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An Allometric Approach to Evaluate Physiological and Production Efficiencies in Tree Size for Tart Cherry and Apple Orchard Systems

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AN ALLOMETRIC APPROACH TO EVALUATE PHYSIOLOGICAL AND

PRODUCTION EFFICIENCIES IN TREE SIZE FOR TART CHERRY

AND APPLE ORCHARD SYSTEMS

by

Zachary T. Brym

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

_____

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UTAH STATE UNIVERSITY
Logan, Utah

2016

ABSTRACT

AN ALLOMETRIC APPROACH TO EVALUATE PHYSIOLOGICAL AND

PRODUCTION EFFICIENCIES IN TREE SIZE FOR TART CHERRY

AND APPLE ORCHARD SYSTEMS

by

Zachary T. Brym, Doctor of Philosophy

Utah State University, 2016

Major Professor: Dr. S. K. Morgan Ernest
Research Advisor: Dr. Brent L. Black
Program: Ecology

Improving production efficiency is a major challenge for modern orchard

systems. The primary response in horticulture is to develop high-density orchard systems

that use dwarfing rootstocks and intense management strategies to maintain small tree

size. As development and evaluation of novel orchard systems is resource and time

intensive, modeling approaches of existing orchard systems may help improve

understanding of plant physiology for the development of high-density systems. The

effect of tree size and architecture on physiological and production efficiency was

evaluated for tart cherry (*Prunus cerasus*, *P. mahaleb*) and apple (*Malus* spp.) orchard

systems using a physiologically driven modeling approach, called allometry. Branch

dimensions, canopy dimensions and biomass were measured for 24-year-old tart cherry

individuals and 10-year-old 'Golden Delicious' apple individuals on various rootstocks in

experimental blocks at the Kaysville Research Farm in Davis Co., Utah. Tree size was

related to annual fruit biomass that had been collected over the duration of the apple trial. Branch dimensions, canopy dimensions, yield, and fruit quality were collected in commercial tart cherry orchards of Utah Co.

Tree size, architecture, and biomass of tart cherry and apple expressed strong allometric relationships that were broadly consistent among the two orchard tree species and the theoretical expectations derived from wild plants. The most consistent relationship was the trunk diameter (or trunk cross sectional area) ~ stem biomass relationship, which broadly followed the 8/3-power law. Branch and canopy dimensions that include a measure of length, such as branch length and canopy height, demonstrated architecture indicative of high water efficiency and metabolic activity that is relieved from biomechanical constrains of weight bearing. The apple rootstocks differed from each other in production efficiency with individuals that express smaller branch and canopy dimensions producing a higher proportion of fruit relative to tree size. In the commercial tart cherry orchards, smaller individuals with relatively higher canopy height and spread expressed higher yield and fruit quality.

Overall, this research supported the continued development of training systems that maintain small trees to improve physiological and production efficiency. Further research must reconcile other consequences of intense management and overproduction that arise with the increased efficiency facilitated by small tree size and high-density orchard systems to maintain sustainable fruit production.

(144 pages)

PUBLIC ABSTRACT

AN ALLOMETRIC APPROACH TO EVALUATE PHYSIOLOGICAL AND

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In orchard systems, the size of a tree and the physical structure of its canopy influences how the tree gathers resources and uses them to produce fruit. Smaller orchard trees produce a higher proportion of fruit relative to their size. Small trees also produce higher quality fruit than larger trees. These relationships were demonstrated for apples and tart cherries grown in Utah. In physiological ecology, models called allometries have been developed that explain how the size of wild plants is related to growth, architecture, and reproduction. These models were applied to apple and tart cherry orchard systems and revealed consistent patterns in plant architecture among domesticated orchard trees. Allometries were also used to provide insights into how the size of a tree impacts its efficiency in producing fruit. Patterns in plant architecture and reproduction may be broadly consistent across crop plants and may help researchers and growers use fundamental knowledge of plant physiology to develop resource conserving, economically viable, and sustainable cropping systems.

Stay Curious.

ACKNOWLEDGMENTS

What an adventure! I was never really a dreamer until I started my PhD. The process really forced me to reflect on what I wanted to do with my life and my career. I am happy with where my journey has taken me and excited for what my vision might have in store for me next. After all, why would I voluntarily put myself through so many hours in the cold meticulously measuring tree branches? I feel extremely fortunate for the many meaningful and supportive relationships that I gained through the process and hope to maintain as many connections as possible as I start my career.

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Zachary T. Brym

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Plants, or eukaryotic photoautotrophs, are sessile organisms that have evolved

highly adaptive and efficient ways to access their environment (Niklas, 1992). Plants

must first establish at a favorable site and then grow to access essential resources such as

water and light. As plants grow, plant size and structure directly affects physiological

function and interaction with the environment (Meinzer et al, 2011). The function of

plants and their interaction with the environment is limited in two fundamental ways,

through mechanical constraints imposed by supporting structural biomass (McMahon &

Kronauer, 1976; Niklas and Spatz, 2004) and hydraulic constraints imposed by resistance

to resource transport (McCulloch and Sperry, 2005; Price et al., 2007). In response to

these physiological constraints, plant species evolve a unique balance of trade-offs in the

uptake, transport, and allocation of resources to maintenance, vegetative growth, and

reproductive output.

The adaptation of plant growth strategies is constrained by physiological limits

that can be understood using process-based models of plant size and structure called

allometry. Allometric relationships are mathematical relationships among body size (e.g.,

trunk diameter, plant height) and other biological characteristics or functions (e.g., stem

biomass, canopy volume, fruit production). Allometric relationships arise from general

patterns in growth and resource partitioning that are constrained by fundamental physical

and chemical properties (Preistley, 1962; Huxley, 1972) and emerge universally among

plant species in natural systems (West et al., 1997; Niklas, 2004). For example,

unmanaged forest trees have evolved to minimize resistance of the resource transport

system (West et al., 1999), yet must also grow vertically towards the light-filled canopy imposing biomechanical constraints from gravity (Enquist and Niklas, 2001). These individuals only achieve reproductive maturity upon reaching the canopy when surplus resources are available that may be diverted from vegetative to reproductive growth (Niklas and Enquist, 2003).

With the domestication of plants, humans have added novel forces that drive plant evolution (Pollan, 2002). Humans select for desirable traits to improve food, fiber, and medicinal plant products. In the case of orchard trees, selective breeding programs attempt to maximize yield while reducing requirements of water, fertilizer, and other inputs (Robinson, 2007). Such human manipulation to maximize reproductive yield and economic efficiency alters the survival requirements that wild orchard trees experience in forest ecosystems. However, it remains unclear how selective breeding in orchard trees has impacted the physiological constraints found universally among naturally occurring plants.

The evolution of modern agriculture drives crop plants to grow and produce at maximum efficiency. Crop plants are typically evaluated for their production efficiency, or ratio of harvestable to non-harvestable products. Research of plant size and structure largely began as a means to estimate production efficiency in perennial agricultural systems where non-harvestable products are difficult to measure most years (Westwood and Roberts, 1970). Production efficiency can be improved in two fundamental ways, through increased photosynthetic potential or increased resource partitioning to harvestable products. As improvements to photosynthesis have largely eluded breeding programs, most research focus has been on developing genetic material and cropping

systems that maximize production efficiency through resource partitioning.

Modern cropping systems maximize production efficiency by choosing genetic material and management systems that effectively partition resources to fruit production over structural materials. Although energy for fruit production is primarily derived in the current season through photosynthesis in nearby leaves (Murneek, 1933; Marsal et al., 2003), reduced vegetative growth is desirable as long as sufficient photosynthesis is achieved to support fruit growth. Furthermore, reproductive organs are preferred over other resource sinks, so any crop load reduces vegetative growth and leaf development (Grossman and DeJong, 1995). Leaf area tends to decrease with a heavy crop load (Hansen, 1980), though an increase in resource transport may compensate for the reduction in leaf area (Preistley, 1970; Roper et al., 1988; Kappel, 1991). The development of rootstock selections and high-density management practices facilitates improved production efficiency in modern orchard systems.

Dwarfing rootstocks and high-density management practices comprise the major advancements in modern orchard systems to improve production efficiency (Mika and Piskor, 1997; Marini et al. 2014). The primary goal for modern orchard systems is to improve light interception through high-density planting systems while maintaining or decreasing vegetative growth potential so that a maximum investment can be made to fruit production. Genetic material is selected to increase dwarfing, leaf area, and precocity in favored varieties (Hrotkó, 2007). Dwarfing reduces overall plant vigor, size, and biomass. Dwarfing rootstocks are grafted to scion cultivars that express favorable tree architecture and fruit production to control vigor and also improve disease resistance. Increased leaf area affects the available photosynthetic materials to the plant for

allocation of energy to growth and reproduction. Precocity describes early maturity, reducing time to marketable product. High-density systems require higher start-up capital, though initial investments are returned faster because of early maturity and an increase in yield and fruit quality (Robinson et al., 2007). High-density systems also reduce labor and input requirements, as trees are more uniform and accessible (Lang, 2005).

