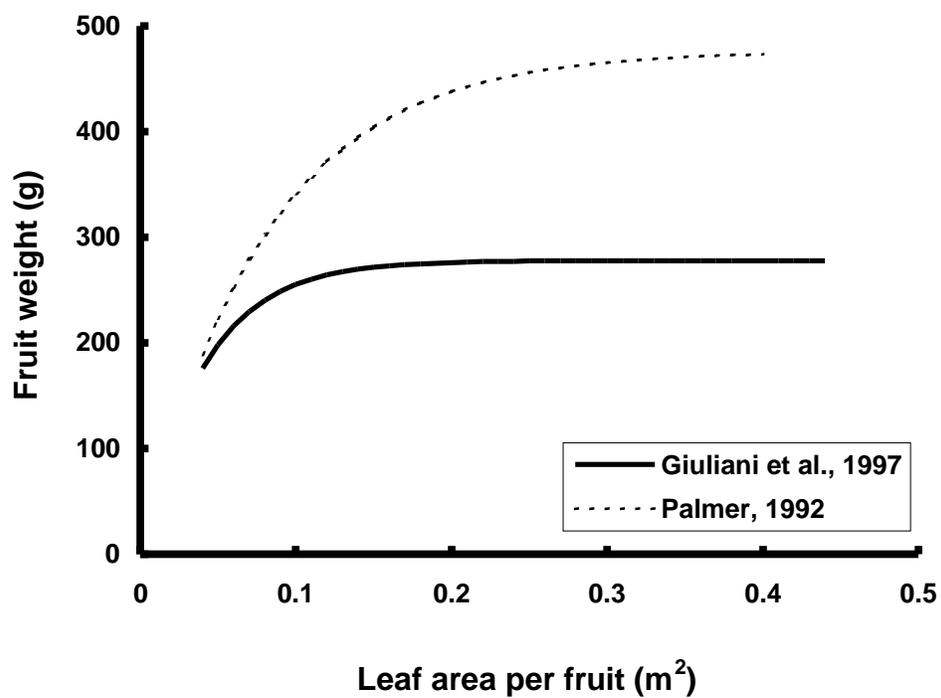


Figure 4.9 Fruit fresh weight of 'Smoothie'/'Pajam 2' (Giuliani et al., 1997) and 'Crispin'/'M.27' (Palmer, 1992) apples is exponentially correlated to crop load as in term of leaf area per fruit.

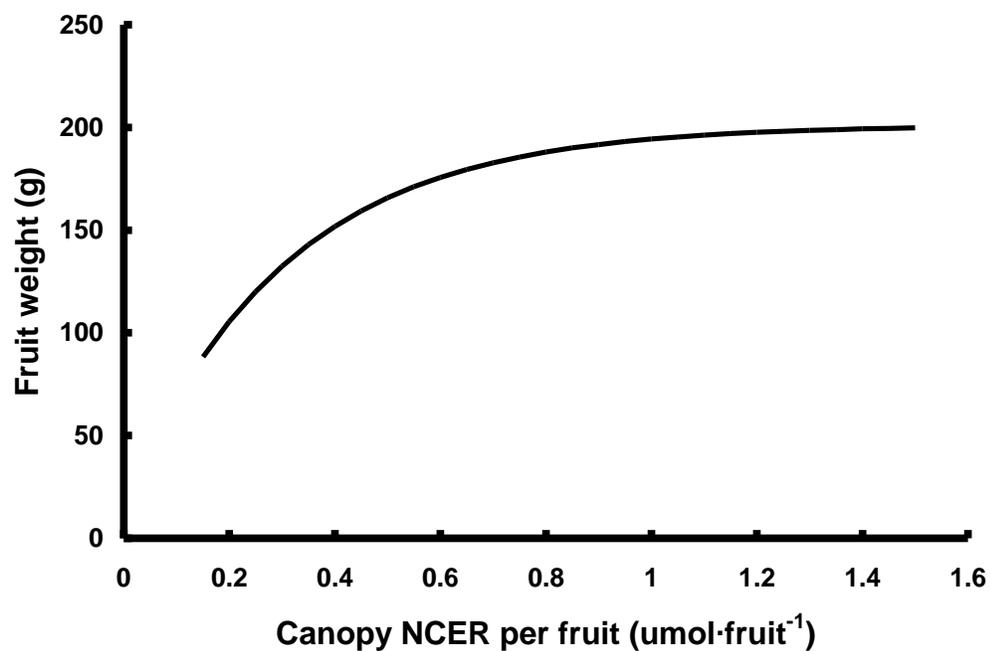


Figure 4.10 Fruit weight of 'Starkrimson Delicious' apples is exponentially correlated to crop load as in term of whole canopy net carbon exchange rate (NCER) per fruit (Francisconi et al., 1996).

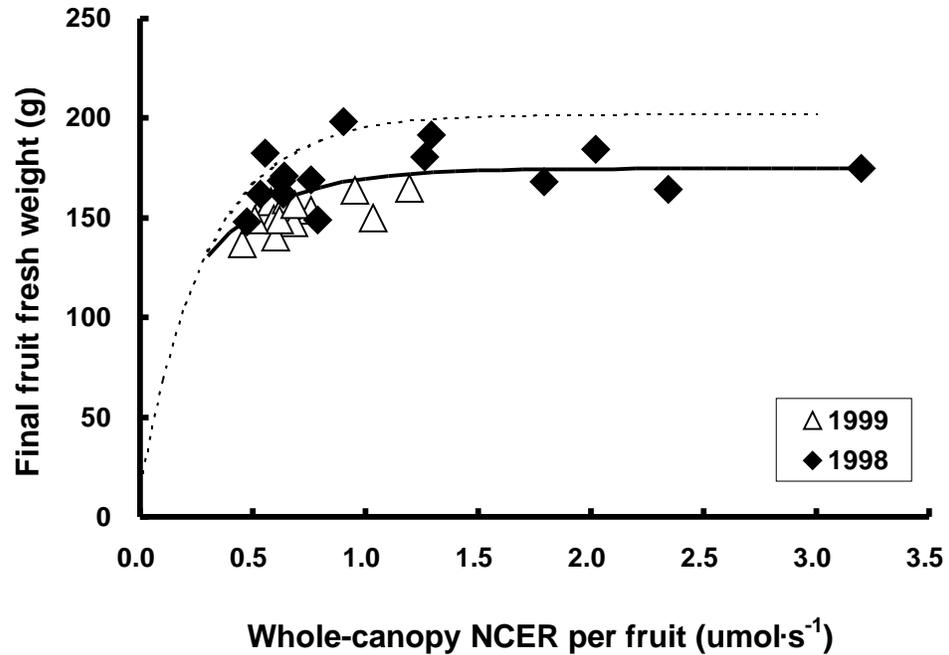


Figure 4.11 Correlation between final fruit weight and physiological crop load ($\mu\text{mol s}^{-1} \text{fruit}^{-1}$) after summer pruning on 20-year-old slender spindle 'Empire' /M.9 apple trees. The NCER represents mid-day maximum under sunny conditions. The regression (solid line) is $y=63.4+111.3(1-0.0451^x)$, $r^2=0.31$. Dash line is adopted from the result of European red mite effect on 'Starkrimson Delicious' apples (Francesconi et al., 1996).

strongly affect fruit growth (Figure 4.11) because the NCER per fruit did not fall below $0.5 \mu\text{mol s}^{-1}$ per fruit. Francesconi et al. (1996) found that 0.5 was a reasonable threshold of response.

Although carbohydrate balance appears to explain the lack of strong effects on fruit growth, it alone was not able to clearly explain the variations in final fruit size. As mentioned in Chapter three, canopy transpiration was also reduced in relation to summer pruning severity. Since both 1998 and 1999 were drought years, the reduction in transpiration and the consequent improved stem water status might have benefited fruit growth. Future research on the relationship between carbohydrate and water is required.

Fruit Color

Fruits were well-colored in both years. No relationship between percentage blushing area of fruit and summer pruning has been found in both experiment years in this study (data not shown). Color estimation on labeled fruits showed that fruits located inside the canopy had 10% to 20% lower blushing than fruits on the outer canopy. However, no pruning treatment difference was recorded. Interestingly, fruit coloring is slightly reduced with increasing fruit number per tree. It is likely due to the increase in the percentage spurs with more than one fruit in higher-cropping trees, and therefore increased shading from adjacent fruits on the same spurs.

It is expected that the benefit of summer pruning on fruit coloring might only appear on fruit from a dense canopy or from the most shaded part of an open canopy (Warrington et al., 1984; Morgan et al., 1984). This explains the insignificant effect of summer pruning on fruit coloring usually reported from young trees with small canopy or training systems with wide spacing

and thin canopy such as horizon trellis (Myers and Ferree, 1983a; Upshall and Barkovic, 1963). The well-maintained canopy structure and training system of the experimental orchard in this study might already ensure light intensity of the inner canopy that exceeds the threshold without summer pruning, leading to a general acceptable fruit color on each tree.

Fruit Maturity and Internal Quality

Fruit maturity estimated by starch index was not related to either pruning severity or cropping in both years. No significant difference between fruit from inner and outer canopy were recorded either. The average starch index was 5.0 and 4.1 in 1998 and 1999, respectively. The variance between years was most likely due to the difference in harvest time.

Fruit firmness was not affected either by pruning treatment or cropping regulation. Average firmness reading was $7.1 \text{ kg} \cdot \text{cm}^{-2}$ and $7.4 \text{ kg} \cdot \text{cm}^{-2}$ in 1998 and 1999, respectively.

Although increasing in fruit firmness due to shade or decreasing in firmness by improving light exposure was expected (Palmer and Warrington, 2000; Robinson et al., 1983), most prior studies suggested that summer pruning did not show a consistent influence on fruit firmness (Autio and Greene, 1990; Barden and Marini, 1984; Lawson et al., 1998, Myers and Ferree, 1983b; Shupp, 1992).

Soluble solids was also not affected either by summer pruning or cropping in this study. Average value from random samples was $12.2 \text{ }^\circ\text{Brix}$ and $12.6 \text{ }^\circ\text{Brix}$ in 1998 and 1999, respectively. Measurements from labeled fruit suggested that fruits from inner canopy had lower soluble solids content than fruit located on outer canopy by 0.5 to 0.6 $^\circ\text{Brix}$ in both experiment years,

but these differences were also not related to either pruning treatment or cropping.

Insignificant effects on soluble solids content by summer pruning have also been reported by Lawson et al. (1998) and Morgan et al. (1984). While a number of studies suggested summer pruning reduced fruit soluble solids content (Link, 1984; Myers and Ferree, 1983b; Struklec, 1981; Ystaas, 1989, 1992), Taylor (1982) and Taylor and Ferree (1984) reported that summer pruning affects on soluble solids only happened on fruits in the middle level canopy where a combination of both light reduction and leaf area reduction occurred. Redalen (1992) found fruits from summer pruned trees contained slightly lower soluble solids. However, he also found the decreased soluble solids content seems better correlated with cropping, suggesting fruit load had greater influence than pruning treatment alone.

Summer Pruning and Physiological Fruit Disorders

In this study, similar to other fruit quality parameters, incidence of internal breakdown was not related to either pruning or cropping treatments or the interaction between each other. Incidence of internal breakdown was undetectable from any fruits from six of the 16 tested trees, while the rest showed a highly varied incident rate from 10% to 70%.

Reports of summer pruning on postharvest fruit disorders were highly varied and were associated with fruit Ca content or K:Ca ratio (Link, 1984; Olszewski and Mika, 1999; Struklec 1981; 1994; Taylor and Ferree, 1986).

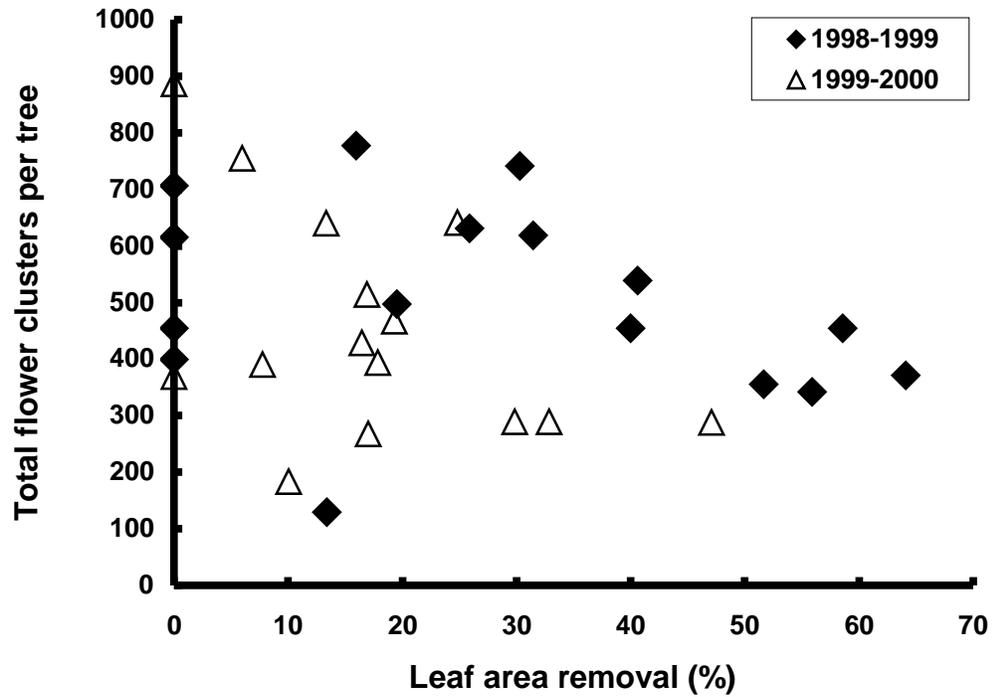


Figure 4.12 Return bloom on 20-year-old slender spindle 'Empire' / M.9 trees related to previous year's summer pruning severity. Data represents number of flower cluster per test tree.

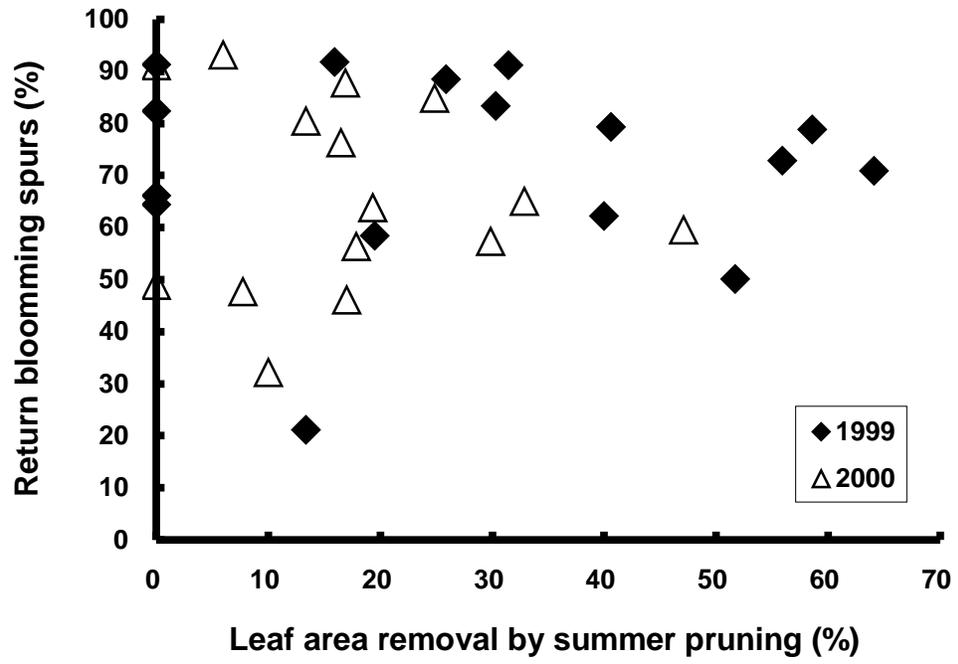


Figure 4.13 Return blooming spurs related to summer pruning severity on 20-year-old slender spindle 'Empire' / M.9 apple trees. Summer pruning was carried out on 30 July 1998 and 3 Aug. 1999, respectively.

Return Bloom

In this study, total flower clusters per tree and the percentage flowering spurs following summer pruning were not related to previous year's pruning treatment (Figure 4.12 and Figure 4.13).

Insignificance effects of summer pruning on return bloom have also been reported by others (Chandler, 1923; Ferree, 1979; Lord et al., 1979; Marini and Barden 1982a; Morgan et al., 1984; Myers and Ferree, 1983c).

Although the summer pruning effect was insignificant, a linear relationship between the percentage spurs flowering in 1999 and the crop in 1998 (expressed as fruit per tree) was found (Figure 4.14). However, the relationship was very poor in the next year, likely due to the changes in tree size and structure after the pruning treatments in 1998, leading to unequal number of spurs and laterals. A similar negative effect of cropping and return bloom has also been reported by Lawson et al. (1998) and Palmer (1992), indicating that variations in cropping likely interact with the summer pruning effect on return bloom.

Consequently, exponential curves representing the correlation between physiological crop load and return bloom were obtained in this study (Figure 4.15 and Figure 4.16). This suggests that carbohydrate balance theory may be a good model to understand summer pruning effects on return blooming. In addition, return bloom showed greater effects and higher saturation point of the exponential curve compared to fruit growth (about 0.5 for fruit growth in Figure 4.11 versus 1.0 to 1.5 for return bloom in Figure 4.15). This suggests that compared to fruit growth the development of flower buds might be relatively sensitive to changes of carbohydrate balance caused by summer pruning, cropping, or other internal and environment factors.

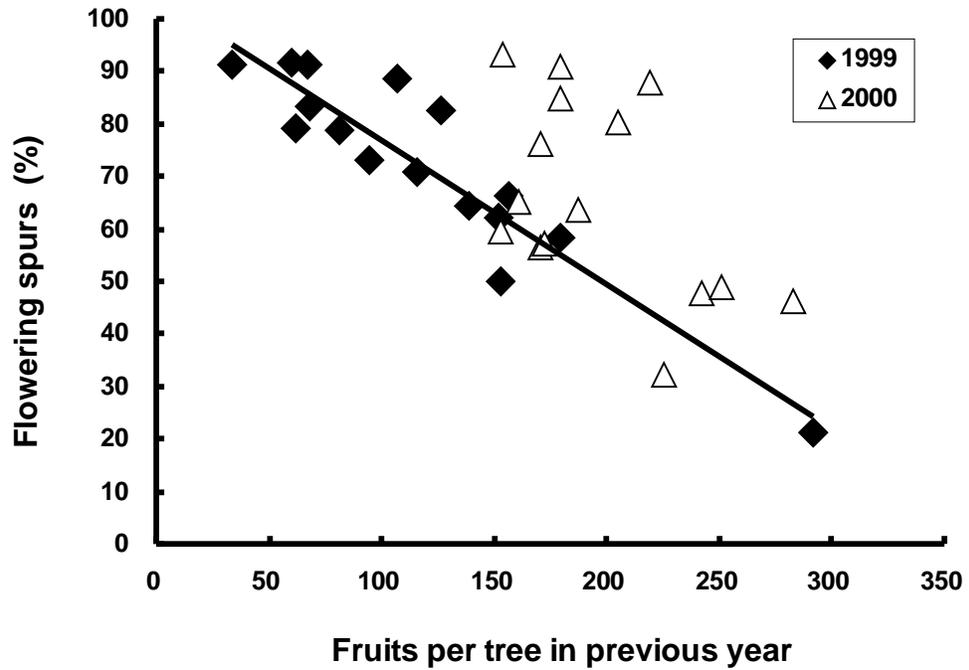


Figure 4.14 Correlation between the percentage return bloom on spurs and the previous year's cropping on 20-year-old slender spindle 'Empire' /M.9 apple trees. The regression for return bloom in 1999 is $y = -0.275x + 104.5$, $r^2 = 0.86$.

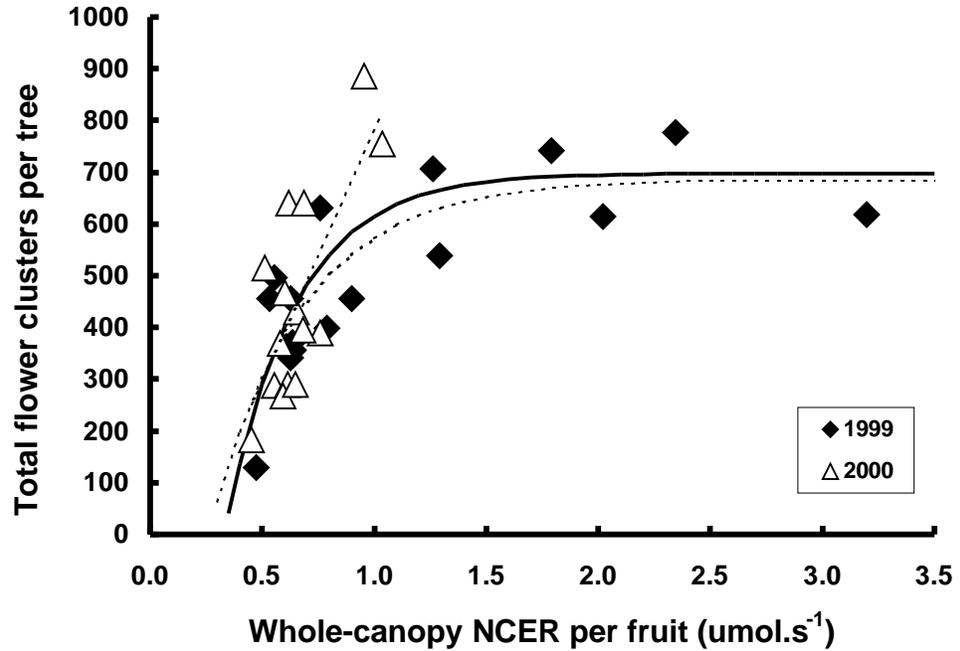


Figure 4.15 Correlation between total flower clusters per tree and physiological crop load following summer pruning on 20-year-old slender spindle 'Empire' /M.9 apple trees. The regression for return blooming in 1999 (dash exponential), 2000 (dash linear), and combination of both year (solid exponential) are $y=967.9-187.7x$, $r^2=0.56$, $y=-1311+2009(1-0.04121^x)$, $r^2=0.67$, and $y=-610.4+1296(1-0.08723^x)$, $r^2=0.55$, respectively.

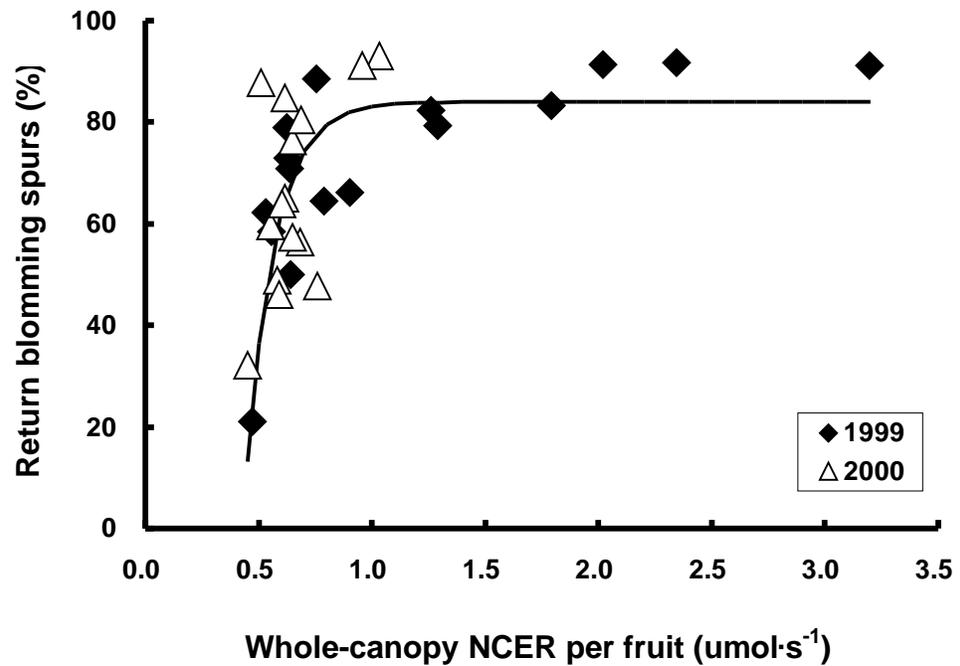


Figure 4.16 Correlation between return blooming spurs and physiological crop load (NCER/fruit) following summer pruning on 20-year-old slender spindle 'Empire' /M.9 apple trees. The regression is $y = -2436 + 2520(1 - 0.00036^x)$, $r^2 = 0.74$.

