

Spring 2015

Growth parameters of 'Golden Delicious' apple trees (*Malus x domestica* Borkh)

Biyong Shi
Purdue University

Follow this and additional works at: https://docs.lib.purdue.edu/open_access_theses

 Part of the [Horticulture Commons](#)

Recommended Citation

Shi, Biyong, "Growth parameters of 'Golden Delicious' apple trees (*Malus x domestica* Borkh)" (2015). *Open Access Theses*. 610.
https://docs.lib.purdue.edu/open_access_theses/610

This document has been made available through Purdue e-Pubs, a service of the Purdue University Libraries. Please contact epubs@purdue.edu for additional information.

**PURDUE UNIVERSITY
GRADUATE SCHOOL
Thesis/Dissertation Acceptance**

This is to certify that the thesis/dissertation prepared

By Biying Shi

Entitled

GROWTH PARAMETERS OF 'GOLDEN DELICIOUS' APPLE TREES (MALUS × DOMESTICA BORKH.)

For the degree of Master of Science

Is approved by the final examining committee:

Peter M. Hirst

Chair

Bedrich Benes

Bruce P. Bordelon

To the best of my knowledge and as understood by the student in the Thesis/Dissertation Agreement, Publication Delay, and Certification Disclaimer (Graduate School Form 32), this thesis/dissertation adheres to the provisions of Purdue University's "Policy of Integrity in Research" and the use of copyright material.

Approved by Major Professor(s): Peter M. Hirst

Approved by: Hazel Y. Wetzstein

Head of the Departmental Graduate Program

04/23/2015

Date

GROWTH PARAMETERS OF 'GOLDEN DELICIOUS' APPLE TREES (MALUS ×
DOMESTICA BORKH.)

A Thesis

Submitted to the Faculty

of

Purdue University

by

Biying Shi

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

May 2015

Purdue University

West Lafayette, Indiana

ACKNOWLEDGMENTS

I would like to express my sincere appreciation to my advisor, Dr. Peter Hirst, for his invaluable guidance, continuous support and kindness through the course of this work. Dr. Peter Hirst has been a true mentor with extensive knowledge, vision and creative thinking and I learned so much from him. Thank you so much for all you have done to make my stay in Purdue such an unforgettable experience.

I would like to thank my committee members, Dr. Bedrich Benes and Dr. Bruce Bordelon, for their continuous support and invaluable guidance in directing my research.

I thank my dear parents, Baoyi and Jinmei, my brother, Zhiying, my dear grandparents, Changzhong and Dongzhen, for all their love and support.

I thank Siwen, and the ones that I loved. Without your encouragement, I would not be here today.

TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT.....	x
CHAPTER 1 INTRODUCTION.....	1
1.1 Plant Simulation Models	1
1.2 Tree Architecture.....	2
1.2.1 Branching and Fruiting Habits	3
1.2.2 Horticultural Manipulation of Apple Trees	4
1.2.2.1 Use of Rootstocks	5
1.2.2.2 Canopy Form	6
1.3 Shoot Development.....	7
1.3.1 Bud Development.....	8
1.3.2 Non-growing Buds	9
1.3.3 Shoot Category	10
1.3.3.1 Vegetative Shoots	10
1.3.3.2 Flowering Spurs	10
1.3.4 Branching Characteristics.....	11
1.4 Light Distribution.....	12
1.4.1 Factors Affecting Light Distribution	12
1.4.1.1 Cultivar-rootstock Combination	13
1.4.1.2 Canopy Form	13
1.4.1.3 Tree Spacing and Row Orientation.....	14
1.5 Fruit Quality	15
1.5.1 Fruit Quality Indicators	15
1.5.1.1 Size and Weight	15
1.5.1.2 Sugar Content.....	16
1.5.1.3 Background Color.....	17
1.5.1.4 Firmness.....	18
1.5.1.5 Other Quality Indicators	18

	Page
1.6 References	19
CHAPTER 2 VEGETATIVE GROWTH AND BRANCHING CHARACTERISTICS OF ‘GOLDEN DELICIOUS’ APPLE TREES (MALUS X DOMESTICA BORKH.)...	30
2.1 Introduction	30
2.1.1 Vegetative Growth.....	30
2.1.2 Branching Characteristics.....	31
2.2 Materials and Methods.....	32
2.2.1 Tree Materials.....	32
2.2.2 Leaf Growth.....	33
2.2.3 Shoot Elongation	34
2.2.4 Branching Characteristics of Two-year-old Branch.....	34
2.2.5 Statistical Analysis	35
2.3 Results	36
2.3.1 Leaf Growth.....	36
2.3.2 Shoot Elongation	41
2.3.3 Branching Characteristics of Two-year-old Branches.....	43
2.4 Discussion	46
2.5 Conclusions	48
2.6 References	50
CHAPTER 3 INFLUENCE OF LIGHT DISTRIBUTION ON FRUIT QUALITY IN ‘GOLDEN DELICIOUS’ APPLE TREES (MALUS × DOMESTICA BORKH.).....	54
3.1 Introduction	54
3.2 Materials and Methods.....	56
3.2.1 Tree Materials.....	56
3.2.2 Light Measurement.....	56
3.2.3 Fruit Analysis	59
3.2.3.1 Weight.....	59
3.2.3.2 Background Color.....	59
3.2.3.3 Firmness.....	60
3.2.3.4 Soluble Solid Concentration	60
3.2.3.5 Starch Test	60
3.2.4 Statistical Analysis	61
3.3 Results	61
3.3.1 Light Distribution	61

	Page
3.3.2 Fruit Quality	65
3.3.2.1 Position Effects on Fruit Quality	65
3.3.2.2 Light Effects on Weight.....	65
3.3.2.3 Light Effects on Background Color	67
3.3.2.4 Light Effects on Firmness.....	67
3.3.2.5 Light Effects on Soluble Solid Concentration	67
3.3.2.6 Light Effects on Starch Pattern Index	68
3.4 Discussion	68
3.5 Conclusions	71
3.6 References	72

LIST OF TABLES

Table	Page
Table 2.1 Tagging dates for different leaves in flowering spur, vegetative spur and bourse shoot.....	33
Table 3.1 Effect of canopy location on light distribution and fruit quality of ‘Golden Delicious’/G.16 trees in 2014.	63

LIST OF FIGURES

Figure	Page
Figure 1.1 The four branching and fruiting types of apple trees (Lespinasse & Delort, 1986).	3
Figure 1.2 ‘Cox Orange Pippin’ scion grafted on a range of Malling and Malling-Merton rootstocks (Webster & Wertheim, 2003).	5
Figure 1.3 Canopy forms of apple trees trained for commercial orchards. (a) slender-spindle, (b) vertical-axis, (c) central-leader, (d) horizontal-palmette, (e) Y-trellis (Robinson et al., 2003).	6
Figure 1.4 Axillary shoot positions and terminology regarding branching types. (a) sylleptic, (b) proleptic, (c) acrotonic, (d) mesotonic, (e) basitonic (Costes et al., 2006).	9
Figure 2.1 Example of an apple branch. Zones are defined according to their spatial distance to the proximal end of two-year-old branch, with zone 1 located at the proximal 1/3 portion and zone 3 at distal 1/3 portion of the branch. Figure is from Costes et al. (2006).	35
Figure 2.2 Growth curve of leaves in flowering spur, vegetative spur and bourse shoot in ‘Golden Delicious’/G.16 trees in 2014. Measurements were made from prior to full bloom (May 6) to the end of the growing season. Error bars indicate standard errors.	37

Figure	Page
Figure 2.3 Relative growth rate (RGR) of leaves in flowering spur, vegetative spur and bourse shoot in ‘Golden Delicious’/G.16 trees in 2014. RGR was calculated based on the leaf length measured from bloom time to the end of growing season.	38
Figure 2.4 Frequency distribution of final leaf length for flowering spur (FS), vegetative spur (VS) and bourse shoot (BS) in ‘Golden Delicious’/G.16 trees in 2014.....	39
Figure 2.5 Frequency distribution of final length for different leaves in (a) vegetative spur and (b) bourse shoot in ‘Golden Delicious’/G.16 trees in 2014.	40
Figure 2.6 Shoot growth curve of ‘Golden Delicious’/G.16 trees throughout the growing season of 2014. TS: terminal shoot, (n=102), VS: vegetative shoot (n=100), BS: bourse shoot (n=93). Error bars indicate standard errors.	41
Figure 2.7 Frequency distribution of shoot length for (a) bourse shoot (n=93), (b) vegetative spur (n=100), (c) terminal shoot (n=102) of ‘Golden Delicious’/G.16 trees in May, June, August and November in 2014.....	42
Figure 2.8 Frequency distribution of spur density for two-year-old branch sections (n=35) in ‘Golden Delicious’/G.16 trees in 2014. Spurs include both vegetative and reproductive ones.	44
Figure 2.9 Plot of spur density and the length of the two-year-old branch in ‘Golden Delicious’/G.16 trees (n=35) in 2014.	44

Figure	Page
Figure 2.10 Percentage of growing laterals (a) and reproductive laterals (b) in different zones of two-year-old branch in ‘Golden Delicious’/G.16 trees measured in 2014. Zone 1 to zone 3 represent the relative position on shoot with zone 1 located at the proximal and zone 3 at the distal part of the branch. Values with different letters are significant at the 0.05 level. ns: not significant. Means were separated by F-test and by Tukey’s multiple range test at the 5% level. Error bars indicate standard errors.....	45
Figure 3.1 Illustration of light measurement on a tree. (a) The frame for light measurement. The dimension of the frame is 3 m × 3 m × 3 m. The tree was girded into 216 equal sized cubes with 0.5 m at each side, by using ropes and PVC plastic pipes. (b) Close look of one cube. The solid lines indicating the positions where nine light reading were taken in each cube.	58
Figure 3.2 Relative light intensity within tree canopy in the morning, at noon and in the afternoon. Data were collected from four replicate ‘Golden Delicious’/G.16 trees. Layers 1 to 6 represent the vertical distance to the ground, 0.5 m, 1 m, 1.5 m, 2 m, 2.5 m and 3 m, respectively.	64
Figure 3.3 Correlation between fruit quality and the relative light intensity in ‘Golden Delicious’/G.16 trees. Fruit from the same light level were grouped together to calculate the average values for fruit quality (n=868). Ten light levels were determined by relative light intensity from 0 to 100% with 10% interval. Error bars indicate standard errors. (a) weight of individual fruit, (b) hue angle, (c) chroma, (d) firmness, (e) soluble solid concentration (SSC), (f) starch pattern index (SPI).....	66

ABSTRACT

Shi, Biying. M.S., Purdue University, May 2015. Growth Parameters for 'Golden Delicious' Apple Trees (*Malus × domestica* Borkh.). Major Professor: Peter Hirst.

High yield and high quality of tree fruit result from appropriate orchard design and management practices. This requires an accurate knowledge of vegetative growth, branching, and flowering processes of fruit trees. Tree development knowledge is the fundamental information necessary to build functional-structural tree models, which have various applications in agriculture. To build such models, information is needed on the distributions of growth parameters, not merely means as are often reported. The objective of this study was to quantitatively analyze shoot development and examine the correlations between fruit quality and light distribution in apple trees. This study was conducted in 2014, on 'Golden Delicious'/G.16 apple trees grown at the Purdue Meigs Research Farm. Measurements of shoot development were taken to determine the shoot growth rates, the frequency of leaf and stem length distribution, as well as the branching characteristics of two-year-old branches. The light distribution in tree canopies was measured and fruit quality was analyzed to determine correlations between them. Results showed a heterologous growth pattern of different types of shoots in trees. Vegetative spurs had the largest leaves, reaching a length of 90 mm, while flowering spurs had the smallest ones, which were about 40 mm. Most vegetative spurs and bourse shoots were

less than 5 cm in length. For terminal shoots, however, the lengths were evenly distributed between 5 and 16 cm. The highest branching frequency was found in the middle section of two-year-old shoots, while more reproductive laterals were found in the distal portion as opposed to the basal or middle portions of shoots. Light intensity was a good predictor of soluble solid concentration and skin background color, but was poorly correlated with individual fruit weight, firmness and starch pattern index. The data collected in this study are being incorporated into a model of apple tree growth in collaboration with colleagues in the Department of Computer Graphics Technology at Purdue University.

CHAPTER 1 INTRODUCTION

1.1 Plant Simulation Models

Computer-based plant models or "virtual plants" are able to represent the appearance as well as simulate biological processes of living plants (Tomita, 2001; Prusinkiewicz, 2004). Modeling plant development allows agronomists and foresters to test hypotheses and carry out virtual experiments concerning plant architecture and growth processes, while obtaining the results almost immediately.

There are a number of mathematical methods to describe and predict the dynamic development of plant architecture. Among those, the L-system is the most widely adopted one to model plant structure. The L-system was introduced by Lindenmayer in 1968, and is now a well-established methodology serving as a framework for the modeling of plant architecture (Lindenmayer, 1968). L-PEACH, based on L-system, was developed to simulate the carbon assimilation and allocation in peach trees. It can also simulate the tree response to pruning and fruit thinning (Lopez, Favreau, Smith, & Dejong, 2010).

Efforts have also been made to simulate interactions between plants and the environment. MAppleT constituted an effective tool to simulate the bending effects on branches imposed by gravity (Costes, Smith, Renton, Guédon, Prusinkiewicz, & Godlin, 2008). The crop yield of cotton, affected by environmental factors such as water

availability, nitrogen status and temperature, was modeled by Hanan and Hearn (2003). Moreover, the influence of wind on the developmental process of a tree was simulated based on wind intensity, duration and the actual exposure of the tree (Pirk, Niese, Haedrich, Benes, & Deussen, 2014).

Some models aim at simulating a specific part of a plant, while other model trees in a larger scale. The ROOTMAP has been developed to simulate complex interactions between plant root system and the below-ground environment (soil water, nutrients, barriers) (Dunbabin et al., 2011). Lim and Honjo (2003) intended to simulate an entire forest as a result of human disturbances such as planting, thinning and harvesting. This forest model is used in landscape design and forest management.

1.2 Tree Architecture

Significant effort has been made to analyze tree architecture, because it affects various aspects of plant development including light interception, flower bud induction, fruit yield and quality (Lauri, Terouanne, Lespinasse, Regnard, & Kelner, 1995). Tree architecture refers to the dynamic development of topology and geometry of trees at various scales from node, branch to whole tree canopy (Barthélémy, 1991; White, 1979). Topology describes the physical relationships (e.g., position) between tree organs, while geometry deals with size, shape and orientation of tree components (Godin, Costes, & Sinoquet, 1999). Although the tree architecture is genetically controlled, it can be influenced by environmental factors such as planting site, temperature, light, wind, soil nutrition status and water availability.

1.2.1 Branching and Fruiting Habits

Many researchers have been working on analyzing the structure of apple trees, to establish a system to describe branching and fruiting habits for various apple cultivars (Lapins, 1969). Growth characteristics such as shoot vigor, internode length, diameter and branching frequency were used in distinguishing ideotypes of apple cultivars (Lespinasse & Delort, 1986). Based on these growth characteristics, four ideotypes of apple cultivars were determined (Fig. 1.1).

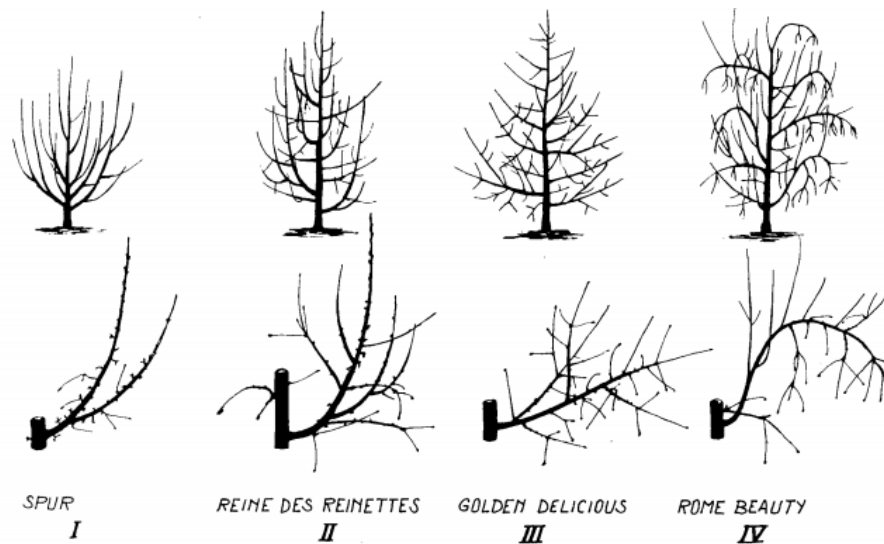


Figure 1.1 The four branching and fruiting types of apple trees (Lespinasse & Delort, 1986).

Type I trees (spur type), such as ‘Gravenstein’, usually have erect branches with greatest tendency to develop branches on lower part of trunk (basitony). The majority of the fruiting spurs are located close to the trunk.