Despite clear evidence that dwarfing rootstocks and high-density systems are more economically and production efficient, at least for apple systems, the consequences of such manipulation on plant architecture and function across orchard trees remain less understood. Specifically, how do efforts to improve production efficiency in orchard fruit affect metabolic efficiency and physiological limitations? Can the study of orchard fruit allometry better inform selective breeding programs and orchard system development? This dissertation seeks to evaluate allometry and production efficiency for two variably managed orchard tree species: apple (*Malus* spp.) and tart cherry (*Prunus cerasus*). Driven by consumer demand for high quality, large, and uniform fruits, apple has historically been the most studied, developed, and heavily managed of orchard tree species. Accordingly, apple provides the industry standard for high-density systems. On the other hand, tart cherry is among the least studied orchard trees with minimal canopy management required after initial establishment of the orchard. The two systems are compared for their allometry (Chapter II) and evaluated independently for the effects of tree size and structure on fruit production (apple, Chapter III; tart cherry, Chapter IV).

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CHAPTER II

PROCESS-BASED ALLOMETRY DESCRIBES THE INFLUENCE OF

MANAGEMENT ON ORCHARD TREE ABOVEGROUND

ARCHITECTURE

Summary

We evaluated allometric relationships in length, diameter, and mass of branches for two variably managed orchard tree species (tart cherry, *Prunus cerasus*; apple, *Malus* spp.). Empirically estimated allometric exponents (*a*) were compared to expectations of *a* described by two processed-based allometry models: the West, Brown and Enquist fractal branching model (WBE) and the recently introduced Flow Similarity model (FS). These process-based allometric models were derived from physics and suggest all plants encounter physiological constraints on growth and architecture. We compared the empirical estimates of *a* to the model expectations to provide context for allometries that vary across plants and may reveal the physiological implications of pruning and management in orchard systems. Our study found strong allometric relationships among the species and individuals studied with broad agreement with the expectations of both models. The 8/3-power law prediction of the mass ~ diameter relationship by the WBE, indicative of biomechanical limitations, was supported by this study, while the length-including allometric relationships deviated from the WBE expectations and shifted towards the flow similarity expectation of FS that describes aboveground architecture with high efficiency of water use and transport. In this way, managed orchard trees deviated from strict adherence to the idealized expectations of the models, but still fall

largely within the range of FS model expectations despite intensive management.

Keywords: allometry, WBE model, Flow Similarity, Malus spp., Prunus cerasus

Introduction

      The physical structure of a plant emerges from species-specific growth strategies to access scarce environmental resources such as light, water, and nutrients (Pacala and Tilman 1994; Grossman and Dejong 1995; Kobe 2006). While species vary in their strategies for growing in resource-limited environments, even when resources are not limited, growth is constrained by physiological limits on processes such as photosynthesis and resource transport (Murneek and Logan 1932; Niklas and Kirchner 1984). The diversity of plant form that exists in nature reveals the many ways that plants evolved to balance trade-offs between external environmental and internal physiological limitations (Niklas 1997). Despite the diversity of plant form, however, there are still emergent patterns in plant structure that may reflect the impact of underlying constraints on plant physiology (Price et al. 2010).

      One aspect of plant form where physiological constraints on plant growth may be evident is aboveground morphology or architecture (Niklas 2004). Aboveground morphology of plants often exhibits regular patterns referred to as allometric relationships (Huxley 1972; Lacointe 2000). Allometric relationships describe how plant size (e.g., mass or diameter) relates to other dimensions of morphology such as branch length, surface area, or volume. These relationships are often highly constrained (i.e., show limited variance) and are typically well described by power law equations of the form:

$$y = y_0 x^a$$

where y is the measurement of some trait of interest, x is a measure of plant size, and y_0

and a are fitted parameters. Various models exist attempting to explain why this

relationship often takes the general form of a power law and to explain the narrow range

of allometric exponent values (a) often seen in data. Because many of these models

predict only a single value of a for any particular x-y relationship, the exact value and

importance of a is much debated (Coomes et al. 2011; Price et al. 2012) as is the

usefulness of an allometric approach to describing plant form (Le Roux et al. 2001).

Determining whether empirically estimated a support an expected value is challenging

because while the values of exponents tend to be constrained, there is still variation

within and across species.

A recently proposed model called Flow Similarity (FS) attempts to explicitly

explain the variation in a by incorporating two fundamental physical processes

constraining plant growth: hydraulics and biomechanics (Price et al *preprint*). The

hydraulic constraint is described as 'flow similarity', which is the condition where a

constant flow rate and velocity of water is maintained through the plant vascular network

by area-preserving branching (McCulloh and Sperry 2005). The biomechanical constraint

is described as 'elastic similarity', where each branch grows to the structural limit at

which if it were to grow any larger it would break under its own weight (McMahon and

Kronauer 1976; Niklas 1992). FS explicitly recognizes that a tree grows dynamically in

order to optimize water use while providing a sufficient structural architecture. New

growth and branches at the distal end of a plant are likely to express flow similarity,

while the trunk and basal structural branches that bear the majority of weight of the plant

are likely to express elastic similarity. From this dynamic view of interacting physical constraints, FS predicts a range of a that falls within the bounds of hydraulic and biomechanical constraints instead of a single prediction (Table 2-1). The FS approach to expressing dynamic constraints between hydraulic and biomechanical limits is in contrast to a similar but more static model derived by West, Brown and Enquist (WBE; 1997). WBE assumes that the way biomechanical and hydraulic processes interact is fixed within and across species. The two models we explore in this study are built on similar processes but make different predictions for the same allometric relationships (Table 2-1).

We use a unique dataset from destructively sampled orchard trees to explore the ability of FS and WBE to predict the allometries of manipulated tree architectures. Allometries have been widely used in the management of orchard systems to predict carbon partitioning to fruit (Westwood and Roberts 1970; Lacointe 2000). However, the allometric relationships used in horticulture can be rigid and lack linkages to the underlying processes generating estimates of a. If process-based allometry models can be applied to orchard trees, it provides the opportunity to understand how human management interacts with fundamental physiological constraints and how these constraints influence how managed trees respond to human manipulation.

Orchard trees offer a unique opportunity for examining allometric models because the genetic material and management regimen provides a distinct manipulated environment and set of growing conditions. Clonal rootstocks that influence tree growth and partitioning are grafted to scion wood that produces favorable fruit (Robinson 2007). The orchard environment is heavily subsidized with water and nutrients, reducing the

Table 2-1. Predicted allometric relationships between a.) length, diameter, surface area and volume as formulated by the Flow Similarity model (FS) and b.) length, diameter, and mass as formulated by the West, Brown, Enquist model (WBE). Y and X variables are listed in the first two columns. An expression for each relationship is in the third column, where α_F is the expected exponent for the FS length to diameter prediction and where α_M represents the set of expected exponents for the WBE predictions. The following columns represent the predicted exponents. For FS, the predictions are broken down into flow similarity, elastic similarity, and the change in exponent expected going from small to large plants (flow to elastic). This table is modified from Price et al (*preprint*) with permission.

a. FS

Y-variable	X-variable	Expression	Flow Similarity	Elastic Similarity	Changing Exponent
Length	Diameter	$L=D^{\alpha_F}$	2	2/3	2 to 2/3
Surface Area	Volume	$SA=V^{(\alpha_F+1)/(\alpha_F+2)}$	3/4	5/8	3/4 to 5/8
Diameter	Volume	$D=V^{1/(\alpha_F+2)}$	1/4	3/8	1/4 to 3/8
Length	Volume	$L=V^{\alpha_F/(\alpha_F+2)}$	1/2	1/4	1/2 to 1/4
Diameter	Surface Area	$D=SA^{1/(\alpha_F+1)}$	1/3	3/5	1/3 to 3/5
Length	Surface Area	$L=SA^{\alpha_F/(\alpha_F+1)}$	2/3	2/5	2/3 to 2/5

b. WBE

Y-variable	X-variable	Expression	Predicted Exponent
Length	Diameter	$L=D^{\alpha}_M$	2/3
Length	Mass	$L=M^{\alpha}_M$	1/4
Mass	Diameter	$M=D^{\alpha}_M$	8/3

effect of resource limitation on plant architecture. With high subsidies of water and nutrients, physiological constraints should be the primary influence on plant growth (Deng et al. 2012). However, tree architecture is also directly manipulated by pruning and training to improve light penetration, airflow, and fruit production (Lauri et al. 2011). Dormant season pruning, the destructive removal of branches in winter months, impacts the growth trajectory of trees by removing growing nodes and displacing growth hormones. Trees respond to pruning the following growing season with localized invigoration of retained buds and branches and an overall dwarfing of tree size (Ferree and Schupp 2003). How controlled genetic material, environmental manipulation, and pruning interact to affect the overall allometry of an orchard tree is unknown. Are the allometric relationships of managed trees still consistent with expectations from process-based allometric models built to explain plant architecture of unmanaged trees? Or, does human manipulation of the natural architecture push orchard trees away from basic physical and biological constraints to exhibit forms with little comparison in unmanaged systems?