Summer Pruning Effects on Trunk Growth

Our result showed no significant difference between pruning severity (Figure 4.17). Over the 2-year experiment, average TCSA increased 6.0 to 6.7 cm².

Most reports indicated summer pruning suppressed trunk growth (Engel, 1974; Kikuchi et al., 1989; Myers and Ferree 1983c; Taylor and Ferree, 1981; Upshall and Barkovic, 1963). Säkö and Laurine (1982) reported that summer pruning on 5 to 7-year-old apple trees reduced trunk growth by 20% to 25%. Some other reports showed summer pruning has no effect on trunk growth or the effect varied among varieties or training systems (Barden and Marini 1984; Ferree, 1979; Marini and Barden, 1982a, Platon and Zagrai, 1997). Promotion on trunk growth by summer pruning has only been reported by Platon and Zagrai (1997) from young slender spindle 'Golden Delicious' trees.

Although in this study trunk growth was also not related to cropping or physiological crop load, Mika et al. (1983) indicated that the effect of summer pruning in their study was likely affected by fruiting. Marini and Barden (1982a) and Barden and Marini (1984) indicated that summer pruning reduced trunk growth in 'Golden Delicious' but not in 'Stayman' or 'Delicious' in the same experiment. Noticeably, another report (Marini and Barden, 1982d) showed a higher crop load of 'Golden Delicious' than the other two varieties. These results suggested that similar to fruit growth or return bloom, fruiting and the carbohydrate supply and demand balance might help explain the summer pruning effect on trunk growth.

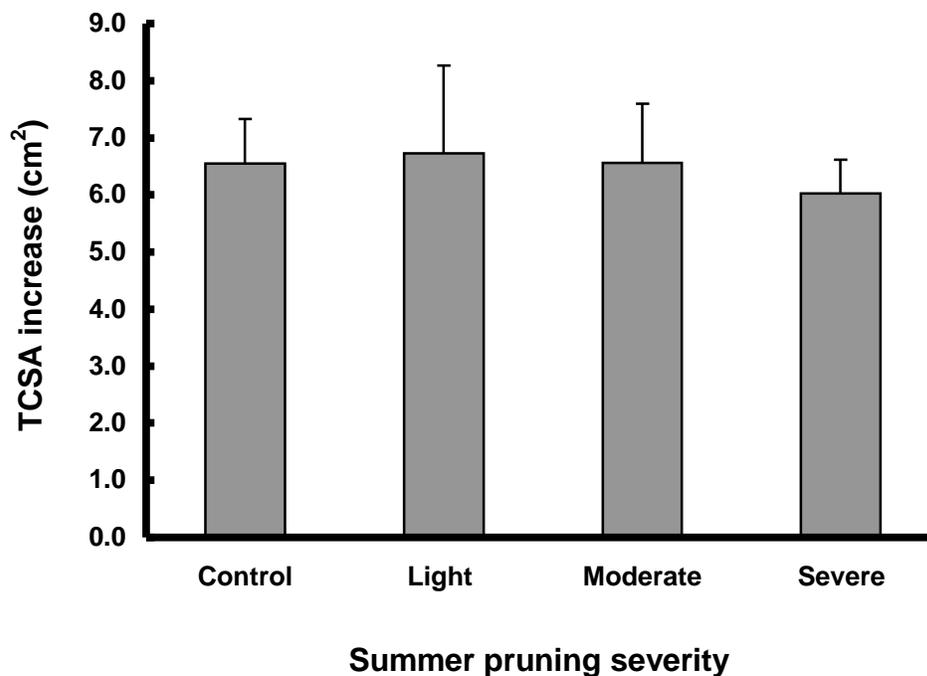


Figure 4.17 Summer pruning effect on trunk growth of 20-year-old slender spindle 'Empire' / M.9 apple trees. Data represent average value of four replicates after summer pruning treatment for two consecutive years (1998 and 1999). Vertical bars represent standard errors.

Summer Pruning Effects on Apple Root Growth

We found that new root growth started in May or June with a major growing peak during June and July (Figure 4.18). Most new roots were recorded before summer pruning. A minor growth period in 1999 was also recorded during the late growth season, mainly after harvest and before leaf fall (Figure 4.18), similar to the reports from Rogers (1933; 1939).

Seasonal apple root growth has been reported by a number of studies with excavation or minirhizotron approaches (Atkinson, 1978, 1980; Head, 1966, 1967; Psarras et al., 2000; Rogers, 1933; 1939). Although Priestley (1963) indicated that late season root growth on young apple trees was related to the accumulation of assimilate from foliage, no relationship between pruning treatments and the onset as well as number of roots in the late growth season was observed from our test trees. In Ithaca, N.Y., Psarras et al. (2000) also found little spring or autumn root growth with M.9 roots. In addition to carbohydrate and nutrient resources, other environmental factors such as soil temperature or moisture might be involved in the late season root growth (Rogers 1939).

A similar growth pattern from the same test trees was observed in 2000, but with fewer roots observed (Figure 4.19). However, a significant difference in root survival between the two years was found. Since there were relatively few roots and no significant effect of summer pruning, the data from all trees were pooled to examine root survivorship. Fifty percent of new roots recorded in early growing season of 1999 remained white until 4 weeks after emergence, similar to results from 'Mutsu' /M.9 (Psarras et al., 2001). However, more than 50% of new roots in 2000 changed color in 2 weeks (Figure 4.20). In addition, 60% of new roots in 1999 survived up to 110 days after first recorded in the

early season, while the longevity decreased to 40 days in 2000 (Figure 4.21). The survivorship of 1999 is much longer than report from 'Red Delicious'/M.26 (Eissenstat et al., 2000) but close to 'Mutsu'/M.9 (Psarras et al., 2001). Annual variations of root survivorship have also been reported from 'Mutsu'/M.9 (Psarras et al., 2001). The lower number of roots and shorter lifespan of roots recorded in 2000 was also likely due to the reduction of orchard fertilization and pest control (the orchard was being removed). This may have resulted in an overall decay of resource supply for root growth.

Suppression of root growth following summer pruning or defoliation has been reported by a number of studies. Head (1969) observed that the complete defoliation 4 to 6 weeks before leaf-fall reduced the number of white roots and delayed the root growth in the following spring. Marked suppression of root growth of 1- or 2-year-old apple trees after summer pruning has been reported (Ferree, 1979; de Haas and Hein, 1973; Kikuchi et al., 1983; Myers and Ferree, 1983a; Taylor and Ferree, 1981). Priestley (1963) suggested that carbohydrate status of young apple trees after mid-summer may affect root growth in the fall and the following spring. In addition to summer pruning, decreased root growth of potted trees with high fruit set has also been reported (Ebert, 1992; Ebert and Lenz, 1991).

These results indicated that the apple root system might respond to the changes of carbohydrate supply and demand balance after summer pruning. However, in this study, although root growth was not recorded until mid-June 1999, records from 2000 indicated no root growth was observed until early June. Psarras et al. (2000) found similar results in the N.Y. climate. Summer pruning treatment and cropping regulation in 1999 did not affect the onset and number of new root emergence in 2000 (data not shown).

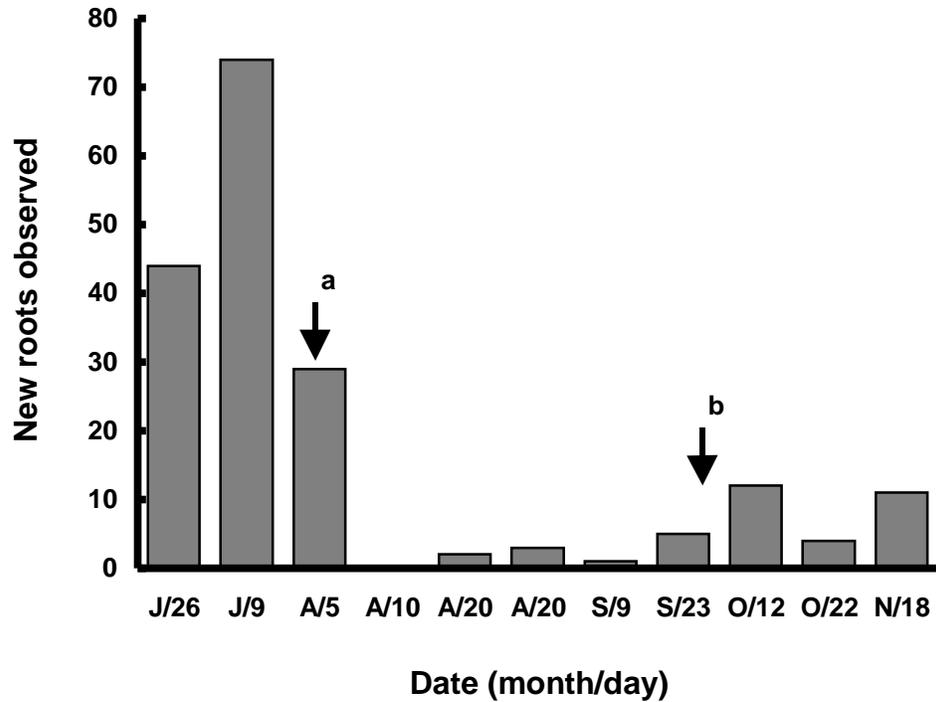


Figure 4.18 Root growth pattern of 20-year-old slender spindle 'Empire' / M.9 apple trees in 1999. Data represents total number of new root recorded from 27 minirhizotrons of nine test trees. Summer pruning was carried out on 30 July 1999 (arrow a) and fruits were harvested on 28 Sept. 1999 (arrow b).

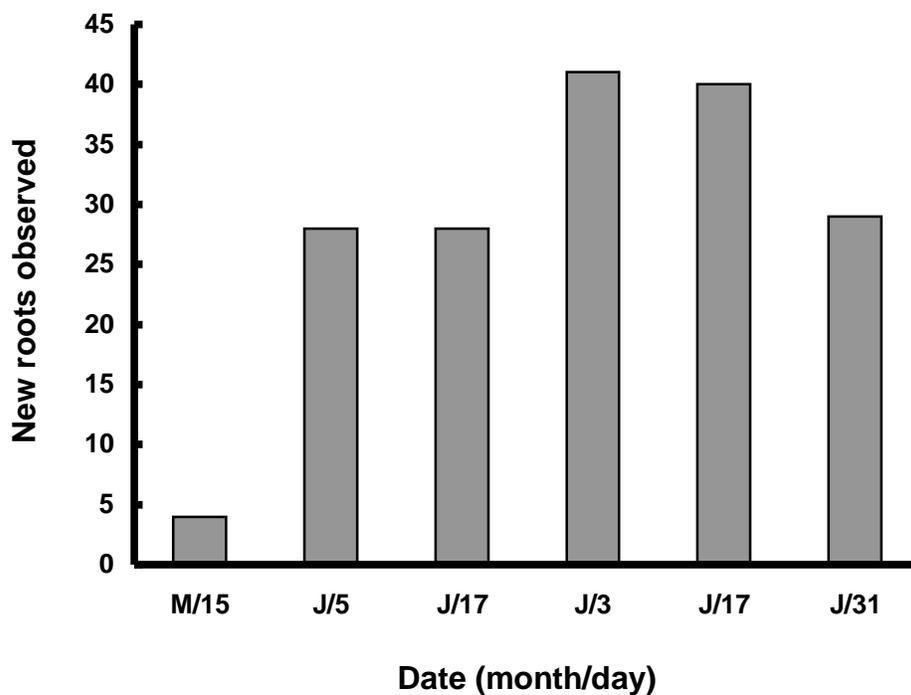


Figure 4.19 Root growth pattern of 20-year-old slender spindle 'Empire' / M.9 apple trees in 2000. Data represents total number of new root recorded from 22 minirhizotrons of nine test trees.

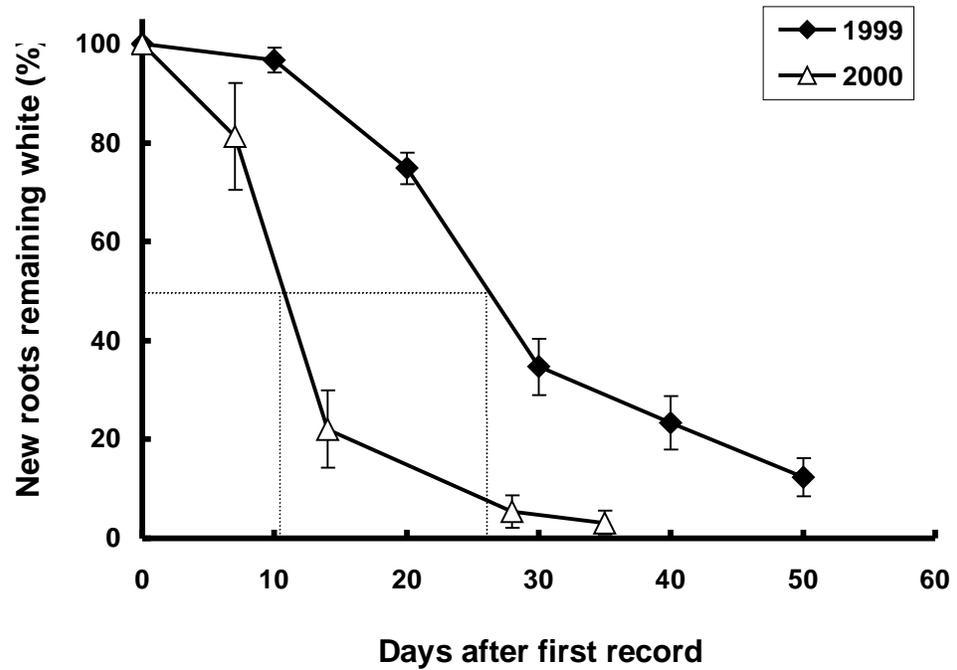


Figure 4.20 Time curves of new root remaining white of 20-year-old slender spindle 'Empire' /M.9 apple trees. Data represents average value of total new root recorded from nine test trees in June and July of 1999 and 2000. Vertical bars represent standard errors.

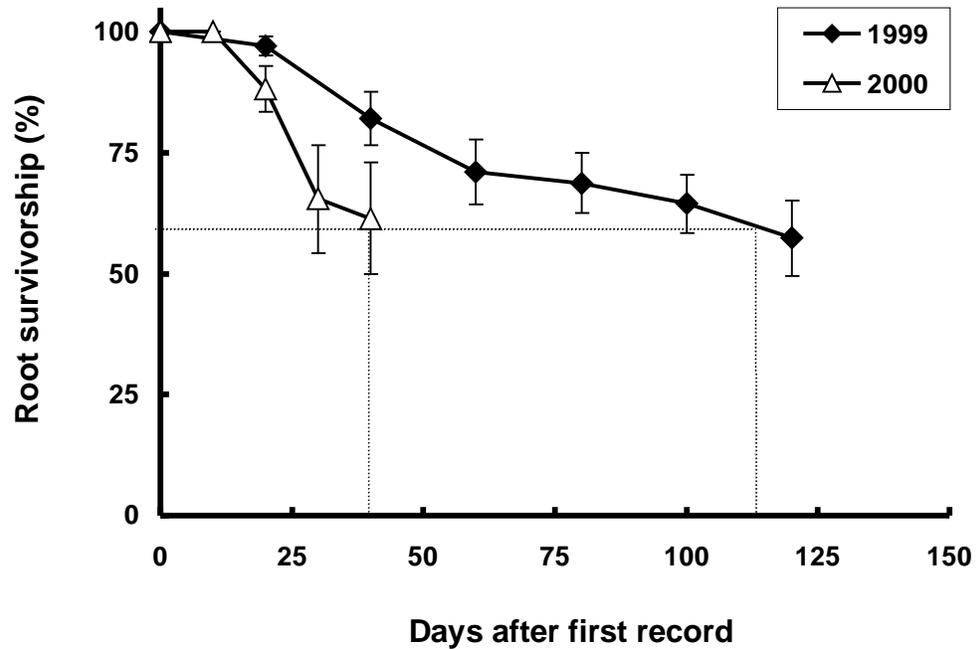


Figure 4.21 Root survivorship curves of 20-year-old slender spindle 'Empire' /M.9 apple trees in 1999 and 2000. Data represents average value of survivorship (longevity of new roots before turning black or invisible) of new root recorded from nine test trees in June and July of 1998 and 1999. Vertical bars represent standard errors.

Noticeably, almost all the previous reports of negative effect of summer pruning on root growth were obtained from young nursery trees or potted plants as model systems. These reports indicated the possible impact of decreased carbohydrate supply after summer pruning on root growth. However, compared to a young apple tree, a mature tree will likely show a less significant impact due to: a) the relatively low proportion of carbon partitioned to the root systems and b) the timing of maximum root growth occurring before summer pruning. It must be acknowledged that the limited number of minirhizotrons used in this study might not be able to provide a large enough sample size due to the low root density of apples and the highly variable distribution the apple root system in the soil (Atkinson, 1980; Green and Clothier, 1999; Hughes and Gandar, 1993).

There were no significant differences between test trees on the onset and number of new roots produced in 1999, or the correlation between final root survivorship and current year's physiological crop load (Figure 4.23). However, root survivorship at 40 days was correlated to the physiological crop load of 1998, in an exponential relationship similar to that of fruit growth or return bloom (Figure 4.22). The relationship between root survivorship and the crop load of previous year has also been found in grapes (Eissenstat and Lakso, unpublished results). This result suggested that similar to young apple trees, root growth or survival of mature apple trees might also be affected by the changes of carbohydrate balance due to summer pruning and cropping. Due to the timing of root growth and summer pruning, the involvement of carbohydrate supply and demand might be more complicated.

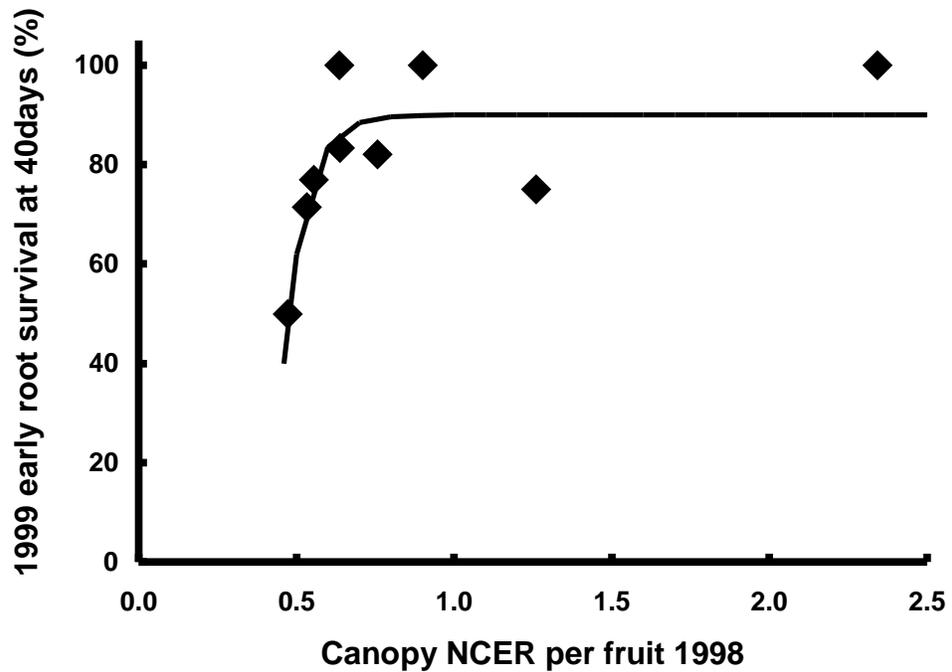


Figure 4.22 Correlation between early root survival in 1999 and physiological crop load (NCER per fruit) of 1998 on 20-year-old slender spindle 'Empire' /M.9 apple trees received summer pruning treatment on 30 July 1998. Data represent survivorship (longevity of new roots before turning black or invisible) of root recorded in June and July 1999. The regression is $y = -39640 + 39730(1 - 0.0000005^x)$, $r^2 = 0.69$.

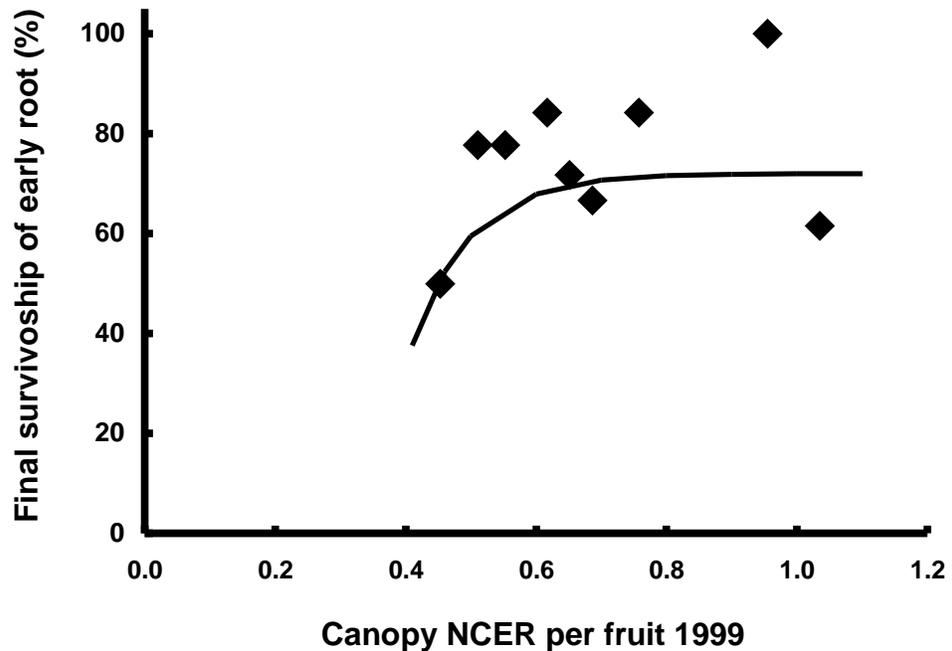


Figure 4.23 Correlation between final root survival and physiological crop load (NCER per fruit) of 1999 on 20-year-old slender spindle 'Empire' /M.9 apple trees received summer pruning treatment on 30 July 1998 and 3 Aug. 1999, respectively. Data represents survivorship (longevity of new roots before turning black or invisible) of root recorded in June and July 1999. The regression is $y = -3451 + 3532(1 - 0.0000123^x)$, $r^2 = 0.31$.

Carbohydrate Supply and Demand Balance

In this study the carbohydrate supply and fruit demand balance concept showed its flexibility in explaining and clarifying the complexity of the summer pruning influences on fruit growth (Figure 4.11), return bloom (Figure 4.15 and 4.16), and root survivorship (Figure 4.22) of mature apple trees. It also showed the possibility to determine the sink strengths and to identify the priority of summer pruning impact by comparing the curves and inflection point of exponential lines from the results. For example, return bloom appeared to be more sensitive to the reduced NCER per fruit than did fruit growth or root growth.