Type II trees have strong wide angled branches. The central leader branch shows greater dominance than Type I trees. Fruiting zones move away from trunk with the

majority of fruiting spurs located on two to four-year-old branches. Examples are ‘McIntosh’ and ‘Spartan’.

Type III trees tend to have stronger and wider angled (60° to 90°) crotches. They bear fruit on spurs and one to three-year-old shoots. The fruiting zones move away from the center of the tree, causing bending of fruiting branches. Example is ‘Golden Delicious’.

Type IV trees (tip bearing) develop lateral shoots on distal portion of the branches. Trees have strong tendency to fruit on the ends of the previous year’s shoots resulting in a weeping canopy form. Examples are ‘Cortland’ and ‘Granny Smith’.

Fruiting pattern, alternate vs. regular, is closely related to the tree type. For example, ‘Oregon Spur Delicious’ belongs to Type II (spur type) category and has a strong biennial bearing tendency. ‘Granny Smith’, belonging to Type IV (tip bearing type), has a regular fruiting habit (Lauri et al., 1995, Lauri, Térouanne, & Lespinasse, 1997).

1.2.2 Horticultural Manipulation of Apple Trees

Most apple cultivars tend to develop large umbrella-shaped trees of 7-10 m in height if left undisturbed. This large of a tree is not desirable for commercial apple production. First of all, it is difficult to prune, spray and harvest. Second, it has poor light illumination inside the canopy. Moreover, large trees tend to have low yield efficiency and delayed cropping habit (Gjamovski & Kiprijanovski, 2011; Hirst & Ferree, 1995). In commercial apple orchards, tree canopy is highly manipulated to increase the fruit yield

and quality, as well as to improve orchard management efficiency. The canopy of an apple tree is mainly controlled by the use of rootstocks, as well as training and pruning. These horticultural practices on fruiting trees make the architecture analysis more complex.

1.2.2.1 Use of Rootstocks

Using dwarf rootstocks is the primary way to control tree height, spread and vigor. Rootstocks have profound effects on regulating tree canopy size, ranging from super dwarf (M.27), dwarf (M.9), semi-dwarf (M.26), semi-vigorous (M.106) to vigorous (M.25) (Webster & Wertheim, 2003) (Fig. 1.2).

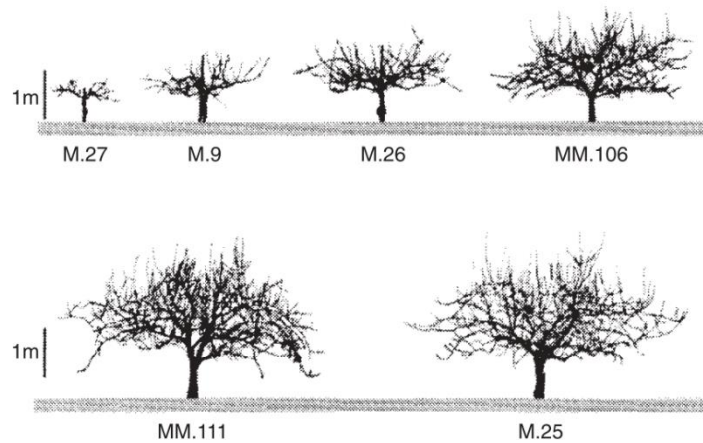


Figure 1.2 'Cox Orange Pippin' scion grafted on a range of Malling and Malling-Merton rootstocks (Webster & Wertheim, 2003).

1.2.2.2 Canopy Form

Robinson et al. (2003) reviewed several apple tree forms trained for commercial production. Trees trained to different forms varied a lot in terms of branch orientation, canopy size and shape (Fig. 1.3).

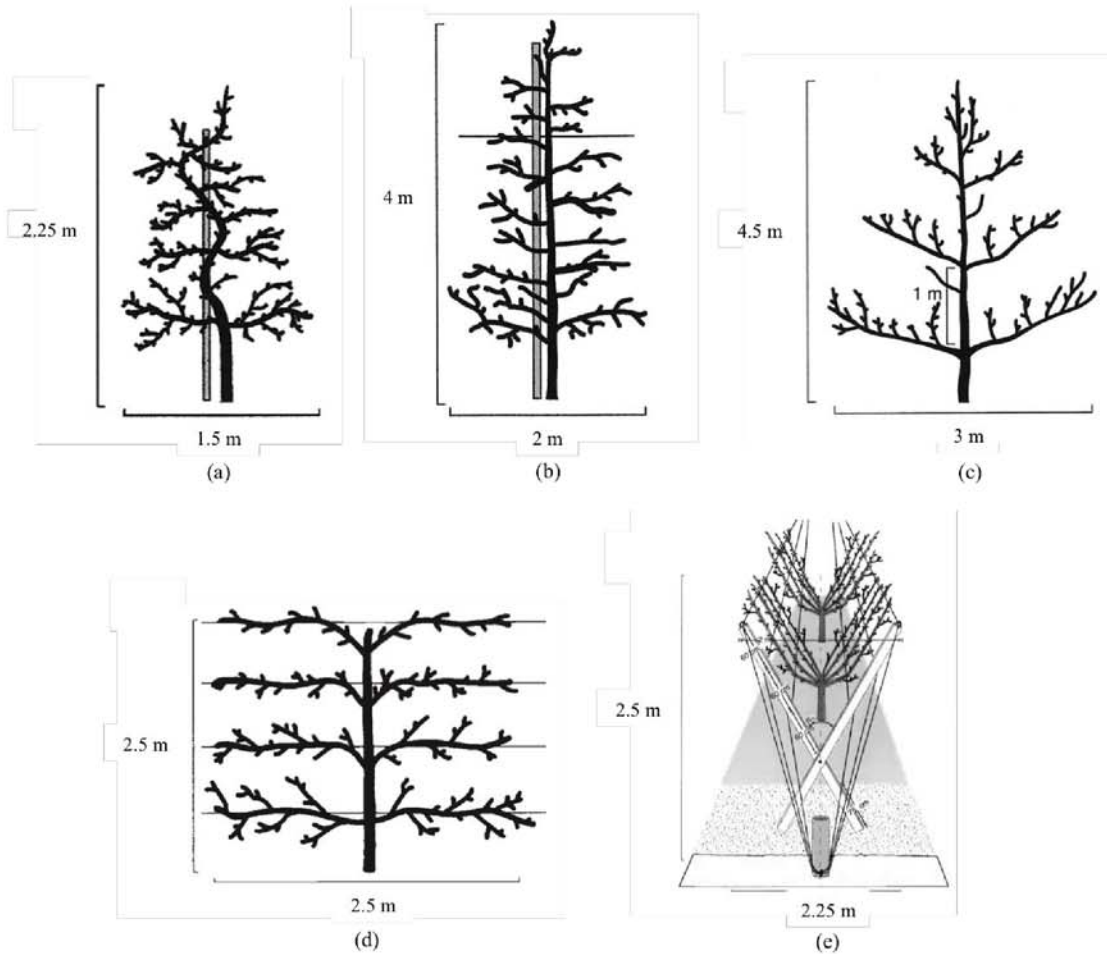


Figure 1.3 Canopy forms of apple trees trained for commercial orchards. (a) slender-spindle, (b) vertical-axis, (c) central-leader, (d) horizontal-palmette, (e) Y-trellis (Robinson et al., 2003).

Slender-spindle, vertical-axis and central-leader are among the most popular training systems adopted in the US and Europe. These tree forms have a single vertical leader trunk with several side branches spaced along the trunk. Trees trained to slender

spindle and vertical axis are used for high density plantings ranging from 1500 to 4000 trees ha^{-1} , so the canopy of those trees are narrower and more conic shaped with shorter, smaller side branches than the central leader tree form.

Palmette training system restricts the tree canopy to a two-dimensional plane, creating a fruiting wall to improve labor efficiency. Trees are usually 4-5 m high and supported by four to six-wire trellis. Branches at each tier are tied to wires. Side branches not in the two-dimensional plane are removed.

The V-shaped canopy systems were introduced for commercial orchards (Chalmers, Van Den Ende, & Van Heek, 1978) to improve light interception and penetration to the center of the canopy. The trained tree has two main scaffold arms about 50 to 70 degrees above the horizontal. The supporting trellis is about 2-3 m high and 6 wires at each side. Trees are planted with 1-2 m spacing in rows and 4-5 m between rows depends on specific trellis systems.

1.3 Shoot Development

The shoot system plays a major role in forming a specific tree structure. In apple, shoots develop from buds. Normally a tree has a large population of buds (Wilson & Kelty, 1994). There are many terms used to describe types of buds according to different criteria. Based on location, buds at the distal end of a shoot are called terminal buds; buds in the axils of leaves are called axillary buds (Forshey & Elfving, 1989). Based on function, buds could be either vegetative or mixed (reproductive and vegetative).

Vegetative buds only develop leaves and stems, while mixed buds develop leaves, stems along with flower clusters.

1.3.1 Bud Development

The shoot developing process includes two stages: the formation and differentiation of bud meristems, and the subsequent growth of buds (Landsberg, 1974; Shimizu-Sato & Mori, 2001). In apple trees, the formation and differentiation of buds usually happens in middle to late summer when the shoot growth ceases (Abbott, 1970). However, it varies with cultivar-rootstocks combination, as well as crop load and environmental condition (Forshey & Elfving, 1989). Flower bud induction is reportedly under complex regulations of internal (crop and hormones) and external factors (environmental conditions and management practices) (Buban & Faust, 1982), but many regulation theories are still controversial (Barlow, 1994).

Usually, buds of woody plants in the temperate zone undergo winter dormancy, which allows plants to survive under unfavorable environmental conditions (Beikircher & Mayr, 2013; Faust, Liu, Wang, & Stutte, 1995). Buds resume growth when the chilling requirement is fulfilled and environmental conditions are favorable. Chilling requirements need to be fully satisfied for obtaining desired vegetative growth and fruit bearing capacity, dormancy release and growth resumption. Different apple cultivars have various chilling requirements (Powell, 1985). Shoot growth begins in the period around the time of full bloom (Forshey & Elfving, 1989). Shoots that grow from a bud after a period of dormancy are termed proleptic shoots. In contrast, sylleptic shoots grow

from buds that have not gone through dormancy (Costes, Lauri & Regnard, 2006) (Fig. 1.4).

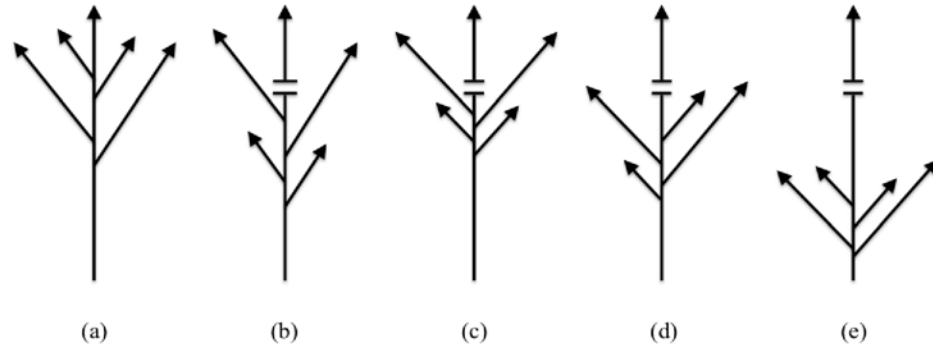


Figure 1.4 Axillary shoot positions and terminology regarding branching types. (a) sylleptic, (b) proleptic, (c) acrotonic, (d) mesotonic, (e) basitonic (Costes et al., 2006).

1.3.2 Non-growing Buds

Lauri (2009) addressed two categories of non-growing buds. The first category are those buds that are dormant in spring, but will resume growth later. These buds serve as reserve growing points of the tree. Another category is buds that permanently lose the ability of growth, termed meristem extinction or lateral abortion. Internal regulation such as apical dominance (Booker, Chatfield, & Leyser, 2003; Cline & Sadeski, 2002), external factors such as unfavorable temperature, low light intensity and low hydraulic conductance (Girault, Bergougnoux, Combes, Viemont, & Leduc, 2008; Han, Coutand, Cochard, Trottier, & Lauri, 2007) could all result in bud extinction.

1.3.3 Shoot Category

Based on developmental characteristics, annual shoots of apple tree are divided into two categories: vegetative shoots and flowering spurs (Pratt, 1988).

1.3.3.1 Vegetative Shoots

Vegetative shoots include long extension shoots, short spurs and bourse shoots. Vegetative spurs refer to those shoots shorter than 5 cm (Lauri & Kelner, 2001; Pratt, 1990). Leaves and nodes of spurs are entirely preformed and internodes do not elongate very much. Long extension shoots could be only preformed with elongating internodes, or have both preformed and neofomed growth (Barthélémy & Caraglio, 2007; Costes et al., 2006). Water sprouts are also vegetative shoots. They are vigorous upright shoots developing from buds on the upper surface of old limbs or buds close to pruning cuts. Water sprouts usually cast shade in the canopy decreasing the fruit quality (Fink, 1983).

1.3.3.2 Flowering Spurs

In apple trees, flower spurs are mixed with a whorl of leaves and a cluster of flowers. The development of flowering spurs proceeds the vegetative shoots (Forshey & Elfving, 1989). Later in growing season, one or more bourse shoots may arise from beneath the mixed buds (Pratt, 1988). The leaves of flowering spurs emerge first in spring and comprise the majority of the foliage until after bloom. Although leaves of flowering spurs are smaller than that of extension shoots, they play an essential role in early flower

development and fruit set (Forshey & Elfving, 1989). In addition, defoliation of spur and bourse shoot leaves caused the reducing of fruit set, fruit calcium level and return bloom (Abbott, 1960; Proctor & Palmer, 1991).

1.3.4 Branching Characteristics

The complexity of branching depends on the temporal and spatial development of laterals. The size, vigor, distribution of laterals (Barthélémy & Caraglio, 2007), as well as their yearly developmental sequences are used to characterize branching pattern of the parent shoot (Lauri et al., 1995). The branching pattern is cultivar specific and influenced by environmental conditions (Costes & Guédon, 2002, Hirst & Ferree, 1995).

Branching pattern can be described as acrotonic or basitonic. Acrotony is a term used to describe the phenomenon of increased vigor of lateral shoots from proximal to the distal portion of the shoot (Cook, Rabe, Keulemans, & Jacobs, 1998; Wilson, 2000) (Fig 1.4). In apple trees, acrotony is characterized as the increased potential of growing axillary meristems from the proximal to the distal zone of annual shoots, along with increased proportion of reproductive laterals among growing laterals (Lauri, 2007). Studies show that the bud diameter, spur leaf number, as well as fruit size are all increasing from proximal to distal position on acrotonic shoots (Rom & Barritt, 1990). Basitony describes the opposite phenomenon of acrotony.

1.4 Light Distribution

Light intercepted by the leaf is the driving force of all activities of plant development, from bud formation to fruit growth. Maximum fruit yields are limited by light interception, while fruit quality is largely determined by the local light environment in the fruiting zone (Campbell & Marini, 1992; Lakso, Robinson, & Pool, 1989; Palmer, 1988). High quality fruiting spurs have a large leaf area and large fruit are mainly located in well-illuminated canopy regions (Barritt, Rom, Konishi, & Dilley, 1991). Similarly, Jackson (1970) found that the main fruiting zone of tree canopy receives a minimum of 30% of full sun. Studies show that red color development and soluble solid concentration are largely diminished due to shading on fruit (Doud & Ferree, 1980; Hirst, Tustin, & Warrington, 1990). Light also affects the initiation of flowering buds for the following year as well (Marini & Sowers, 1990). As a consequence, the goal of orchard design and tree training is to intercept a high proportion of available light as well as to ensure adequate light distribution within the canopy (Lakso et al., 1989).

1.4.1 Factors Affecting Light Distribution

Fruit growers can improve the light microclimate using various horticultural practices. At the orchard level, light penetration depends on planting pattern such as row system (single versus multiple) (Wertheim, De Jager, & Duyzens, 1986), row orientation (Jackson & Palmer, 1972, Palmer, 1989) and tree spacing (Palmer, Avery, & Wertheim, 1992). At the individual tree level, light distribution is mainly influenced by selection of cultivar-rootstocks combination, training and pruning.

1.4.1.1 Cultivar-rootstock Combination

Four ideotypes of apple tree form, from upright, highly branched scaffolds to low-branched, tip-bearing cultivars, affect the light illumination in tree canopy (Lespinasse & Delort, 1986). Light intensity in large trees decreases rapidly with increased depth of the canopy. The innermost part of tree receives light intensity as low as 6% of full sunlight due to the shading by outer portion of foliage (Robinson, Lakso, & Ren, 1991). Generally small sized trees have less internal shading (Jackson, 1980; Warrington, Stanley, Tustin, Hirst, & Cashmore, 1996).