Materials and Methods

System

Two Rosaceous species from experimental orchard blocks at the Utah State University Kaysville Research Farm (2011-2013) in Davis County, Utah were used in this study: tart cherry (*Prunus cerasus*) and apple (*Malus* spp.). The production systems sampled for tart cherry and apple differ in management intensity and genetic complexity.

The sampled tart cherry orchard block was twenty-four years-old, near the end

of peak production age for similar orchard systems. Individuals consisted of a clonal scion (cultivar: 'Montmorency') grafted on to closely related seedling rootstocks (*Prunus mahaleb*). These individuals are described generally by vigorous growth and wide crotch angles ($57.1^O \pm 27.9$). Fruit-bearing spurs, stubby twigs that grow off of main branches, tend to be located on the proximal two-thirds of parent branches (Maguylo et al. 2004). A multiple leader 'open-vase' canopy was developed in the first few years of growth by selecting three to five main structural branches for ideal orientation and branching angle. Following initial canopy development, individuals received relatively minor annual pruning, ~10% total biomass, to improve light penetration, air flow, and fruit set. No pruning occurred for five years prior to the study.

The apple block was ten years-old and part of the NC-140 Regional Rootstock Research Project - 2003 'Golden Delicious' Trial (Marini et al. 2014). The individual trees consisted of clonal scions (cultivar: 'Golden Delicious') grafted on to several clonal rootstocks ('Budagovsky 9', 'Geneva® 41', 'Geneva® 210', 'Malling 26', 'Japan-Morioka 8', 'Pi-AU 56-83'). The 'Golden Delicious' cultivar is described as moderately vigorous with wide crotch angles ($56.4^O \pm 36.6$) and bears fruit on spurs or terminals of short shoots (Ferree and Schupp 2003). Rootstocks primarily drive growth potential and disease resistance and provide a gradient in tree size, introduced from smallest to largest. Budagovsky 9 (B.9) is highly dwarfing, highly productive, and winter hardy (Budagovsky 1974; Stehr 2007; Hoover et al. 2011). Geneva® 41 (G.41) is a dwarf rootstock with wide crotch angles that expresses good yield and fruit size, disease resistance, and winter hardiness (Robinson and Hoying 2004; Fazio et al. 2013). Geneva® 210 (G.210) is a semi-dwarf with wide crotch angles that is disease resistant, free

standing, precocious and productive (Fazio et al. 2013). Malling 26 (M.26) is one of

the most common dwarf rootstocks in commercial planting but is susceptible to disease

and winter freezing (Hoover et al. 2011; Marini et al. 2009; Robinson et al. 2007). In the

western United States it grows more like a semi-dwarf, as observed in our study as an

intermediate-sized rootstock. Japan-Morioka 8 (JM.8) is reported as a dwarfing rootstock

that is disease resistant; however, it also expresses a semi-dwarf size in some

environments, as we observe in our study (Marini et al. 2009; Soejima et al. 2010). Pi-

AU 56-83 is reported as a dwarfing rootstock from trials in Germany (Fischer 2001), but

other reports suggest it expresses as a semi-dwarf with high survival, vigor and fruit

weight, but low production (Marini et al. 2009). All apple trees were trained, pruned, and

managed consistently according to NC-140 protocols (www.nc140.org). Individuals were

trellised and pruned heavily each year, ~25% total biomass, to maintain one dominant

central trunk, or single leader, and whorled terraces of lateral branches for bearing fruit.

Data Collection

We sampled five tart cherry trees for a total of 449 branches and 19 apple trees for

a total of 375 branches. The five tart cherries were chosen from a stratified random

sample of over 300 available trees in the block while excluding senescent or diseased

individuals. Six apple rootstocks were chosen from the experimental block to represent a

gradient in tree size and superior survivorship. Three to four individuals of each rootstock

were then chosen randomly, except for the industry standard rootstock, M.26, which only

had one individual surviving. For each individual sampled, all branches were identified

and measured for diameter and length. Branches were defined as a continuous stem

between two branching nodes, while twigs were defined as stems supporting only buds

or short fruit-bearing stems less than two centimeters in diameter. Branches and twigs

were removed from the tree and dried in a large oven for a minimum of one week at

65^OC and weighed for biomass. Twig length and biomass measurements were limited to

one random individual for cherry and each apple rootstock. Sampling occurred at least

one full growing season following the last pruning event.

Branch Classification

Branch morphology was classified in two ways to explore allometric patterns

below the individual-level: segment and subtree (Figure 2-1). *Segment* values are the data

gathered directly for each branch. Segment length, for instance, is the distance between

the proximal end of the branch at one branching node and its distal end at the next

branching node. *Subtree* values are the diameter of a given branch and the total length or

mass of that branch and all distil branches. The multi-dimensional morphological

characteristics, surface area (π * diameter * length) and volume (π * (diameter / 2)^2 *

length), are calculated at a segment level with subtree level values generated as the

appropriate sum of segment level calculations.

Data Analysis

To estimate *a*, log-log transformed linear relationships for combinations of

morphological characteristics were evaluated using reduced major axis regression

(Warton et al. 2006). For each pairwise relationship and branch classification, an

estimated *a* with 95% confidence intervals and an *r^2* value were determined using the

Branch-level Classification: Segment   Subtree
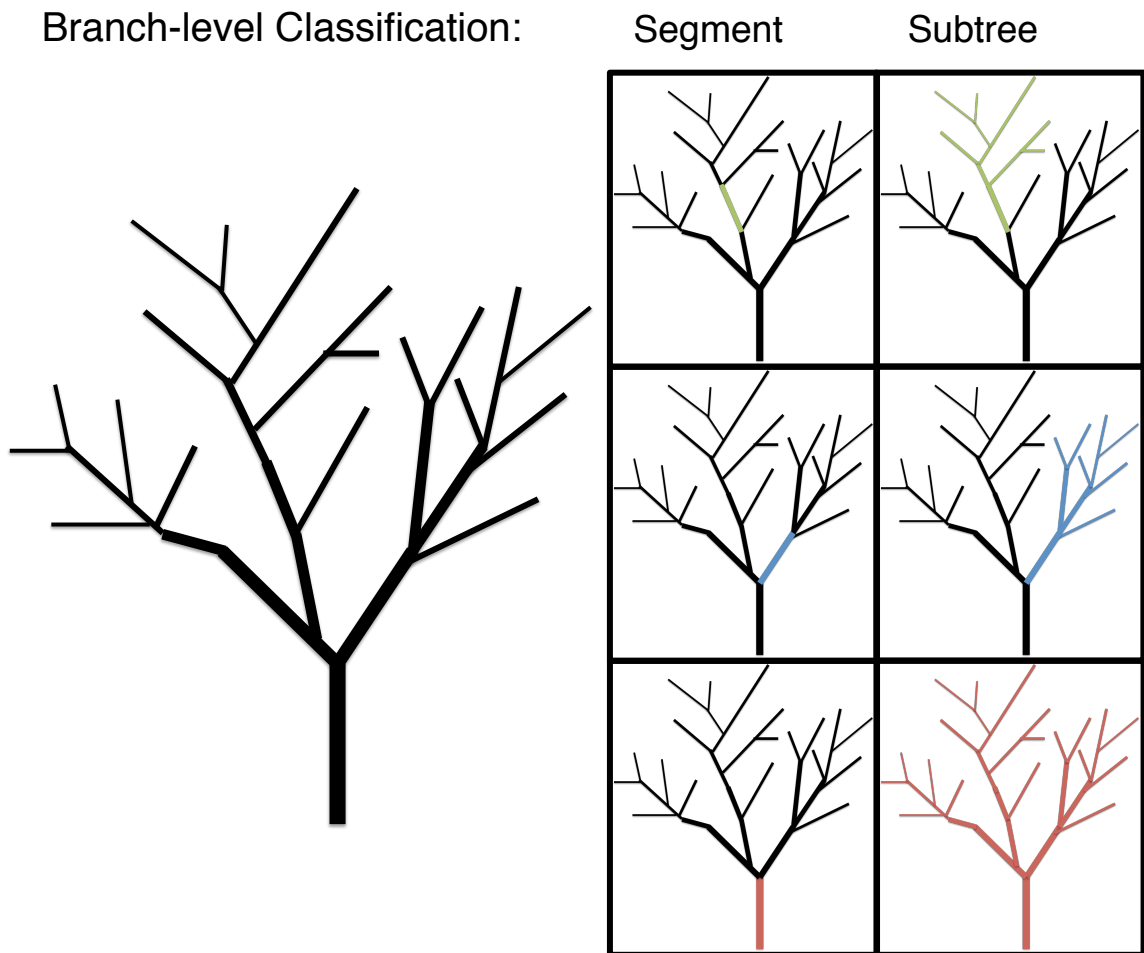
Figure 2-1. An illustration of the branch-level classifications: segment and subtree. The allometric analysis was conducted at both segment and subtree branch classifications for each relationship.