However, there are likely many other factors that contribute to summer pruning influences by acting independently or interacting with carbohydrate balance. For example, the well-managed and open canopy of the test orchard used in this study probably reduced the benefit of summer pruning on improving light distribution within canopy, resulting in less significant effects on fruit coloring enhancement. In addition, as we reported previously (Chapter three), summer pruning also reduced canopy transpiration, which would be expected to favor fruit growth especially in drought periods such as the summer 1999. The better water status might potentially mediate the impact of reduction in carbohydrate supply after summer pruning on fruit growth. The interaction between water and carbohydrates is certainly an interesting topic for the future research. Finally, weather needs to be considered in our analysis. As we demonstrated in Chapter two, leaf photosynthesis ability is mainly determined by the pre-summer pruning light availability. The above normal total solar radiation in the spring of 1999 might strengthen the Pn ability of leaves in the inner canopy and relieve the impact

of decreasing carbohydrate supply by summer pruning when comparing to similar treatment in a bad or normal year. Weather might also play an interesting role on manipulating the interaction between canopy carbon balance and water status, and consequently changing the summer pruning influence. For example, a growing season or area with high solar radiation and low precipitation might furthermore minimize the negative effect of decreased canopy NCER and strengthen the benefit of lower canopy transpiration. In contrast, years or areas with cloudy weather and high precipitation during the growing season might drive the relationship to the opposite direction.

Conclusions

Many apple varieties, including 'Empire' tend to set too many fruits. However, nowadays growers have better control of crop load by chemical thinning. It is expected that the carbohydrate demand for fruit growth will be more stable from year to year. Therefore, the impact of carbohydrate shortage after summer pruning is possibly not as severe in the current orchard management as before when over cropping occurred more often. In addition, maintaining an open canopy year around, as was the case in the test trees in this study, may ensure sufficient light exposure for leaf development and would also reduce the negative effect of summer pruning on canopy photosynthesis.

Overall, in this study summer pruning alone did not show significant influence on fruit size, color, internal quality, postharvest disorder, return bloom, trunk growth, and root growth. The physiological crop loads did not reach the critical levels identified earlier by Francesconi et al. (1996). However,

we demonstrated the possibility of using carbohydrate model to explain the balance between suppressing in carbohydrate supply by summer pruning and the demand for fruit growth.

In addition, the interaction between canopy water status and carbohydrate supply, and the possibility of annual modification by weather pattern might also play significant roles in the dynamic of carbohydrate balance. More information and studies is required in the future before we can clearly illustrate this issue.

References

- Andris, H.L, C.H. Crisosto, and Y.L. Grossman. 1998. The use of reflective films to improve the apple fruit red color. *Plasticulture* 116:33-42.
- Atkinson, D. 1978. The use of soil resources in high density plating systems. *Acta Hort.* 65:79-89.
- Atkinson, D. 1980. The distribution and effectiveness of the roots of tree crops. *Hort. Rev.* 2:424-490.
- Autio, W.R., and D.W. Green. 1990. Summer pruning affects yield and improves fruit quality of 'McIntosh' apples. *J. Amer. Soc. Hort. Sci.* 115(3):356-359.
- Barden, J.A. and R.P. Marini. 1984. Summer and dormant pruning of apple: A four year summary. *Acta Hort.* 146:263-268.
- Belter, H. and T.M. Thomas. 1980. Preliminary experiences in summer pruning of apples in Michigan. *Compact Fruit Tree* 13:100-101.
- Buwalda, J.G. 1993. The carbon costs of root systems of perennial fruit crops. *Environ. & Eex. Bot.* 33:131-140.
- Cain, J.C. 1973. Foliage canopy development of 'McIntosh' apple hedgerows in relation to mechanical pruning, the interception of solar radiation, and fruiting. *J. Amer. Soc. Hort. Sci.* 98:357-360.
- Chandler, W.H. 1923. Results of some experiments in pruning fruit trees. *Cornell Univ. Agr. Exp. Sta. Bul.* 415
- Cheng, W., D.C. Coleman, and E. Box Jr. 1991. Measuring root turnover using the minirhizotron technique. *Agri. Eco. Environ.* 34: 261-267.
- Curry, E.A. 1997. Temperatures for optimum anthocyanin accumulation in apple tissue. *J. Hort. Sci.* 72(5):723-729.
- Doud, D.S. and D.C. Ferree. 1980. Influence of altered light levels on growth and fruiting of mature 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 105(3):325-328.

- Ebert, G. 1992. Die Wurzelatmung von Apfelbäumen II. Einfluß von innerpflanzlichen Faktoren. *Erwerbsobstbau* 34:165-168.
- Ebert, G., and F. Lenz. 1991. Jahresverlauf der Wurzelatmung von Apfelbäumen und ihr Beitrag zur CO₂-Bilanz. *Gartenbauwissenschaft* 56:130-133.
- Eissenstat, D.M., C.E. Wells, R.D. Yanai, and J.L. Whitbeck. 2000. Building roots in a changing environment: Implications for root longevity. *New Phytol.* 147:33-42.
- Engel, G. 1974. Einfluß des Sommerschnittes auf den Wuchs und Ertrag von Äpfeln auf Sämling. *Erwerbsobstbau* 16:47-48.
- Ferree, D.C. 1979. Current experiences with summer pruning. *Proc. New York Sta. Hort. Soc.* 124:77-79.
- Ferree, D.C., S.C. Myers, C.R. Rom, and B.H. Taylor. 1984. Physiological aspects of summer pruning. *Acta Hort.* 146:243-251.
- Forshey, C.G. and D.C. Elfving. 1989. The relationship between vegetative growth and fruiting in apple trees. *Hort. Rev.* 11:229-287.
- Francesconi, A.H.D., A.N. Lakso, J.P. Nyrop, J. Barnard, and S.S. Denning. 1996. Carbon balance as a physiological basis for the interactions of European red mite and crop load on 'Starkrimson Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 12(5):959-966.
- Giuliani, R., L. Corelli-Grappadelli, and E. Magnanini. 1997. Effects of crop load on apple photosynthetic responses and yield. *Acta Hort.* 451:303-311.
- Green, S. and B. Clothier. 1999. The root zone dynamics of water uptake by a mature apple tree. *Plant & Soil* 206:61-77.
- Haas, P.G.D., and K. Hein. 1973. Über die Beeinflussung des Wachstumsverlaufs von Apfelwurzeln durch verschiedene Baumschnittmaßnahmen und durch Entblätterung. *Erwerbsobstbau* 15:137-141.

- Head, G.C. 1966. Estimating seasonal changes in the quantity of white unsubscriberized root on fruit trees. *J. Hort. Sci.* 41:197-206.
- Head, G.C. 1967. Effects of seasonal changes in shoot growth on the amount of unsubscriberized root on apple and plum trees. *J. Hort. Sci.* 42:169-180.
- Head, G.C. 1969. The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. *J. Hort. Sci.* 44:175-181.
- Heinicke, A.J. 1935. Root growth In young apple trees made shortly before and after defoliation. *Proc. Amer. Soc. Hort. Sci.* 33:164-165.
- Hughes, K.A. and P.W. Gandar. 1993. Length densities, occupancies and weights of apple root systems. *Plant & Soil* 148:211-221.
- Iglesias, I., J. Graell, G. Echeverría, and M. Vendrell. 2000. Orchard cooling with overtree sprinkler irrigation to improve fruit color of 'Delicious' apples. *HortScience* 35(7):1207-1208.
- Jackson, J.E. and J.W. Palmer. 1977. Effects of shade on the growth and cropping of apple trees II. Effects on components of yield. *J. Hort. Sci.* 52:253-266.
- Jackson, J.E., J.W. Plamer, M.A. Perring, and R.O. Sharples. 1977. Effects of shade on the growth and cropping on apple trees. III. Effects on fruit growth, chemical composition and quality at harvest and after storage. *J. Hort. Sci.* 52:267-282.
- Jackson, J.E., R.O. Sharples, and J.W. Palmer. 1971. The influence of shade and within-tree position on apple fruit size, colour and storage quality. *J. Hort. Sci.* 46:277-286.
- Johnson, M.G., D.T. Tingey, D.L. Phillips, and M.J. Strons. 2001. Advancing fine root research with minirhizotrons. *Environ. & Exp. Bot.* 45:263-289.
- Katzler, H. and L. Wurm. 1998. Auswirkungen verschiedener Schnittvarianten auf Ertrag sowie äußere und innere Fruchtqualität bei den Apfelsorten Jonagold und Golden Delicious. *Mitteilungen Klosterneuburg* 48:137-144.

- Kikuchi, T., T. Asada, and Y. Shiozaki. 1989. Effect of summer pruning on the next season's shoot growth of young apple trees. *J. Japan. Soc. Hort. Sci.* 58(3):491-497.
- Lakso, A.N. 1980. Correlations of fisheye photography to canopy structure, light climate, and biological responses to light in apple trees. *J. Amer. Soc. Hort. Sci.* 105(1):43-46.
- Lakso, A.N., M. Bepete, M.C. Goffinet, and L. Corelli-Grappadelli. 1998. Aspects of carbon supply and demand in apple fruits. *Acta Hort.* 466:13-18.
- Lakso, A.N. and L. Corelli-Grappadelli. 1992. Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Hort.* 322:231-239.
- Lakso, A.N. and T.L. Robinson. 1997. Principles of orchard systems management optimizing supply, demand and partitioning in apple trees. *Acta Hort.* 451:405-415.
- Lawson, D.S., W.H. Reissig, and A.M. Agnello. 1998. Effects of summer pruning and hand fruit thinning on obliquebanded leafroller (Lepidoptera: Tortricidae) fruit damage in New York State apple orchards. *J. Agric. Entomol.* 15(2):113-123.
- Link, H. 1984. Auswirkungen verschiedener Schnittmaßnahmen auf das Wachsen und Fruchten von Apfelbäumen. *Erwerbsobstbau* 26:28-34.
- Lord, W.J., D.W. Greene, W.S. Bramlage, and M. Drake. 1979. Induction flowering of apple trees and increasing fruit quality by summer pruning. *Compact Fruit Tree* 12:23-39.
- Maggs, D.H. 1963. The reduction in growth of apple trees brought about by fruiting. *J. Hort. Sci.* 38:19-128.
- Marini, R.P. and J.A. Barden. 1982a. Growth and flowering of vigorous apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):34-39.
- Marini, R.P. and J.A. Barden. 1982b. Light penetration on overcast and clear days, and specific leaf weight in apple trees as affected by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(1):39-43.

- Marini R.P. and J. A. Barden. 1982c. 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(1):170-174.
- Marini, R.P. and J.A. Barden. 1982d. Yield, fruit size, and quality of three apple cultivars as influenced by summer or dormant pruning. *J. Amer. Soc. Hort. Sci.* 107(3):474-479.
- Marini, R.P. and J.A. Barden. 1987. Summer pruning of apple and peach trees. *Hort. Rev.* 9:351-371.
- Mika, A. 1986a. Physiological responses of fruit trees to pruning. *Hort. Rev.* 8:337-378.
- Mika, A. 1986b. Treatments improving illumination of the fruit zone of the tree, p. 42-45. In: A.N. Lakso and F. Lenz (eds.). *The regulation of photosynthesis in fruit trees. Symp. Proc. Publ., N.Y. Stat. Agr. Exp. Sta., Geneva, N.Y.*
- Mika, A., M.J. Grochowska, and A. Karaszewska, and M.W. Williams. 1983. Effects of dormant and summer pruning, disbudding, and growth retardants on growth, flower bud formation, and fruiting of young apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):655-660.
- Moreshet, S., G. Stanhill, and M. Fuchs. 1975. Aluminum mulch increases quality and yield of 'Orleans' apples. *HortScience* 10(4):390-391.
- Morgan, D.C., C.J. Stanley, R. Volz, and I.J. Warrington. 1984. Summer pruning of 'Gala' apple: the relationships between pruning time, radiation penetration, and fruit quality. *J. Amer. Soc. Hort. Sci.* 109(5):637-642.
- Myers, S.C. and D.C. Ferree. 1983a. Influence of summer pruning and tree orientation on net photosynthesis, transpiration, shoot growth, and dry-weight distribution in young apple trees. *J. Amer. Soc. Hort. Sci.* 108(1):4-9.
- Myers, S.C. and D.C. Ferree. 1983b. Influence of time of summer pruning and limb orientation on yield, fruit size, and quality of vigorous 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):630-633.

- Myers, S.C. and D.C. Ferree. 1983c. Influence of time of summer pruning and limb orientation on growth and flowering of vigorous 'Delicious' apple trees. *J. Amer. Soc. Hort. Sci.* 108(4):634-638.
- Ogata, R., H. Kikuchi, T. Hatayama, and H. Komatsu. 1986. Growth and productivity of vigorous 'Fuji' apple trees on M.26 as affected by summer pruning. *Acta Hort.* 160:157-165.
- Olszewski, T. and A. Mika. 1999. The effect of summer pruning and calcium foliar spraying of 'Jonagold' and 'Šampion' apple trees on fruit storage quality. *Acta Hort.* 485:287-291.
- Palmer, J.W. 1988. Annual dry matter production and partitioning over the first 5 years of a bed system of Crispin-M.27 apple trees at four spacings. *J. Appl. Ecol.* 25:569-578.
- Palmer, J.W. 1992. Effects of varying crop load on photosynthesis, dry matter production and partitioning of Crispin/M.27 apple trees. *Tree Physiol.* 11:19-33.
- Palmer, J.W. and I.J. Warrington. 2000. Underlying principles of successful apple planting systems. *Acta Hort.* 513:357-363.
- Platon, I. and L. Zagrai. 1997. The influence of training system and pruning time on growth and apple fruiting. *Acta Hort.* 451:513-518.
- Poll L., A. Rindom, T.B. Toldam-Andersen, and P. Hansen. 1996. Availability of assimilates and formation of aroma compounds in apples as affected by the fruit/leaf ratio. *Physiol. Plantarum* 97:223-227.
- Priestley, C.A. 1963. The importance of autumn foliage to carbohydrate status and root growth of apple trees. *East Malling Res. Sta. Ann. Rep.* 1963:104-106.
- Psarras, G., I.A. Merwin, A.N. Lakso, and J.A. Ray. 2000. Root growth phenology, root longevity, and rhizosphere respiration of field grown 'Mutsu' apple trees on 'Malling 9' rootstock. *J. Amer. Soc. Hort. Sci.* 125(5):596-602.
- Redalen, G. 1992. Yield and grading result of 'Aroma' apples as influenced by pruning treatments. *Acta Hort.* 322: 299-303.

- Robinson, T.L., E. J. Seeley, and B.H. Barritt. 1983. Effect of light environment and spur age on 'Delicious' apple fruit size and quality. *J. Amer. Soc. Hort. Sci.* 108(5):855-561.
- Robinson, T.L., J. Wünsche and A. Lakso. 1993. The influence of orchard system and pruning severity on yield, light interception, conversion efficiency, partitioning index and leaf area index. *Acta Hort.* 349: 123-127.
- Rogers, W.S. 1933. Root studies IV. A method of observing root growth in the field; illustrated by observations in an irrigated apple orchard in British Columbia. *East Malling Res. Sta. Ann. Rep.* 1933:86-91.
- Rogers, W.S. 1939. Root studies VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. *J. Pom. & Hort. Sci.* 17:99-130.
- Saure, M. 1985. Der Einfluss von Schnittzeitpunkt und Schnittintensität auf Wachstum und Wuchsleistung junger Apfelbäume. *Erwerbsobstbau* 27:169-173.
- Saure, M.C. 1990. External control of anthocyanin formation in apple. *Sci. Hort.* 42:181-218.
- Saure, M.C. 1987. Summer pruning effects in apple: A review. *Sci. Hort.* 30:253-282.
- Säkö, J. and E. Laurinen. 1982. Effect of summer pruning on the growth and yield of apple trees. *Ann. Agr. Fennial* 21:8-12.
- Schupp, J.R. 1992. Effect of root pruning and summer pruning on growth, yield, quality, and fruit maturity of McIntosh apple trees. *Acta Hort.* 322:173-175.
- Seeley, E.J., W.C. Micke, and R. Kammereck. 1980. 'Delicious' apple fruit size and quality as influenced by radiant flux density in the immediate growing environment. *J. Amer. Soc. Hort. Sci.* 105(5):645-647.
- Smock, R.M. 1963. Red color study on apples: a progress report. *Proc. New York Hort. Soc.* 108:163-167.

- Smock, R.M. 1964. Red color study on apples: a second progress report. Proc. New York Hort. Soc. 109:185-188.
- Stiles, W.C. 1980. Pruning, growth regulator, and nutrition studies with apples. Maine State Pomo. Soc. Ann. Rep. 1980:25-34.
- Struklec, A. 1981. Einfluß des Schnittermins beim Sommerschnitt auf Blatt und Frucht beim Apfel. Gartenbauwissenschaft 46(6):S. 268-276.
- Struklec, A. 1994. Kann Sommerschnitt die Kalziumkonzentration der Apfelfrucht erhöhen und damit das Auftreten physiologischer Krankheiten verringern? Erwerbsobstbau 36:158-160.
- Taylor, B.H. 1982. The influence of summer pruning and fruit cropping on growth, carbohydrate and nutrient element status of apple trees. PhD dissertation. The Ohio State Univ., Columbus, Ohio.
- 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(3):389-393.
- Taylor, B.H. and D.C. Ferree. 1984. The influence of summer pruning and cropping on growth and fruiting of apple. J. Amer. Soc. Hort. Sci. 109(1): 17-24.
- Taylor, B.H. and D.C. Ferree. 1986. The influence of summer pruning and fruit cropping on the carbohydrate, nitrogen, and nutrient composition of apple trees. J. Amer. Soc. Hort. Sci. 111(3):342-346.
- Upshall, W.H. and J. Barkovic. 1963. Summer pruning of dwarf apple and pear trees. Ontario Hort. Exp. Sta. & Prod. Lab. Ann. Rep. 1963:16-19.
- Warrington, I.J., C.J. Stanley, R. Volz, and D.C. Morgan. 1984. Effects of summer pruning on Gala apple quality. The Orchardist of New Zealand 12:518-522.
- Ystaas, J. 1989. Yield, fruit size and fruit quality of two apple cultivars as influenced by summer pruning. Norsk Landbruksforskning 3:195-204.

Ystaas, J. 1992. Effects of summer pruning on yield, fruit size, and fruit quality of the apple cultivar 'Summerred'. Acta Hort. 322:277-282.

CHAPTER FIVE

COMPUTER MODELING SIMULATION OF SUMMER PRUNING EFFECTS AND WEATHER PATTERNS ON CARBOHYDRATE BALANCE IN APPLE TREES

Abstract

Computer modeling is a potential approach for integrating information and illustrating the consequences of summer pruning. To learn the modeling environment and test this approach, the carbohydrate balance model developed by Lakso et al. (2001) was used to simulate the responses of mature slender spindle 'Empire' /M.9 apple trees (*Malus domestica* Borkh.) to summer pruning severity and crop regulations under the average weather condition or certain growing seasons. To simplify the simulation process, fruit number was regulated at full bloom. Leaf area was adjusted 110 days after budbreak by reducing the total active leaf area to simulate the pruning treatments. The model generated a continuous seasonal trend of canopy photosynthesis (Pn) in relation to pruning severity. Results also suggested that with unlimited water and nutritional resources, the effect of summer pruning could be interpreted with the carbohydrate supply and demand balance in relation to the severity of leaf area removal by summer pruning and the fruit number. Seasonal weather pattern might also affect the supply and demand balance and consequently change the plant sensitivity to summer pruning.

Additional Index Words

Malus domestica, photosynthesis, light interception, carbohydrate supply and demand balance

Introduction

With the canopy balloon gas exchange system, our previous studies (Chapter two and three) suggested that summer pruning in apple trees (*Malus domestica* Borkh.) can significantly reduce canopy photosynthesis (Pn), resulting in a reduction in carbohydrate supply, and might consequently lead to suppression of growth and development of fruit, flower, and root (Chapter four). However, the instant readings obtained on a limited number of dates and under specific weather conditions might not be able to provide sufficient information to demonstrate the effect of summer pruning on the carbohydrate supply and demand balance over the entire growing season. The time and labor-consuming field task and the number of replicates reduced the possibility of the application of the balloon system for continuous monitoring of the canopy performance over the growing season. Therefore, alternate strategies are required to estimate the effects at other times.

Computer modeling offers an useful tool for generating information and for developing quantitative hypotheses (Atkins, 1999; Murase, 2000). Several computer models specific for apples have been developed to simulate production practices and physiological performance (Atkins et al., 1996; Costes et al., 1999; Johnson and Lakso, 1991; Porter, 1989; Smith et al., 1992). The model originally developed by Lakso and Johnson (1991) has been used to estimate carbohydrate supply/demand balances (Lakso and Corelli-

Grappadelli, 1992; Lakso and Robinson, 1997). It has also been used for simulations of the reduction in carbon supply due to European red mite damage (Lakso et al., 1998). Therefore, the potential of the model to evaluate summer pruning effects was highly interesting.

The objectives of this study were to acquaint the modeling environment and to test the feasibility of simulating the effects of summer pruning in apple trees. The carbohydrate balance model was used to simulate the output of different severities of summer pruning and cropping treatments on canopy photosynthesis, light interception, carbohydrate supply and fruit demand. In addition, as discussed in previous chapters, the annual weather conditions might regulate the effects of summer pruning on canopy photosynthesis and transpiration (Chapter three) and consequently modify the significance on the balance of carbohydrate supply and demand. The capacity of driving the model with different temperature and radiation input might also allow us to explore the tree performance under different weather patterns.

The results from this study were expected to provide some valuable perspectives for increasing our understanding of summer pruning. In addition, the comparison between simulation and field measurements also offers an opportunity for the development of new strategies to improve either field measurement or the computer model.

Model Description and Simulation Strategies

Description of the Model

The model described by Lakso et al. (2001) was adopted in our study. This model was originally designed by Lakso and Johnson (1990) with a

dynamic modeling program (Stella, High Performance Systems, Inc., Hanover, N.H.) for simulating carbon supply/demand balance of apple trees through the growing season on a daily basis. The basic components of the model include daily canopy gas exchange, leaf area development, fruit growth and abscission, and carbohydrate partitioning. The canopy photosynthesis sub model is a "big leaf" model with a daily time step as developed by Charles-Edwards (1982). Inputs of tree descriptions and weather information are required to drive the model. The initial major inputs of tree information include numbers of shoots and flowers, spacing, and wood surface area. Daily radiation and maximum and minimum temperature are the weather data necessary for simulation. The original weather input was the average temperature and radiation data of 1971 to 1990 from Geneva, New York, but weather from 1999 was also used.

The model is initially designed for a mature slender spindle 'Empire' /M.9 apple tree at a 1957 tree ha^{-1} density, with 13.3 m^2 leaf area when fully developed and 2400 initial flower number.

Simulation of Summer Pruning Severity and Cropping Effects

To simplify the simulation process, fruit number was reduced from 2400 to 150 fruit per tree at full bloom (32 days after budbreak) with the pollination factor option. Active leaf area was adjusted with a fraction foliage option at 110 days after budbreak to simulate the summer pruning effect. In addition to control (unpruned), 15%, 30%, 50%, and 60% leaf area removal was simulated.

For simulating fruit demand, the original active leaf area was adopted. Fruit number was adjusted at full bloom to 150, 200, and 250 fruits per tree, respectively.