Dwarfing rootstocks are widely used to reduce the tree volume (Barritt, Konishi, & Dilley, 1995). Previous studies showed that vigor controlling rootstocks influenced light interception and light distribution by altering total leaf area of apple trees. Large leaf areas generally cast more shade on the interior area of the canopy as shown in rootstock testing studies (Verheij & Verwer, 1973). Dwarf trees have more leaf area per hectare that received more than 30% of full sun than do standard large trees (Robinson et al., 1991).

1.4.1.2 Canopy Form

Numerous experiments have been conducted to compare the performance of various canopy forms in terms of light interception, distribution and energy conversion efficiency.

The palmette-leader tree form was proposed to increase yield and improve light distribution inside the canopy (Lakso et al., 1989). The upper east- and west-growing

branches were removed, creating large openings in the canopy to ensure good light exposure to all parts of the tree. However, in a study comparing performance of palmette-leader with central-leader tree forms, the results did not show any advantage of the former in terms of light distribution, productivity and fruit quality (Elfving, Schechter, Cline, & Pierce, 1990). V-trellis, Y-trellis, and multilayered trellis are also designed to improve light penetration into the canopy (Robinson et al., 2003). The Y-trellis training system on M.26 rootstock (semi-dwarf) showed the highest light interception and energy conversion efficiency compared with slender spindle and central-leader training system on dwarf rootstocks (Robinson & Lakso, 1991).

1.4.1.3 Tree Spacing and Row Orientation

A desirable planting system is aimed for maximum light interception as well as good light distribution throughout the tree canopy. Tree spacing and planting density varies with training systems, ranging from 1000 (central-leader) to 6000 (super-spindle) trees per hectare, with some systems reaching a density up to 10,000 trees per hectare (Robinson et al., 2003). In commercial orchards, single-rows are the most commonly used; however, double-row, triple-row and even full field plantings have also been used. Research shows that the single-row system gives relatively high yields per tree compared to the other multiple row systems (Jackson, 1989; Wertheim et al., 1986).

Because of solar angle, tree rows oriented north-south are preferred to maximum light interception (Jackson & Palmer, 1972).

1.5 Fruit Quality

Fruit quality is defined by the degree of excellence or superiority in terms of sensory properties, nutrition values, mechanical properties and functional properties. In terms of apple, the most influential quality indicators are external (skin color, size) and internal (texture, taste, aroma) ones, based on consumer preference studies (Kühn & Thybo, 2001; Pathare, Opara & Al-Said, 2013).

Some fruit reach their best quality when left to ripen on the plant such as strawberry, cherry, tangerine and grape. However, some fruit are usually picked mature but unripe to prevent damage or perish from post harvesting processes. Examples of such fruit are apple, pear, apricot, peach and passion fruit. For these fruit, the ripening process continues after removal from the plant (Kader, 1999). In apple, ripening processes are reflected with increased respiration, degradation of chlorophyll in skin, disintegration of starch and softening of flesh. These physiological processes happen simultaneously (Valero & Serrano, 2010). Depending on the cultivar, apples require 80 to 200 days from bloom to attain the acceptable fruit maturity (Forshey & Elfving, 1989).

1.5.1 Fruit Quality Indicators

1.5.1.1 Size and Weight

Fruit size is among the most important commercial traits, which is generally determined by mean cell number and mean cell size (Bain & Robertson, 1951). Fruit size

is genetically regulated. For example, the fruit of ‘Grand Gala’, which is a mutant of ‘Gala’, are 15% larger and 38% heavier than that of ‘Gala’ (Malladi & Hirst, 2010).

However, many tree factors can influence the final fruit size, such as crop load and pollen source. After thinning the crop, fruit size was largely increased (Link, 2000). The timing of thinning is also essential. The size of fruit from those trees thinned near bloom are larger than those from trees thinned later (Goffinet, Robinson, & Lakso, 1995). Pollen source also largely affects the fruit size. When ‘Freedom’ and ‘Prima’ were used as pollinizer on ‘Rewena’, fruit gained high marketing value due to the large size and nice shape (Bodor, Gaál, & Tóth, 2008).

1.5.1.2 Sugar Content

Sugars contribute to the nutritional and sensory qualities of apples. Sweetness in apple is largely determined by the concentrations of fructose, glucose, sucrose, and the sugar-alcohol sorbitol (Fuleki, Pelayo, & Palabay, 1994).

As fruit ripens, starch is hydrolyzed to sugars. This process occurs first in the inner cortex, followed by the core, and then proceeds to outer cortex region (Ohmiya & Kakiuchi, 1990). Staining the equatorial region of apple with iodine-potassium iodide solution is the fastest and easiest way to indicate starch hydrolysis level and to predict harvest time (Brookfield, Murphy, Harker, & MacRae, 1997). Soluble solid concentration, expressed in Brix unit, is widely used to assess apple fruit sugar and acid level (Miller & Hall, 1953).

1.5.1.3 Background Color

Apple background color is correlated with maturity in apple. The decreasing intensity of green coloration is caused by degradation of chlorophyll, which results in yellowing in skin (Gierson & Kader, 1986).

The CIE L*a*b* system is widely adopted for the measurement of fruit skin color (Munsell, 1971). The parameter L* indicates the luminance or lightness, ranging from 0 to 100. a* and b* are two chromatic components ranging from -120 to +120 with a* measuring the degree of red (+) or green (-) and b* indicating the degree of blue (-) to yellow (+). Values of a* and b* are converted into hue angle ($H^\circ = \tan^{-1} b^*/a^*$, when $a^* < 0$ and $b^* > 0$, $H^\circ = 180^\circ + \tan^{-1} b^*/a^*$) and chroma ($\text{chroma} = (a^{*2} + b^{*2})^{1/2}$). Hue angle defines the color, reported in degrees, with 0° to 359° indicating the change of color from red (0°), yellow (60°), green (120°), blue (180°) to purple (270°). Chroma indicates color saturation and intensity, and its value varies from 0 (achromatic gray) to 60 (pure chromatic color). Hue angle and chroma were more appropriate parameters to describe the color (Greer, 2005).

Background color is a good indicator of apple maturity. Different cultivars have different thresholds of color indicating fruit quality. For example, 'Ligol' apples had the best quality when a* values ranged between -13.5 and -15.5, while for 'Jonagored' apples, the values were from -4.9 to -5.7 (Lysiak, Kurlus, Zydlik, & Walkowiak-Tomczak, 2014).

1.5.1.4 Firmness

Previous studies showed that fruit firmness was progressively decreased with ripening (Jackman, Marangoni, & Stanley, 1990). Fruit softening is a physiological process caused by dissolution of the middle lamella, the cementing material between cells (Ben-Arie, Kislev, & Frenkel, 1979).

1.5.1.5 Other Quality Indicators

Many other quality indicators are also used to determine the fruit quality. Seeds of apples become brown as the fruit matures, but seed color development has considerable seasonal variations and thus is less reliable as a maturity index (Kingston, 1992). The release of aromatic and nonaromatic volatiles (e.g., ethylene, acetate esters) increases as the fruit ripens, but the measurement of gas concentration requires sophisticated devices (Abbott, 1999). Other maturity index such as titratable acidity, fruit retention strength, and respiration rate are also adopted commercially (Kingston, 1992).

1.6 References

- Abbott, D. L. (1960). The bourse shoot as a factor in the growth of apple fruits. *Annals of Applied Biology* 48(2), 434–438.
- Abbott, D. L. (1970). The role of bud scales in the morphogenesis and dormancy of the apple fruit bud. In: L.C. Luckwill & C. Cutting (Eds.). *Physiology of Tree Crops* (pp. 65–82). London: Academic Press.
- Abbott, J. A. (1999). Quality measurement of fruits and vegetables. *Postharvest Biology and Technology*, 15(3), 207-225.
- Bain J. M., & Robertson, R. N. (1951). The physiology of growth in apple fruits. I. Cell size, cell number and fruit development. *Australian Journal of Biological Science*, 4(2), 75–91.
- Barlow, P. W. (1994). From cell to system: repetitive units of growth in the development of roots and shoots. In M. Iqbal (Ed.), *Growth patterns in vascular plants* (pp.19-58). Oregon: Dioscorides Press.
- Barritt, B. H., Konishi, B. S., & Dilley, M. A. (1995). Performance of three apple cultivars with 23 dwarfing rootstocks during 8 seasons in Washington. *Fruit Varieties Journal*, 49, 158–170.
- Barritt, B. H., Rom, C. R., Konishi, B. J., & Dilley, M. A. (1991). Light level influences spur quality and canopy development and light interception influence fruit production in apple. *HortScience*, 26(8), 993-999.
- Barthélémy, D. (1991). Levels of organization and repetition phenomena in seed plants. *Acta Biotheoretica*, 39(3-4), 309-323.

- Barthélémy, D., & Caraglio, Y. (2007). Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany*, *99*(3), 375-407.
- Beikircher, B., & Mayr, S. (2013). Winter peridermal conductance of apple trees: lammas shoots and spring shoots compared. *Trees*, *27*(3), 707-715.
- Ben-Arie, R., Kislev, N., & Frenkel, C. (1979). Ultrastructural changes in the cell walls of ripening apple and pear fruit. *Plant Physiology*, *64*(2), 197-202.
- Bodor, P., Gaál, M., & Tóth, M. (2008). Metaxenia in apples cv. 'Rewena', 'Relinda', 'Baujade' as influenced by scab resistant pollinizers. *International Journal of Horticultural Science*, *14*(3), 11-14.
- Booker, J., Chatfield, S., & Leyser, O. (2003). Auxin acts in xylem-associated or medullary cells to mediate apical dominance. *The Plant Cell Online*, *15*(2), 495-507.
- Brookfield, P., Murphy, P., Harker, R., & MacRae, E. (1997). Starch degradation and starch pattern indices; interpretation and relationship to maturity. *Postharvest Biology and Technology*, *11*(1), 23-30.
- Buban, T., & Faust, M. (1982). Flower bud induction in apple trees: internal control and differentiation. *Horticultural Reviews*, *4*, 174-203.
- Campbell, R. J., & Marini, R. P. (1992). Light environment and time of harvest affect 'Delicious' apple fruit quality characteristics. *Journal of the American Society for Horticultural Science*, *117*(4), 551-557.
- Chalmers, D., Van den Ende, B., & Van Heek, L. (1978). Productivity and mechanization of the Tatura Trellis orchard [Peaches, pears, apricots]. *HortScience*, *13*, 517-521.

- Cline, M. G., & Sadeski, K. (2002). Is auxin the repressor signal of branch growth in apical control. *American Journal of Botany*, 89(11), 1764-1771.
- Cook, N. C., Rabe, E., Keulemans, J., & Jacobs, G. (1998). The expression of acrotony in deciduous fruit trees: a study of the apple rootstock M. 9. *Journal of the American Society for Horticultural Science*, 123(1), 30-34.
- Costes, E., & Guédon, Y. (2002). Modelling branching patterns on 1-year-old trunks of six apple cultivars. *Annals of Botany*, 89(5), 513-524.
- Costes, E., Lauri, P. E., & Regnard, J. L. (2006). Analyzing fruit tree architecture: Implications for tree management and fruit production. *Horticultural Reviews*, 32, 1-61.
- Costes, E., Smith, C., Renton, M., Guédon, Y., Prusinkiewicz, P., & Godin, C. (2008). MAppleT: simulation of apple tree development using mixed stochastic and biomechanical models. *Functional Plant Biology*, 35(10), 936-950.
- Doud, D. S., & Ferree, D. C. (1980). Influence of altered light levels on growth and fruiting of mature 'Delicious' apple trees. *Journal of the American Society for Horticultural Science*, 105(3), 325-328.
- Dunbabin, V. M., Airey, M., Diggle, A. J., Renton, M., Rengel, Z., Armstrong, R., ... & Siddique, K. H. M. (2011). Simulating the interaction between plant roots, soil water and nutrient flows, and barriers and objects in soil using ROOTMAP. In R.S. Anderssen, F. Chan, & D. Marinova (Eds.), *19th international congress on modelling and simulation* (pp. 975-981). Perth, Western Australia: Modelling and Simulation Society of Australia and New Zealand.

- Elfving, D. C., Schechter, I., Cline, R. A., & Pierce, W. F. (1990). Palmette-leader and central-leader tree forms compared for light distribution, productivity, and fruit quality of 'McIntosh' Apple Trees. *HortScience*, 25(11), 1386-1388.
- Faust, M., Liu, D., Wang, S. Y., & Stutte, G. W. (1995). Involvement of apical dominance in winter dormancy of apple buds. *Acta Horticulturae*, 395, 47-56.
- Fink, S. (1983). The occurrence of adventitious and preventitious buds within the bark of some temperate and sub-tropical trees. *American Journal of Botany*, 70, 532-542.
- Forshey, C. G., & Elfving, D. C. (1989). The relationship between vegetative growth and fruiting in apple trees. *Horticultural Reviews*, 11, 229-287.
- Fuleki, T., Pelayo, E., & Palabay, R. B. (1994). Sugar composition of varietal juices produced from fresh and stored apples. *Journal of Agricultural and Food Chemistry*, 42(6), 1266-1275.
- Gierson, D., & Kader, A. A. (1986). Fruit ripening and quality. In J. Atherton & j. Rudich (Eds.), *The tomato crop* (pp. 241-280). Netherlands: Springer.
- Girault, T., Bergougoux, V., Combes, D., Viemont, J.D. & Leduc, N. (2008). Light controls shoot meristem organogenetic activity and leaf primordia growth during bud burst in *Rosa* sp. *Plant, Cell & Environment*, 31(11), 1534-1544.
- Gjamovski, V., & Kiprijanovski, M. (2011). Influence of nine dwarfing apple rootstocks on vigour and productivity of apple cultivar 'Granny Smith'. *Scientia Horticulturae*, 129(4), 742-746.
- Godin, C., Costes, E., & Sinoquet, H. (1999). A method for describing plant architecture which integrates topology and geometry. *Annals of Botany*, 84(3), 343-357.

- Goffinet, M. C., Robinson, T. L., & Lakso, A. N. (1995). A comparison of 'Empire' apple fruit size and anatomy in unthinned and hand-thinned trees. *Journal of Horticultural Science*, 70(3), 375-387.
- Greer, D. H. (2005). Non-destructive chlorophyll fluorescence and colour measurements of 'Braeburn' and 'Royal Gala' apple (*Malus domestica*) fruit development throughout the growing season. *New Zealand Journal of Crop and Horticultural Science*, 33(4), 413-421.
- Han, H. H., Coutand, C., Cochard, H., Trottier, C., & Lauri, P. E. (2007). Effects of shoot bending on lateral fate and hydraulics: invariant and changing traits across five apple genotypes. *Journal of Experimental Botany*, 58(13), 3537-3547.
- Hanan, J. S., & Hearn, A. B. (2003). Linking physiological and architectural models of cotton. *Agricultural Systems*, 75(1), 47-77.
- Hirst, P. M., & Ferree, D. C. (1995). Rootstock effects on shoot morphology and spur quality of 'Delicious' apple and relationships with precocity and productivity. *Journal of the American Society for Horticultural Science*, 120(4), 622-634.
- Hirst, P. M., Tustin, D. S., & Warrington, I. J. (1990). Fruit colour responses of 'Granny Smith' apple to variable light environments. *New Zealand Journal of Crop and Horticultural Science*, 18(4), 205-214.
- Jackman, R. L., Marangoni, A. G., & Stanley, D. W. (1990). Measurement of tomato fruit firmness. *HortScience*, 25(7), 781-783.
- Jackson, J. E. (1970). Aspects of light climate within apple orchards. *Journal of Applied Ecology*, 207-216.

- Jackson, J. E. (1980). Light interception and utilization by orchard systems. *Horticultural Reviews*, 2, 208-267.
- Jackson, J. E. (1989). World-wide development of high density planting in research and practice. *Acta Horticulturae*, 243, 17-27.
- Jackson, J. E., & Palmer, J. W. (1972). Interception of light by model hedgerow orchards in relation to latitude, time of year and hedgerow configuration and orientation. *Journal of Applied Ecology*, 9, 341-357.
- Kader, A. A. (1999). Fruit maturity, ripening, and quality relationships. *Acta Horticulturae*, 485, 203-208.
- Kingston, C. M. (1992). Maturity indices for apple and pear. *Horticultural Reviews*, 13, 407-432.
- Kühn, B. F., & Thybo, A. K. (2001). The influence of sensory and physiochemical quality on Danish children's preferences for apples. *Food Quality and Preference*, 12(8), 543-550.
- Lakso, A. N., Robinson, T. L., & Pool, R. M. (1989). Canopy microclimate effects on patterns of fruiting and fruit development in apples and grapes. In C. J. Wright (Ed.), *Manipulation of fruiting* (pp. 263-274). London: Butterworths.
- Landsberg, J. J. (1974). Apple fruit bud development and growth; analysis and an empirical model. *Annals of Botany*, 38(5), 1013-1023.
- Lapins, K. (1969). Segregation of compact growth types in certain apple seedling progenies. *Canadian Journal of Plant Science*, 49(6), 765-768.