'SMATR' package in R: (R version 3.1.1). Estimates of *a* were evaluated by aggregating all branches at the individual and species level. This analysis was further summarized at the individual-level by calculating the percent of individuals where the estimated 95%

confidence interval overlapped the elastic similarity and flow similarity expectations and the percent of individuals where the estimated exponent fell between the elastic and flow similarity expectations.

Because these relationships are not always linear on log-log plots, we also examined whether polynomial fits to the data performed better. Polynomial fits were tested against linear fits by comparing the AICc values, but did not strongly alter the analysis (see appendix, Figure A-1). Only results of the linear models are reported in the paper.

The addition of twig lengths and mass to branch-level calculations were evaluated among the subset of individuals with the extra sampling effort, with only minor shifts in estimated a (see appendix, Figure A-2).

Data and programming code for this analysis can be found freely available online at github.com/weecology/branch-arch/GeneralAllometry. The authors license this work under a Creative Commons Attribution 3.0 Unported License (CC BY 3.0).

Results

Species level results are reported from this study for each allometric relationship examined (Figure 2-2). We also report the summarized individual-level results (Table 2-2), but the detailed individual level results can be found in the appendix (Figure A-2) along with data visualizations for all branches sampled separated by individual (Figure A-3) and aggregated (Figure A-4).
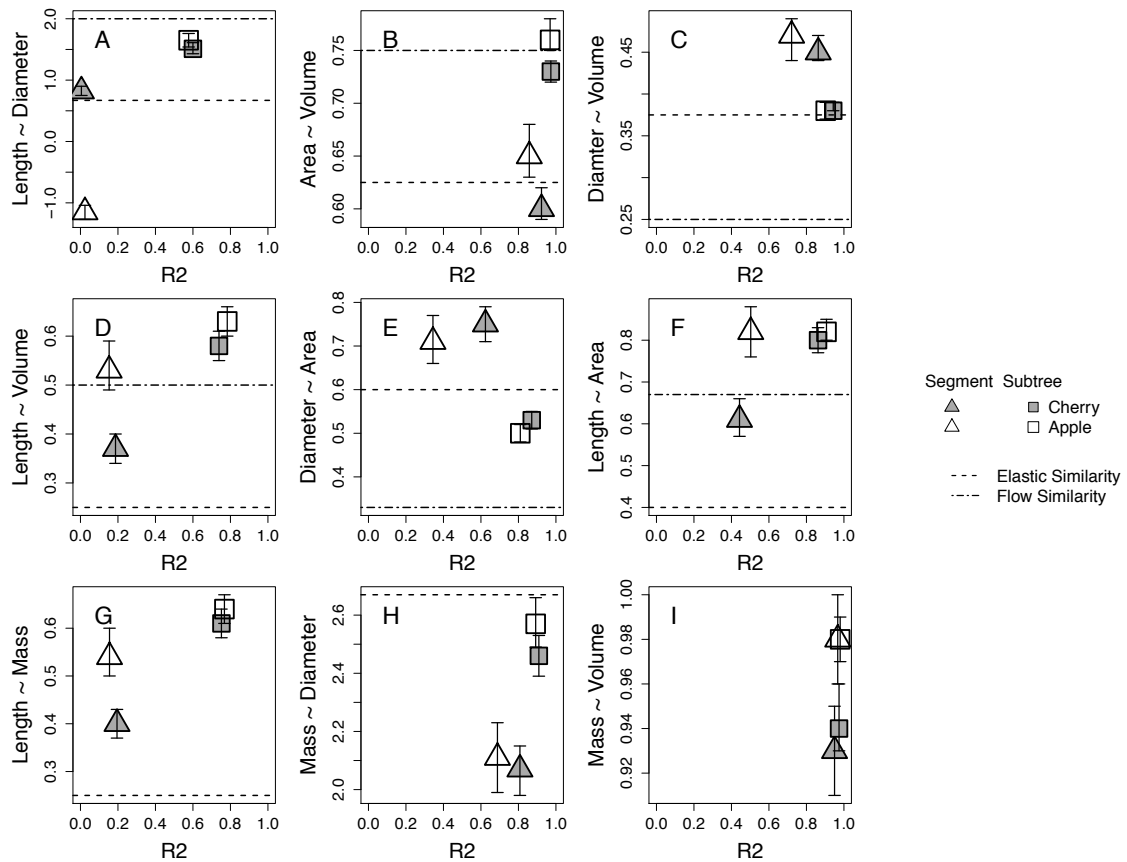
Figure 2-2. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P. mahaleb*) and nineteen 10-year-old 'Golden Delicious' apple (*Malus* spp.; various rootstocks) for each branch-level classification. Segment level estimates are marked by triangles and subtree by squares with tart cherry shaded and apple open symbol. The predicted *a* from the process-bases models are marked as horizontal lines. A-F) The predicted *a* from the FS model: elastic similarity is marked by a dashed line and flow similarity by a dot-dash line. G-H) The predicted *a* from the WBE model is marked by a dashed line.

Table 2-2. The percent of individuals that are described by an estimated allometric
exponent 95% confidence interval that overlaps with the elastic similarity expectation
('Elastic'), that overlaps with the flow similarity expectations ('Flow'), or that are
described by an estimated mean exponent occurring within the range of elastic and flow
similarity expectations ('Between') for each species: a) cherry and b.) apple. Dash
indicates 'no comparison' where neither the Flow Similarity model nor the West, Brown,
Enquist model provides an exponent expectation.

a. Cherry

Branch Class	Segment			Subtree		
Reference	Elastic	Between	Flow	Elastic	Between	Flow
Length ~ Diameter	80^z	0	0	0	100	40
Area ~ Volume	80	0	0	0	40	100
Diameter ~ Volume	0	0	0	100	20	0
Length ~ Volume	20	100	40	0	0	20
Diameter ~ Area	0	0	0	20	80	0
Length ~ Area	0	40	100	0	0	0
Length ~ Mass	0	-	-	0	-	-
Mass ~ Diameter	0	-	-	80	-	-
Mass ~ Volume	-	-	-	-	-	-

[z] Values are expressed as percent of total cherry individuals [n = 5].

b. Apple

Branch Class	Segment			Subtree		
Reference	Elastic	Between	Flow	Elastic	Between	Flow
Length ~ Diameter	26^y	5	47	0	79	100
Area ~ Volume	95	58	84	0	0	53
Diameter ~ Volume	53	5	11	95	47	11
Length ~ Volume	11	21	74	0	0	5
Diameter ~ Area	79	11	11	37	95	11
Length ~ Area	0	5	47	0	0	0
Length ~ Mass	5	-	-	0	-	-
Mass ~ Diameter	47	-	-	100	-	-
Mass ~ Volume	-	-	-	-	-	-

[y] Values are expressed as percent of total apple individuals [n = 19].

Branch classification

Allometric relationships at the subtree–level exhibit equal or higher r^2 values over segment classification r^2 values across all morphological characteristics (Figure 2-2). A shift in *a* occurs in most cases between segment and subtree level estimations. Allometric relationships of multi-dimensional morphological characteristics, like surface area and volume, tend to exhibit higher r^2 values over allometric relationships including linear morphological characteristics, like length and diameter (Figure 2-2). The mass ~ volume relationship is strongest, overall (Figure 2-2I). The surface area ~ volume relationship, both multi-dimensional terms, expresses the next strongest fit (Figure 2-2B). The diameter ~ volume and length ~ surface area relationships follow with strong relationships at the subtree level (Figures 2-2C, 2-2F). Mass ~ diameter, a component of the WBE, is also extremely strong (Figure 2-2H).

Model expectations

All but two estimated 95% confidence intervals overlap between species and are therefore interpreted as statistically indistinguishable (Figure 2-2). The exceptions are surface area ~ volume (Figure 2-2B) and mass ~ volume (Figure 2-2I). Four of six pair of species level subtree *a* estimations fall within the expected ranges in *a* described by FS (Figure 2-2). Estimated *a* shift between segment and subtree level of branch organization with a few subtree estimated *a* omitted from the expected range: length ~ volume (Figure 2-2D) and length ~ surface area (Figure 2-2F). Shifts occur in the direction towards the flow similarity expectation. At a species level, the subtree mass ~ diameter relationship expresses a very strong relationship close to the expected value from WBE at the subtree

level and overlapping with the empirical estimation of 2.53 by Brown (1997; Figure 2-2H). The length ~ mass relationship at a species level appears to deviate significantly from the WBE prediction (Figure 2-2G).