Simulation of Weather Pattern Effect

In addition to the original long-term weather input, simulations was made under the input of weather data of 1999. Due to the various developments of accumulation degree-day, fruit set was adjusted to 200 fruits per tree at 32 days and 35 days after budbreak in the original weather set and in 1999 weather set, respectively. Original active leaf area was adopted in the simulation over the growing season.

Results and Discussions

Simulation of Summer Pruning Severity and Cropping Effects

By simply reducing the active leaf area after canopy was fully developed in early summer (110 days after budbreak), the carbon balance model generated the daily photosynthesis trend resembling the canopy response to summer pruning measured in the field (Figure 5.1). The trend demonstrated the proportional reduction in canopy photosynthesis in relation to the leaf area removal until leaf fall (220 days after budbreak). There was a slight difference between the simulation output and our previous field measurements on the prediction of the impact of summer pruning (Figure 5.2). The prediction from field study was based on the average value of three instant mid-day readings in ideal sunny weather conditions after summer pruning in 1998 and 1999. The outputs from the model data are based on total daily photosynthesis. These data might not truly represent the canopy net

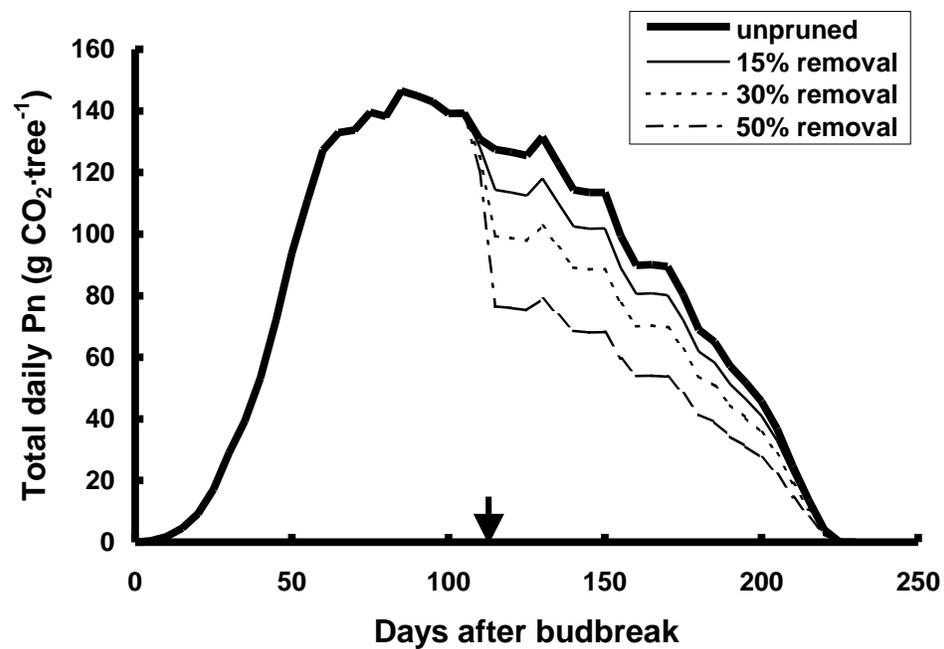


Figure 5.1 Simulation of summer pruning effect on daily canopy photosynthesis (Pn) of mature slender spindle 'Empire' /M.9 apple trees. Leaf area was adjusted to simulate pruning severity at 110 days after budbreak (arrow).

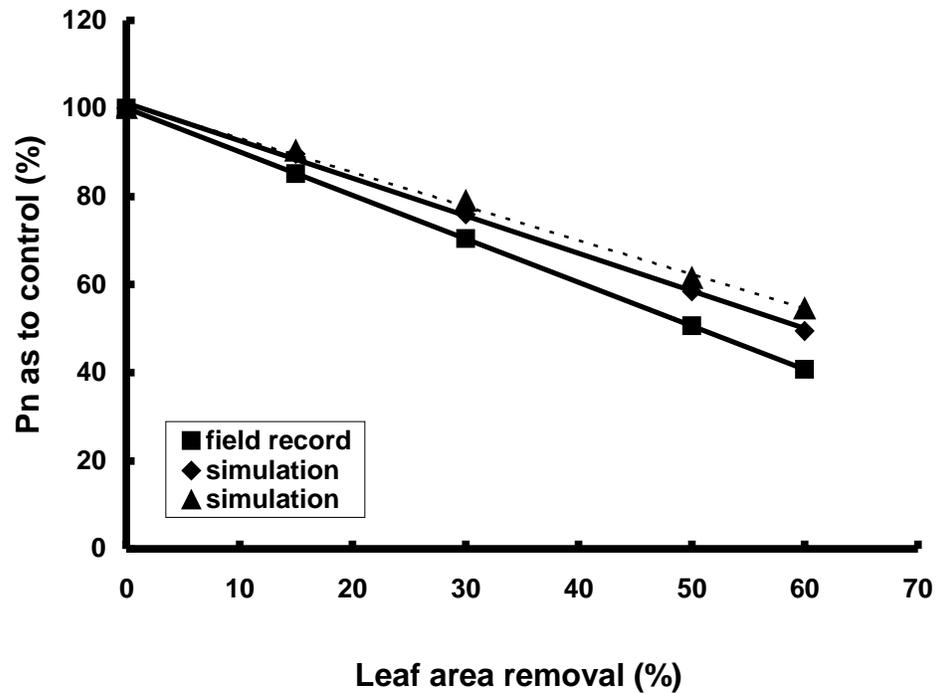


Figure 5.2 Instant measurements of canopy net gas exchange rate (NCER) and simulation of final photosynthesis (Pn) accumulations in relation to summer pruning severity in mature slender spindle 'Empire' /M.9 apple trees. Simulation outputs represent daily Pn at 115 days after budbreak (solid line) and the total Pn accumulation after summer pruning until leaf fall (dash line). Field record represents predictions from average values of three instant readings after summer pruning.

carbon exchange rate (NCER) in inferior weather conditions. The higher percentage of direct light and lower percentage of diffuse light on sunny days is expected to increase the proportion of well-exposed shoot leaves and reduce the proportion of shade leaves contributing to total canopy photosynthesis. In contrast, cloudy and haze conditions would drive the proportion to the opposite direction. Since summer pruning mainly removes the well-exposed shoot leaves, the prediction based on the instant readings from sunny days possibly over estimated the impact of summer pruning on seasonal total photosynthesis.

On the other hand, due to the assumption of uniform leaf function, output of simulation by reducing leaf area according to summer pruning severity might under estimate the final impact on canopy photosynthesis. Therefore, the actual seasonal photosynthetic reduction in relation to summer pruning can be located between the field measurements and simulation output.

Due to the limitation on the tree materials and orchard size, a great variance on canopy light interception measurement was observed from our field study (Chapter three). The computer simulation provides a possibility to modify the correlation (Figure 5.3). However, as in many other computer models, the light interception in this model is based on canopy leaf area and canopy light extinction coefficient (k), which assumes uniform distribution and orientations of leaves within the canopy volume. Simply reducing the leaf area from the model does not change the uniformity and the canopy k .

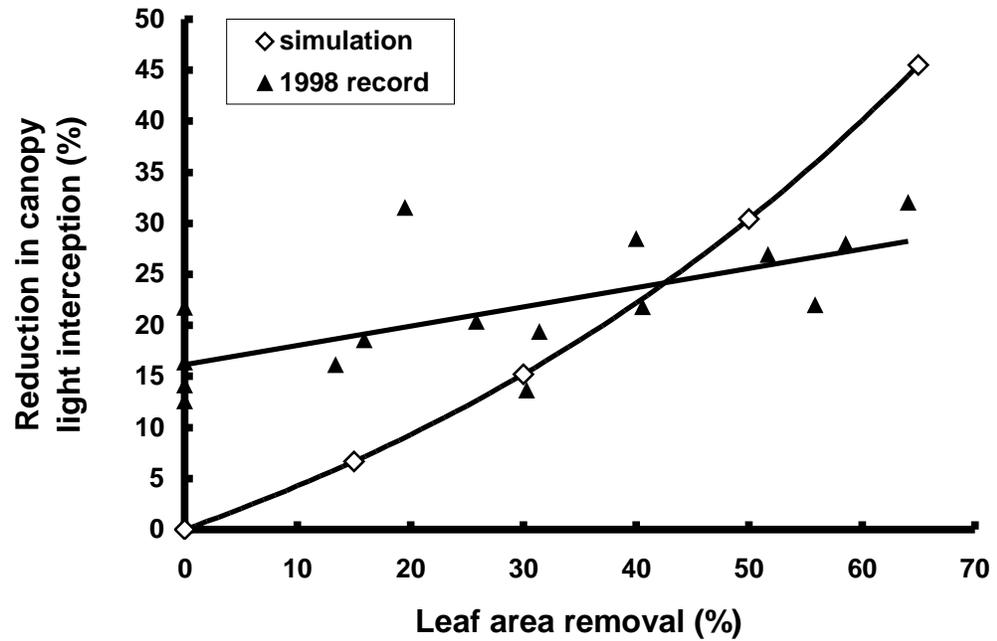


Figure 5.3 In situ measurements and computer simulations of canopy light interception in relation to summer pruning severity in mature slender spindle 'Empire'/M.9 apple trees.

Therefore, the model simulates the pruning as a homogeneous removal of leaves within the same dimensions. However, in practice only the exterior extension shoots were removed from the canopy by summer pruning. This would change the canopy k and the canopy dimensions. Therefore, the canopy light interception effects are more complicated than simulated.

With a final fruit set at 150 fruits per tree, the computer simulation suggested that fruit weight should be reduced in relation to percentage leaf area removal (Figure 5.4). However, in the model the fruit weight is estimated according to the balance of carbohydrate partitioning to the fruit and the demand for supporting the potential fruit growth. Due to the scarcity and uncertainty of the quantitative information, the estimate of crop demand and competing sink strength is not well tested. Therefore, crop demand was estimated independently based on the measured fruit growth in the field. The growth rate in grams fresh weight per day was adjusted to dry weight (15%) and dry weight-to-fixed CO₂ (1.67 x dry weight) construction costs.

Previous study suggested that root and shoot growth mainly occurs before our summer pruning treatment (Chapter three and four). Fruit growth is possibly the major carbohydrate sink from the mid-summer until harvest and may have the first priority to use any extra carbohydrate, e.g. total photosynthesis – total respiration (Figure 5.5). Therefore, simulation results of daily carbohydrate availability and fruit demand might provide a better interpretation on summer pruning and fruit growth. The relationship suggest that with a moderate crop load (150 or less per tree), a mature slender spindle 'Empire'/M.9 apple tree after light or moderate summer pruning would still be able to provide sufficient carbohydrate for fruit demand, as we concluded in the previous study (Chapter four).

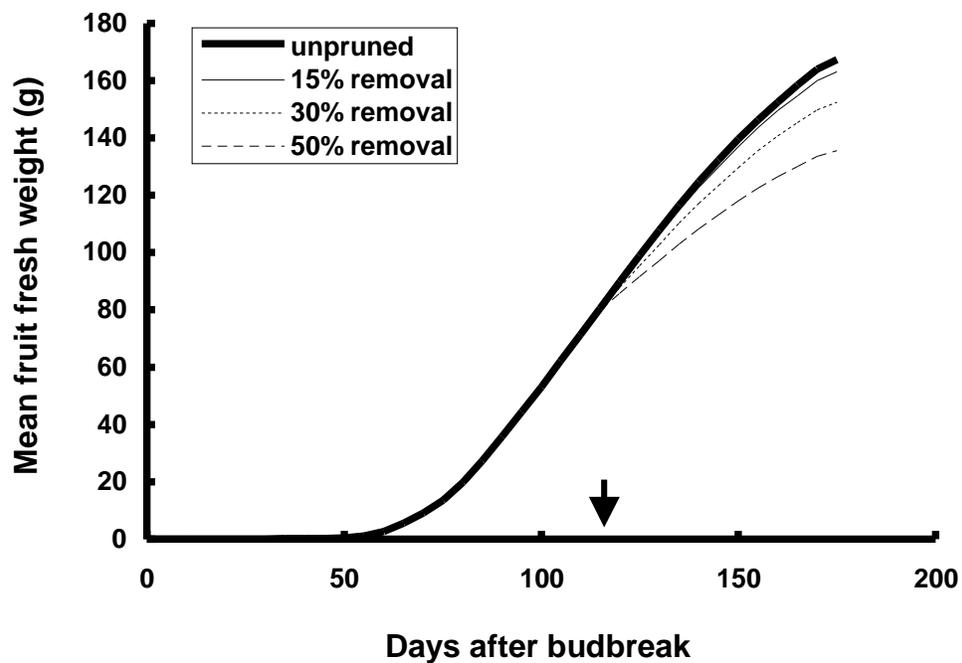


Figure 5.4 Simulation of summer pruning effect on fruit growth of mature slender spindle 'Empire' /M.9 apple trees with 150 fruit per tree. Leaf area was adjusted 110 days after budbreak (arrow).

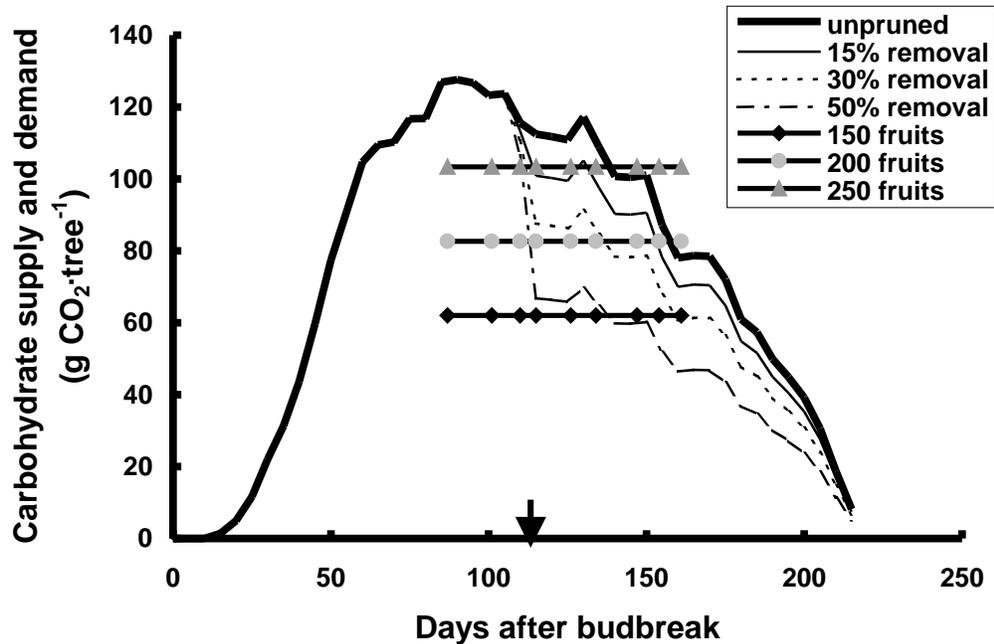


Figure 5.5 Simulation of carbohydrate availability (lines without symbols) and demand for fruit growth (lines with symbols) of mature slender spindle 'Empire' / M.9 apple trees in relation to summer pruning and cropping. Leaf area was adjusted 110 days after budbreak (arrow). The availability curves represent total daily photosynthesis – total daily respiration. Fruit demands were estimated from the average growth rate from field measurement in 1998.

Simulation of Weather Pattern Effect

A few researchers have noticed that the result of summer pruning might be modified by annual weather patterns. Lord et al. (1979) indicated that the result of increasing in flower bud formation in some varieties following summer pruning might be attribute to favorable weather conditions rather than pruning procedures. With a computer modeling program on potential apple production, Wagenmakers (1996) suggested that a 25% greater fruit production in seasons with 'good' weather than that in 'bad' year. The increase might be attributed to adequate temperature, better light availability and sufficient water supply. In 1999, the better radiation over the growing season (Figure 5.6), the lower temperature in the early spring and higher than normal day and night temperature later (Figure 5.7), and the lower precipitation might affect the results of summer pruning. The simulation output of 1999 weather set indicated slight reductions in total daily photosynthesis (Figure 5.8) and in daily carbohydrate available for fruit growth (Figure 5.9), comparing to the results from average weather conditions. However, the precipitation and water-plant relationships were not considered in the carbon balance model. The simulation results and our field records suggested that the tree water status might be as important as carbohydrate balance on influencing the result of summer pruning. More information on the water-fruit growth and water-carbohydrate relationships is needed.

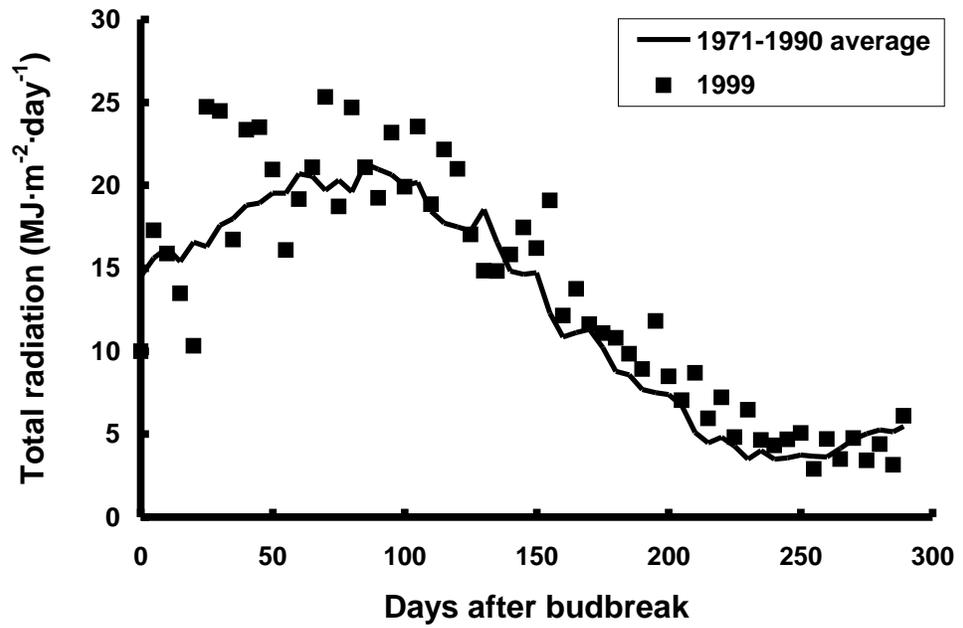


Figure 5.6 Seasonal daily total radiations of Geneva, New York (42°52.6' N) of 1999 and average value of 1971-1990.

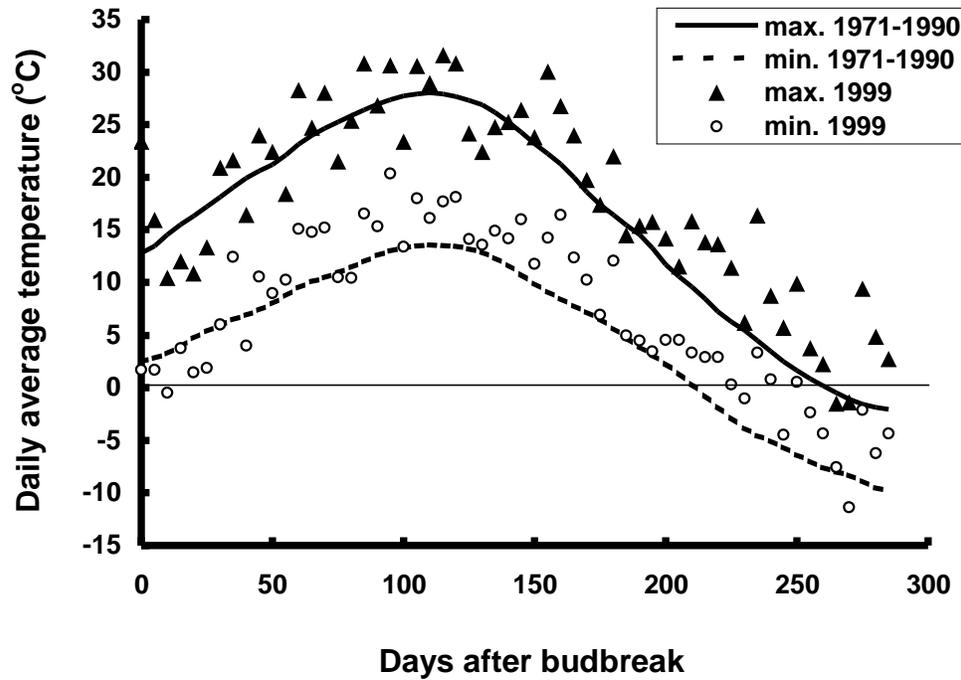


Figure 5.7 Seasonal daily maximum and minimum temperature of Geneva, New York ($42^{\circ}52.6'$ N) of 1999 and average value of 1971 to 1990.

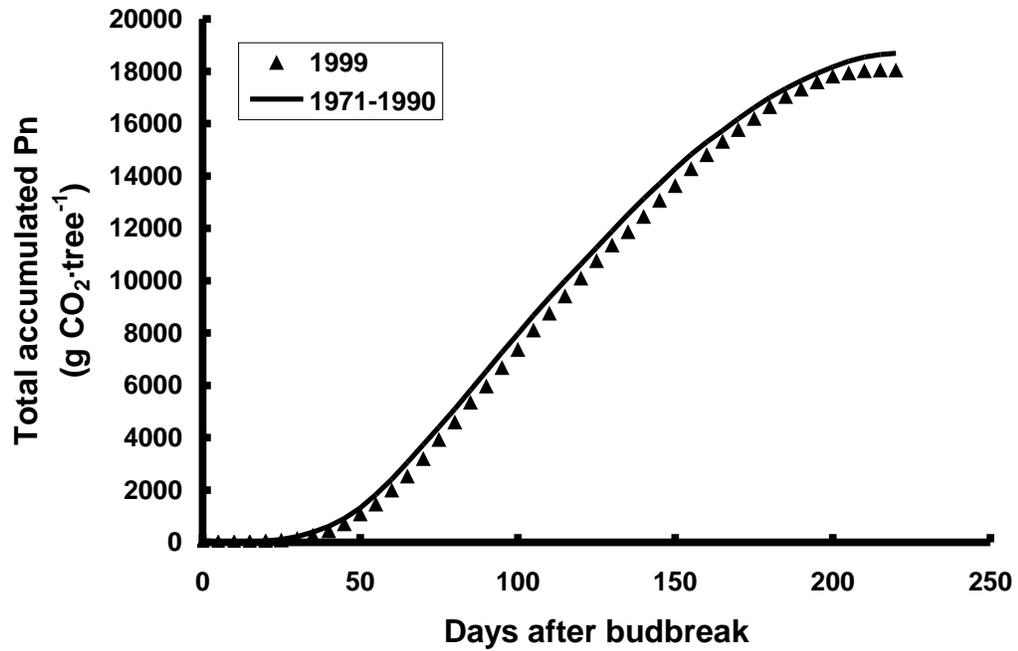


Figure 5.8 Simulation of total Pn accumulation of mature slender spindle 'Empire' /M.9 apple trees in 1999 and average weather conditions from budbreak until leaf fall.