- Lauri, P. E. (2007). Differentiation and growth traits associated with acrotony in the apple tree (*Malus× domestica*, Rosaceae). *American Journal of Botany*, 94(8), 1273-1281.
- Lauri, P. E. (2009). Does plant architecture only result from growing meristems? Atlan's principle of life and death as regulated morphogenetic processes. In W. P. Karam (Ed.), *Tree growth: influences, layers and types* (pp. 45-55). Hauppauge, New York: Nova Science Publishers.
- Lauri, P. E., Kelner, J. J. (2001). Shoot type demography and dry matter partitioning: A morphometric approach in apple (*Malus x domestica*). *Canadian Journal of Botany* 79(11), 1270–1273.
- Lauri, P. E., Térouanne, E., & Lespinasse, J. M. (1997). Relationship between the early development of apple fruiting branches and the regularity of bearing: An approach to the strategies of various cultivars. *Journal of Horticultural Science (United Kingdom)*, 72, 519–530.
- Lauri, P. E., Térouanne, E., Lespinasse, J. M., Regnard, J. L., & Kelner, J. J. (1995). Genotypic differences in the axillary bud growth and fruiting pattern of apple fruiting branches over several years—an approach to regulation of fruit bearing. *Scientia Horticulturae*, 64(4), 265-281.
- Lespinasse, J. M., & Delort, J. F. (1986). Apple tree management in vertical axis: Appraisal after ten years of experiments. *Acta Horticulturae* 160, 139–155.
- Lim, E. M., & Honjo, T. (2003). Three-dimensional visualization forest of landscapes by VRML. *Landscape and Urban Planning*, 63(3), 175-186.

- Lindenmayer, A. (1968). Mathematical models for cellular interactions in development
II. Simple and branching filaments with two-sided inputs. *Journal of Theoretical Biology*, 18(3), 300-315.
- Link, H. (2000). Significance of flower and fruit thinning on fruit quality. *Plant Growth Regulation*, 31, 17-26.
- Lopez, G., Favreau, R. R., Smith, C., & DeJong, T. M. (2010). L-PEACH: A computer-based model to understand how peach trees grow. *HortTechnology*, 20(6), 983-990.
- Lysiak, G., Kurlus, R., Zydlik, Z., & Walkowiak-Tomczak, D. (2014). Apple skin colour changes during harvest as an indicator of maturity. *Acta Scientiarum Polonorum-Hortorum Cultus*, 13(3), 71-83.
- Malladi, A., & Hirst, P. M. (2010). Increase in fruit size of a spontaneous mutant of 'Gala' apple (*Malus domestica* Borkh.) is facilitated by altered cell production and enhanced cell size. *Journal of Experimental Botany*, 61(11), 3003-3013.
- Marini, R. P., & Sowers, D. L. (1990). Net photosynthesis, specific leaf weight, and flowering of peach as influenced by shade. *HortScience*, 25(3), 331-334.
- Miller, E. V., & Hall, G. D. (1953). Distribution of total soluble solids, ascorbic acid, total acid, and bromelin activity in the fruit of the natal pineapple (*Ananas comosus* L. Merr.). *Plant Physiology*, 28(3), 532.
- Munsell, A. H. (1971). *A colour notation: An illustrated system defining all colours and their relationships by measured scales of hue, value, and chroma*. Baltimore, MD: Munsell Colour Company, Inc.

- Ohmiya, A., & Kakiuchi, N. (1990). Quantitative and morphological studies on starch of apple fruit during development. *Journal of the Japanese Society for Horticultural Science*, 59(2), 417-423.
- 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. *Journal of Applied Ecology*, 25, 569-578.
- Palmer, J. W. (1989). Canopy manipulation for optimum utilization of light. In C. J. Wright (Ed.), *Manipulation of Fruiting* (pp. 245-262). London: Butterworths.
- Palmer, J. W., Avery, D. J., & Wertheim, S. J. (1992). Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Scientia Horticulturae*, 52(4), 303-312.
- Pathare, P. B., Opara, U. L., & Al-Said, F. A. J. (2013). Colour measurement and analysis in fresh and processed foods: A review. *Food and Bioprocess Technology*, 6(1), 36-60.
- Pirk, S., Niese, T., Haedrich, T., Benes, B., & Deussen, O. (2014). Windy trees: computing stress response for developmental tree models. *ACM Transactions on Graphics (TOG)*, 33(6), 204:1-204:11.
- Powell, L. E. (1985). The chilling requirement in apple and its role in regulating time of flowering in spring in cold-winter climates. In L.C. Luckwill (Ed.), *V International Symposium on Growth Regulators in Fruit Production* (pp. 129-140). Rimini, Italy.
- Pratt, C. (1988). Apple flower and fruit: Morphology and anatomy. *Horticultural Reviews*, 10, 273-308.

- Pratt, C. (1990). Apple trees: Morphology and anatomy. *Horticultural Reviews*, 12, 265-305.
- Proctor, J. T. A., & Palmer, J. W. (1991). The role of spur and bourse leaves of three apple cultivars on fruit set and growth and calcium content. *HortScience*, 26(6), 789.
- Prusinkiewicz, P. (2004). Modeling plant growth and development. *Current Opinion in Plant Biology*, 7(1), 79-83.
- Robinson, T. L., & Lakso, A. N. (1991). Bases of yield and production efficiency in apple orchard systems. *Journal of the American Society for Horticultural Science*, 116(2), 188-194.
- Robinson, T. L., Ferree, D. C., & Warrington, I. J. (2003). Apple-orchard planting systems. *Apples: Botany, Production and Uses*, 345-407.
- Robinson, T. L., Lakso, A. N., & Ren, Z. (1991). Modifying apple tree canopies for improved production efficiency. *HortScience*, 26(8), 1005-1012.
- Rom, C. R., & Barritt, B. (1990). Spur development of 'Delicious' apple as influenced by position, wood age, strain, and pruning. *HortScience*, 25(12), 1578-1581.
- Shimizu-Sato, S., & Mori, H. (2001). Control of outgrowth and dormancy in axillary buds. *Plant Physiology*, 127(4), 1405-1413.
- Tomita, M. (2001). Whole-cell simulation: a grand challenge of the 21st century. *Trends in Biotechnology*, 19(6), 205-210.
- Valero, D., & Serrano, M. (2010). *Postharvest biology and technology for preserving fruit quality*. Boca Raton, USA: CRC-Taylor & Francis.

- Verheij, E. W. M., & Verwer, F. L. J. A. W. (1973). Light studies in a spacing trial with apple on a dwarfing and a semi-dwarfing rootstock. *Scientia Horticulturae*, *1*(1), 25-42.
- Warrington, I. J., Stanley, C. J., Tustin, D. S., Hirst, P. M., & Cashmore, W. M. (1996). Light transmission, yield distribution, and fruit quality in six tree canopy forms of 'Granny Smith' apple. *Journal of Tree Fruit Production*, *1*(1), 27-54.
- Webster, A. D., & Wertheim, S. J. (2003). Apple rootstocks. In: D. C. Ferree & I. J. Warrington, (Eds.), *Apples: Botany, production and uses* (pp. 91–124). Cambridge, MA: CAB International.
- Wertheim, S. J., De Jager, A., & Duyzens, M. J. J. P. (1986). Comparison of single-row and multi-row planting systems with apple, with regard to productivity, fruit size and colour, and light conditions. *Acta Horticulturae*, *160*, 243-258.
- White, J. (1979). The plant as a metapopulation. *Annual Review of Ecology and Systematics*, 109-145.
- Wilson, B. F. (2000). Apical control of branch growth and angle in woody plants. *American Journal of Botany*, *87*(5), 601-607.
- Wilson, B. F., & Kelty, M. J. (1994). Shoot growth from the bud bank in black oak. *Canadian Journal of Forest Research*, *24*(1), 149-154.

CHAPTER 2 VEGETATIVE GROWTH AND BRANCHING CHARACTERISTICS OF 'GOLDEN DELICIOUS' APPLE TREES (MALUS X DOMESTICA BORKH.)

2.1 Introduction

The complexity of the tree architecture depends on the temporal and spatial development of plant components (Lauri, Térouanne, Lespinasse, Regnard, & Kelner, 1995). The architecture analysis is based on morphological traits of tree components at various scales from bud, leaf, shoot to whole canopy (Barthélémy & Caraglio, 2007; Rom & Barritt, 1990). In studies of fruit tree structure, efforts were put into analyzing shoot development, including vegetative growth and branching characteristics (Costes & Guédon, 2002).

2.1.1 Vegetative Growth

Based on developmental characteristics, annual shoots of apple tree were divided into four categories: long extension shoots, vegetative spurs, flowering spurs, and bourse shoots (Pratt, 1988; Pratt, 1990). Spur is a term referring to shoots that are shorter than 5 cm. The nodes of spurs are entirely preformed and their internodes do not elongate very much. Long extension shoots could only be preformed with elongating internodes, or have both preformed and neoformed growth (Barthélémy & Caraglio, 2007; Costes,

Lauri, & Regnard, 2006). Flowering spurs develop from mixed buds containing a whorl of spur leaves and flower clusters. Bourse shoots are vegetative shoots arising from beneath the flowering spurs (Pratt, 1988). However, flowering spurs are not guaranteed to set fruit.

Leaves from different categories of shoots differ in size and affect the tree growth in different manners (Pratt, 1990). Generally, leaves of shoots are larger than that of spurs. By the time of the full leaf canopy, the total leaf area of shoots was more than twice of that of spurs (Forshey, Weires, & VanKirk, 1987). However, spur leaves play an important role in flower initiation and fruit set, and the majority of new carbohydrates for early fruit growth were from primary leaves of flowering spurs (Hansen, 1971). Similarly, Proctor and Palmer (1991) found that the defoliation of spur and bourse shoot leaves caused reduction of fruit set, fruit calcium level and return bloom. From a functional perspective, leaves of fruiting spurs had a 20% increase in photosynthesis rate than that of non-fruiting spurs (Fujii & Kennedy, 1985).

2.1.2 Branching Characteristics

Branching characteristics of apple is cultivar specific and influenced by environmental conditions (Costes & Guédon, 2002; Hirst & Ferree, 1995). Distribution of laterals along the parent shoot, as well as their growth traits (size, vigor) and yearly developmental sequences are used to characterize branching patterns for apple cultivars (Lauri, 2007; Lauri & Trottier, 2004). There are numerous studies analyzing branch developmental characteristics. For example, the growth characteristics of one-year-old

vegetative spurs were studied on several commercial ‘Delicious’ apple strains to evaluate their degree of spur-bearing habit of the tree (Warrington, Ferree, Schupp, Dennis, & Baugher, 1990). In a detailed statistical analysis of lateral branch traits for several one-year-old seedlings on own roots, genetic variation in terms of number, position, and length of sylleptic shoots was clearly found (De Wit, Keulemans, & Cook, 2002). Shoot length, spur density and quality on two-year-old branch sections of trees growing on 17 different rootstocks were studied by Hirst and Ferree (1995) for six years, and the results showed that rootstocks had large effects on scion branching characteristics.

This experiment was conducted on ‘Golden Delicious’/G.16 apple trees to better understand the development of apple trees and to build database for tree modeling and simulation. The objectives of this study were 1) to examine growth rates of leaf and shoot as well as the frequency distribution of leaf and shoot length among different shoot categories, and 2) to quantitatively analyze the branching characteristics on two-year-old branch sections.

2.2 Materials and Methods

2.2.1 Tree Materials

This experiment was conducted in 2014 on ‘Golden Delicious’/G.16 apple trees. Trees were planted in 2003 at the Purdue Meigs Farm, Lafayette, IN, USA, trained as central leader system and pruned annually according to commercial standards. Rows were oriented in a north-south direction, with 3.5 m in-row and 5.5 m between-row

spacing. Seven trees were selected for uniformity of trunk size and general appearance.

Full bloom time in 2014 was on May 6.

2.2.2 Leaf Growth

Fifteen shoots from each shoot category, flowering spurs (FS), vegetative spurs (VS) and bourse shoots (BS), were randomly chosen in each of seven trees before bloom. Three leaves on each shoot or spur were tagged to track their growth throughout the growing season of 2014. For flowering spurs, the three leaves were tagged on the same day because leaves of flowering spur developed at the same time. For vegetative spurs and bourse shoots, the three leaves were tagged on different days to capture the growth of new leaves. Table 2.1 shows the tagging dates for leaves, referring to first, second and third leaf, according to tagging time. The newest unfolded leaf was selected at each time. The length of leaf blade was measured with a digital caliper throughout the growing season. Relative growth rate (RGR) was calculated from the formula: $RGR = (L2 - L1) / L1 (T2 - T1)$, where L1 and L2 were the length of leaves measured at two times, T1 and T2, respectively.

Table 2.1 Tagging dates for different leaves in flowering spur, vegetative spur and bourse shoot.

	Flowering spur	Vegetative spur	Bourse shoot
First leaf	Apr 27 (n=217)	May 2 (n=90)	May 8 (n=82)
Second leaf	*	May 8 (n=81)	June 3 (n=77)
Third leaf	*	June 3 (n=57)	**

*For flowering spurs, the three leaves were tagged on the same day because those leaves developed at the same time

**Very few bourse shoots developed the new leaf after June 3.

2.2.3 Shoot Elongation

A sample of 15 shoots for each shoot category (flowering spurs (FS), vegetative spurs (VS) and terminal shoots (TS)) from each of seven trees was randomly tagged before blooming. The length of individual shoot or spur was measured with a digital caliper at monthly intervals through the end of the growing season in 2014.

2.2.4 Branching Characteristics of Two-year-old Branch

Five two-year-old branch sections were randomly selected on each tree in November 2014. Individual shoot length was measured with a digital caliper. Three zones were determined based on the distance from the proximal end of the two-year-old branch section, referred as zone 1 (proximal 1/3 portion of the branch) to zone 3 (distal 1/3 portion of the branch) (Fig. 2.1). The number of total buds, growing buds as well as flowering buds were counted separately in each zone. The method was modified from Lauri (2007).

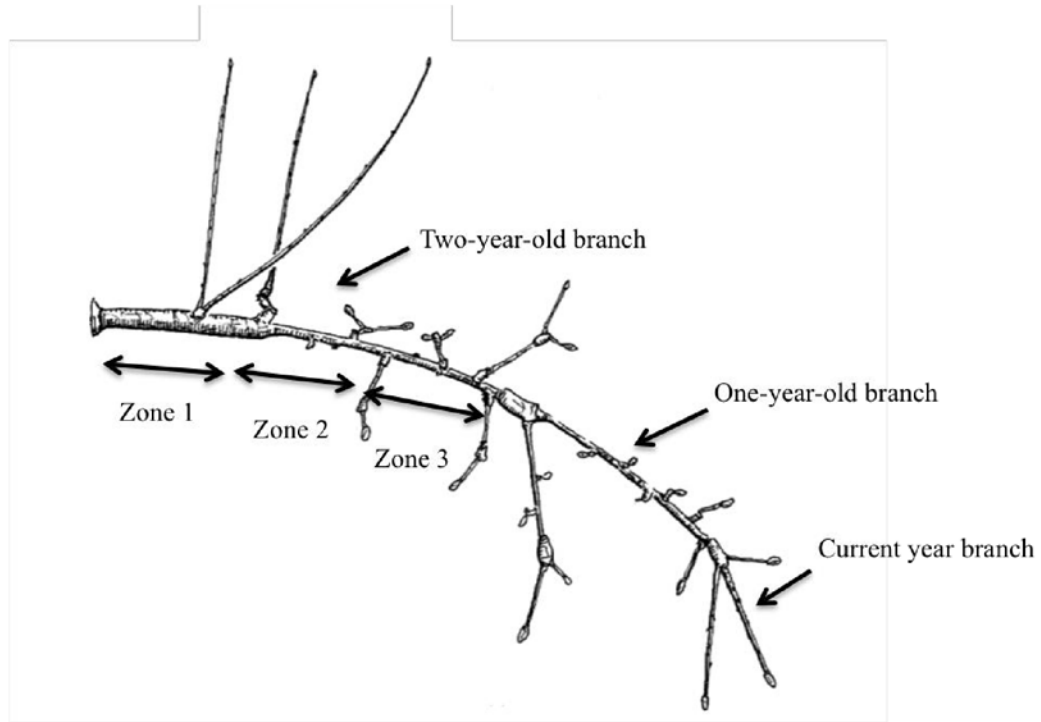


Figure 2.1 Example of an apple branch. Zones are defined according to their spatial distance to the proximal end of two-year-old branch, with zone 1 located at the proximal 1/3 portion and zone 3 at distal 1/3 portion of the branch. Figure is from Costes et al. (2006).

2.2.5 Statistical Analysis

Data were subjected to analysis of variance and the means were separated by F-test and by Tukey's multiple range test at the 5% level, using SAS (SAS 9.3; SAS Institute Inc., Cary, NC).