Individual data summaries largely support the conclusions of the aggregated species level results (Table 2-2). For length ~ diameter, all cherry individuals at a subtree level fall between the elastic and flow similarity expectations with four of five individuals overlapping with elastic similarity, while all apple at a subtree level overlap with flow similarity. Surface area ~ volume has a high variation of a at the individual level with high overlap of both elastic and flow similarity expectations. The individual level data confirm the species level overlap of the elastic similarity expectation for diameter ~ volume at the subtree level. The individual level data similarly confirms the estimations between elastic and flow similarity expectations of diameter ~ surface area at the subtree level. Four of five of the cherry individuals and all of the apples overlap with the mass ~ diameter elastic similarity expectation from the WBE at a subtree level.

Discussion

Our study describes the allometry of two variably managed orchard tree species drawing from existing process-based allometric models. Overall, the allometric relationships evaluated for tart cherry and apple individuals sampled are well described by a power law (Figures A1-4). Estimates of a shift significantly for both species between segment and subtree branch classifications, with higher confidence intervals and more similar estimates of a among species at the subtree-level than the segment-level (Figure 2-2). We find overlap in 95% confidence intervals of estimated a for tart cherry

and apple for most (7/9) of the allometric relationships evaluated at the subtree-level

indicating a consistent pattern in growth and resulting tree architecture.

Strong allometric relationships in orchard trees provide support for similar

patterns in plant growth, despite different genetic material and management approaches

driving growth and architecture among cherry and apple systems and within apple

rootstocks. Allometric relationships with multi-dimensional branch dimensions (i.e.,

surface area and volume) are stronger than relationships with linear dimensions (i.e.

length and diameter; Figure 2-2). This could be because these multi-dimensional branch

dimensions better reflect resource transport and environmental exposure (Price et al.

preprint; West, Brown and Enquist 1997). For instance, surface area might relate to the

number of leaves distributed on a branch, dictating the photosynthetic capacity of that

location on the plant (Allen et al. 2005). The volume of a branch might be a better

predictor of water use than either length or diameter independently (McCulloh and Sperry

2005). Better performance of multi-dimensional parameters linked to environmental

exposure could explain why we find stronger morphological relationships also emerge at

the subtree level; though, many of the strongest allometric relationships are represented

by the highest r^2 values for both subtree and segment levels (Figures 2-2B,C,H,I).

Existing process-based allometric models, WBE and FS, derive expectations of a

for idealized plants from physics first principles. These models provide context for

understanding how physiological mechanisms drive the conservation or deviation of plant

growth from the idealized expectations (Table 2-1). The mass ~ diameter relationship is

most consistent among species and individuals within our study and is in general

agreement with the expected a of the WBE, despite genetic and management differences

(Figure 2-2H, Table 2-2). The other allometric relationships explored including length dimensions also do not distinguish among species or rootstocks, but are consistently described by estimated *a* that shift within the expectations of idealized plants described by FS towards flow similarity and away from the biomechanical constraint of elastic similarity (Figure 2-2).

The shift in *a* towards flow similarity for allometries including length dimensions may be attributed to the genetic selection for improved production efficiency or to substantial manipulation of tree architecture for commercial fruit production. This study represents two distinct species with clonal genetic material developed through selective breeding. The cherries are clonal scion material with closely related seedling rootstocks, while the apples are clonal scion with five distinct clonal rootstocks that were selected for known differences in tree growth, architecture, and production efficiency (Marini et al. 2014). Manipulation of tree architecture through pruning directly influences length and length-including branch dimensions (i.e., surface area, volume). As much as 25% of total aboveground biomass is removed annually, which reduces the growth potential of a tree by reducing leaf area and altering the root:shoot balance (Ferree and Schupp, 2003). Localized effects of pruning changes the load-bearing status and growth potential in basal branches. Remaining branches are mainly structurally important branches with wide crotch angles and relatively stubby dimensions suited for bearing a commercial fruit load (Feree and Schupp 2003). Regrowth is invigorated with increased investment in nearby fruit-bearing spurs and lateral branches, potentially driving the shift in *a* towards flow similarity (Grochowska et al. 1984; Fumey et al. 2011). In addition, training of tree architecture with structural supports may influence branch dimensions and localized

constraints on branch physiology. Though not statistically significant, we observe that apple is described by an *a* that shifts slightly more towards flow similarity in relation to tart cherry. The greater shift towards flow similarity in apple is consistent with a relaxation of biomechanical constraints due to direct structural support provided by trellises in the apple system and more intensive 'length-reducing' pruning cuts. In contrast, the tart cherries are free standing and receive minimal 'branch-removing' pruning cuts that may be less of a factor in relaxing biomechanical constraints.

The biological process behind strong and consistent allometric relationships is linked to physiological limitations of plant growth in unmanaged plants (McMahon and Kronauer 1976; Niklas and Spatz 2004; Savage et al. 2010). It has remained difficult to disentangle the limiting effects of biomechanical and hydraulic processes, but the insights of FS provide the opportunity for a first attempt at exploring these constraints in domesticated plants. From this study, it appears that both biomechanical and hydraulic constraints are limiting plant function in orchard systems, but perhaps are acting at different levels of branch classification as represented by the shift in estimated *a* among scales (Figure 2-2). This may support the concept of 'incomplete branch autonomy' by which branches organize themselves independently due to the localized distribution of leaves and the resulting photosynthetic material but ultimately interact within a tree-wide network of nutrient transport and hormone signaling pathways (Marsal et al. 2003). Branch diameter may be driven primarily by biomechanical constraints as its relationships with surface area and volume fall firmly in the elastic similarity region (Figure 2-2C,E). Individual segments are more constrained by load-bearing than what is observed at the subtree level as the segment level estimated *a* generally shifts towards the

biomechanically driven elastic similarity expectation while the subtree level estimated

a generally shifts towards the hydraulically driven flow similarity expectation (Figure 2-

2). Because FS is expected to operate more in the terminal parts of the network, pruning

there should shift *a* toward the elastic similarity limitation expected of the load-bearing

basal branches that remain unpruned. This within-canopy shift from elastic similarity to

flow similarity is something that needs further testing. The development of theory that

disentangles biomechanical and hydraulic constraints provides the opportunity for further

exploration of these physiological mechanisms as they relate to plant allometry.

Continued use of a process-based allometric approach in orchard systems may

lead to a more general understanding of plant growth that can be linked to physiology

and, in the case of orchard trees, can inform management techniques and research

programs designed to maintain plant health, increase yields, and reduce resource use

(Costes 2004; Niklas 2004; Lauri and Claverie 2008). Describing common allometric

relationships and physiological limitations for orchard systems can reveal a boundary

where constraints from physics drive plant function more than human intervention. This

study finds that allometric relationships are largely invariant between the two orchard

species and rootstocks tested, but that the estimated *a* vary within the idealized

expectations of process-based allometric models likely due to the extreme human

influence on the plants studied. Both tart cherries and apples were heavily pruned at some

stage of their development and received fertilizer, water, and biocide applications at

levels optimal for reproductive growth. We posit that the two orchard species explored

are performing at a high efficiency of water use facilitated by reduced biomechanical

demands. Despite the large removal of biomass for each of these species, growth

following management appears compensatory in such a way that the mass ~ diameter relationship returns to consistent and expected relationships, while length ~ diameter relationships fluctuate potentially according to pruning intensity. Future research might focus on the facets of management that drive allometry the farthest from model expectations or use measurements of body size to standardize treatments that could provide improved analysis of competing orchard systems and varieties. Breeding programs might better identify varieties that are approaching the yield ceiling while optimizing for resource use efficiency and yield improvements in the varieties with greatest potential for improvement.

Conclusion

Process-based allometric models describe conserved morphological relationships across plants governed by physiological constraints on growth and architecture. Common rules generated from models can link physical form to physiological mechanism and function. Our study finds strong allometric relationships in two variably managed orchard species. Agreement with idealized expectations of FS and WBE is limited to the mass ~ diameter relationship. This study reveals the potential for continued use of process-based allometry within agricultural systems; however, expectations derived for idealized plants may be insufficient alone for the description of orchard systems due the human manipulation of plants' physiology and environment. Although orchard trees are particularly complex candidates due to genetic, environmental and physical manipulation, process-based allometry may still provide a mechanistic understanding of the effects of management for optimal reproductive growth.

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CHAPTER III

AN ALLOMETRIC APPROACH TO DISTINGUISH TREE SIZE, ARCHITECTURE,

AND YIELD AMONG APPLE ROOTSTOCKS

Abstract. The influence of rootstock on tree size, tree architecture and fruit production was evaluated among six apple rootstocks (*Malus* spp.) from the NC-140 2003 'Golden Delicious' Dwarf Rootstock Trial. Log-log transformed relationships between tree size and biomass, called allometric relationships, were strongly conserved among rootstocks. Stem biomass was most strongly related to stem volume and trunk cross sectional area. Total stem length was most correlated to cumulative yield. Smaller rootstocks demonstrated yield higher than expected based on tree size when compared to larger rootstocks in the study. The dwarf rootstocks, Budagovsky 9, Geneva® 41 and semi-dwarf Geneva® 210 were confirmed to demonstrate high yield efficiency as determined in previous studies. These results were consistent with observed harvest index and modeled harvest index that used biomass as the indicator of tree size. Yield efficiency remains a strong and practical predictor of production efficiency in orchard systems; however, modeling harvest index using an allometric relationship of trunk cross sectional area and biomass was a better representative of harvest index than yield efficiency and allows for comparison of production efficiency across size classes.