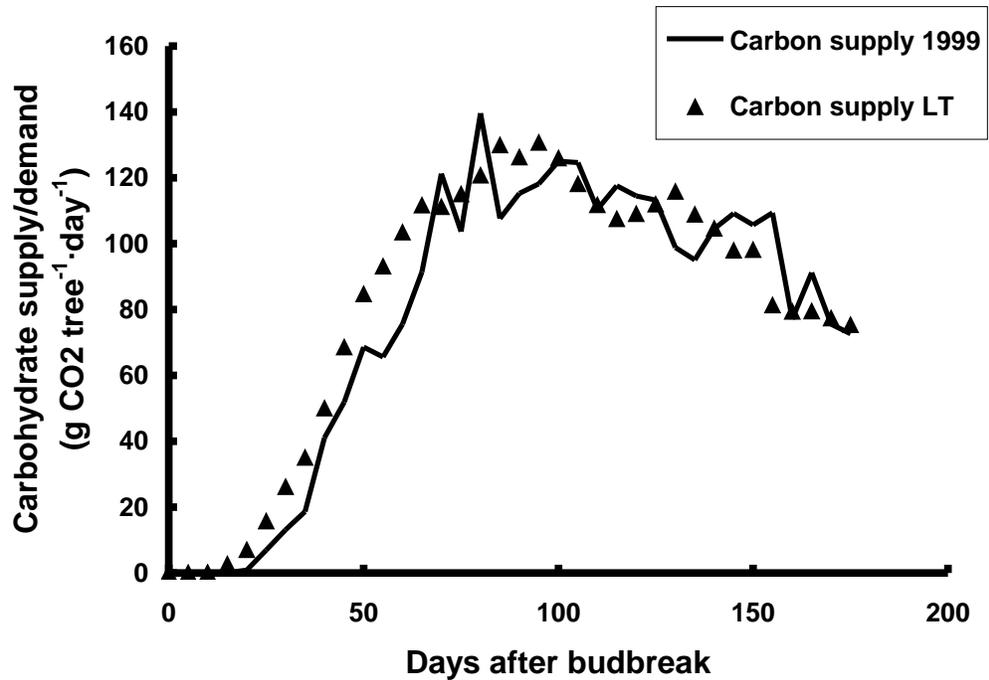


Figure 5.9 Simulation of carbohydrate availability for fruit growth of slender spindle 'Empire' / M.9 apple trees in long-term (1971-1990 average) and annual (1999) weather conditions. The supply curves represent total daily photosynthesis - total daily respiration. The demands curves represent 200 fruits per tree.

Conclusions

This preliminary study indicated the potential of computer modeling approaches for understanding the physiological responses of apple trees to summer pruning and weather pattern. The simulation process also revealed the limitations of the current carbohydrate balance model. It is possible to improve the active leaf area and canopy k components by separating the leaf type and the proportion to the total canopy leaf area. To improve the simulation of canopy light interception especially for summer pruning study it might require more reliable information from in situ measurement of light. Other modeling approaches such as 3D topological databases for single canopy architecture study (Costes et al., 1999) as well as multiscale model for plant topological structure (Godin and Caraglio, 1998) might provide other strategies for quantifying the selective leaf and shoot removal by summer pruning and the consequent changes in light interception.

More work on the growth of root and trunk, and the seasonal consumption and restoration of carbohydrate reserves are required to improve the estimation of carbohydrate demand and partitioning of the model. In the future, introducing the interaction between carbohydrate and other resources such as water or nutrient into the model will greatly enhance the ability of the model to simulate performance under all conditions.

References

- Atkins, T.A. 1999. Directions in modeling fruit growth and orchard processes. *Acta Hort.* 499:31-36.
- Atkins, T.A., R.O. O'Hagan, W.J. Rogers, M.W. Pearson, and E.A. Cameron. 1996. Virtual reality in horticultural education: pruning simulated fruit trees in a virtual environment. *Acta Hort.* 416:243-245.
- Charles-Edwards, D.A. 1982. *Physiological determinants of crop growth.* Academic Press, Sydney.
- Costes, E., H. Sinoquet, C. Godin, and J.J. Kelner. 1999. 3D digitizing based on tree topology: application to study the variability of apple quality within the canopy. *Acta Hort.* 499:271-280.
- Godin C. and Y. Caraglio. 1998. A multiscale model of plant topological structure. *J. Theor. Biol.* 191:1-41.
- Johnson, R.S. and A.N. Lakso. 1991. Approaches to modeling light interception in orchards. *HortScience* 26(8):1002-1004.
- Lakso, A.N., M. Bepete, and M.C. Goffinet. 1998. Aspects of carbon supply and demand in apple fruits. *Acta Hort.* 466:13-18.
- Lakso, A.N. and L. Corelli-Grappadelli. 1992. Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Hort.* 322:231-239.
- Lakso, A.N. and R.S. Johnson. 1990. A simplified dry matter production model for apple using automatic programming simulation software. *Acta Hort.* 276:141-148.
- Lakso, A.N. and T.R. Robinson. 1997. Principles of orchard systems management optimizing supply, demand and partitioning in apple trees. *Acta Hort.* 451:405-415.
- Lakso, A.N., M.D. White, and D.S. Tustin. 2001. Simulation modeling of the effects of short and long-term climatic variations on carbon balance of apple trees. *Acta Hort.* (In press.).

- Lord, W.J., D.W. Greene, W.S. Bramlage, and M. Drake. 1979. Inducing flowering of apple trees and increasing fruit quality by summer pruning. *Compact Fruit Tree* 12:23-29.
- Murase H. 2000. Computer applications and "phytotechnology" in horticulture. *Acta Hort.* 519:19-36.
- Porter, J.R. 1989. Pruning, canopy architecture and plant productivity, p. 293-304. In: C.J. Wright (ed.). *Manipulation of fruiting*. Butterworths, London.
- Smith G.S., J.P. Curtis, and C.M. Edwards. 1992. A method for analysis plant architecture as it relates to fruit quality using three-dimensional computer graphics. *Ann. Bot.* 70:265-269.
- Wagenmakers, P.S. 1996. Effects of light and temperature on potential apple production. *Acta Hort.* 416:191-197.

CHAPTER SIX

GENERAL CONCLUSIONS AND FUTURE STUDIES

Many years of grower experience has shown that there are many advantages of summer pruning for canopy control, apple fruit coloring, and orchard management. However, the diversity of pruning strategies and the inconsistency of plant responses have also troubled growers and scientists for more than a century (Gardner et al., 1922). In this study the possibility of interpreting the summer pruning effects by carbohydrate balance theory was tested and demonstrated with field measurements and computer simulation approaches. The results suggested that although summer pruning was efficient on improving canopy light transmission and on controlling canopy vigor, the removal of a great amount of well-functioned leaves during the growing season immediately and directly impaired the canopy photosynthetic ability, which might be detrimental to fruit and vegetative growth and development if the canopy carbohydrate supply could not fulfill the demand.

Therefore, maintaining the balance of carbohydrate supply and demand is the principle to relieve the impact of summer pruning. Due to the different requirements according to varieties, marketing, planting area, weather, and orchard conditions, it is not practical to develop a standard summer pruning procedure. However, the principle can be achieved by:

- 1) Maintaining a year round well open canopy by proper training systems, winter pruning, or delayed dormant pruning to improve canopy

light environment and thus reduce the amount of leaf area needed to be removed by summer pruning.

2) Adjusting crop load by chemical or hand thinning to avoid excessive demand for carbohydrates.

In addition, the field test indicated that several environmental and physiological factors might potentially affect the carbohydrate dynamics after summer pruning. Future studies required to document this issue include:

1) To determine the influence of decreased canopy transpiration after summer pruning on canopy water status, and the interaction between water status and carbon balance (Figure 6.1).

2) To determine the influence of environmental conditions, mainly temperature, radiation, and precipitation/soil water content, on tree carbon and water balance after summer pruning (Figure 6.2).

3) To improve the estimation of light interception for individual trees. Strategies may include better buffering with multiple adjacent trees and multiple adjacent rows, measurement in an artificial environment or under controlled light sources, direct measurement with the 'Whirligig' radiometer (Green et al., 1995; McNaughton et al., 1992), and computer modeling (Wagenmakers and Tazelaar, 1999).

Simulations with the computer model of carbohydrate balance generated intriguing information to illustrate the result of summer pruning.

Modifications to increase the precision of simulation require:

1) Separating canopy leaf area submodel for spur leaves and shoot leaves to represent the selective shoot leaf removal by summer pruning.

2) Developing flexible canopy extinction coefficient (k) according to the severity of summer pruning since spurs and shoots have different k values.

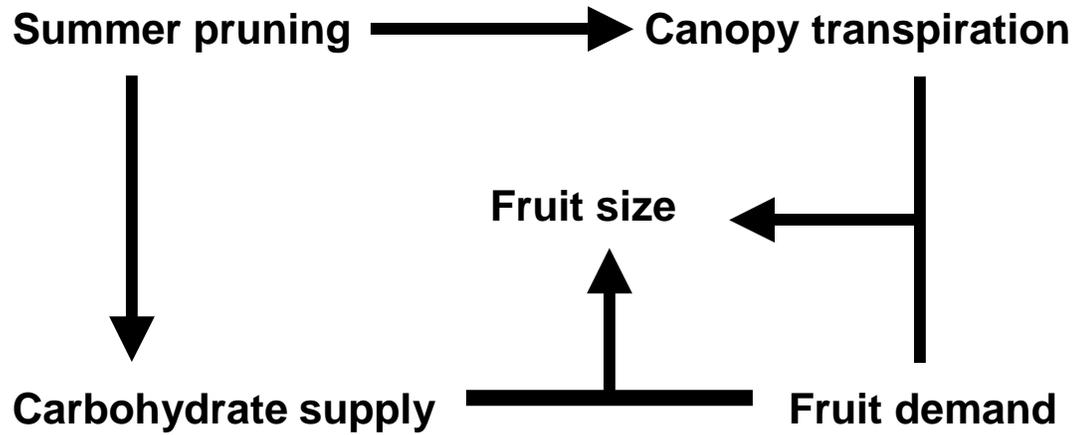


Figure 6.1 Fruit demand and final fruit size in relation to canopy carbohydrate supply and transpiration after summer pruning.

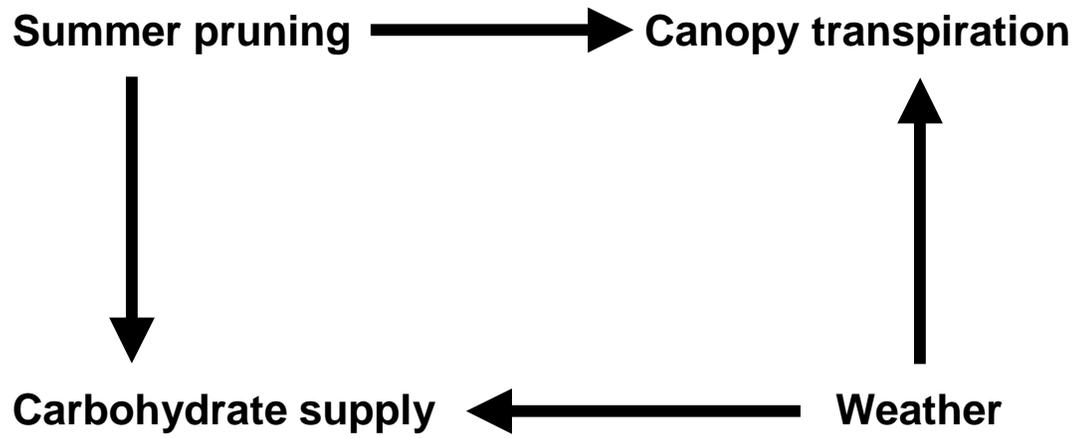


Figure 6.2 Diagrams of canopy carbohydrate supply and transpiration in relation to summer pruning and weather patterns.

3) Obtaining more information on the seasonal growth demand of root, shoot, and trunk to improve the estimations of carbohydrate demand and partitioning.

References

- Gardner, V.R., F.C. Bradford, and H.D. Hooker. Jr. 1922. The fundamentals of fruit production. 1st ed. McGraw-Hill, New York.
- Green, S.R., K.G. McNaughton, D.H. Greer, and D.J. McLeod. 1995. Measurement of the increased PAR and net all-wave radiation absorption by an apple tree caused by applying a reflective ground covering. *Agric. For. Meteorol.* 76:163-183.
- McNaughton, K.G., S.R. Green, T.A. Black, B.R. Tynan, and W.R.N. Edwards. 1992. Direct measurement of net radiation and photosynthetically active radiation absorbed by a single tree. *Agric. For. Meteorol.* 62:87-107.
- Wagenmakers, P.S. and M. Tazelaar. 1999. Modelling light interception on the basis of sunfleck measurements. *Acta Hort.* 499:297-303.

APPENDIX A

CLIMATOLOGICAL SUMMARY OF GENEVA, NEW YORK

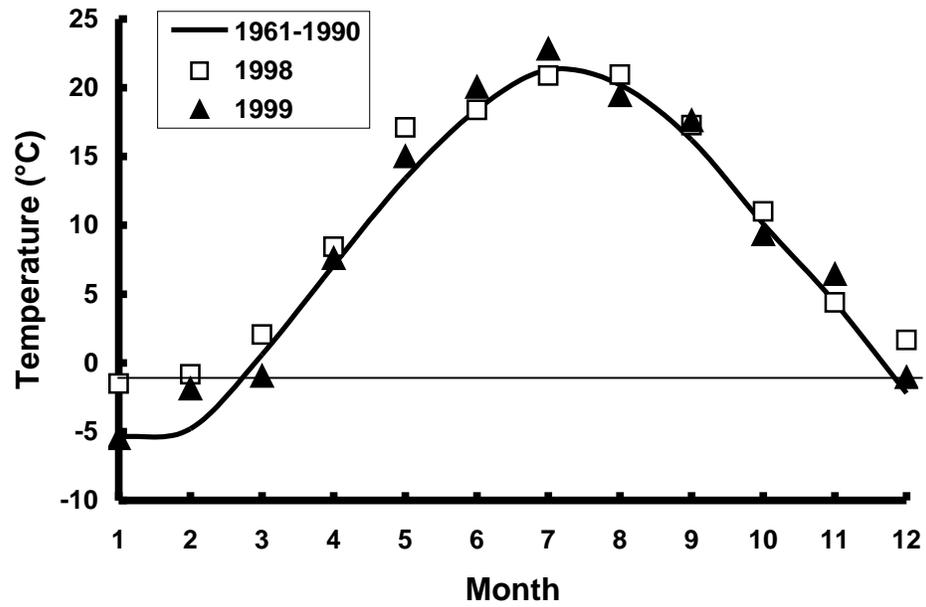


Figure A.1 Monthly mean temperature of Geneva, N.Y. (primary source: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

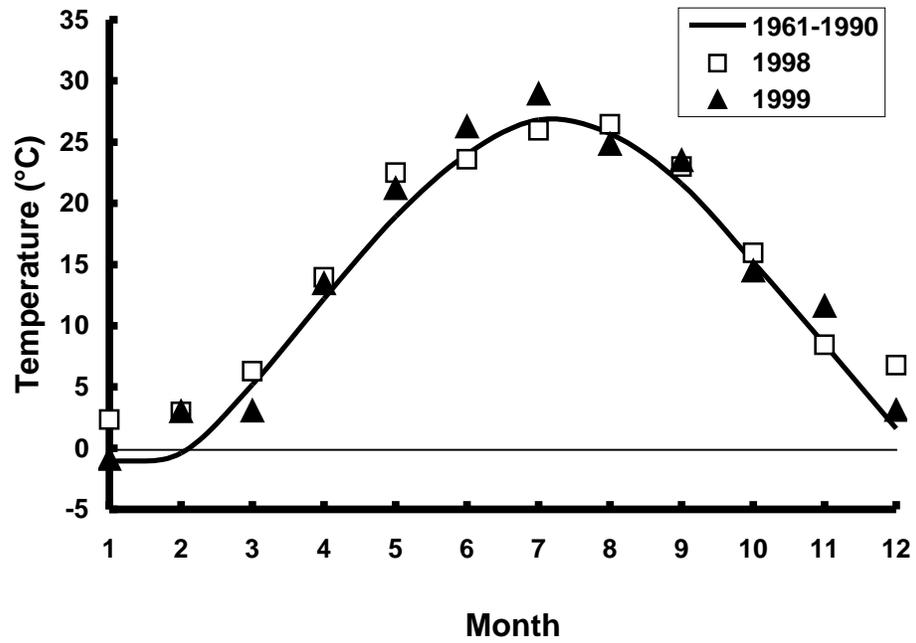


Figure A.2 Monthly maximum temperature of Geneva, N.Y. (primary source: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

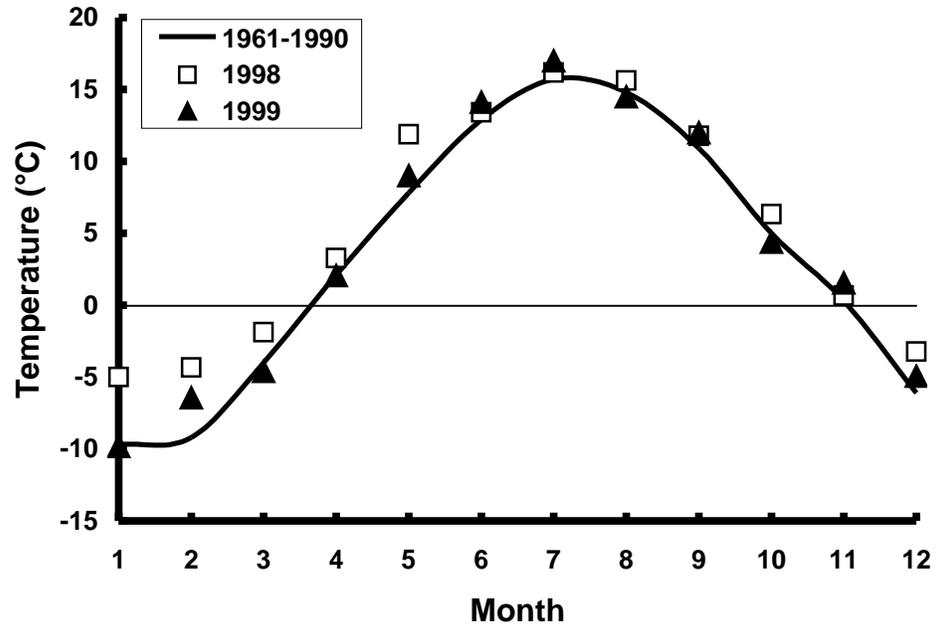


Figure A.3 Monthly minimum temperature of Geneva, N.Y. (primary source: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

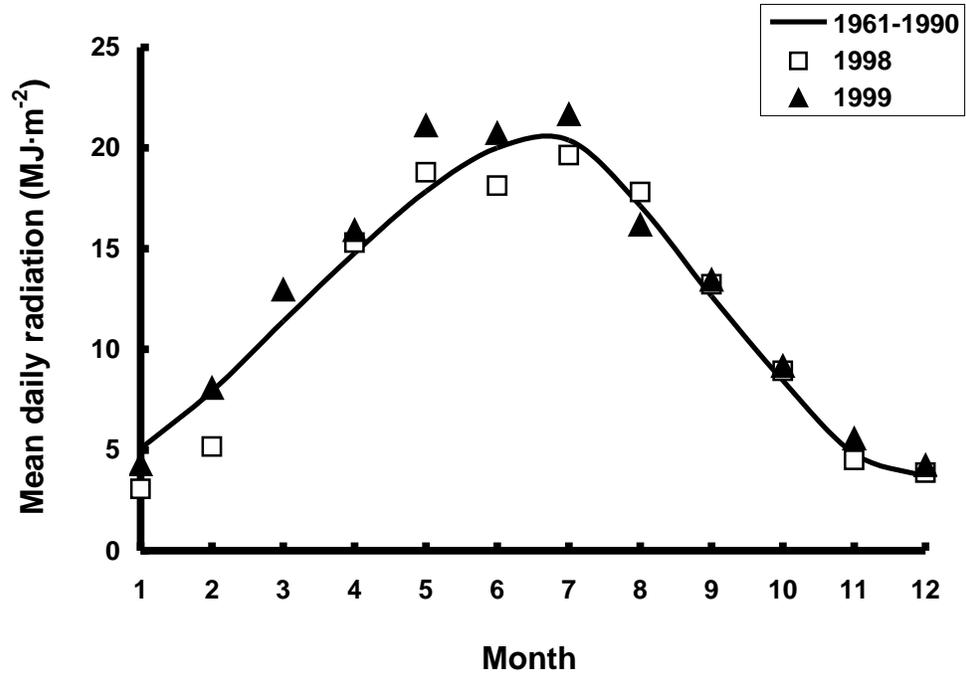


Figure A.4 Mean daily radiation of Geneva, N.Y. (primary sources: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

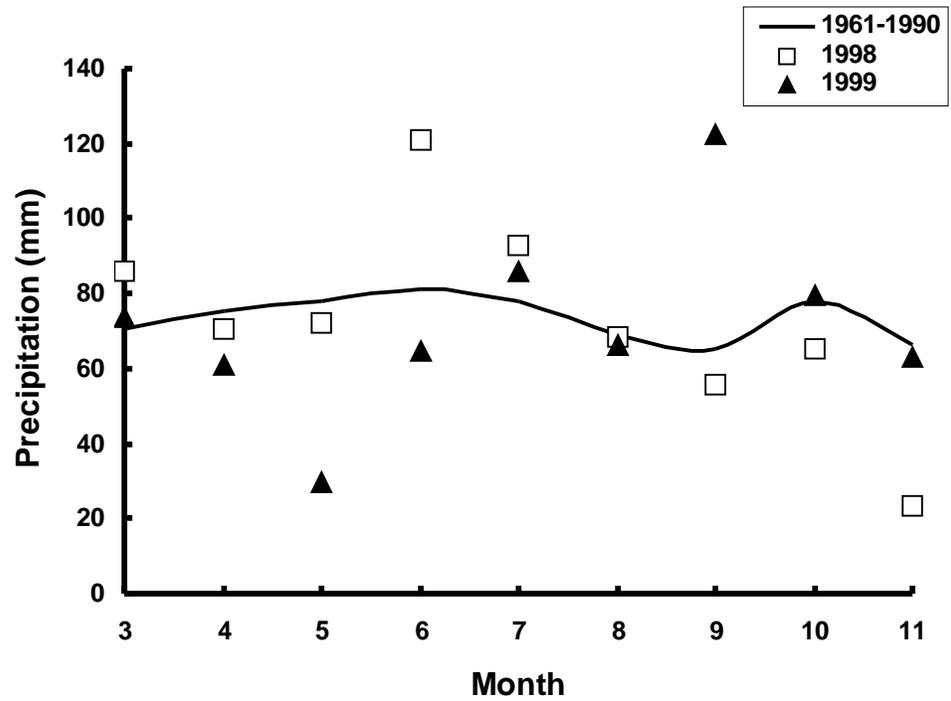


Figure A.5 Monthly precipitation of Geneva, N.Y. (primary source: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

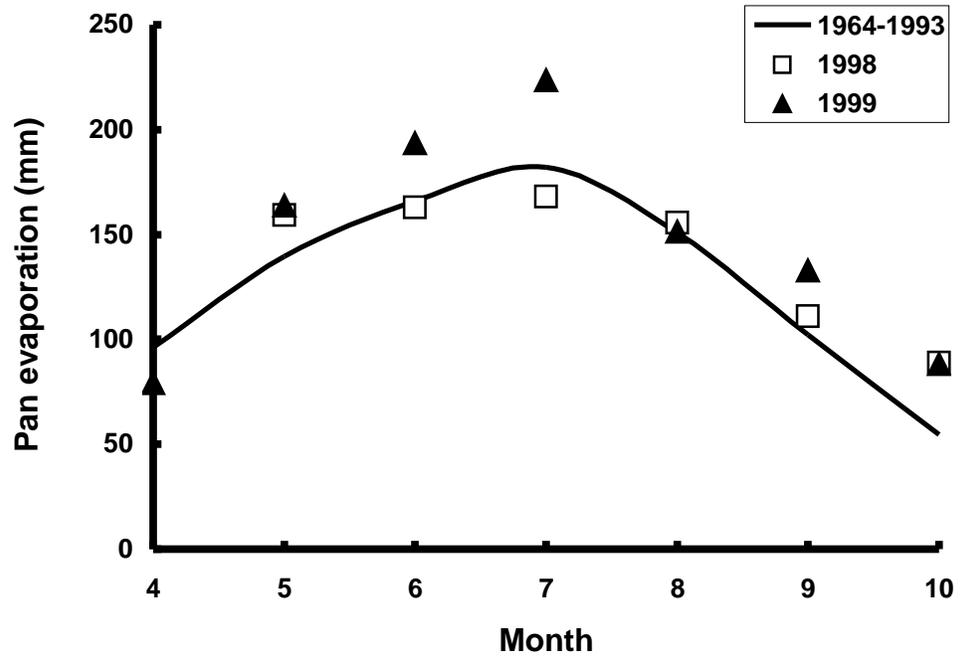


Figure A.6 Monthly pan evaporation of Geneva, N.Y. (primary source: Climatological Reference Station at New York State Agricultural Experiment Station, Geneva, N.Y.).