2.3 Results

2.3.1 Leaf Growth

Leaves that developed early in the season (FS, BS first leaf, VS first and second leaf) exhibited a similar growth pattern (Fig. 2.2). A linear increase in leaf length was noted until May 26, which was 20 days after full bloom. Similarly, the largest relative growth rate (RGR) occurred in early May after which there was a sharp decline until May 26 (Fig. 2.3). Leaf length remained the same after this period. FS leaves reached 90% of their final length by the time of full bloom and ceased earlier than other leaves. As for those leaves that developed later in the season (BS second leaf and VS third leaf), they continued growing until June 20, which was 45 days after full bloom. On average, final leaf length of VS and BS was 1.4 and 1.2 times greater than that of FS, respectively. For FS, the range of final leaf length was between 10 and 60 mm, and more than 40% of leaves were around 45 mm in length (Fig. 2.4). For VS and BS leaves, the range of final leaf length was between 30 and 120 mm and the leaves were evenly distributed within the range. Moreover, for VS and BS, leaves that emerged at different times had a large difference in length (Fig. 2.5). A 45 % difference in the final leaf length was noticed in VS leaves and a 35% difference was found in BS leaves.

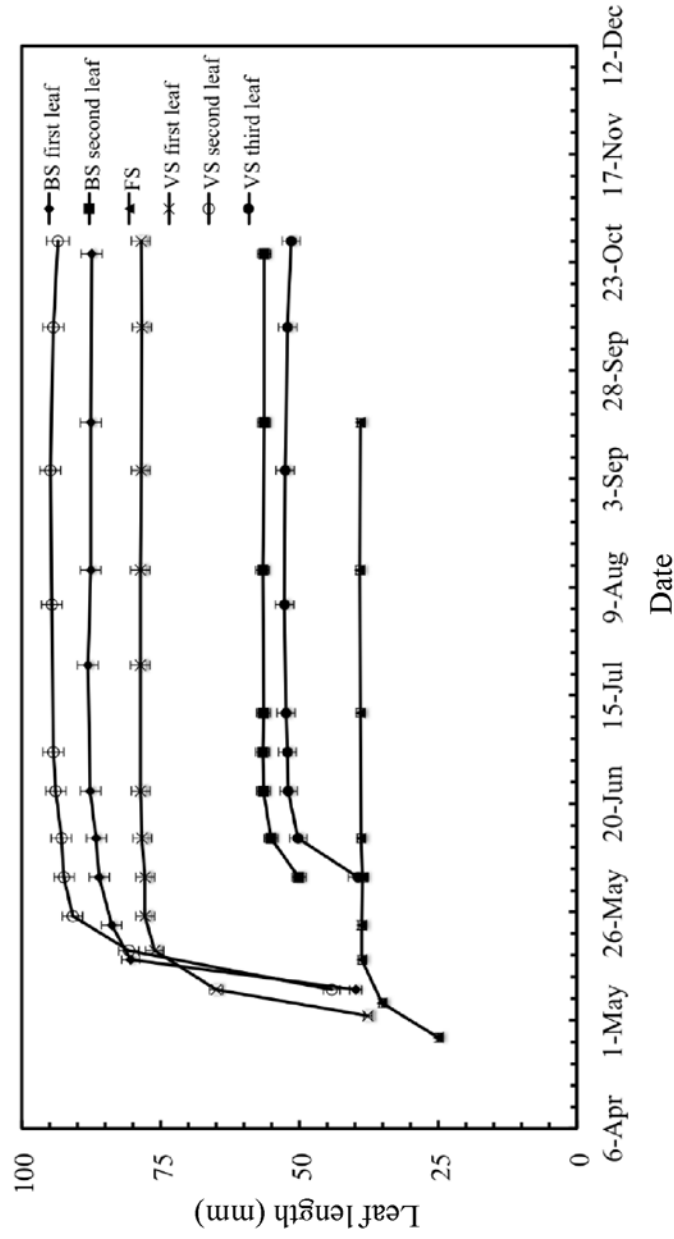


Figure 2.2 Growth curve of leaves in flowering spur, vegetative spur and bourse shoot in 'Golden Delicious' /G.16 trees in 2014. Measurements were made from prior to full bloom (May 6) to the end of the growing season. Error bars indicate standard errors.

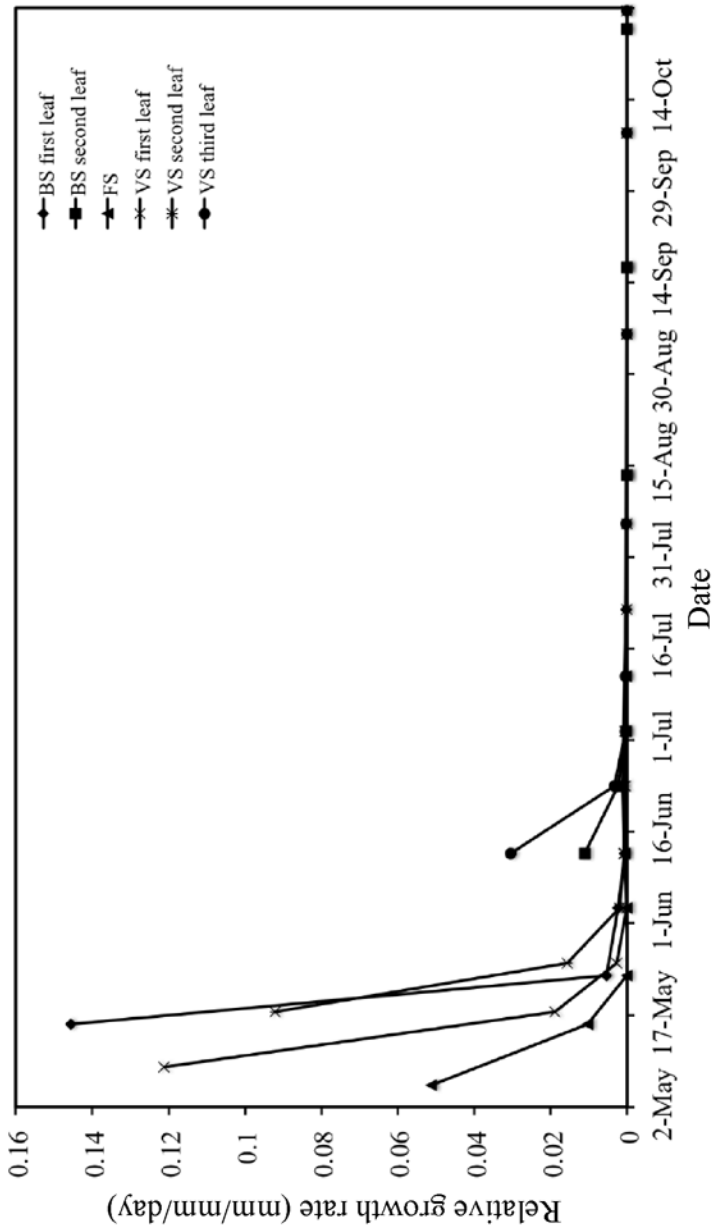


Figure 2.3 Relative growth rate (RGR) of leaves in flowering spur, vegetative spur and bourse shoot in 'Golden Delicious'/G.16 trees in 2014. RGR was calculated based on the leaf length measured from bloom time to the end of growing season.

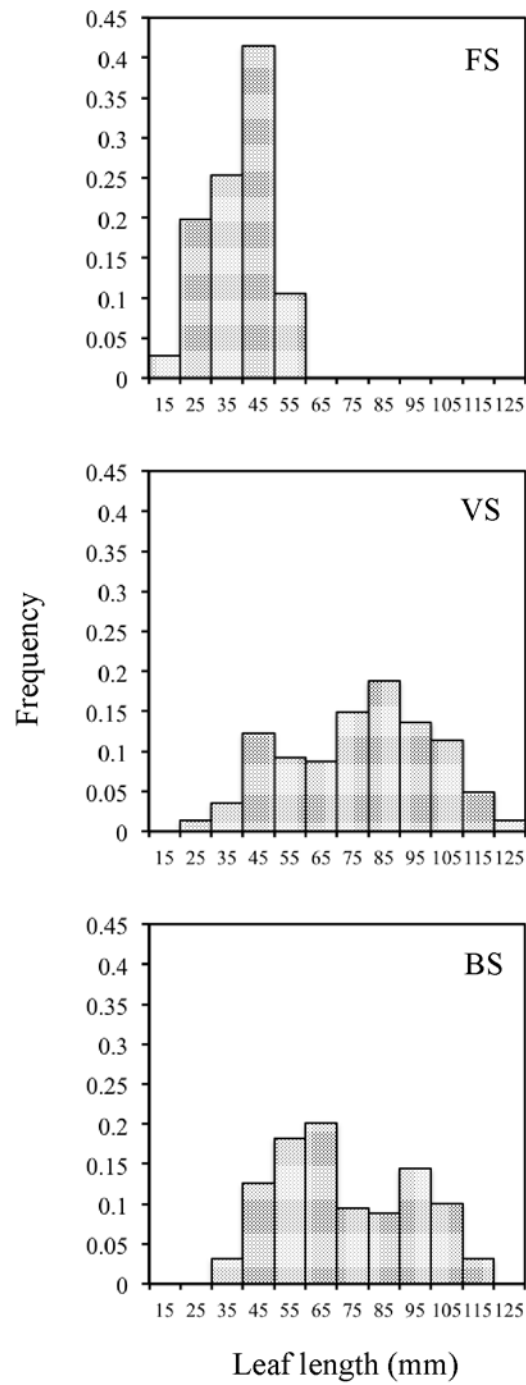


Figure 2.4 Frequency distribution of final leaf length for flowering spur (FS), vegetative spur (VS) and bourse shoot (BS) in 'Golden Delicious'/G.16 trees in 2014.

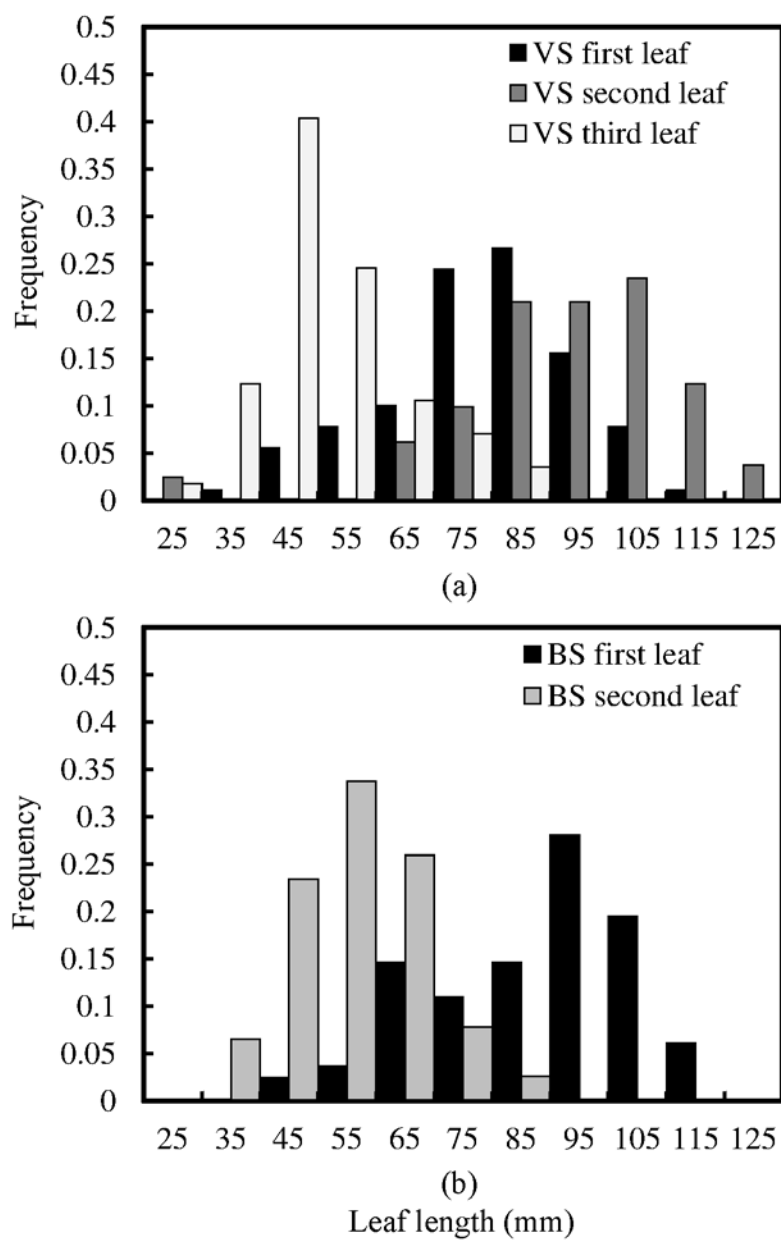


Figure 2.5 Frequency distribution of final length for different leaves in (a) vegetative spur and (b) bourse shoot in 'Golden Delicious'/G.16 trees in 2014.

2.3.2 Shoot Elongation

All the shoots grew rapidly in May (Fig. 2.6). The growth of VS and BS ceased after about 45 days after full bloom, however, for TS, a little increase in shoot length was noticed in late August and early September. Small differences were found in the distribution of shoot length in different months for VS and BS (Fig. 2.7). Most of VS and BS shoots were less than 5 cm long. In contrast, less than 20% of TS were less than 5 cm, and their length were evenly distributed between 5 and 16 cm. Some TS were over 30 cm in length.

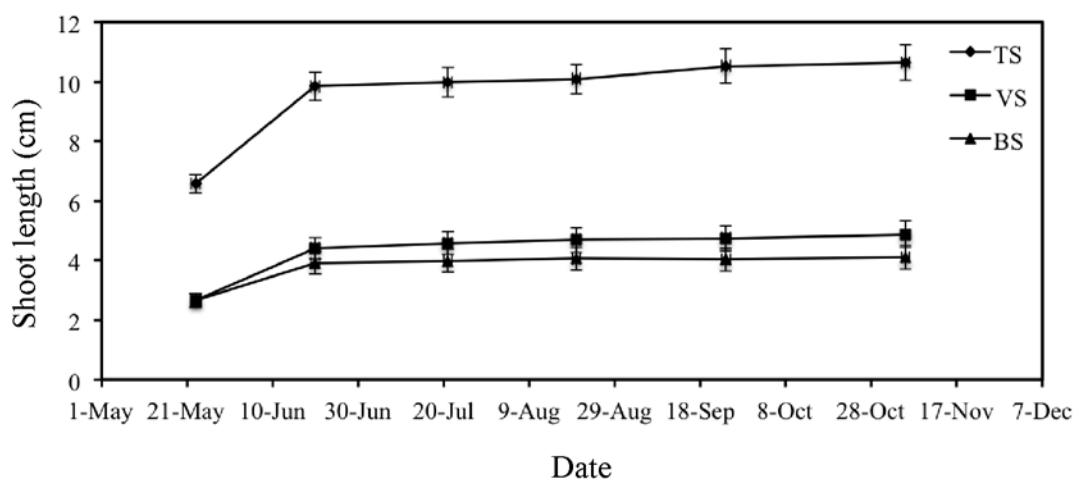


Figure 2.6 Shoot growth curve of ‘Golden Delicious’/G.16 trees throughout the growing season of 2014. TS: terminal shoot, (n=102), VS: vegetative shoot (n=100), BS: bourse shoot (n=93). Error bars indicate standard errors.