Additional Index Words: biomass partitioning, trunk cross sectional area, harvest index, yield efficiency, yield per canopy spread, yield per height

The improvement of production efficiency in modern cropping systems is largely a result of shifts in biomass allocation from structural to harvestable products. Harvest index (HI) is used in annual cropping systems to evaluate production efficiency and distinguish cropping systems that partition the highest proportion of available biomass to harvestable product (Unkovich et al., 2000). HI is the proportion of yield biomass to total plant biomass (including yield). In annual systems, HI is fairly straightforward to calculate because both the yield and the remaining structural biomass can be collected without impacting future yield. Studying biomass partitioning in orchard systems is more complex than annual systems because fruit trees crop for many years and the non-harvested structural biomass (i.e., wood) cannot be directly measured without also destroying future yield.

As direct measures of structural biomass are not possible in orchard systems, indirect measures that represent tree size and biomass of orchard trees are often used to estimate production efficiency. Trunk cross sectional area (TCSA) is the most common representative of tree size used in experimental analysis and evaluation of orchard system design (Grossman and DeJong, 1998; Costes et al., 1999). TCSA serves as an indirect estimate of stem biomass (Westwood and Roberts, 1970) and takes the place of total plant biomass in the harvest index. Cumulative yield biomass across years takes the place of annual yield biomass. This ratio of cumulative yield and TCSA used for orchard systems is called yield efficiency (YE; Autio et al, 1996). YE works well as an index to compare production efficiency of rootstocks, training systems, and management practices. YE is easy to measure, but remains a coarse approximation of complex physiological processes driving biomass partitioning.

An approximation of total biomass that is derived from physiological models could improve the comparison of production efficiency among orchard systems through direct evaluation of biomass partitioning. Physiological models that describe limits of water transport and weight bearing on tree growth and architecture provide insights into the physiological drivers of partitioning biomass between fruit and wood. Training and pruning systems can then be evaluated within the context of plant physiology for their effect on the manipulation of tree architecture and biomass partitioning.

One physiological model used to describe links between tree size and biomass allocation is called allometry. Allometric relationships are robust in wild plants and appear relevant to even intensely managed orchard systems (Strong and Azarenko, 2000; Deng et al., 2012; Chapter II). Allometric relationships take the form of:

$$Log_{10}Y = b + m*Log_{10}X$$

where X is a measure of branch or tree size, Y is a physiological function or structural measure of interest (e.g., biomass, fruit production, annual growth), b is the intercept, and m is the slope of the relationship between $Log_{10}X$ and $Log_{10}Y$. In plants, these allometric relationships emerge from the interaction between plant size and the operation of hydraulic and biomechanical constraints on plant function (Niklas, 2004). These fundamental physiological constraints drive the indirect relationship between TCSA and biomass allocation through the vascular and structural network of the plant. Physiological constraints on the vascular and structural network of the plant are also expressed in other branch and canopy dimensions, which creates the potential for other measures of plant size and form (i.e., height, branch length, canopy spread) to provide additional information on biomass allocation and fruit production. Empirical assessments of this

suite of measures of tree size and architecture might be useful in describing biomass allocation in orchard fruit and in particular understanding physiological processes constraining biomass allocation.

Allometry may provide a complementary approach to existing production efficiency metrics to evaluate tree size and biomass partitioning in orchard systems. It has been well established in horticulture that analyzing relationships in tree size, biomass, and fruit production is important because different sized trees differ in their ability to sustain growth with maximal fruit production. Larger individuals produce more in general simply due to their size and allometry (Thomas, 2011), but are less efficient producers given the structural requirements of their size (Fideghelli et al., 2003). Differences among rootstocks, training systems, and management practices can have important impacts on biomass partitioning and fruit production and using the physiologically derived models from allometry may provide insights into the physiological impacts of different horticultural approaches.

Here we use an allometric approach to investigate differences in biomass partitioning and tree architecture among experimental rootstocks from the NC-140 Regional Rootstock Research Project 2003 'Golden Delicious' Trial (Marini et al., 2014). The NC-140 project compares rootstock selections across a range of tree size for planting in high-density apple orchard systems (*Malus* spp.). Apple is the most studied and most widely adopted high-density crop, though high-density systems are being developed for many orchard crops to increase production efficiency. Rootstocks are used in high-density apple systems to moderate vigor and improve fruit quality (Webster and Wertheim, 2003). We tested the ability of simple tree size measurements and allometric

transformations to predict aboveground stem biomass and to evaluate biomass partitioning and production efficiency among a selection of rootstocks in a standardized trial.

Materials and Methods

Data Collection. We sampled 19 ten-year-old 'Golden Delicious' apple trees (*Malus* spp.) from the NC-140 Regional Rootstock Research Project experimental block at the Utah State University Kaysville Research Farm (2012-2013) in Davis County, UT (Marini et al., 2009, 2014). Six rootstocks were chosen from the block with superior survivorship to represent a gradient in tree size. From smallest to largest TCSA, these rootstocks were: Budagovsky 9 (B.9), Geneva® 41 (G.41), Geneva® 210 (G.210), Malling 26 (M.26), Japan-Morioka 8 (JM.8) and the Pillnitz rootstock selection Pi-AU 56-83. B.9 is a highly dwarfing, highly productive, winter hardy rootstock of a size similar to Malling 9 (M.9; Budagovsky, 1974; Perry, 1997; Stehr, 2007). However, it was found to be less yield efficient when compared to M.9 (Hoover et al., 2011). G.41 is a dwarf rootstock that expresses good fruit size and wide crotch angles but a brittle graft union (Robinson and Hoying, 2004; Fazio et al., 2013). G.41 is very similar in dwarfing to M.9 and more yield efficient (Marini et al., 2014; Robinson et al., 2007). It is resistant to fire blight, *Phytophthora*, apple replant disease, woolly apple aphids and is cold resistant (Robinson and Hoying, 2004). G.210 is a semi-dwarf with a size between M.26 and M.7. It is fire blight resistant, free standing, precocious and productive (Fazio et al., 2013). It outperforms M.7 in yield with a better graft union and wider crotch angles (Robinson and Hoying, 2004). M.26 is one of the most common dwarf rootstocks in commercial

planting but is susceptible to fire blight, woolly apple aphid, and winter freezing

(Hoover et al., 2011; Marini et al., 2009; Robinson et al., 2007). However, in the western

United States it grows more like a semi-dwarf, as observed in this study as an

intermediate-sized rootstock. JM.8 is reported as a dwarfing rootstock like Malling 27

that is resistant to *Phytophthora* crown and root rot and woolly apple aphid; however it

also expresses a semi-dwarf size in some environments, as observed in this study (Marini

et al., 2009; Soejima et al., 2010). Pi-AU 56-83 is reported as similar to an M.9 dwarf in

trials in Germany with slightly higher yield (Fischer, 2001). Other reports suggest it

expresses as a semi-dwarf with high survival, vigor and fruit weight, but low yield

efficiency (Marini et al., 2009, 2014).

Each tree was planted in the spring of 2003, trained to the vertical axis system,

and was managed as previously described by Marini et al. (2014). The planting originally

consisted of eight trees per rootstock. Data on fruit yield were collected from 2005 to

2012, and cumulative yield and yield efficiency were previously reported (Marini et al.

2009, 2014). At the completion of the trial in 2012, three to four individuals of each

rootstock were chosen randomly, except for M.26, which only had one surviving

individual. For each individual, TCSA and height were measured. Tree height was

determined as the distance from the ground to the top of the canopy directly over the

trunk leader. For each individual, all branches were measured for stem diameter and

length. Branches were defined as a continuous stem between two branching nodes, while

twigs were defined as short fruit bearing shoots less than two centimeters in diameter or

shoots supporting only buds. Branches and twigs were removed from the tree and dried in

a large oven for a minimum of one week at $65^{O}C$ and weighed for biomass. The surface

area and volume of a stem were calculated as $\pi * (diameter / 2)^2$ and $\pi * (diameter / 2)^2$ * length, respectively. Total stem length, surface area, and volume are reported for each individual. Canopy spread was calculated as the sum of two maximum distance measurements of the canopy from the tree row towards the grass aisle at each side. Canopy volume was calculated from three vertical diamond-shaped canopy area measurements taken at the center and 1 m to each side of the trunk, including the measurements for height and spread.