APPENDIX B

THE WHOLE-TREE CARBON BALANCE/DRY MATTER PRODUCTION MODEL FOR APPLE

This appendix contains the equations and structures of the carbon balance model used in Chapter five. For details and update please contact Dr. Alan Lakso.

Equations

$$\text{AccDegDays}(t) = \text{AccDegDays}(t - dt) + (\text{DailyDegDay}) * dt$$

$$\text{INIT AccDegDays} = 0$$

DOCUMENT: Accumulated degree-days=Sum of daily degree-days, base 4 C,
over the season, starting at budbreak

INFLOWS:

$$\text{DailyDegDay} = (\text{TempMax} + \text{TempMin}) / 2 - 4$$

DOCUMENT: Daily-degree days= Average of daily maximum and minimum temperatures (C), subtracted by 4C (base temperature, minimum necessary for growth)

$$\text{AccDMtoFrt}(t) = \text{AccDMtoFrt}(t - dt) + (\text{DailyCtoFrt}) * dt$$

$$\text{INIT AccDMtoFrt} = 0$$

INFLOWS:

$$\text{DailyCtoFrt} = \text{CO2toFrts} * \text{FrtDMtoCO2}$$

DOCUMENT: Once CO₂ is partitioned to the fruit, it is expressed as dry matter based on the dry matter-to-CO₂ relation (FrtDMtoCO₂) .

$$\text{AccDMtoRoots}(t) = \text{AccDMtoRoots}(t-dt) + (\text{DailyCtoRoots}) * dt$$

$$\text{INIT AccDMtoRoots} = 0$$

INFLOWS:

$$\text{DailyCtoRoots} = \text{CO}_2\text{toRoots} * \text{VegDMtoCO}_2$$

DOCUMENT: Once CO₂ is partitioned to the fruit, it is expressed as dry matter based on the dry matter-to-CO₂ relation (VegDMtoCO₂) .

$$\text{AccDMtoShts}(t) = \text{AccDMtoShts}(t-dt) + (\text{DailyCtoShts}) * dt$$

$$\text{INIT AccDMtoShts} = 0$$

INFLOWS:

$$\text{DailyCtoShts} = \text{CO}_2\text{toShts} * \text{VegDMtoCO}_2$$

DOCUMENT: Once CO₂ is partitioned to the fruit, it is expressed as dry matter based on the dry matter-to-CO₂ relation (VegDMtoCO₂) .

$$\text{AccDMtoWood}(t) = \text{AccDMtoWood}(t-dt) + (\text{DailyCtoWood}) * dt$$

$$\text{INIT AccDMtoWood} = 0$$

INFLOWS:

$$\text{DailyCtoWood} = \text{CO}_2\text{toWood} * \text{VegDMtoCO}_2$$

DOCUMENT: Once CO₂ is partitioned to the fruit, it is expressed as dry matter based on the dry matter-to-CO₂ relation (VegDMtoCO₂) .

$$\text{AccFrtResp}(t) = \text{AccFrtResp}(t - dt) + (\text{DlyFrtResp}) * dt$$

$$\text{INIT AccFrtResp} = 0$$

DOCUMENT: Accumulated fruit respiration (gCO₂.tr-1)

INFLOWS:

$$\text{DlyFrtResp} = \text{DayFrtResp}$$

DOCUMENT: Daily fruit respiration (gCO₂.tr-1.day-1)

$$\text{AccLeafDM}(t) = \text{AccLeafDM}(t - dt) + (\text{LeafDM_day}) * dt$$

$$\text{INIT AccLeafDM} = 0$$

DOCUMENT: Accumulated leaf dry matter (g)

INFLOWS:

$$\text{LeafDM_day} = (\text{DailyExtshLAI} + \text{DailySprLAI}) * \text{LeafDMperA}$$

DOCUMENT: Leaf dry matter produced per day (g DM.tr-1.dy-1)

$$\text{AccLeafResp}(t) = \text{AccLeafResp}(t - dt) + (\text{DlyLeafResp}) * dt$$

$$\text{INIT AccLeafResp} = 0$$

DOCUMENT: Accumulated leaf respiration (gCO₂.tr-1)

INFLOWS:

$$\text{DlyLeafResp} = \text{DayRleaf}$$

DOCUMENT: Daily leaf respiration (gCO₂.tr-1.day-1)

$$\text{AccPnTot}(t) = \text{AccPnTot}(t - dt) + (\text{DlyPnTot}) * dt$$

$$\text{INIT AccPnTot} = 0$$

DOCUMENT: Accumulated total gross photosynthesis (gCO₂.tr-1)

INFLOWS:

$$\text{DlyPnTot} = \text{DailyPnTot}$$

DOCUMENT: Daily integral of total photosynthesis per area allotted to the tree (gCO₂.m-2.day-1)

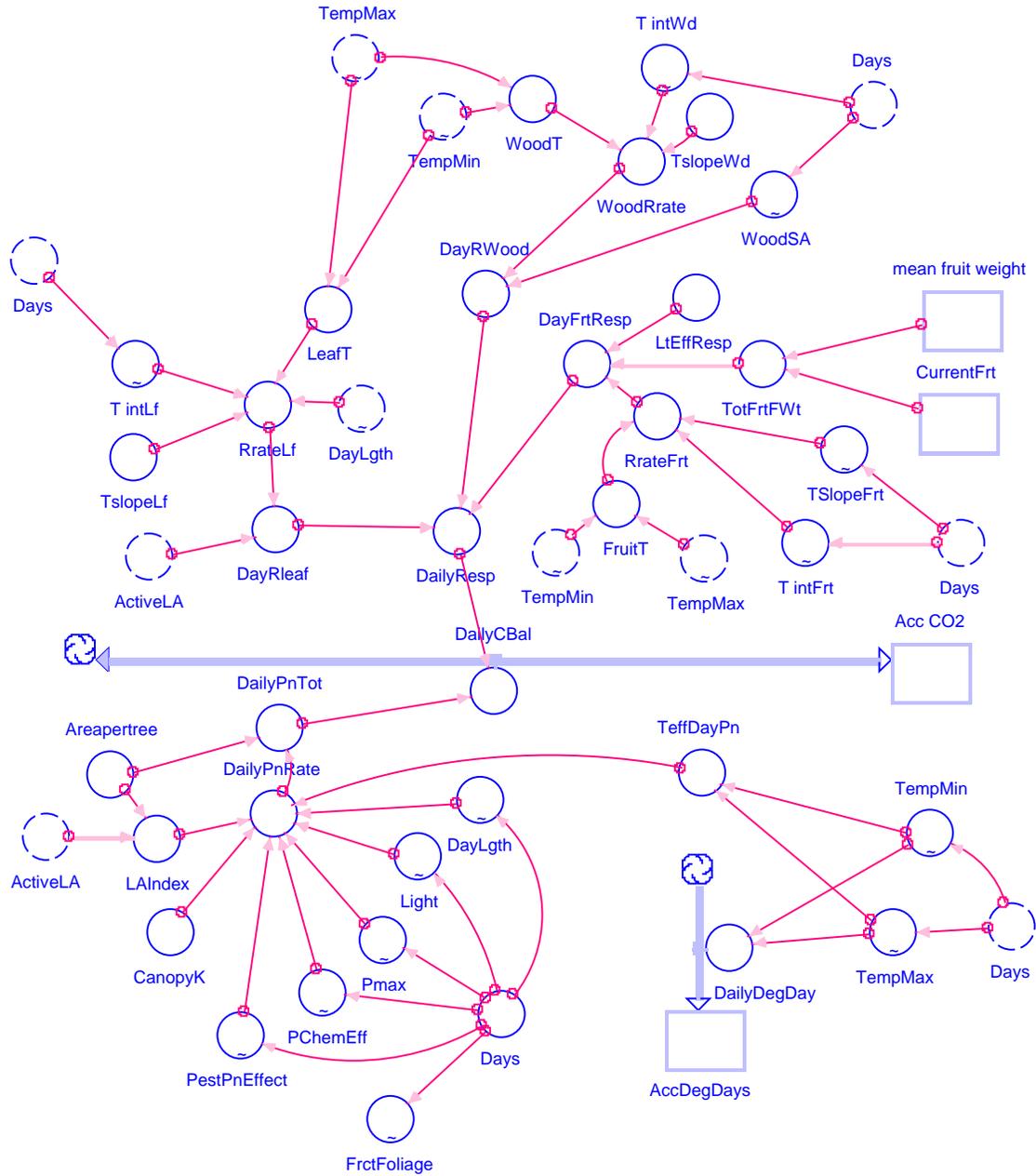


Figure B.1 Structure of the whole-tree carbon balance/dry matter production model- submodel of carbohydrate supply.

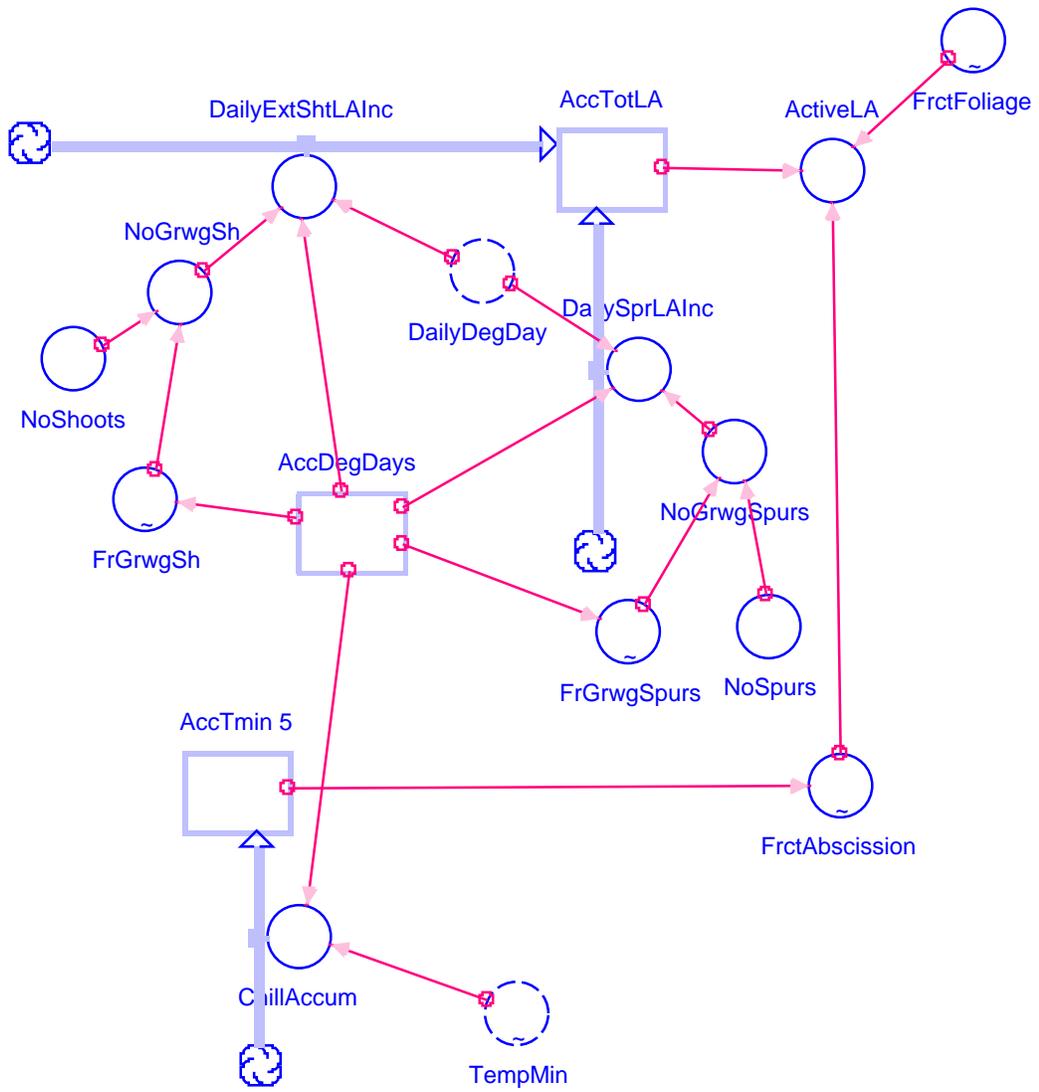


Figure B.2 Structure of the whole-tree carbon balance/dry matter production model— submodel of leaf area.

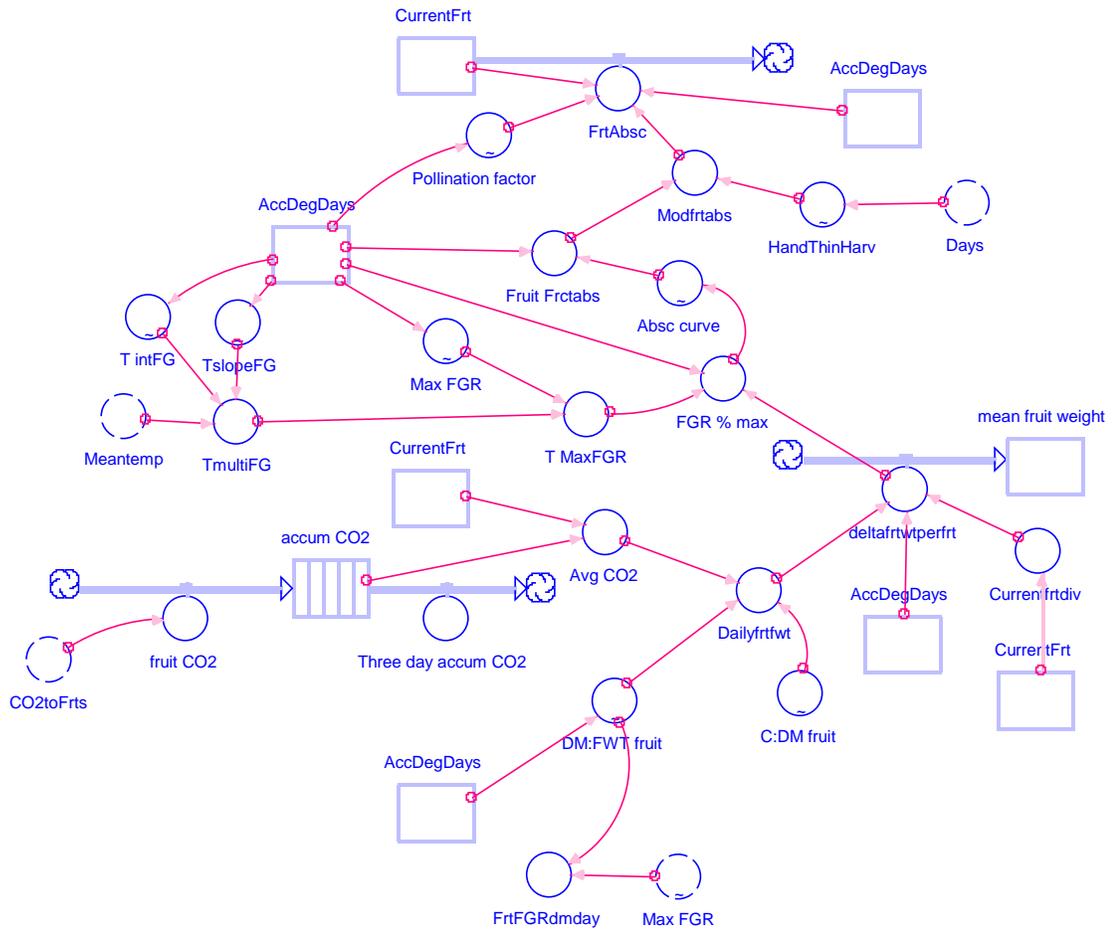


Figure B.3 Structure of the whole-tree carbon balance/dry matter production model— submodel of fruit growth.

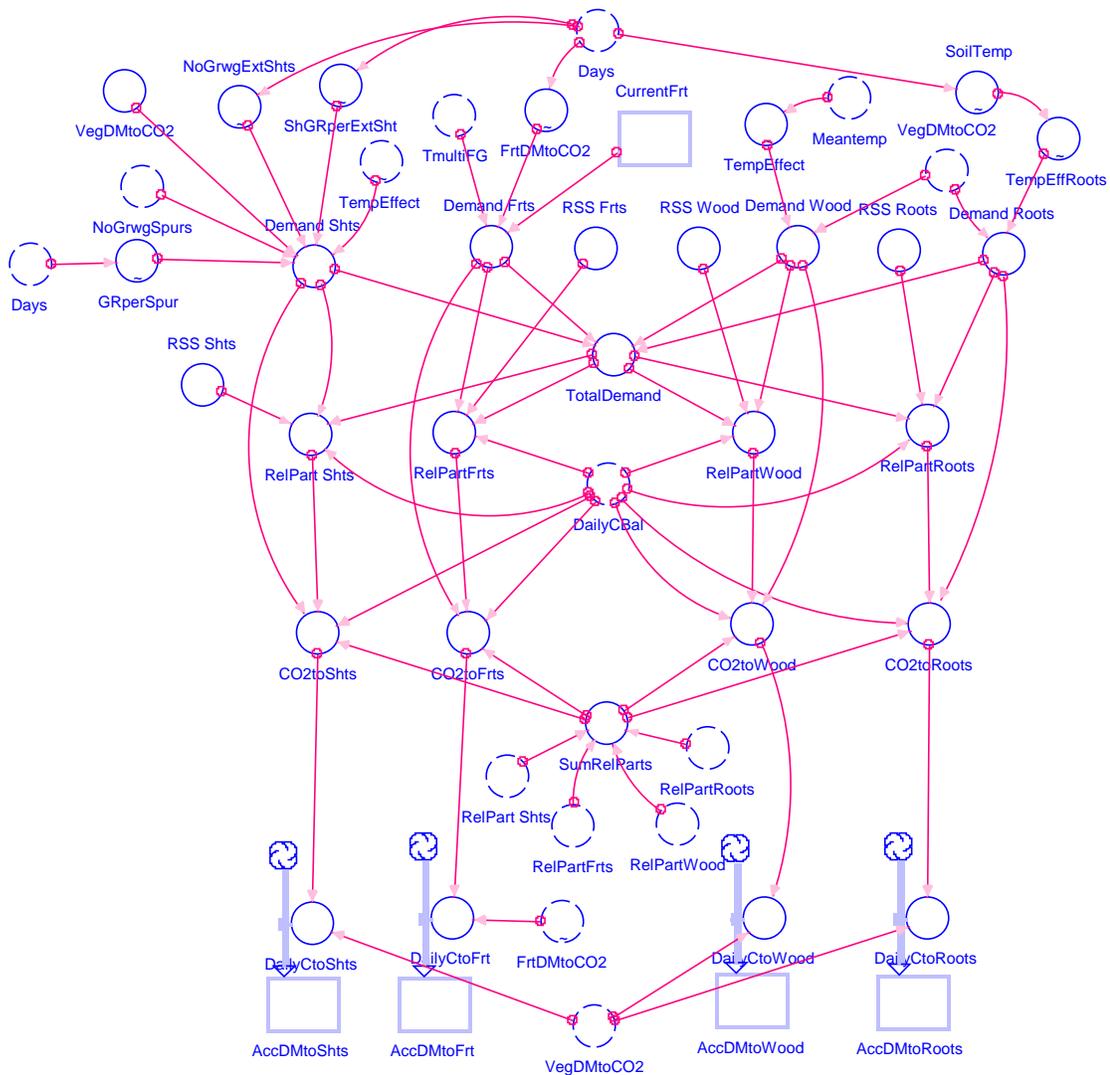


Figure B.4 Structure of the whole-tree carbon balance/dry matter production model— submodel of carbohydrate demand.

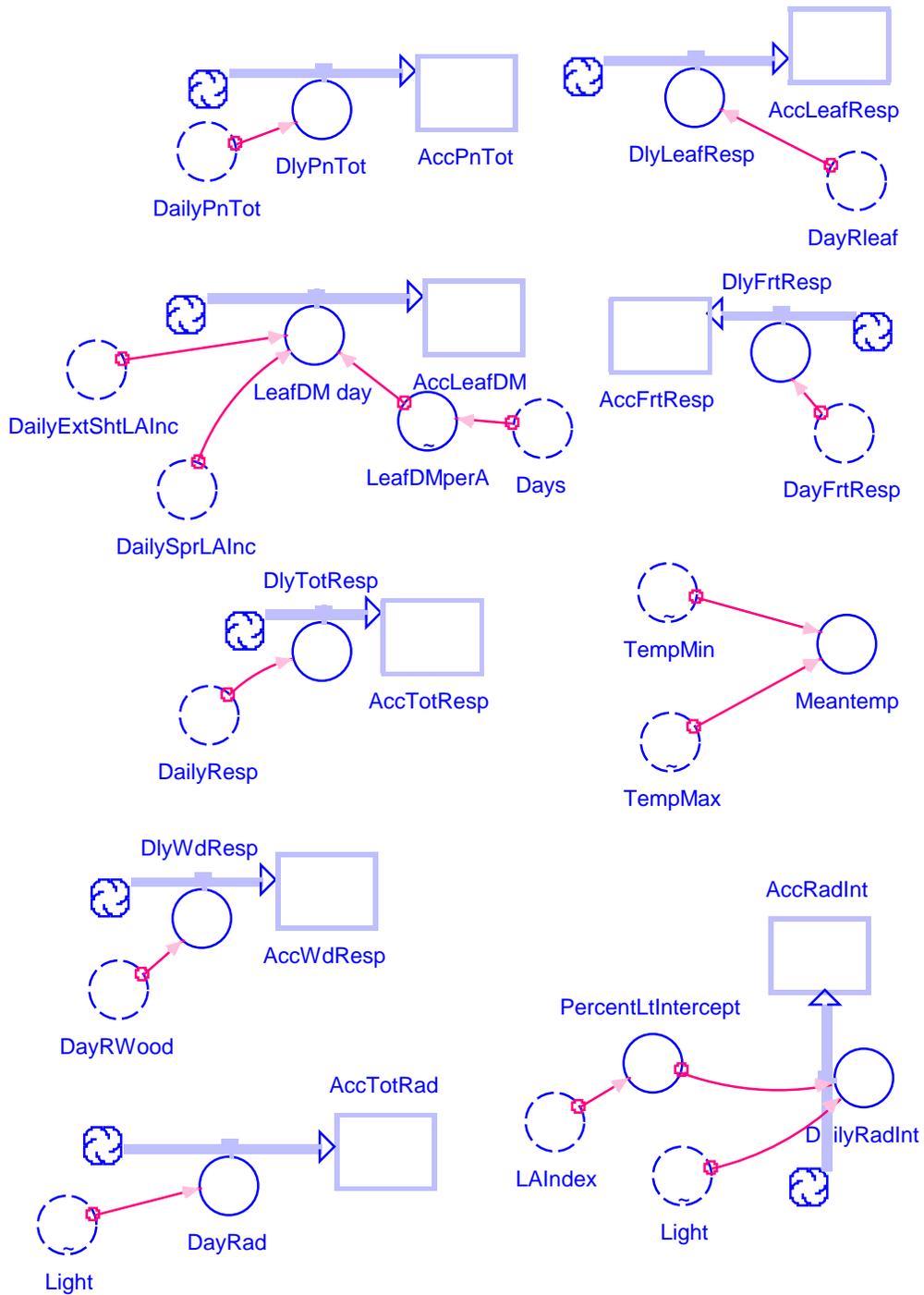


Figure B.5 Structure of the whole-tree carbon balance/dry matter production model— submodels of accumulated respiration, radiation, and leaf dry matter.

$$\text{AccRadInt}(t) = \text{AccRadInt}(t - dt) + (\text{DailyRadInt}) * dt$$

$$\text{INIT AccRadInt} = 0$$

INFLOWS:

$$\text{DailyRadInt} = \text{Light} * \text{PercentLtIntercept} / 100$$

$$\text{AccTmin}_5(t) = \text{AccTmin}_5(t - dt) + (\text{ChillAccum}) * dt$$

$$\text{INIT AccTmin}_5 = 0$$

INFLOWS:

$$\text{ChillAccum} = \text{IF} (\text{AccDegDays} > 600) \text{ THEN } (5 - \text{TempMin}) \text{ ELSE } 0$$

$$\text{AccTotLA}(t) = \text{AccTotLA}(t - dt) + (\text{DailyExtShtLAInc} + \text{DailySprLAInc}) * dt$$

$$\text{INIT AccTotLA} = 0$$

DOCUMENT: Accumulated leaf area=Sum of Daily leaf area increment per tree (m²)

INFLOWS:

$$\text{DailyExtShtLAInc} = \text{If AccDegDays} > 100 \text{ then}$$

$$(0.00007 * \text{DailyDegDay}) * \text{NoGrwgSh} \text{ ELSE } (0.00004 * \text{DailyDegDay})$$

DOCUMENT: Daily leaf area increment per tree (m²)

$$\text{DailyLAInc per shoot(m}^2\text{)} = 0.00008 * \text{DegDay4C}.$$

Rate of leaf area development on apple shoots is quite consistent as a function

of DegDay4C with an average value of 0.00008m² per DegDay4C

(unpublished data and Johnson, R.S., and A.N. Lakso. 1985.