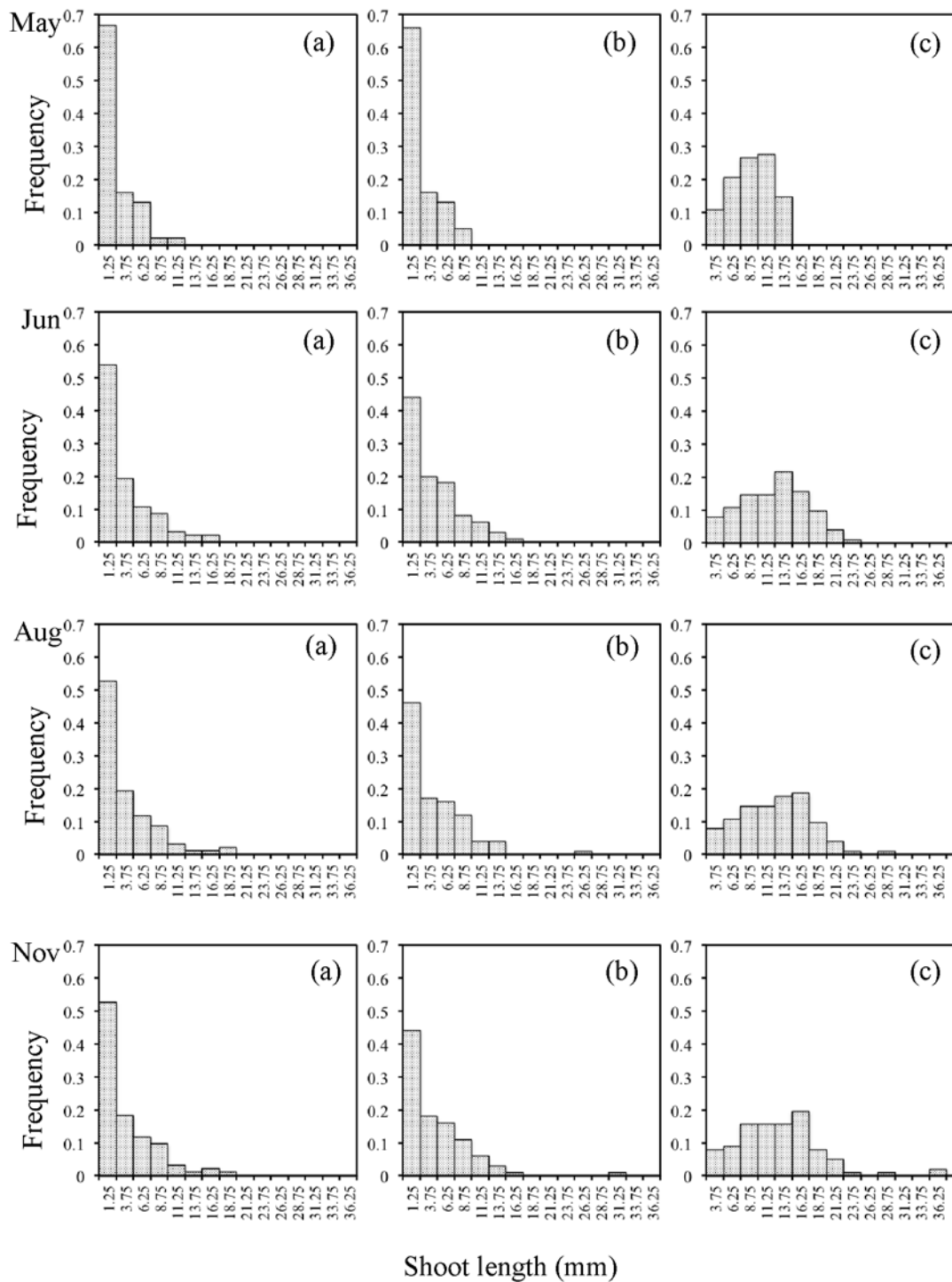


Figure 2.7 Frequency distribution of shoot length for (a) bourse shoot (n=93), (b) vegetative spur (n=100), (c) terminal shoot (n=102) of 'Golden Delicious'/G.16 trees in May, June, August and November in 2014.

2.3.3 Branching Characteristics of Two-year-old Branches

The highest spur density for two-year-old branch sections was 60 spurs per meter of the branch, however, about 5% of branches did not develop laterals at all (Fig. 2.8). For over 30% of branches, the spur density was around 25 spurs per meter of the branch. A positive relation was found between spur density and shoot length although some variability existed (Fig. 2.9).

The percentage of growing laterals among all buds in zone 2 was over 45%, which was significantly higher than zone 1 of 25% ($P < 0.05$) (Fig. 2.10 a). The percentage of reproductive laterals among growing laterals increased from zone 1 (15%) to zone 3 (30%), but no significant difference was found ($P > 0.05$) (Fig. 2.10 b).

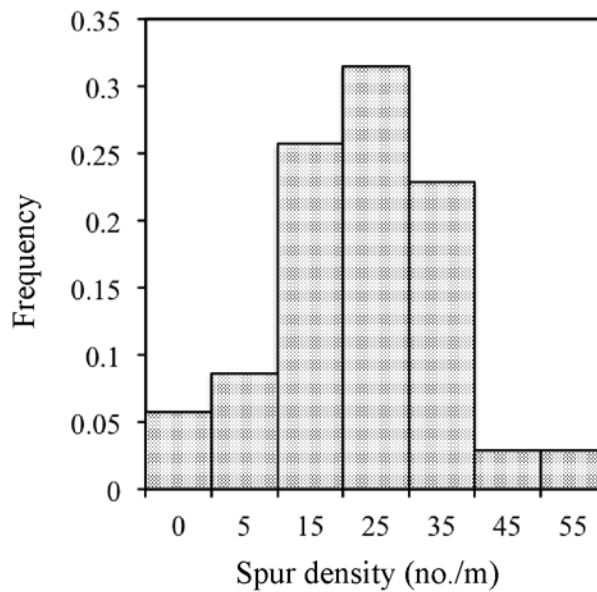


Figure 2.8 Frequency distribution of spur density for two-year-old branch sections (n=35) in 'Golden Delicious'/G.16 trees in 2014. Spurs include both vegetative and reproductive ones.

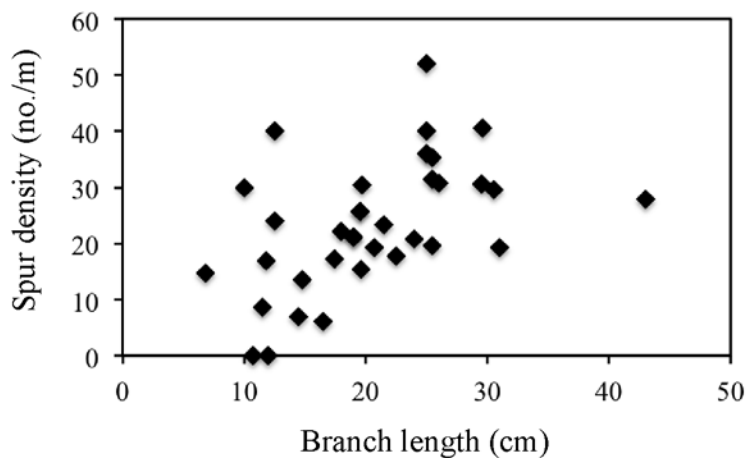


Figure 2.9 Plot of spur density and the length of the two-year-old branch in 'Golden Delicious'/G.16 trees (n=35) in 2014.

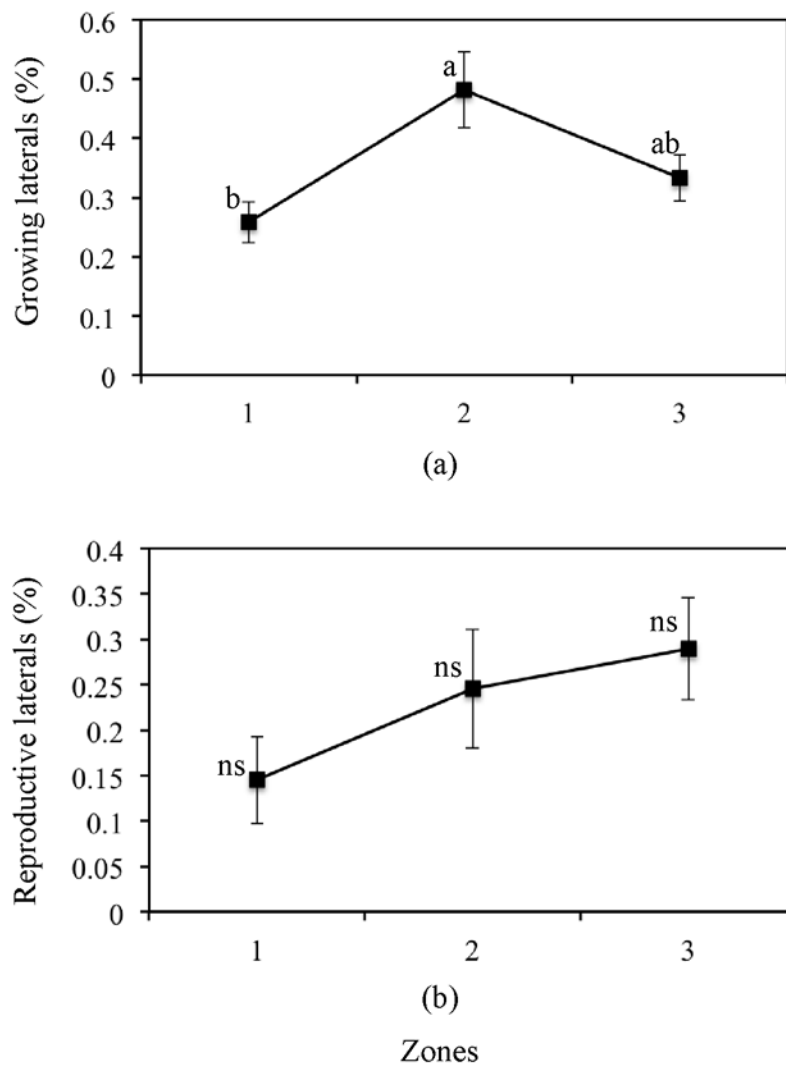


Figure 2.10 Percentage of growing laterals (a) and reproductive laterals (b) in different zones of two-year-old branch in 'Golden Delicious'/G.16 trees measured in 2014. Zone 1 to zone 3 represent the relative position on shoot with zone 1 located at the proximal and zone 3 at the distal part of the branch. Values with different letters are significant at the 0.05 level. ns: not significant. Means were separated by F-test and by Tukey's multiple range test at the 5% level. Error bars indicate standard errors.

2.4 Discussion

Many studies focus on vegetative growth in fruiting trees because of its importance in understanding physiological processes, such as photosynthesis, respiration and carbon allocation (Palmer, 1987), which have large effects on fruit yield and fruit quality (Forshey & Elfving, 1989; Wunsche & Lakso, 2000). Generally, cultivars with a larger average spur leaf size had a higher accumulated yields according to a study examined over a 17-years period (Rom & Ferree, 1984). Moreover, vegetative development has important implications in aspects of cultural practices such as tree training, pruning, and spraying (Palmer, Avery, & Wertheim, 1992).

Our results showed a dramatic increase in leaf length around the time of full bloom. Leaves of FS reached 90% of their full length by the time of full bloom. Lakso (1984) found the similar results that total leaf area at and shortly after full bloom nearly doubled in the unpruned 'Empire'/M7 apple trees. Lakso (1984) indicated that it was mainly due to the increased leaf area in rapid growing spurs. Our results showed that the leaf length of VS and BS was 1.4 and 1.2 times greater than that of FS, respectively. In this research, branch factors such as the age of shoots and their position in tree canopy were not taken into consideration, but other studies showed these factors influence leaf growth as well. For example, Volz, Ferguson, Hewett, and Woolley (1994) revealed that at harvest, one-year terminals had the largest bourse leaf areas, followed by two-year spurs and the one-year laterals had the lowest leaf areas in several apple cultivars investigated. Palmer (1987) indicated that in dense plantings, the mean leaf size tended to be smaller at the top of the tree than at the bottom. The difference in leaf size does not only

exist among different shoot categories. Our results also revealed a large difference among leaves from the same shoot category. A 45 % difference of leaf length was found for VS leaves and a 35% difference found for BS leaves. Most studies on leaves have been limited to use one mean leaf size of a particular shoot type (Barlow, 1980; Palmer, 1987; Wunsche & Lakso, 2000). However, the difference among leaves from the same shoot type is an important factor to consider.

Shoot elongation was very rapid in the first month and ceased by mid-summer. Lakso and Corelli-Grappadelli (1992) indicated that early cessation of shoot growth was critical for fruit development, because it allowed rapid export of carbon to fruit from extension shoots. A similar conclusion was made by Borchert (1976) that the increased competition between tree components was the reason that adult trees had shorter periods for growing and had only a single flush per growing season, unlike young non-fruiting trees. Both vegetative spurs and bourse shoots have high percentages of short shoots (< 5 cm), while for terminal shoots, they were much longer and the length were more evenly distributed, ranging from 5 cm to 25 cm. Our results agree with the previous study that the terminal shoots grew more vigorously than lateral and bourse shoots (Forshey & Elfving, 1989). However, the length of shoots and the duration of growth can vary considerably by factors such as cultivar, rootstock, vigor, crop load and environmental factors such as weather, water status and soil fertility (Ebel, Proebsting, & Evans, 1995; Lauri & Kelner, 2001; Wunsche & Ferguson, 2005).

Branching characteristics affect the structure of trees so it has important implications in understanding and modeling the dynamics of tree architecture. Our results showed that two-year-old branches of 'Golden Delicious'/G.16 trees tend to have high

percentage of reproductive laterals in distal position of branches. This acrotonic gradient in the reproductive lateral development was similar with cultivars ‘Pirchounette’ and ‘Chantecler’ as investigated by Lauri (2007). The results also confirmed that ‘Golden Delicious’ is a Type III tree, in which the fruiting zones moved away from the center of the trunk. Our results showed a positive relationship between spur density and shoot length although some variability existed, which conflicted with the results reported by Hirst and Ferree (1995) who found a negative relationship between those two variables in their studies on ‘Starkspur Supreme Delicious’ trees grafted on 17 different rootstocks. However, the divergence could be expected because trees with different cultivar-rootstock combinations exhibit large variance in branching characteristics. For example, Greene and Autio (1994) found a larger proportion of dormant buds in the proximal and medial zones than in the distal zone on ‘Redspur Delicious’ trees grafted on MM.111 rootstock, however, our study found more dormant buds in proximal and distal zones than in medial ones.

2.5 Conclusions

The first part of this experiment was to examine the vegetative growth in ‘Golden Delicious’/G.16 apple trees. The growth rates, in this case, the rates of leaf and stem elongation, are important parameters in analyzing vegetative development of trees. Our results show that in general, vegetative spurs had the highest leaf growth rate as well as the largest leaves, while flowering spurs had the smallest ones. Terminal shoots grew more vigorously than either vegetative spurs or bourse shoots. In addition, this study

quantitatively analyzed branching characteristics of 'Golden Delicious'/G.16 trees by examining the spatial distribution of growing and reproductive laterals along two-year-old branches, revealing a high branching frequency in the middle section. Analysis of fruit tree development has practical implications in orchard management, helping horticulturists and fruit growers improve skills in tree training and pruning, as well as predicting crop yield (Costes et al., 2006). The data gathered could also be used to simulate and model tree growth in other disciplines such as computer graphics and engineering.

2.6 References

- Barlow, H. W. B. (1980). The relationship between leaf size and shoot length in apple. *Journal of Horticultural Science*, 55(3), 279-283.
- Barthélémy, D., & Caraglio, Y. (2007). Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany*, 99(3), 375-407.
- Borchert, R. (1976). Differences in shoot growth patterns between juvenile and adult trees and their interpretation based on systems analysis of trees. *Acta Horticulturae*, 56, 123-130.
- Costes, E., & Guédon, Y. (2002). Modelling branching patterns on 1-year-old trunks of six apple cultivars. *Annals of Botany*, 89(5), 513-524.
- Costes, E., Lauri, P. E., & Regnard, J. L. (2006). Analyzing fruit tree architecture: Implications for tree management and fruit production. *Horticultural Reviews*, 32, 1-61.
- De Wit, I., Keulemans, J., & Cook, N. C. (2002). Architectural analysis of 1-year-old apple seedlings according to main shoot growth and sylleptic branching characteristics. *Trees*, 16(7), 473-478.
- Ebel, R. C., Proebsting, E. L., & Evans, R. G. (1995). Deficit irrigation to control vegetative growth in apple and monitoring fruit growth to schedule irrigation. *HortScience*, 30(6), 1229-1232.
- Forshey, C. G., & Elfving, D. C. (1989). The relationship between vegetative growth and fruiting in apple trees. *Horticultural Reviews*, 11, 229-287.

- Forshey, C. G., Weires, R. W., & VanKirk, J. R. (1987). Seasonal development of the leaf canopy of 'Macspur McIntosh' apple trees. *HortScience*, 22, 881-883.
- Fujii, J. A., & Kennedy, R. A. (1985). Seasonal changes in the photosynthetic rate in apple trees a comparison between fruiting and nonfruiting trees. *Plant Physiology*, 78(3), 519-524.
- Greene, D. W., & Autio, W. R. (1994). Notching techniques increase branching of young apple trees. *Journal of the American Society for Horticultural Science*, 119(4), 678-682.
- Hansen, P. (1971). ¹⁴C studies on apple trees. VII. The early seasonal growth in leaves, flowers and shoots as dependent upon current photosynthates and existing reserves. *Physiologia Plantarum*, 25(3), 469-473.
- Hirst, P. M., & Ferree, D. C. (1995). Rootstock effects on shoot morphology and spur quality of 'Delicious' apple and relationships with precocity and productivity. *Journal of the American Society for Horticultural Science*, 120(4), 622-634.
- Lakso, A. N. (1984). Leaf area development patterns in young pruned and unpruned apple trees [Fisheye photography]. *Journal of the American Society for Horticultural Science*, 109, 861-865
- Lakso, A. N., & Corelli-Grappadelli, L. (1992). Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Horticulturae*, 322, 231-239.
- Lauri, P. E. (2007). Differentiation and growth traits associated with acrotony in the apple tree (*Malus domestica*, Rosaceae). *American Journal of Botany*, 94(8), 1273-1281.