Data Analysis. Tree size measurements (TCSA, height, stem length, stem area, stem volume, canopy spread, canopy area, canopy volume, and stem biomass) were evaluated independently for significant variation among rootstocks using a single-factor ANOVA in R (R version 3.1.1; R stats, `aov()`) and the Duncan's multiple range post-hoc test (R package 'Agricolae'). Cumulative yield was evaluated similarly among rootstocks. Allometric relationships of tree size measurements with stem biomass and cumulative yield were evaluated using reduced major axis regression. The correlation (r^2) of each log-log transformed linear relationships was determined using the 'SMATR' package in R (`sma()`; Warton et al., 2006).

Production efficiency metrics, including HI, were established as the ratio of cumulative yield to the evaluated tree size measurements. Observed HI (HI_o) was established directly from the cumulative yield and stem biomass data. Modeled HI (HI_m) was determined by transforming TCSA of each individual to stem biomass using the estimated values of stem biomass from the stem biomass ~ TCSA allometry (Table 3-1) with cumulative yield (Strong and Azarenko, 2000). The stem biomass ~ TCSA

allometry predicted mass from TCSA with high accuracy ($r^2 = 0.984$) and was robust

to greater than 5% changes in the slope parameter. Production efficiency metrics were

evaluated for significant variation among rootstocks using an ANOVA similarly to tree

size measurements. The correlation (r^2) of tree size measurements and YE was evaluated

using ordinary least squares regression in R (R stats, `lm()`).

Code License. Data and programming code to replicate this analysis can be found freely

available on-line at github.com/weecology/branch-arch/NC140. The authors

Table 3-1. Trunk cross sectional area (TCSA), height, branch volume and biomass

allometries of 10-year-old 'Golden Delicious' individuals of various rootstocks in the

form: $Log_{10}Y = b + m * Log_{10}X$. [z]

Y	X	b [95% CI]	m [95% CI]	r^2
Stem Biomass [kg] [y]	TCSA [cm^2]	1.835 [1.71; 1.96]	1.245 [1.18; 1.31]	0.990
Height [m]	TCSA [cm^2]	-0.192 [-0.31; -0.07]	0.398 [0.34; 0.46]	0.916
Stem Biomass [kg]	Height [m]	2.436 [2.13; 2.73]	3.127 [2.67; 3.67]	0.901
Stem Volume [m^3] [x]	TCSA [cm^2]	3.910 [3.79; 4.03]	1.243 [1.18; 1.31]	0.991
Stem Biomass [kg]	Stem Volume [m^3]	-2.081 [-2.33; -1.83]	1.002 [0.96; 1.04]	0.994

[z] Estimated allometric parameters and 95% confidence intervals were generated using

reduced major axis regression.

[y] Stem Biomass represents total dry weight of aboveground woody biomass.

[x] Stem Volume represents the total volume of branch segments (i.e., conduit volume).

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Results

Tree size measurements. All tree size measurements reported were determined to be significantly different among rootstocks (Table 3-2). The Duncan's post-hoc test indicates the greatest separation among rootstocks in TCSA, stem area, and stem volume. Overall, the differences among rootstocks were organized generally according to tree size.

Allometries. TCSA and stem biomass were highly correlated on log-log scales and demonstrated consistent allometries among rootstocks (Fig. 3-1A). Stem biomass and TCSA were not as strongly correlated to cumulative yield (Fig. 3-1B, C), though all tree size measurements were well correlated with stem biomass and cumulative yield on log-log scales (Table 3-3). Stem biomass is best predicted by stem volume ($r^2 = 0.994$) and TCSA (0.990) while cumulative yield is best predicted by stem length (0.846).

Production efficiency metrics. HI_o represented the greatest separation in production efficiency metrics among rootstocks (Table 3-4, Fig. B-1). HI_m and yield per stem volume also demonstrated high separation. HI_m ($r^2 = 0.982$) and YE ($r^2 = 0.913$; Fig. B-2) were well correlated with HI_o using linear models. A polynomial model improved the fit of YE with HI_o ($r^2 = 0.970$). A strong signal of tree size remains in the production efficiency metrics as TCSA remains the most correlated tree size

measurement to YE ($r^2 = 0.889$). Height ($r^2 = 0.843$), canopy volume ($r^2 = 0.838$) and stem volume ($r^2 = 0.821$) are also strongly correlated with YE. In contrast, cumulative yield is not significantly correlated with YE ($r^2 = 0.306$) and only weakly correlated with HI_o ($r^2 = 0.548$).

Discussion

Our study used an allometric approach to inform our understanding of biomass partitioning, tree architecture, and production efficiency in apple. A gradient in tree size of similarly aged and consistently managed 'Golden Delicious' on dwarfing rootstocks demonstrated increased partitioning of biomass to fruit production in smaller rootstocks. TCSA showed a strong allometric relationship to stem biomass (Table 3-1) and remained the best metric to evaluate tree size and partitioning to fruit. YE performed well to approximate differences in HI_o with a polynomial relationship where small rootstocks had a shallow slope compared to large rootstocks (Fig 3-2A). In contrast, a HI_m that used an allometric transformation of TCSA to stem biomass directly related to the HI_o across all rootstock sizes (Fig 3-2B). The direct relationship of HI_o or HI_m achieved from modeling biomass from TCSA allows comparison of production efficiency among rootstock size classes when biomass data are unavailable. Yield per height and yield per canopy spread were also important production efficiency metrics that may represent different dimensions of tree size affecting yield. Height and canopy spread may represent dimensions of tree size that are driven by available canopy space and pruning strategy chosen for the orchard system.

We found strong and consistent allometric relationships among the apple

Table 3-2. Average size and mass of 10-year-old 'Golden Delicious' on various

rootstocks.[z]

	B.9	G.41	G.210	M.26	JM.8	Pi-AU 56-83
TCSA [cm^2]	23.5a	59.9b	90.8c	145.7d	249.3e	274.5e
Height [m]	2.20a	3.45b	4.05b	5.20c	5.63c	5.53c
Stem Length [m]	6.07a	12.36ab	17.57bc	19.14bc	19.76c	23.63c
Stem Area [m^2]	4.91a	13.43b	18.52bc	26.10c	34.94d	43.65e
Stem Volume [m^3]	0.39a	1.47ab	2.21b	3.99c	7.06d	9.07e
Canopy Spread [m]	1.83a	2.90ab	3.14bc	3.80bc	3.55bc	4.14c
Canopy Area [m^2]	2.64a	6.78ab	8.22abc	11.34bc	9.91bc	13.68c
Canopy Volume [m^3]	7.01a	12.81b	16.99b	28.06c	27.63c	30.66c
Stem Biomass [kg]	3.29a	12.97ab	18.32bc	29.62c	63.29d	76.56d
Cumulative Yield [kg]	95.7a	214.1b	298.4cd	243.7bc	254.0bc	327.8d

[z] Mean separation in branch metrics by Duncan's multiple range test at $P < 0.05$

Table 3-3. Correlation (r^2) of tree size with total dry weight of above-ground woody biomass and cumulative yield among 10-year-old 'Golden Delicious' individuals and within various rootstocks.[z]

	Stem Biomass		Cumulative Yield	
	individuals	rootstocks	individuals	rootstocks
TCSA	0.990	0.993	0.695	0.728
Height	0.902	0.952	0.703	0.773
Stem Length	0.803	0.907	0.846	0.928
Stem Area	0.973	0.987	0.801	0.821
Stem Volume	0.994	0.997	0.734	0.761
Canopy Spread	0.737	0.899	0.716	0.866
Canopy Area	0.737	0.890	0.716	0.890
Canopy Volume	0.935	0.934	0.711	0.732

[z] r^2 values determined by linear regression at an individual level.