Relationships between stem length, leaf area, stem weight, and

accumulated degree-days in apple shoots. J. Amer. Soc. Hort. Sci.

110(4):586-590.)

**DailySprLAInc = If AccDegDays<200 Then
 (0.00002*DailyDegDay*NoGrwgSpurs)ELSE
 (0.00004*DailyDegDay*NoGrwgSpurs)**

AccTotRad(t) = AccTotRad(t - dt) + (DayRad) * dt

INIT AccTotRad = 0

INFLOWS:

DayRad = Light

AccTotResp(t) = AccTotResp(t - dt) + (DlyTotResp) * dt

INIT AccTotResp = 0

DOCUMENT: Accumulated total respiration (gCO₂.tr-1)

INFLOWS:

DlyTotResp = DailyResp

**DOCUMENT: Daily integral of total respiratory losses of leaves, fruits and
 tree structure per tree, i.e. per area allotted to the tree (gCO₂.tr-1.day-1)**

**accum_CO2(t) = accum_CO2(t - dt) + (fruit_CO2 - Three_day_accum_CO2) *
 dt**

INIT accum_CO2 = 0

TRANSIT TIME = 3

INFLOW LIMIT = INF

CAPACITY = INF

**DOCUMENT: Conveyor is set with a transit time of 3. Therefore the conveyor
 accumulates CO₂ values over the preceding three days. Allows an**

average to be taken of the CO₂ values partitioned to the fruit over a three day period.

INFLOWS:

$$\text{fruit_CO2} = \text{CO2toFrts}$$

OUTFLOWS:

$$\text{Three_day_accum_CO2} = \text{CONVEYOR OUTFLOW}$$

$$\text{AccWdResp}(t) = \text{AccWdResp}(t - dt) + (\text{DlyWdResp}) * dt$$

$$\text{INIT AccWdResp} = 0$$

DOCUMENT: Accumulated wood respiration (gCO₂.tr-1)

INFLOWS:

$$\text{DlyWdResp} = \text{DayRWood}$$

DOCUMENT: Daily wood respiration (gCO₂.tr-1.day-1)

$$\text{Acc_CO2}(t) = \text{Acc_CO2}(t - dt) + (\text{DailyCBal}) * dt$$

$$\text{INIT Acc_CO2} = 0$$

INFLOWS:

$$\text{DailyCBal} = (\text{DailyPnTot} - \text{DailyResp})$$

DOCUMENT: Daily Carbon Balance (g CO₂ per tree per day-1). Biflow allows negative Carbon Balance values to occur when carbon losses due to respiration are higher than carbon fixed by photosynthesis.

$$\text{CurrentFrt}(t) = \text{CurrentFrt}(t - dt) + (- \text{FrtAbsc}) * dt$$

$$\text{INIT CurrentFrt} = 2400$$

DOCUMENT: Current fruit number carried by the tree. Initially set at 2400.

OUTFLOWS:

**FrctAbsc = IF (AccDegDays<190) THEN CurrentFrct*Pollination_factor
ELSE CurrentFrct*Modfrctabs**

DOCUMENT: Fruit abscission rate is calculated by multiplying current fruit number by abscission factor or hand thinning factor depending on which is the active process. Before 190 accumulated GDD only abscission factor used is the pollination factor. 190 GDD is assumed to be the point of full bloom using the 1997 Empire data used to obtain the maximum fruit growth rate.

mean_fruit_weight(t) = mean_fruit_weight(t - dt) + (deltafrctwtperfrct) * dt

INIT mean_fruit_weight = 0.10

DOCUMENT: Mean fruit weight (grams)

INFLOWS:

deltafrctwtperfrct = IF (AccDegDays>170) THEN

Dailyfrctfwt/Currentfrctdiv ELSE 0.0

DOCUMENT: Calculates the available fresh weight (grams) available to each fruit. Calculated by dailyfrctfwt divided by the current fruit carried by the tree. Below 170 accumulated degree days (base 4) (8 days before bloom) fruit fresh weight set at 0 as deemed not to be growing and not receiving significant amounts of carbon.

**ActiveLA = (IF AccTotLA>0 THEN AccTotLA*(1-FrctAbscission) ELSE
0)*FrctFoliage**

Areapertree = 5.1

DOCUMENT: Area per tree=5.1 m² based on the standard Empire/M9,
Slender Spindle, mature orchard, 14 y-old, spacing:1.5m within

row*3.4m between rows, 1957 tr/ha, 5.1m²/tr, mature tree height=2.5 m (Wunsche, J.'s Ph.D. Dissertation)

Avg_CO2 = If (CurrentFrts=0) THEN 0 ELSE accum_CO2/3

DOCUMENT: Avg CO2: averages CO2 over a three day period partitioned to the fruit. This is to account for variations in light and photosynthesis so the fruit abscission is responding to longer variations in climatic conditions.

CanopyK = 0.3

DOCUMENT: Canopy light extinction coefficient

Spur type/clumped canopy: k<0.5

Extension shoots/closed canopy: k>0.5

Orchard basis k was estimated from the data and regression of Wunsche et. al., 1996 (JASHS) for several orchard systems in which the "standard" spindle tree was one measured.

With a k=0.3 and an orchard LAI=2.5 (as measured in the standard orchard), the light interception will maximize at about 55%.

CO2toFrts = If (DailyCBal/SumRelParts)<1 then

RelPartFrts*(DailyCBal/SumRelParts) else Demand_Frts

CO2toRoots = If (DailyCBal/SumRelParts)<1 then

RelPartRoots*(DailyCBal/SumRelParts) else Demand_Roots

$CO2toShts = IF (DailyCBal/SumRelParts) < 1 \text{ Then}$
 $RelPart_Shts * (DailyCBal/SumRelParts) \text{ else Demand_Shts}$

$CO2toWood = If (DailyCBal/SumRelParts) < 1 \text{ then}$
 $RelPartWood * (DailyCBal/SumRelParts) \text{ else Demand_Wood}$

$Currentfrtdiv = IF (CurrentFrft=0) \text{ THEN } 1.0 \text{ ELSE CurrentFrft}$

DOCUMENT: Currentfrtdiv is the current fruit number carried by the tree
 which defaults to one if tree carries no fruit.

$Dailyfrtftwt = Avg_CO2 * C:DM_fruit * DM:FWT_fruit$

DOCUMENT: The daily carbon partitioned to fruit in terms of fruit fresh
 weight (grams).

$DailyPnRate = (PChemEff * Light * DayLgth * Pmax * (1 - EXP(-$
 $CanopyK * LAIndex)) / (PChemEff * CanopyK * Light + DayLgth * Pmax)) * Te$
 $ffDayPn * PestPnEffect$

DOCUMENT: DailyPnRate=Daily gross photosynthetic rate per unit ground
 area allotted per tree ($gCO_2.m^{-2}.day^{-1}$)

PChemEff=leaf photochemical efficiency or quantum yield ($ugCO_2.J^{-1}$ total
 radiation); Light=Daily integral of total radiation incident on a
 horizontal surface ($MJ.m^{-2}.day^{-1}$); Daylength=(s); Pmax=rate of light
 saturated leaf photosynthesis per unit leaf area ($g CO_2.m^{-2}.s^{-1}$);
 Canopy k=canopy light extinction coefficient; LAIndex=leaf area index
 per total area allotted per tree; TeffDayPn=Temperature effects on

photosynthetic rate, i.e. Fractional reduction (or no change) of daily Pn due to temperature.

This integral model was described by Charles-Edwards, D.A. 1982.

Physiological determinants of crop growth. Academic Press, Sydney. chapter 4. p.65-85. eq.4.10c, with an additional correction factor due to temperature effects on photosynthesis.

$$\text{DailyPnTot} = \text{DailyPnRate} * \text{Areapertree}$$

DOCUMENT: Daily integral of total photosynthesis per tree (gCO₂ per day⁻¹)

$$\text{DailyResp} = \text{DayRleaf} + \text{DayRWood} + \text{DayFrtResp}$$

DOCUMENT: Daily integral of total respiratory losses of leaves, fruits and tree structure per tree, i.e. per area allotted to the tree (gCO₂.tr⁻¹.day⁻¹)

The respiration submodels are all based on exponential response of the respiration rate (R) to temperature (0-42C): $R = a * e^{kT}$, where a=R at T=0C (the intercept of lnR versus T); k=temperature coefficient of R (the slope of lnR versus T); T=temperature in C. The plot of lnR versus T contains lines of various slopes and/or intercepts depending on the tissue and/or time of the season.

$$\text{DayFrtResp} = \text{RrateFrt} * \text{TotFrtFWt} * \text{LtEffResp}$$

DOCUMENT: Daily fruit respiration (gCO₂.tr⁻¹.day⁻¹)

$$\text{DayRleaf} = (\text{RrateLf} * \text{ActiveLA})$$

DOCUMENT: Daily leaf respiration (gCO₂.tr⁻¹.day⁻¹)

Total daily leaf respiration includes a factor that increases R as a proportion of the DailyPnTot.

Preliminary trial on potted apple tree under constant temperature in a growth chamber suggested that dark leaf respiration rate after higher leaf photosynthetic rate (high light) was higher than after lower leaf photosynthetic rate (low light) (data not published).

$\text{DayRWood} = \text{WoodRate} * \text{WoodSA}$

DOCUMENT: Daily wood respiration (gCO₂.tr-1.day-1)

$\text{Days} = \text{TIME}$

DOCUMENT: The basic time step is one day. Using the daily integral eliminates the complexity of diurnal changes in radiation geometry.

$\text{Demand_Frts} = \text{CurrentFrt} * \text{FrtFGRdmday} * \text{TmultiFG} / \text{FrtDMtoCO2}$

$\text{Demand_Roots} = 20 * \text{TempEffRoots} / \text{VegDMtoCO2}$

$\text{Demand_Shts} =$

$((\text{NoGrwgExtShts} * \text{ShGRperExtSht}) + (\text{NoGrwgSpurs} * \text{GRperSpur})) * \text{TempEffect} / \text{VegDMtoCO2}$

DOCUMENT: Dry weight demand of the shoots is estimated from several studies of shoot growth rates of active shoots of Empire trees with normal temps (averaging perhaps 28/20C). Shoots grew about 0.2 g Dry Wt/day in dry weight/day.

To express the demand in g of fixed CO₂ a cost of construction of vegetative tissue is used. This is based on a 1.22 g glucose/g dry weight construction cost for leaf and shoot growth, and 0.68 g glucose/g fixed CO₂ giving a 0.55 g of dry matter from a g of fixed CO₂, so divided by the VegDMtoCO₂ factor of 0.55.

$$\text{Demand_Wood} = 20 * \text{TempEffect} / \text{VegDMtoCO2}$$

$$\text{FGR_}\% _ \text{max} = \text{IF} (\text{AccDegDays} > 170) \text{ Then } (\text{deltafrtwtperfrt} / \text{T_MaxFGR} * 100) \\ \text{ELSE } 100$$

DOCUMENT: The percentage fruit growth rate obtained of the maximum temperature adjusted fruit growth rate. Units: %. Set to zero below 170 accumulated growing degree days (base 4) as fruit assumed not to be growing.

$$\text{FrtFGRdmday} = \text{Max_FGR} / \text{DM:FWT_fruit}$$

$$\text{FruitT} = (\text{TempMin} + \text{TempMax}) / 2$$

DOCUMENT: Fruit temperature (C) = Tmean

$$\text{Fruit_Frctabs} = \text{IF} (\text{AccDegDays} < 700) \text{ THEN } \text{Absc_curve} \text{ ELSE } 0$$

DOCUMENT: Abscission curve is used to abscise fruit up to 720 accumulated growing degree days (base 4). This corresponds to 39 days after full bloom using 1986 empire maximum fruit growth data. After this period it is assumed that the tree retains the current fruit number.

$$\text{LAIndex} = (\text{ActiveLA})/\text{Areapertree}$$

DOCUMENT: Leaf area index per total area allotted per tree

$$\text{LeafT} = (\text{TempMax} + \text{TempMin} + \text{TempMin})/3$$

DOCUMENT: Leaf temperature (C) during the dark period was estimated by Tmax and double-weighted Tmin

$$\text{LtEffResp} = 0.75$$

DOCUMENT: The effect of light exposure of the fruit on respiration is estimated, averaged over the crop, to reduce fruit respiration rate by 25% compared to the dark respiration rates used in the main calculation of fruit respiration. Based on data of Bepete et al (1997 Acta Hort 451).

$$\text{Meantemp} = (\text{TempMax} + \text{TempMin})/2$$

$$\text{Modfrtabs} = \text{IF} (\text{HandThinHarv}) > 0 \text{ Then HandThinHarv else Fruit_Frctabs}$$

$$\text{NoGrwgSh} = \text{NoShoots} * \text{FrGrwgSh}$$

DOCUMENT: Number of growing shoots=final number of shoots per tree multiplied by the fraction of growing shoots at any given day during the season.

$$\text{NoGrwgSpurs} = \text{NoSpurs} * \text{FrGrwgSpurs}$$

NoShoots = 194

DOCUMENT: Final number of long shoots as an average for our Standard Empire/M9 tree.

NoSpurs = 686

DOCUMENT: Number of short shoots (fruiting and non-fruiting spurs and lateral short shoots) on the standard Empire/M9 trees.

PercentLtIntercept = $69.3 * (1 - \text{EXP}(-42.3 * \text{LAIIndex} / 69.3))$

DOCUMENT: This equation is from Jens Wunsche's research on several orchard systems that relates LAI to Light Interception in a 13-year old orchard that good vigor. The standard Empire/M9 Slender spindle trees used here as models had about 75-80% of shoot being spurs or short lateral shoots while 20-25% being extension shoots. The mean number of total shoots/tree was 890, giving a leaf area of 13.3 m²/tree

RelPartFrts = Demand_Frts - (Demand_Frts * (1 - RSS_Frts) * (1 - (DailyCBal/TotalDemand)))

DOCUMENT: The Relative Partitioning to each organ is calculated from the equation in Buwalda's kiwifruit model (1992). It depends on the demand of the sink at the time, the relative sink strength (RSS) and the fraction of total demand that is met by available carbon. If the $C_Avail/TotalDemand$ is <1, then the right side is subtracted from the demand.

The higher the demand and the RSS, the higher the relative partitioning.

$$\text{RelPartRoots} = \text{Demand_Roots} - (\text{Demand_Roots} * (1 - \text{RSS_Roots}) * (1 - (\text{DailyCBal} / \text{TotalDemand})))$$

$$\text{RelPartWood} = \text{Demand_Wood} - (\text{Demand_Wood} * (1 - \text{RSS_Wood}) * (1 - (\text{DailyCBal} / \text{TotalDemand})))$$

$$\text{RelPart_Shfts} = \text{Demand_Shfts} - (\text{Demand_Shfts} * (1 - \text{RSS_Shfts}) * (1 - (\text{DailyCBal} / \text{TotalDemand})))$$

$$\text{RrateFrt} = (\text{T_intFrt} * \text{EXP}(\text{TSlopeFrt} * \text{FruitT})) * 0.0864$$

DOCUMENT: Fruit respiration rate (gCO₂.g-1fruit weight.day-1)

$$\text{RrateLf} = ((\text{T_intLf} * \text{EXP}(\text{TslopeLf} * \text{LeafT})) * (86400 - \text{DayLgth})) / 1000$$

DOCUMENT: Leaf dark respiration rate (gCO₂.m-2 leaf area.day-1)

$$\text{RSS_Frts} = 0.07$$

DOCUMENT: RSS is Relative Sink Strength and is a fraction of 1 (total sink strength of all sinks = 1). The higher the value the greater the relative competitiveness and the better the sink's ability to attract carbon under limiting conditions.

In this model the shoots have the highest RSS with fruits the next in priority, with wood and roots the lowest.

$$\text{RSS_Roots} = 0.01$$

DOCUMENT: RSS is Relative Sink Strength and is a fraction of 1 (total sink strength of all sinks = 1). The higher the value the greater the relative

competitiveness and the better the sink's ability to attract carbon under limiting conditions.

In this model the shoots have the highest RSS with fruits the next in priority, with wood and roots the lowest.

RSS_Shts = 0.9

DOCUMENT: RSS is Relative Sink Strength and is a fraction of 1 (total sink strength of all sinks = 1). The higher the value the greater the relative competitiveness and the better the sink's ability to attract carbon under limiting conditions.

In this model the shoots have the highest RSS with fruits the next in priority, with wood and roots the lowest.

RSS_Wood = 0.02

DOCUMENT: RSS is Relative Sink Strength and is a fraction of 1 (total sink strength of all sinks = 1). The higher the value the greater the relative competitiveness and the better the sink's ability to attract carbon under limiting conditions.

In this model the shoots have the highest RSS with fruits the next in priority, with wood and roots the lowest.

SumRelParts = RelPart_Shts+RelPartFrts+RelPartRoots+RelPartWood

TeffDayPn = .33*(0.535+0.0384*TempMax-0.0004126*TempMax^2-0.00001576*TempMax^3)+.67*(0.535+0.0384*(.75*TempMax+.25*Temp

$$\text{Min}) - .0004126 * (.75 * \text{TempMax} + .25 * \text{TempMin})^2 -$$

$$.00001576 * (.75 * \text{TempMax} + .25 * \text{TempMin})^3$$

DOCUMENT: T_{effDayPn} = Temperature effects on daily photosynthetic rate.
 Fractional reduction (or no change) of daily Pn due to temperature is estimated by the normalized equation:

T_{effDayPn} (basic eq) = $0.535 + 0.0384T - 0.0004126T^2 - 0.00001576T^3$,
 which gives a maximum Pn at about 21C and zero at -7C and 45C.

From analysis of the relative diurnal temperature patterns, the FINAL TEMPERATURE EFFECT CALCULATED above is comprised of 1/3 of the light period at Tmax, and 2/3 of the period at a temperature between Tmax and Tmin.

$$T_{\text{multiFG}} = T_{\text{intFG}} * \text{EXP}(T_{\text{slopeFG}} * \text{Meantemp})$$

DOCUMENT: Temperature multiplier : both slope and intercept scaled where max fruit growth rate (Max FGR) is reached at temperature = 25C. ie at rates above 25C then actual fruit growth rate can exceed Max FGR. No units.

$$\text{TotalDemand} = \text{emand_Shts} + \text{Demand_Frts} + \text{Demand_Roots} + \text{Demand_Wood}$$

$$\text{TotFrtFWt} = \text{CurrentFrt} * \text{mean_fruit_weight}$$

DOCUMENT: Total fruit weight per tree (g)

$$\text{TslopeLf} = 0.069$$

DOCUMENT: k=Temperature coefficient of leaf respiration (the slope of lnLeafResp versus Temperature); 0.069 gives a standard

$$Q_{10}=2$$

$$\text{TslopeWd} = 0.069$$

DOCUMENT: k=Temperature coefficient of wood respiration (the slope of lnWoodResp versus Temperature)

$$T_MaxFGR = Max_FGR * TmultiFG$$

DOCUMENT: Temperature adjusted maximum growth rate: fresh weight (grams) per day.

$$\text{VegDMtoCO2} = 0.55$$

DOCUMENT: To express the demand in g of fixed CO₂ a cost of construction of vegetative tissue is used. This is based on a 0.81 g DM/g glucose (1.22 g glucose/g DM) construction cost for leaf and shoot growth, and 0.68 g glucose/g fixed CO₂ giving a 0.55 g of dry matter from a g of fixed CO₂, so divided by the VegDMtoCO₂ factor of 0.55.

$$\text{WoodRate} = ((T_intWd * \text{EXP}(\text{TslopeWd} * \text{WoodT})) * 86400) / 1000$$

DOCUMENT: Wood respiration rate (gCO₂.m⁻²wood surface area.s⁻¹)

$$\text{WoodT} = (\text{TempMax} + \text{TempMin}) / 2$$

DOCUMENT: Wood temperature (C) = Tmean

Absc_curve = GRAPH(FGR_%_max)

(0.00, 0.00), (10.0, 0.00), (20.0, 0.00), ..., (100, 0.00)

DOCUMENT: Abscission curve is based on empire fruit thinning and shade studies conducted in 1986, 1991 and 1993. Data contained in excel file abscissionfwt99.

C:DM_fruit = GRAPH(TIME)

(0.00, 0.5), (10.0, 0.5), (20.0, 0.5), (30.0, 0.5), (40.0, 0.5), (50.0, 0.535), (60.0, 0.57), (70.0, 0.6), (80.0, 0.645), (90.0, 0.68), (100, 0.68), (110, 0.68), (120, 0.68), (130, 0.68), (140, 0.68), (150, 0.68), (160, 0.68), (170, 0.68), (180, 0.68)

DOCUMENT: Carbon dioxide conversion into dry matter. Values taken from early version of the model. No units.

DayLgth = GRAPH(Days)

(0.00, 47200), (29.0, 50600), (58.0, 53000), (87.0, 53400), (116, 53000), (145, 50000), (174, 43600), (203, 38600), (232, 34000), (261, 32400), (290, 33200)

DOCUMENT: Daylength (in seconds) is based on Geneva at 43N latitude.