- Lauri, P. E., & Trottier, C. (2004). Patterns of size and fate relationships of contiguous organs in the apple (*Malus x domestica*) crown. *New Phytologist*, *163*(3), 533-546.
- Lauri, P. E., Kelner, J. J. (2001). Shoot type demography and dry matter partitioning: A morphometric approach in apple (*Malus x domestica*). *Canadian Journal of Botany* *79*(11), 1270–1273.
- Lauri, P. E., Térouanne, E., Lespinasse, J. M., Regnard, J. L., & Kelner, J. J. (1995). Genotypic differences in the axillary bud growth and fruiting pattern of apple fruiting branches over several years—an approach to regulation of fruit bearing. *Scientia Horticulturae*, *64*(4), 265-281.
- Palmer, J. W. (1987). The measurement of leaf area in apple trees. *Journal of Horticultural Science*. *62*(1):5-10.
- Palmer, J. W., Avery, D. J., & Wertheim, S. J. (1992). Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Scientia Horticulturae*, *52*(4), 303-312.
- Pratt, C. (1988). Apple flower and fruit: Morphology and anatomy. *Horticultural Reviews*, *10*, 273-308.
- Pratt, C. (1990). Apple trees: Morphology and anatomy. *Horticultural Reviews*, *12*, 265-305.
- Proctor, J. T. A., & Palmer, J. W. (1991). The role of spur and bourse leaves of three apple cultivars on fruit set and growth and calcium content. *HortScience*, *26*(6), 789.

- Rom, C. C., & Ferree, D. C. (1984). Spur leaf characteristics of nine apple cultivars. *Fruit Varieties Journal (USA)*, 38, 2-5.
- Rom, C. R., & Barritt, B. (1990). Spur development of 'Delicious' apple as influenced by position, wood age, strain, and pruning. *HortScience*, 25(12), 1578-1581.
- Volz, R. K., Ferguson, I. B., Hewett, E. W., & Woolley, D. J. (1994). Wood age and leaf area influence fruit size and mineral composition of apple fruit. *Journal of Horticultural Science*, 69(2), 385-395.
- Warrington, I. J., Ferree, D. C., Schupp, J. R., Dennis, F. G., & Baugher, T. A. (1990). Strain and rootstock effects on spur characteristics and yield of 'Delicious' apple strains. *Journal of the American Society for Horticultural Science*, 115(3), 348-356.
- Wunsche, J. N., & Ferguson, I. B. (2005). Crop load interactions in apple. *Horticultural Reviews*, 31, 231-290.
- Wunsche, J. N., & Lakso, A. N. (2000). The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *HortScience*, 35(7), 1202-1206.

CHAPTER 3 INFLUENCE OF LIGHT DISTRIBUTION ON FRUIT QUALITY IN 'GOLDEN DELICIOUS' APPLE TREES (MALUS × DOMESTICA BORKH.)

3.1 Introduction

Light interception and distribution are essential in studies of fruit trees, owing to its role in photosynthesis, its influence on fruit quality, its effects on flower bud formation, and its importance for fruit yield and quality (Rom, 1991). Maximum fruit yields were limited by light interception, while fruit quality were largely determined by local light environment of fruiting zone (Campbell & Marini, 1992; Lakso, Robinson, & Pool, 1989; Palmer, 1988). Light distribution within a tree canopy was largely determined by the foliage development, which was usually influenced by various horticultural practices such as tree spacing (Palmer, Avery, & Wertheim, 1992), cultivar-rootstocks combination, training and pruning (Rom, 1991).

Many studies have focused on analyzing light distribution in the tree canopy and its influence on various aspects of tree development. For vegetative growth, light intensity has positive influence on the specific leaf weight in peach and apple trees (Jackson, 1980; Marini, Sowers, & Marini, 1991). The effect of light on reproductive growth in apple trees has also received much attention. Jackson (1970) found that the main fruiting zone of tree canopy received a minimum of 30% full sun. High quality

fruiting spurs that have a large leaf area and large fruit were generally found in well-illuminated canopy regions (Barritt, Rom, Konishi, & Dilley, 1991). Fruit with higher soluble solid concentration and lighter green background color were mainly located in the uppermost layer of canopy where the fruit had a better exposure to light (Tustin, Hirst, Warrington, & Stanley, 1989). Some studies showed that imposed shading had negative effects on initiation of flowering buds for the following year (Marini et al., 1991). Shading also reduced fruit development in apples resulting from decreased cell division and expansion (Dash, Johnson, & Malladi, 2012). Moreover, shading on fruit diminished red color development (Doud & Ferree, 1980).

A thorough understanding of the interaction between light environment and tree development assists horticulturists and fruit growers in orchard design and crop management. However, conclusions of light effects on fruit development were usually obtained from artificially imposed shading experiments (Marini et al., 1991; Robinson, Seeley, & Barritt, 1983), which are not representative and may not illustrate the relationship between natural light and fruit quality in tree canopies (Campbell & Marini, 1992). The objective of this experiment was to explain and predict the variation in fruit quality of ‘Golden Delicious’ apple by examining light distribution thoroughly in tree canopies.

3.2 Materials and Methods

3.2.1 Tree Materials

This experiment was performed in 2014, conducted on four ‘Golden Delicious’/G.16 trees planted in 2003 at the Purdue Meigs Farm, Lafayette, IN, USA. Trees were trained as central leader system and pruned annually according to commercial standards. Rows were oriented a north-south direction, with 3.5 m in-row and 5.5 m between-row spacing. Trunk circumference of those trees was 34.7 ± 2.3 cm and the height was 3.4 ± 0.4 m in the spring of 2014. Full bloom time was on May 6. The canopy spread was 3.5 ± 0.5 m in east-west and 3.1 ± 0.1 m in north-south orientation, measured in August, 2014.

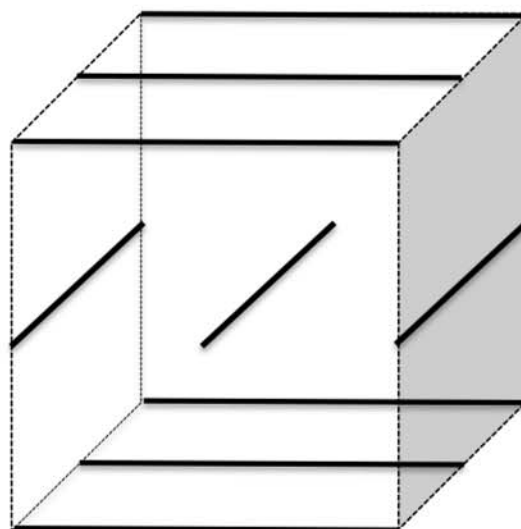
3.2.2 Light Measurement

The light measuring methods were modified from Jackson (1970). The tree was covered with a frame, 3 m at each side. The tree canopy was girded into 216 equal sized cubes with 0.5 m at each side by using ropes and PVC plastic pipes (Fig. 3.1 a). Photosynthetically active radiation (PAR) within the frame was measured with a line quantum meter with 10 sensors on it, giving an average PAR over these sensors (MQ-310, Apogee Instruments Inc., Logan, UT). The light meter is 0.5 m long, fitting the dimension of the cube. A total of nine light measurements were taken on the top, middle, and bottom surfaces of each cube as illustrated in Figure 3.1 b. The cubes next to each other shared the light readings at their attached surfaces. During the measurement, PAR

above the canopy was recorded every minute. For each tree, light measurements were repeated at 8:00 AM, 12:00 PM and 4:00 PM on a clear day in late September. The relative light intensity of each cube was calculated by averaging the nine readings taken from that cube and then dividing it by the PAR above the canopy.



(a)



(b)

Figure 3.1 Illustration of light measurement on a tree. (a) The frame for light measurement. The dimension of the frame is $3\text{ m} \times 3\text{ m} \times 3\text{ m}$. The tree was girded into 216 equal sized cubes with 0.5 m at each side, by using ropes and PVC plastic pipes. (b) Close look of one cube. The solid lines indicating the positions where nine light reading were taken in each cube.

3.2.3 Fruit Analysis

Each fruit was numbered according to the cube it was harvested from so that it could be identified with its light environment based on the light measurements in that cube. All the fruit were harvested at maturity and were analyzed for fruit quality. In this study, fruit from the same light level were grouped together to calculate the average values for fruit quality. Ten light levels were determined by relative light intensity from 0 to 100% with 10% intervals. Only the light measurements made at noon were used for analyzing light effects on fruit quality.

3.2.3.1 Weight

The weight of individual fruit was measured using a digital balance (DL-410D, Ainsworth).

3.2.3.2 Background Color

The background color of apple skin was measured with a hand-held chroma meter (CR-200, Minolta Camera Co., Ltd, Japan). Color was recorded based on the CIE L^* a^* b^* color system (Munsell, 1971). The parameter L^* indicates the luminance or lightness, ranging from 0 to 100. a^* and b^* are two chromatic components ranging from -120 to +120 with a^* measuring the degree of red (+) or green (-) and b^* indicating the degree of blue (-) to yellow (+). Values of a^* and b^* were converted into hue angle ($H^\circ = \tan^{-1} b^*/a^*$, when $a^* < 0$ and $b^* > 0$, $H^\circ = 180^\circ + \tan^{-1} b^*/a^*$) and chroma ($\text{chroma} = (a^{*2} +$

$b^{*2})^{1/2}$). Hue angle defines the color, reported in degrees, with 0° to 359° indicating the change of color from red (0°), yellow (60°), green (120°), blue (180°) and to purple (270°). Chroma indicates color saturation and intensity, and its value varies from 0 (achromatic gray) to 60 (pure chromatic color). Hue angle and chroma are more appropriate parameters to describe the color (Greer, 2005). Two measurements were taken from the skin of each fruit, avoiding the red blush area, to calculate the average hue angle and chroma for background color.

3.2.3.3 Firmness

Flesh firmness of peeled tissue was measured on two opposite sides of each apple with a penetrometer fitted with an 11.1 mm diameter probe (FT327, Effegi, Italy). The firmness value, measured in pound-force (lbf), were converted to Newton (N) by using this formula: $\text{newton (N)} = \text{pound-force (lbf)} \times 4.448$.

3.2.3.4 Soluble Solid Concentration

The soluble solid concentration of the juice pressed from two opposite segments of each apple was measured using a digital refractometer (PAL-1, Atago Co., Ltd, USA).

3.2.3.5 Starch Test

Starch tests were performed by slicing the fruit in half, then dipping the equatorial region of fruit into iodine solution for about 45 seconds. The solution was prepared by dissolving 8.8 grams of potassium iodide in 30 ml of water, adding 2.2 grams of iodine

crystals, and then diluting the mixture with water to make 1.0 liter of iodine solution. The starch pattern index, indicating the relative amounts of starch and sugar, was scored on a scale of 0-8 (Blanpied & Silsby, 1992). A higher score indicates the apple is riper than that of lower score.

3.2.4 Statistical Analysis

Data were subjected to linear mixed modeling at significance level 0.05 using the SAS (SAS 9.3; SAS Institute Inc., Cary, NC) GLIMMIX procedure. Raw data were fitted into the following models to analysis the effect of canopy location on light distribution and fruit quality:

$$\text{Relative light intensity} = \beta_0 + \text{Height } \beta_1 + \text{Distance } \beta_2 + (\text{Height} * \text{Distance}) \beta_{12} + \gamma + \varepsilon$$

$$\text{Fruit quality} = \beta_0 + \text{Height } \beta_1 + \text{Distance } \beta_2 + (\text{Height} * \text{Distance}) \beta_{12} + \gamma + \varepsilon$$

β_0 is the intercept of the model. β_1 , β_2 and β_{12} are fixed effect slopes for Height (the vertical distance to the ground), Distance (the horizontal distance to the tree trunk), and their interaction, respectively. γ is a random effect accounting for the within-subject variation, and ε represents error.

3.3 Results

3.3.1 Light Distribution

PAR on clear days above the tree canopy was between 100 and 500 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ in the morning, 1300 and 1900 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at noon and 1000 and 1500 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ in

the afternoon. Due to the large variation of PAR at different times during the day, relative light intensity was adopted in analyzing the light distribution instead of the absolute PAR value. Relative light intensity of layer one, which was 0.5 m above the ground, ranged from 15% to 55% during the day (Fig. 3.2). While for layer six, which was 3 m above the ground, the relative light intensity was above 70% of full PAR all day long. For all layers, light intensity increased with increasing distance from the trunk, regardless the time of the day. Light intensity declined rapidly from the top to the bottom of tree canopy, ranging from 85% (on top of canopy) to 20% (in lower center) of full PAR. Statistical analysis also shows the light intensity within the canopy was significantly affected by height and the distance to the trunk (Table 3.1).

Table 3.1 Effect of canopy location on light distribution and fruit quality of 'Golden Delicious'/G.16 trees in 2014.

Effect	Fruit quality						
	Relative light intensity (%)	Weight (g)	Hue angle	Chroma	Firmness (N)	Soluble solid concentration (%)	Starch pattern index
Intercept (β_0)	-0.15*	175.33***	106.49***	40.74***	75.52***	14.67***	4.90***
Height (β_1)	0.12***	0.37 ^{NS}	-0.57**	0.52**	0.27 ^{NS}	0.40***	0.16 ^{NS}
Distance (β_2)	0.09***	-2.85 ^{NS}	-0.62*	0.81*	0.69 ^{NS}	0.53***	0.33*
Height \times Distance (β_{12})	0.01*	0.04 ^{NS}	0.03 ^{NS}	-0.34**	0.13 ^{NS}	-0.08 ^{NS}	-0.14**
γ	0.00	458.23	1.32	9.55	10.85	0.10	0.23
ε	0.02	1035.04	6.40	7.17	48.31	0.90	1.29
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
r^2	0.53	0.23	0.16	0.46	0.15	0.16	0.15

Relative light intensity = $\beta_0 + \text{Height } \beta_1 + \text{Distance } \beta_2 + (\text{Height} * \text{Distance}) \beta_{12} + \gamma + \varepsilon$, Fruit quality = $\beta_0 + \text{Height } \beta_1 + \text{Distance } \beta_2 + (\text{Height} * \text{Distance}) \beta_{12} + \gamma + \varepsilon$. β_0 is the intercept of the model. β_1 , β_2 and β_{12} are fixed effect slopes for Height (the vertical distance to the ground of the fruit), Distance (the horizontal distance to the tree trunk), and their interaction, respectively. γ is a random effect accounting for the within-subject variation, and ε represents error^{NS}, *, **, ***, ****, ***** Nonsignificant or significant at $P \leq 0.05, 0.01, 0.001$ or 0.0001 , respectively.

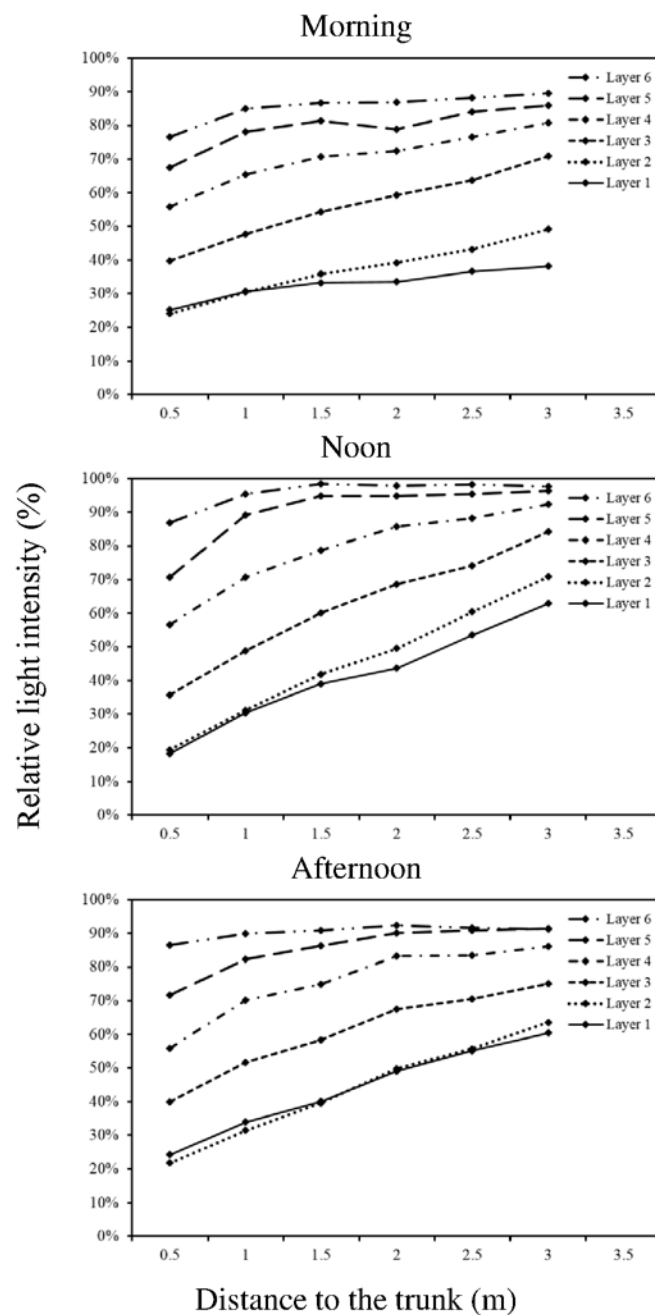


Figure 3.2 Relative light intensity within tree canopy in the morning, at noon and in the afternoon. Data were collected from four replicate ‘Golden Delicious’/G.16 trees. Layers 1 to 6 represent the vertical distance to the ground, 0.5 m, 1 m, 1.5 m, 2 m, 2.5 m and 3 m, respectively.

3.3.2 Fruit Quality

3.3.2.1 Position Effects on Fruit Quality

Fruit quality indices, except for individual fruit weight and firmness, were significantly affected by the height of the fruit and their distance to the trunk ($P < 0.05$). Chroma has a better correlation with the fruit position within tree canopy than other quality indices with a r^2 of 0.46.

3.3.2.2 Light Effects on Weight

The fruit weight varied with light intensity levels (Fig. 3.2 a). The highest fruit weight occurred when the relative light intensity ranged from 90% to 100%, while the lowest value was found when the light intensity was around 75% of full PAR. Additionally, the fruit that came from the 0 to 10 % light level had the largest variance in weight ($SE = 9$).

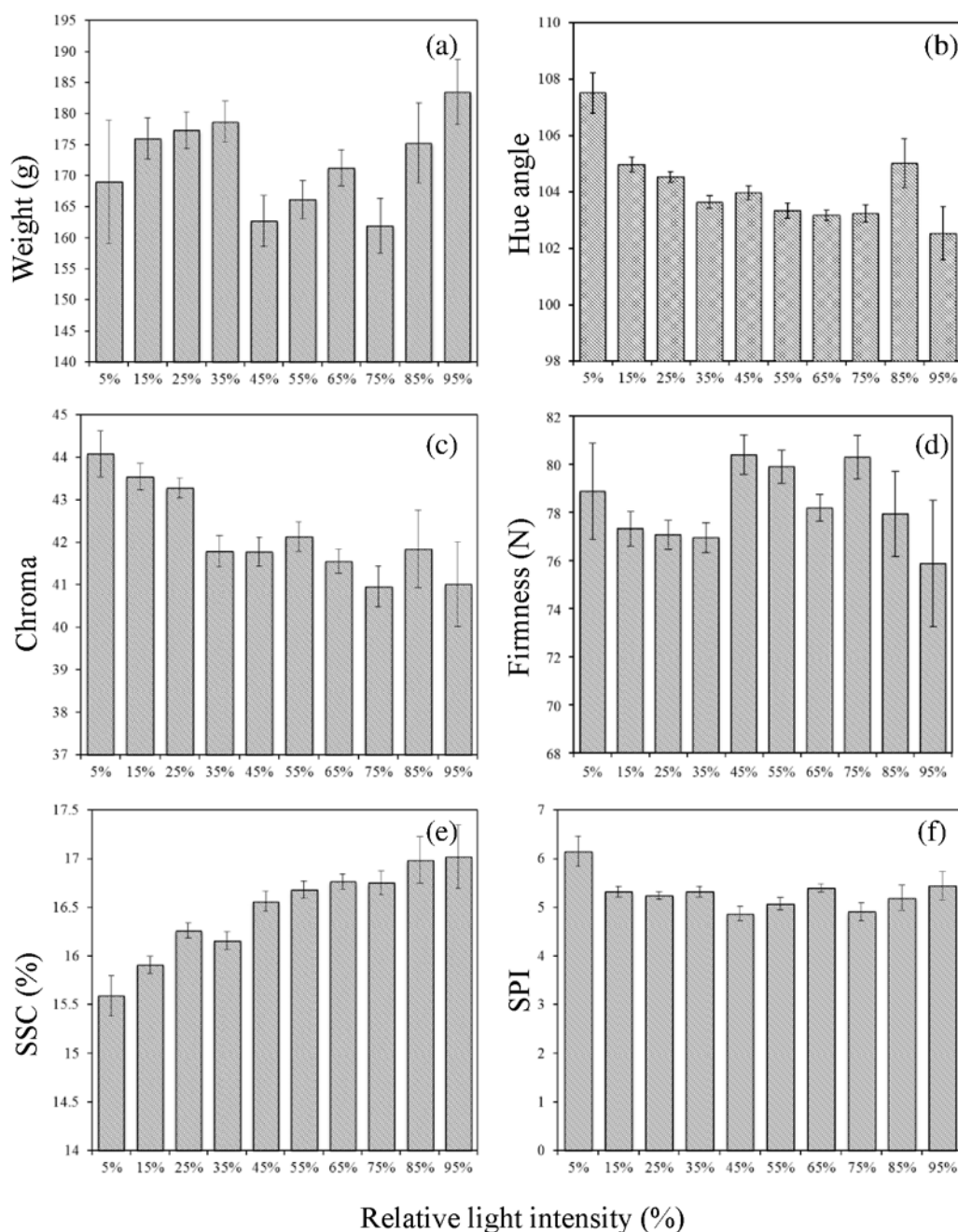


Figure 3.3 Correlation between fruit quality and the relative light intensity in 'Golden Delicious'/G.16 trees. Fruit from the same light level were grouped together to calculate the average values for fruit quality (n=868). Ten light levels were determined by relative light intensity from 0 to 100% with 10% interval. Error bars indicate standard errors. (a) weight of individual fruit, (b) hue angle, (c) chroma, (d) firmness, (e) soluble solid concentration (SSC), (f) starch pattern index (SPI).

3.3.2.3 Light Effects on Background Color

Our results showed that the hue angle of the fruit background color ranged from 102.5° to 107.5° (Fig. 3.2 b), which falls in the yellow-green color region. Generally, the hue angle decreased subsequently from 0 to 100% of relative light intensity except an obvious ascent when the light intensity was between 80% and 90% of full PAR. The chroma of fruit background color ranged from 41 to 44.1, and it decreased subsequently from 0 to 50% of relative light intensity with the highest value found when the light was less than 10% of full PAR (Fig. 3.2 c). Chroma value fluctuated as the light intensity was higher than 50% of full PAR.

3.3.2.4 Light Effects on Firmness

Firmness of flesh ranged from 76 and 81 N (Fig. 3.2 d). The highest firmness value occurred under around 45% of full PAR and the lowest value found when light intensity was higher than 90% of full PAR. We have not found a correlation between firmness and light intensity.

3.3.2.5 Light Effects on Soluble Solid Concentration

Soluble solid concentration ranged from 15.5% to 17% by weight in juice, which was positively related to light intensity (Fig. 3.2 e).

3.3.2.6 Light Effects on Starch Pattern Index

The starch pattern index of fruit was determined using a 0-8 grading system with higher score indicating less starch in fruit. The starch pattern index of fruit ranged between 4.9 and 6.2 (Fig. 3.2 f). The highest value occurred at relative low light intensity (less than 10%) and the lowest value was found in fruit exposed to 45% of full PAR. We have not found a correlation between starch pattern index and the relative light intensity.

3.4 Discussion

Our results show that the light intensity had large variance at different locations of the tree canopy, ranging from 20% (inner and bottom position) to 99% (peripheral and upper position) of full PAR. These results confirm findings from Rom (1991) that the light environment within the canopy is not uniform. Only a very small portion of canopy had a light intensity lower than 30%, mainly found in inner and lower positions in canopy. Poor light illumination may be due to the shade cast by the foliage (Jackson, 1970). Our results show that the light intensity at the peripheral of the tree canopy was very low in the morning (less than 40% of full PAR), which was caused by the shade cast by nearby trees due to the low solar angle.

The light environment around the fruiting zone is a key factor affecting the fruit quality (Lakso et al., 1989). Quality of fresh fruit is determined by appearance, physical characteristics and chemical composition. For apples, the attributes of interest to consumers are color, sensory (soluble solid concentration), texture (firmness), as well as nutrient content (Watada, 1995).

In the present study, there is a negative relationship between hue angle and light intensity. This means that under higher light levels, the background skin color was more yellow. This agrees with the result that fruit from zones with lower light transmission produced greenest ‘Granny Smith’ apples (Tustin, Hirst, & Warrington, 1988). However, Hirst, Tustin and Warrington (1990) found conflicting results that fruit became lighter and yellower with longer duration of artificially imposed severe shade on ‘Granny Smith’ apples. Another parameter describing background color in this study is chroma, which represents the ‘purity’ or the ‘saturation’ of the color, with lower chroma being paler. Our study found a negative correlation between chroma and the light intensity measured around fruit, which indicates a more vivid background color of those fruit from zones with low light intensity in canopy. Given that an increase of greenness resulted in more saturated color according to Hirst et al. (1990), the chroma change revealed that greener fruit appeared in shaded areas, which was consistent with hue angle results.

Our results show that soluble solid concentration has a positive relationship with light intensity, which generally agrees with other studies (Campbell & Marini, 1992; Doud & Ferree, 1980). Doud and Ferree (1980) found that soluble solid concentration was decreased by 22% in fruit imposed by artificial shade in an unknown red strain of ‘Delicious’ on M.9 rootstock. One possible reason for increased soluble solid concentration of fruit under better light illumination conditions is that a high light intensity gives rise to high carbon assimilation in leaves, followed by a high rate of carbon metabolism, leading to high soluble sugar levels in nearby fruit (Ho, 1979; Robbins & Pharr, 1987).

We have not found a clear trend showing that high PAR increased fruit quality in terms of fresh firmness and starch pattern. These results should be expected because the irradiance around fruit is not the only determinant of fruit quality. Research has shown that other factors contribute to fruit quality as well, including internal (e.g., crop load, branch age and spur position) and external factors (e.g., temperature, soil, training and pruning) (Reay, 1999; Tustin et al., 1988).

It should be noted that most light studies on fruit trees have been focused on light in the 400 to 700 nm wavelength. However, light of higher and lower wavelengths has impacts on fruit quality as well (Mancinelli, 1985). Several studies have confirmed that ultraviolet (UV) light, especially UV-B, was most effective at inducing color development in apple skin. Moreover, red light was found to be less effective in inducing color development, but was more effective than the other visible wavelengths (Ritenour & Khemira, 2007). For future studies focusing on light influence on fruit quality, wavelengths other than photosynthetic active wavelengths should be taken into consideration as well (Rom, 1991).

The obtained light data could be used to verify the accuracy of simulated light models. Several approaches have been developed to model the light environment in various scales from individual shoot (Sinoquet, Sonohat, Potel, Monney, & Lauri, 2008) to whole tree canopy (Chelle & Andrieu, 1998; Oyarzun, Stöckle, & Whiting, 2007; Stephan, Sinoquet, Donès, Haddad, Talhouk, & Lauri, 2008). The light simulation models can assist in evaluating the production potential in orchards as a consequence of light interception and distribution, which would help horticulturists and growers in

orchard design and crop management by visualizing the interactions between environmental factors and tree development (Johnson & Lakso, 1991).

3.5 Conclusions

Light intensity in canopies of four 'Golden Delicious'/G.16 apple trees were measured in detail, revealing non-uniform light distribution within the tree canopy. The upper and outer regions of tree canopy received higher light intensity and the inner and lower regions had less light penetration. Soluble solid concentration in apple was found positively related to the amount of light received by fruit. Hue angle and chroma also had good correlations with light intensity. However, no relation was found between flesh firmness and starch pattern with light intensity, indicating that other factors could influence fruit quality as well. One limitation of this study is that the light measurement around the fruit was not so precise by using the 0.5 m cubes, so for future study, more precise light measurements could be collected to better examine the correlation between fruit quality and the light environment around the fruit.

3.6 References

- Barritt, B. H., Rom, C. R., Konishi, B. J., & Dilley, M. A. (1991). Light level influences spur quality and canopy development and light interception influence fruit production in apple. *HortScience*, 26(8), 993-999.
- Blanpied, G. D., Silsby, K., (1992). Predicting harvest date windows for apples. Information Bulletin 221, Cornell Cooperative Extension, Cornell University, Ithaca, NY, USA.
- Campbell, R. J., & Marini, R. P. (1992). Light environment and time of harvest affect 'Delicious' apple fruit quality characteristics. *Journal of the American Society for Horticultural Science*, 117(4), 551-557.
- Chelle, M., & Andrieu, B. (1998). The nested radiosity model for the distribution of light within plant canopies. *Ecological Modelling*, 111(1), 75-91.
- Dash, M., Johnson, L. K., & Malladi, A. (2012). Severe shading reduces early fruit growth in apple by decreasing cell production and expansion. *Journal of the American Society for Horticultural Science*, 137(5), 275-282.
- Doud, D. S., & Ferree, D. C. (1980). Influence of altered light levels on growth and fruiting of mature 'Delicious' apple trees. *Journal of the American Society for Horticultural Science*, 105(3), 325-328.
- Greer, D. H. (2005). Non-destructive chlorophyll fluorescence and colour measurements of 'Braeburn' and 'Royal Gala' apple (*Malus domestica*) fruit development throughout the growing season. *New Zealand Journal of Crop and Horticultural Science*, 33(4), 413-421.

- Hirst, P. M., Tustin, D. S., & Warrington, I. J. (1990). Fruit colour responses of 'Granny Smith' apple to variable light environments. *New Zealand Journal of Crop and Horticultural Science*, 18(4), 205-214.
- Ho, L. C. (1979). Regulation of assimilate translocation between leaves and fruits in the tomato. *Annals of Botany*, 43(4), 437-448.
- Jackson, J. E. (1970). Aspects of light climate within apple orchards. *Journal of Applied Ecology*, 207-216.
- Jackson, J. E. (1980). Light interception and utilization by orchard systems. *Horticultural Reviews*, 2, 208-267.
- Johnson, R. S., & Lakso, A. N. (1991). Approaches to modeling light interception in orchards. *HortScience*, 26(8), 1002-1004.
- Lakso, A. N., Robinson, T. L., & Pool, R. M. (1989). Canopy microclimate effects on patterns of fruiting and fruit development in apples and grapes. In C. J. Wright (Ed.), *Manipulation of Fruiting* (pp. 263-274). London: Butterworths.
- Mancinelli, A. L. (1985). Light-dependent anthocyanin synthesis: a model system for the study of plant photomorphogenesis. *The Botanical Review*, 51(1), 107-157.
- Marini, R. P., Sowers, D., & Marini, M. C. (1991). Peach fruit quality is affected by shade during final swell of fruit growth. *Journal of the American Society for Horticultural Science*, 116(3), 383-389.
- Munsell, A. H. (1971). *A colour notation: An illustrated system defining all colours and their relationships by measured scales of hue, value, and chroma*. Baltimore, MD: Munsell Colour Company, Inc.

- Oyarzun, R. A., Stöckle, C. O., & Whiting, M. D. (2007). A simple approach to modeling radiation interception by fruit-tree orchards. *Agricultural and Forest Meteorology*, 142(1), 12-24.
- 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. *Journal of Applied Ecology*, 25, 569-578.
- Palmer, J. W., Avery, D. J., & Wertheim, S. J. (1992). Effect of apple tree spacing and summer pruning on leaf area distribution and light interception. *Scientia Horticulturae*, 52(4), 303-312.
- Reay, P. F. (1999). The role of low temperatures in the development of the red blush on apple fruit ('Granny Smith'). *Scientia Horticulturae*, 79(1), 113-119.
- Ritenour, M. and H. Khemira. 2007. Red color development of apple: A literature review. In *Postharvest Information Network* (pp. 1-10). Washington State University, WA, USA: Tree Fruit Research and Extension Center.
- Robbins, N. S., & Pharr, D. M. (1987). Regulation of photosynthetic carbon metabolism in cucumber by light intensity and photosynthetic period. *Plant Physiology*, 85(2), 592-597.
- Robinson, T. L., Seeley, E.J., & Barritt, B.H. (1983). Effect of light environment and spur age on 'Delicious' apple fruit size and quality. *Journal of American Society of Horticultural Science*. 108, 855-861.
- Rom, C. R. (1991). Light thresholds for apple tree canopy growth and development. *HortScience*, 26(8), 989-992.

- Sinoquet, H., Sonohat, G., Potel, A. M., Monney, P., & Lauri, P. E. (2008). Using virtual plants to estimate light distribution at intra-canopy scale in apple trees: Method presentation and assessment. *Acta Horticulturae*, 803, 225-234.
- Stephan, J., Sinoquet, H., Donès, N., Haddad, N., Talhouk, S., & Lauri, P. E. (2008). Light interception and partitioning between shoots in apple cultivars influenced by training. *Tree Physiology*, 28(3), 331-342.
- Tustin, D. S., Hirst, P. M., & Warrington, I. J. (1988). Influence of orientation and position of fruiting laterals on canopy light penetration, yield, and fruit quality of 'Granny Smith' apple. *Journal of the American Society for Horticultural Science* 113, 699-073.
- Tustin, S., Hirst, P., Warrington, I., & Stanley, J. (1989). Light distribution and fruit quality through multi-layered trellis apple canopies. *Acta Horticulturae*, 243, 209-212.
- Watada, A. E. (1995). Methods for determining quality of fruits and vegetables. *Acta Horticulturae*, 379, 559-567.