DM:FWT_fruit = GRAPH(AccDegDays)

(100, 6.67), (200, 6.67), (300, 8.70), (400, 9.09), (500, 8.55), (600, 8.33), (700, 8.00), (800, 7.90), (900, 7.80), (1000, 7.69), (1100, 7.60), (1200, 7.50), (1300, 7.45), (1400, 7.41), (1500, 7.24), (1600, 7.14), (1700, 7.02), (1800, 6.90), (1900, 6.90), (2000, 6.67), (2100, 6.67), (2200, 6.67), (2300, 6.67), (2400, 6.67)

DOCUMENT: Fruit dry matter conversion to fresh weight. Using 3 fruit data used to obtain the maximum fruit growth rate (Max FGR).

FrctAbscission = GRAPH(AccTmin_5)

(0.00, 0.00), (10.0, 0.00), (20.0, 0.00), ..., (100, 0.00)

FrctFoliage = GRAPH(Days)

(0.00, 1.00), (1.00, 1.00), (2.00, 1.00), (3.00, 1.00), ..., (248, 1.00), (249, 0.5),
(250, 0.5), (251, 0.5), ..., (290, 0.5)

FrGrwgSh = GRAPH(AccDegDays)

(0.00, 0.5), (50.0, 0.825), (100, 0.98), (150, 0.995), (200, 1.00), (250, 1.00),
(300, 0.995), (350, 0.95), (400, 0.905), (450, 0.83), (500, 0.75), (550, 0.66),
(600, 0.56), (650, 0.425), (700, 0.3), (750, 0.2), (800, 0.145), (850, 0.075),
(900, 0.045), (950, 0.00), (1000, 0.00)

DOCUMENT: Fraction of growing shoots estimated as a function of accumulated degree-days.

Factors that control the cessation of shoot growth are very poorly understood. Consequently, initial modeling was based on estimated shoot cessation derived from information on distribution of shoot lengths and leaf areas at the end of the season and the assumption that shoots all grew at the same rate, but for different durations.

FrGrwgSpurs = GRAPH(AccDegDays)

(0.00, 0.405), (50.0, 1.00), (100, 1.00), (150, 0.565), (200, 0.00), (250, 0.69),
(300, 0.995), (350, 0.91), (400, 0.7), (450, 0.19), (500, 0.00), (550, 0.00), (600,
0.00), (650, 0.00), (700, 0.00), (750, 0.00), (800, 0.00)

FrtdMtoCO2 = GRAPH(Days)

(0.00, 0.5), (5.00, 0.5), (10.0, 0.5), (15.0, 0.5), (20.0, 0.5), (25.0, 0.5), (30.0, 0.5), (35.0, 0.5), (40.0, 0.5), (45.0, 0.5), (50.0, 0.52), (55.0, 0.545), (60.0, 0.57), (65.0, 0.6), (70.0, 0.62), (75.0, 0.635), (80.0, 0.655), (85.0, 0.67), (90.0, 0.68), (95.0, 0.68), (100, 0.68)

DOCUMENT: The ratio of g dry matter from g of fixed CO₂ is needed to adjust potential growth data from dry matter to fixed CO₂ for each organ. Vegetative growth tends to be similar at about 0.55 (see VegDMtoCO₂).

The ratio for fruit starts low at 0.5 g DM/G fixed CO₂ as cell division is the primary growth process and is relatively expensive. Then as cell division declines and cell expansion takes over (from 10 to 60 days after bloom, or 40-90 days after budbreak), the ratio increases to 0.68, then remains constant to harvest. The high ratio indicates that fruit expansion is mostly relatively "cheap" sugars and organic acids.

GRperSpur = GRAPH(Days)

(0.00, 0.02), (10.0, 0.023), (20.0, 0.027), (30.0, 0.032), (40.0, 0.042), (50.0, 0.055), (60.0, 0.065), (70.0, 0.081), (80.0, 0.1), (90.0, 0.1), ..., (290, 0.1)

HandThinHarv = GRAPH(Days)

(0.00, 0.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), ..., (287, 0.00), (288, 0.00), (289, 0.00), (290, 0.00)

DOCUMENT: Hand thinning component. Runs on a day basis so can be handthinned on a particular day. Set to a scale of 1 where 1 would remove 100% of the crop, 0 would remove 0% of the crop.

LeafDMperA = GRAPH(Days)

(0.00, 60.0), (18.0, 72.0), (36.0, 80.0), (54.0, 86.0), (72.0, 90.0), (90.0, 94.0),
 (108, 98.0), (126, 99.0), (144, 100), (162, 100), (180, 100)

Light = GRAPH(Days)

(0.00, 14.5), (1.00, 14.5), (2.00, 14.2), (3.00, 15.2), (4.00, 16.9), (5.00, 17.3),
 (6.00, 16.2), (7.00, 16.4), (8.00, 16.4), (9.00, 16.8), (10.0, 15.3), (11.0, 14.2),
 (12.0, 14.7), (13.0, 15.7), (14.0, 16.3), (15.0, 16.1), (16.0, 16.7), (17.0, 16.3),
 (18.0, 16.8), (19.0, 15.9), (20.0, 17.2), (21.0, 16.3), (22.0, 16.0), (23.0, 16.3),
 (24.0, 16.0), (25.0, 16.9), (26.0, 17.0), (27.0, 18.2), (28.0, 17.7), (29.0, 17.3),
 (30.0, 17.7), (31.0, 18.3), (32.0, 17.7), (33.0, 17.8), (34.0, 17.9), (35.0, 18.3),
 (36.0, 18.0), (37.0, 18.2), (38.0, 19.1), (39.0, 19.7), (40.0, 19.0), (41.0, 18.4),
 (42.0, 18.2), (43.0, 18.8), (44.0, 19.5), (45.0, 19.8), (46.0, 19.9), (47.0, 19.0),
 (48.0, 19.0), (49.0, 19.8), (50.0, 19.9), (51.0, 20.6), (52.0, 19.8), (53.0, 19.5),
 (54.0, 18.8), (55.0, 18.9), (56.0, 20.0), (57.0, 20.9), (58.0, 21.8), (59.0, 21.0),
 (60.0, 19.8), (61.0, 19.7), (62.0, 20.6), (63.0, 21.0), (64.0, 20.7), (65.0, 20.7),
 (66.0, 20.8), (67.0, 20.0), (68.0, 19.3), (69.0, 18.8), (70.0, 19.6), (71.0, 20.2),
 (72.0, 20.7), (73.0, 20.4), (74.0, 20.6), (75.0, 19.7), (76.0, 19.2), (77.0, 18.6),
 (78.0, 19.7), (79.0, 20.2), (80.0, 20.3), (81.0, 20.7), (82.0, 20.5), (83.0, 21.9),
 (84.0, 21.6), (85.0, 21.9), (86.0, 21.3), (87.0, 21.3), (88.0, 21.1), (89.0, 20.6),
 (90.0, 20.5), (91.0, 20.1), (92.0, 20.2), (93.0, 20.2), (94.0, 21.0), (95.0, 21.7),
 (96.0, 21.0), (97.0, 19.7), (98.0, 18.6), (99.0, 19.9), (100, 20.7), (101, 21.3),
 (102, 20.8), (103, 20.2), (104, 19.6), (105, 19.0), (106, 18.9), (107, 18.9), (108,
 18.4), (109, 18.3), (110, 17.7), (111, 17.8), (112, 18.2), (113, 18.1), (114, 17.8),
 (115, 16.7), (116, 17.3), (117, 17.8), (118, 18.0), (119, 17.4), (120, 17.0), (121,
 17.3), (122, 17.2), (123, 17.0), (124, 17.2), (125, 17.5), (126, 18.2), (127, 18.4),
 (128, 19.0), (129, 18.8), (130, 18.3), (131, 16.5), (132, 16.2), (133, 16.3), (134,

17.3), (135, 16.6), (136, 15.0), (137, 13.9), (138, 14.1), (139, 15.5), (140, 15.6),
(141, 15.4), (142, 14.7), (143, 14.6), (144, 14.3), (145, 14.2), (146, 14.8), (147,
14.8), (148, 15.2), (149, 14.6), (150, 14.3), (151, 13.2), (152, 12.7), (153, 12.0),
(154, 12.2), (155, 11.4), (156, 11.3), (157, 10.4), (158, 10.7), (159, 10.7), (160,
11.2), (161, 11.1), (162, 10.7), (163, 10.9), (164, 11.5), (165, 11.4), (166, 10.8),
(167, 10.9), (168, 11.5), (169, 12.1), (170, 11.3), (171, 10.0), (172, 9.30), (173,
9.90), (174, 10.9), (175, 11.0), (176, 10.3), (177, 9.40), (178, 7.70), (179, 7.90),
(180, 8.60), (181, 9.20), (182, 8.60), (183, 8.10), (184, 8.60), (185, 8.40), (186,
8.20), (187, 7.30), (188, 7.40), (189, 7.40), (190, 8.20), (191, 8.10), (192, 7.70),
(193, 7.40), (194, 7.20), (195, 7.10), (196, 7.30), (197, 7.20), (198, 7.40), (199,
7.20), (200, 7.80), (201, 7.80), (202, 7.50), (203, 6.70), (204, 6.00), (205, 5.70),
(206, 5.10), (207, 5.10), (208, 5.20), (209, 5.20), (210, 4.90), (211, 4.20), (212,
4.10), (213, 4.30), (214, 4.70), (215, 5.00), (216, 4.90), (217, 4.80), (218, 4.70),
(219, 4.90), (220, 4.80), (221, 4.40), (222, 4.30), (223, 4.50), (224, 4.20), (225,
4.00), (226, 3.40), (227, 3.70), (228, 3.30), (229, 3.40), (230, 3.70), (231, 3.90),
(232, 4.00), (233, 3.80), (234, 4.20), (235, 4.10), (236, 3.70), (237, 3.60), (238,
3.40), (239, 3.50), (240, 3.30), (241, 3.60), (242, 3.70), (243, 3.70), (244, 3.50),
(245, 3.30), (246, 3.40), (247, 3.60), (248, 4.00), (249, 4.00), (250, 3.70), (251,
3.60), (252, 3.80), (253, 3.70), (254, 3.70), (255, 3.50), (256, 3.60), (257, 3.40),
(258, 3.60), (259, 3.60), (260, 3.90), (261, 3.90), (262, 4.00), (263, 4.10), (264,
4.20), (265, 4.50), (266, 4.60), (267, 4.60), (268, 4.60), (269, 4.70), (270, 4.90),
(271, 5.00), (272, 4.90), (273, 5.00), (274, 5.10), (275, 5.10), (276, 5.10), (277,
5.30), (278, 5.70), (279, 5.30), (280, 4.90), (281, 4.60), (282, 5.20), (283, 5.20),
(284, 5.50), (285, 5.20), (286, 5.30), (287, 5.20), (288, 5.50), (289, 5.90), (290,
6.20)

DOCUMENT: Light=Daily integral of total radiation on a horizontal surface

(MJ.m-2.day-1). Data from Geneva,NY (mean values - 1971-1990)

Conversion: 1MJ.m-2.day-1=0.04187*Langley.day-1

Max_FGR = GRAPH(AccDegDays)

(170, 0.013), (190, 0.022), (210, 0.0367), (230, 0.052), (250, 0.066), (270, 0.081), (290, 0.16), (310, 0.238), (330, 0.317), (350, 0.395), (370, 0.534), (390, 0.672), (410, 0.811), (430, 0.949), (450, 0.999), (470, 1.05), (490, 1.10), (510, 1.15), (530, 1.20), (550, 1.25), (570, 1.30), (590, 1.35), (610, 1.49), (630, 1.62), (650, 1.75), (670, 1.89), (690, 2.02), (710, 2.16), (730, 2.29), (750, 2.29), (770, 2.30), (790, 2.32), (810, 2.32), (830, 2.31), (850, 2.30), (870, 2.30), (890, 2.30), (910, 2.30), (930, 2.30), (950, 2.31), (970, 2.31), (990, 2.31), (1010, 2.31), (1030, 2.31), (1050, 2.31), (1070, 2.31), (1090, 2.31), (1110, 2.32), (1130, 2.32), (1150, 2.32), (1170, 2.32), (1190, 2.33), (1210, 2.33), (1230, 2.33), (1250, 2.33), (1270, 2.33), (1290, 2.34), (1310, 2.34), (1330, 2.34), (1350, 2.34), (1370, 2.35), (1390, 2.35), (1410, 2.34), (1430, 2.33), (1450, 2.32), (1470, 2.32), (1490, 2.31), (1510, 2.30), (1530, 2.29), (1550, 2.28), (1570, 2.28), (1590, 2.27), (1610, 2.26), (1630, 2.25), (1650, 2.24), (1670, 2.23), (1690, 2.22), (1710, 2.21), (1730, 2.20), (1750, 2.19), (1770, 2.18), (1790, 2.17), (1810, 2.15), (1830, 2.14), (1850, 2.13), (1870, 2.12), (1890, 2.13), (1910, 2.13), (1930, 2.13), (1950, 2.13), (1970, 2.14), (1990, 2.14), (2010, 2.14), (2030, 2.15), (2050, 2.15), (2070, 2.15), ..., (2490, 2.15), (2510, 2.15)

DOCUMENT: Maximum fruit growth rate (Max FGR) is based on growth data of three fruit within 24-250 grams from 1987 thinning study. Fruit weights were estimated from Empire 1989 regressions (separated for small and large sizes). Max FGR (fresh weight (grams) per day).

NoGrwgExtShts = GRAPH(Days)

(0.00, 0.00), (10.0, 156), (20.0, 200), (30.0, 200), (40.0, 200), (50.0, 200),
(60.0, 180), (70.0, 116), (80.0, 43.0), (90.0, 13.0), (100, 0.00)

DOCUMENT: The number of growing shoots is empirically set by estimates of when shoots stop growing in field observations.

PChemEff = GRAPH(Days)

(0.00, 2.00), (10.0, 2.63), (20.0, 3.23), (30.0, 3.83), (40.0, 4.00), ..., (160,
4.00), (170, 4.00), (180, 3.85), (190, 3.75), (200, 3.43), (210, 2.60), (220,
0.00), ..., (280, 0.00), (290, 0.00)

DOCUMENT: Leaf photochemical efficiency or quantum yield (ugCO₂J⁻¹total radiation) - Values set to a maximum of 4 following field measurements on Empire, Delicious and Gala in 1999. No cultivar differences were found. Seasonal pattern (especially autumn decline will depend on the climate. Model currently set for NY.

PestPnEffect = GRAPH(Days)

(0.00, 1.00), (10.0, 1.00), (20.0, 1.00), (30.0, 1.00), ..., (290, 1.00)

DOCUMENT: A fractional multiplier that can cause reductions in Pn rate by multiplying by any fraction <1 (e.g. use 0.8 to casue a 20% reduction in Pn due to pest injury).

Pmax = GRAPH(Days)

(0.00, 0.000246), (10.0, 0.000384), (20.0, 0.00057), (30.0, 0.00069), (40.0,
0.00075), (50.0, 0.00075), (60.0, 0.00075), (70.0, 0.000755), (80.0, 0.000755),
(90.0, 0.000755), (100, 0.00075), (110, 0.000735),..., (150, 0.000735), (160,

0.00073), (170, 0.00073), (180, 0.000695), (190, 0.000625), (200, 0.000485),
(210, 0.000315), (220, 1e-005), ..., (290, 5e-006)

DOCUMENT: Rate of light saturated leaf photosynthesis per unit leaf area (g.m⁻².s⁻¹). Current model values based on various data on Empire in NY.

Pollination_factor = GRAPH(AccDegDays)

(0.00, 0.00), (2.00, 0.00), (4.00, 0.00), (6.00, 0.00), ..., (2498, 0.00), (2500, 0.00)

DOCUMENT: Pollination factor assumes that one third of the fruit will be successfully pollinated and continue to develop as fruitlets. The drop of unpollinated flowers is estimated to occur at 300 accumulated degree days. However the peak in the graphical relationship must be sufficiently wide that the model timestep and degree days accumulations are picked up by the model. Note: For environmental simulations the model should be checked to ensure there is only one drop of unpollinated fruitlets.

ShGRperExtSht = GRAPH(Days)

(0.00, 0.02), (4.00, 0.02), (8.00, 0.021), (12.0, 0.022), (16.0, 0.029), (20.0, 0.04), (24.0, 0.056), (28.0, 0.12), (32.0, 0.145), (36.0, 0.15), ..., (80.0, 0.15), (84.0, 0.2), (88.0, 0.2), (92.0, 0.2), (96.0, 0.2), (100, 0.2)

DOCUMENT: The growth demand in dry weight per day of individual growing shoots of Empire apples is estimated from several studies (Lakso, 1984; Johnson and Lakso, 1986a, and unpublished studies). The maximum rate of about 0.2 g dry weight per day was found for the

most vigorous terminal or lateral shoots, however over the whole population of shoots on the tree, an average of 0.15 is probably more reasonable.

SoilTemp = GRAPH(Days)

(0.00, 9.00), (10.0, 11.5), (20.0, 13.4), (30.0, 15.0), (40.0, 17.2), (50.0, 18.8),
(60.0, 21.0), (70.0, 22.0), (80.0, 23.2), (90.0, 24.0), (100, 24.0)

TempEffect = GRAPH(Meantemp)

(0.00, 0.00), (5.00, 0.11), (10.0, 0.28), (15.0, 0.5), (20.0, 0.73), (25.0, 1.00),
(30.0, 1.40), (35.0, 2.00), (40.0, 2.00)

DOCUMENT: The temperature effect on demand is a multiplier that is logarithmic with a Q10 of 2 with zero demand at zero degrees, 1 at 25C , 2 at 35C and above.

TempEffRoots = GRAPH(SoilTemp)

(0.00, 0.1), (5.00, 0.18), (10.0, 0.25), (15.0, 0.36), (20.0, 0.5), (25.0, 0.71),
(30.0, 1.00), (35.0, 1.00), (40.0, 1.00)

TempMax = GRAPH(Days)

(0.00, 12.8), (10.0, 15.0), (20.0, 16.6), (30.0, 18.5), (40.0, 20.3), (50.0, 21.4),
(60.0, 23.6), (70.0, 24.9), (80.0, 26.1), (90.0, 27.1), (100, 27.9), (110, 28.1),
(120, 27.6), (130, 26.7), (140, 24.9), (150, 22.8), (160, 20.8), (170, 18.0), (180,
16.0), (190, 14.2), (200, 11.1), (210, 9.17), (220, 6.72), (230, 5.15), (240, 3.05),
(250, 1.30), (260, -0.1), (270, -1.33), (280, -2.03), (290, -2.00)

DOCUMENT: Daily maximum temperature (C)

Conversion: $C=(F-32)*0.55556$

Data based on Geneva mean temperature data (1971-1990)

TempMin = GRAPH(Days)

**(0.00, 2.50), (10.0, 3.40), (20.0, 5.00), (30.0, 6.20), (40.0, 7.00), (50.0, 8.20),
(60.0, 9.80), (70.0, 10.6), (80.0, 11.6), (90.0, 12.8), (100, 13.4), (110, 13.6),
(120, 13.4), (130, 12.8), (140, 11.4), (150, 9.60), (160, 8.20), (170, 7.00), (180,
5.40), (190, 3.60), (200, 2.10), (210, 0.00), (220, -2.20), (230, -4.20), (240, -
5.20), (250, -6.60), (260, -7.80), (270, -8.40), (280, -9.80), (290, -10.0)**

DOCUMENT: Daily minimum temperature (C)

Conversion: $C=(F-32)*0.55556$

Data from Geneva mean 20-Year temperature data 1971-1990.

TSlopeFG = GRAPH(AccDegDays)

**(170, 0.1), (190, 0.099), (210, 0.099), (230, 0.097), (250, 0.096), (270, 0.095),
(290, 0.094), (310, 0.093), (330, 0.091), (350, 0.088), (370, 0.086), (390,
0.084), (410, 0.082), (430, 0.08), (450, 0.075), (470, 0.07), (490, 0.065), (510,
0.06), (530, 0.059), (550, 0.058), (570, 0.057), (590, 0.056), (610, 0.055), (630,
0.055), (650, 0.055), (670, 0.055), ..., (2490, 0.055), (2510, 0.055)**

DOCUMENT: K = temp coefficient of fruit respiration (the slope of Lnfrresp vs temperature). Slope is modelled against accumulated degree days and is estimated to remain unchanged after 590 accumulated degree days (base 4) (this corresponds to period where fruit growth is due to cell expansion only).

TSlopeFrt = GRAPH(Days)

(0.00, 0.1), (18.0, 0.0985), (36.0, 0.0965), (54.0, 0.0915), (72.0, 0.0795), (90.0, 0.06), (108, 0.055), (126, 0.055), (144, 0.055), (162, 0.055), (180, 0.055)

DOCUMENT: k =Temperature coefficient of fruit respiration (the slope of $\ln FrResp$ versus Temperature)

The high value early reflects a high temp sensitivity of cell division. As the fruit shifts from cell division to cell expansion the K declines. the value of 0.1 early gives a $Q_{10} = 2.7$ while the lowest value of 0.055 gives a $Q_{10} = 1.7$.

$T_{intFG} = GRAPH(AccDegDays)$

(170, 0.082), (190, 0.084), (210, 0.084), (230, 0.088), (250, 0.091), (270, 0.093), (290, 0.095), (310, 0.098), (330, 0.103), (350, 0.111), (370, 0.116), (390, 0.122), (410, 0.129), (430, 0.135), (450, 0.153), (470, 0.174), (490, 0.197), (510, 0.223), (530, 0.229), (550, 0.235), (570, 0.241), (590, 0.247), (610, 0.253), (630, 0.253), (650, 0.253), ..., (2490, 0.253), (2510, 0.253)

DOCUMENT: Fruit respiration rate at temperature = 0 degrees celsius. (the intercept of $\ln fruitresp$ vs temperature).

$T_{intFrt} = GRAPH(Days)$

(0.00, 0.01), (10.0, 0.0101), (20.0, 0.01), (30.0, 0.0098), (40.0, 0.0091), (50.0, 0.008), (60.0, 0.0061), (70.0, 0.0039), (80.0, 0.002), (90.0, 0.001), (100, 0.0007), (110, 0.0007), ..., (280, 0.0007), (290, 0.0007)

DOCUMENT: Fruit respiration rate at Temperature=0C (the intercept of $\ln FruitResp$ versus Temperature)

$T_{intLf} = GRAPH(Days)$

(0.00, 0.025), (18.0, 0.025), (36.0, 0.0239), (54.0, 0.0213), (72.0, 0.0148),
 (90.0, 0.008), (108, 0.00663), (126, 0.006), (144, 0.006), (162, 0.006), (180,
 0.006)

**DOCUMENT: Leaf respiration rate at Temperature=0C (the intercept of
 lnLeafResp versus Temperature)**

T_intWd = GRAPH(Days)

(0.00, 0.005), (18.0, 0.01), (36.0, 0.007), (54.0, 0.0063), (72.0, 0.0059), (90.0,
 0.00555), (108, 0.00525), (126, 0.00495), (144, 0.00465), (162, 0.0043), (180,
 0.004)

**DOCUMENT: Wood respiration rate at Temperature=0C (the intercept of
 lnWoodResp versus Temperature)**

WoodSA = GRAPH(Days)

(0.00, 1.17), (18.0, 1.18), (36.0, 1.20), (54.0, 1.28), (72.0, 1.42), (90.0, 1.45),
 (108, 1.47), (126, 1.50), (144, 1.50), (162, 1.50), (180, 1.50)

DOCUMENT: Wood surface area(m2)

**Respiration is based on wood surface because different aged wood of different
 volumes all give similar respiration when expressed on a surface area
 basis (unpublished data and Butler, D.J., and J.J. Landsberg. 1983.
 Respiration rates of apple trees, estimated by CO₂-efflux measurements.
 Plant, Cell and Environ. 4:153-159)**