Table 3-4. Average production efficiency metric values by rootstock of 10-year-old 'Golden Delicious' on various rootstocks.[z] Modeled Harvest Index is determined by using the allometry: $Log_{10}Stem\ Biomass = 1.83 + 1.25*Log_{10}TCSA$

	B.9	G.41	G.210	M.26	JM.8	Pi-AU 56-83
Observed Harvest Index [kg/kg]	0.967a	0.943b	0.942b	0.892c	0.801d	0.810d
Yield Efficiency [kg/cm^2]	4.11a	3.58a	3.29a	1.67b	1.02b	1.19b
Modeled Harvest Index [kg/kg]	0.964a	0.950a	0.940a	0.877b	0.791c	0.809c
Yield:Height [kg/m]	43.6a	63.4ab	74.3b	46.9a	45.3a	59.6ab
Yield:Stem Length [kg/m]	17.0a	17.4a	17.6a	12.7a	13.0a	14.0a
Yield:Stem Area [kg/m^2]	19.95a	15.96a	16.34a	9.34b	7.27b	7.52b
Yield:Stem Volume [kg/m^3]	248.4a	146.3b	136.9b	61.1c	36.1c	36.0c
Yield:Canopy Spread [kg/m]	52.3a	75.6ab	100.0b	64.1a	71.5ab	78.9ab
Yield:Canopy Area [kg/m^2]	36.4a	35.2a	45.5a	21.5a	25.6a	24.5a
Yield:Canopy Volume [kg/m^3]	13.98ab	17.00a	18.11a	8.68b	9.185	10.65b

[z] Mean separation in branch metrics by Duncan's multiple range test at $P < 0.05$
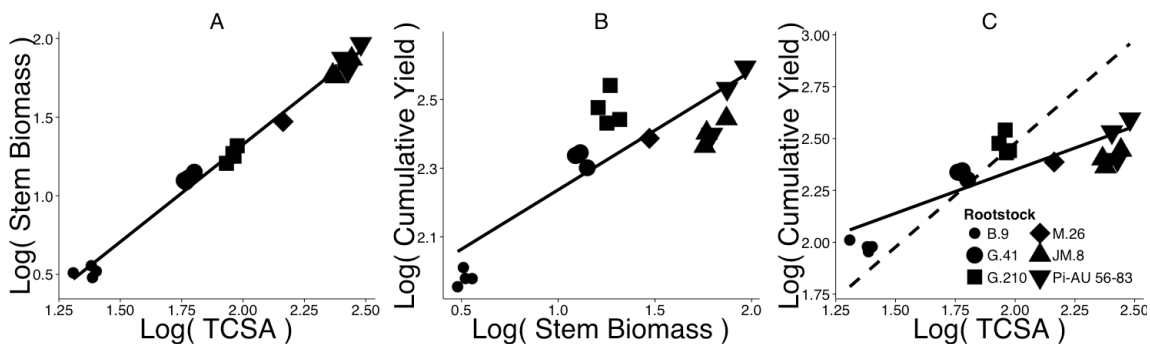
Fig. 3-1. The relationship of log-transformed trunk cross sectional area (TCSA), stem biomass, and cumulative yield of 10-year-old 'Golden Delicious' individuals on various rootstocks. Stem Biomass represents total dry weight of aboveground woody biomass. Correlation (r^2) was determined using reduced major-axis regression (regression line shown in figure). Dashed line in C shows the isocline of Yield Efficiency = 3.
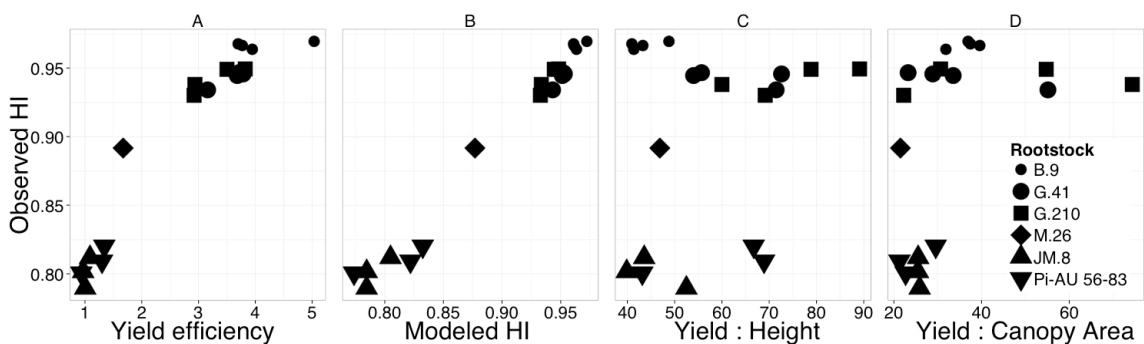
Fig. 3-2. The relationship of observed harvest index (HI_o) to alternate production efficiency metrics (cumulative yield per tree size). Modeled harvest index (HI_m) is determined by using the allometry:

$$Log_{10}\text{Stem Biomass} = 1.83 + 1.25*Log_{10}\text{TCSA}$$

rootstocks sampled (Table 3-1). Stem biomass was strongly related to TCSA (Table 3-3), supporting its continued use as the representative for tree size in horticulture (Westwood and Roberts, 1970). The only higher correlation to stem biomass than TCSA was stem volume.

Stem volume and TCSA are also strongly related, revealing a physiological link among TCSA, stem volume and stem biomass (Price et al., 2010). Stem volume remains difficult to measure, leaving TCSA the best practical field measurement of tree size; though, stem volume may have applications for models of plant growth and production. Allometric relationships with cumulative yield were generally weaker than stem biomass, but remained strong. The top predictor of cumulative yield among rootstocks was stem length (Table 3-3), indicating a physiological link that requires further investigation into the way trees use available branch space to produce fruit. TCSA was not one of the top predictors of cumulative yield as expected; however, tree size remains a driving influence of the relationship with cumulative yield.

Trees with smaller branch and canopy dimensions in our study tended to partition a higher proportion of biomass to fruit than wood as illustrated by HI and YE, distinguishing B.9, G.41, and G.210 from the other rootstocks sampled (Table 3-4). Visual evaluation of production efficiency metrics with canopy dimensions such as yield per height and yield per canopy spread distinguished a subset of G.41 and G.210 individuals for higher performance (Fig. 3-2 C,D). These individuals maintained similar yields to individuals on similar rootstocks that had larger canopies. Yield per height and yield per canopy spread were important alternates to evaluate yield performance in

respect to tree size as both are easily measured and represent additional dimensions of tree size to TCSA and stem biomass.

The maintenance of smaller trees appeared to facilitate an increase in physiological performance and provides strong support for continued development of high-density apple systems. We quantified tree architecture, biomass partitioning, and production efficiency using an allometric approach. The allometric approach broadly evaluated the effect of tree size on yield and confirmed the effectiveness of the commonly used yield efficiency metric used to indirectly estimate production efficiency from TCSA. By approximating biomass from TCSA, the allometric approach improves the evaluation of production efficiency through direct comparison of biomass partitioning among rootstocks of various sizes. The allometric approach to describing similarities and differences in tree size and architecture from the foundation of physiological constraints on the plant vascular and structural network is an important compliment to mechanistic crop physiology research in areas including photosynthesis and fruit set. Future studies may continue the analysis by seeking patterns across orchard species, varieties, and systems to understand underlying physiological levers and favorable traits for selection. Further evaluation of tree size, biomass partitioning and production efficiency among rootstocks and may be helpful to understand the effects of pruning on growth habit and yield and to develop optimized orchard systems for space, light, and nutrients.

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CHAPTER IV

SMALLER 'MONTMORENCY' TART CHERRY TREES WITH LARGER

RELATIVE CANOPY DIMENSIONS PRODUCE MORE FRUIT

WITH HIGHER SUGAR CONTENT

Abstract. 'Montmorency' tart cherry trees (*Prunus cerasus*) commercially grown in Utah in low-density systems (~427 trees/ha) were evaluated along a gradient of age and size. Branch characteristics, canopy dimensions, light distribution, yield, and fruit sugar content were quantified. Overall, smaller trees produced marginally more fruit with significantly higher sugar content. Trees with larger trunk cross sectional area given their age tended to produce more fruit but with lower sugar content. Sugar content was improved by trees with higher crop load and also by trees with relatively larger and less dense canopies facilitated by height and spread dimensions, but not canopy volume. Light distribution within the canopy was only weakly correlated with fruit sugar content, but provided evidence suggesting canopy volume in current commercial plantings quickly becomes too large or overly dense. Data suggest that management should focus on maintaining lower canopy density and volume to improve crop load and fruit sugar content.

Additional Index Words. Trunk cross sectional area, canopy volume, canopy spread, *Prunus cerasus,* sour cherry, dry matter content, soluble solids

High-density orchard systems have emerged as the modern response to demands for increased efficiency in commercial fruit production. High-density orchards increase efficiency both physiologically and economically. Smaller trees present leaves with higher photosynthetic potential and partition a higher proportion of dry matter to fruits improving fruit quality and size (Fideghelli et al., 2003). Small closely arranged canopies improve light capture and yield potential per unit area (Parnia et al., 1986). At least for dwarfing apple rootstocks (*Malus* spp.), trees suitable for high-density plantings reach maturity and fruit sooner than those planted for lower density systems (Webster and Wertheim, 2003). Uniform easily accessible trees facilitate precision management that reduces resource requirements including chemical inputs and labor (Lang, 2005).

The effective control of tree size for high-density systems has been more difficult in systems other than apple, such as cherry (Fideghelli et al., 2003). Sweet cherry trees tend to be overly vigorous when trained to a compact size and are also vulnerable to over cropping (Lang, 2005; Lauri, 2005). Vegetative growth in response to heavy developmental pruning increases time to maturity and first fruit (Hrotko et al., 2005; Long et al., 2005). Sweet cherry systems are advancing with the recent development of vigor controlling rootstocks and pruning systems that facilitate renewal of fruiting branches (Lang, 2005; Andersone et al., 2008). Tart cherry (*Prunus cerasus*) is among the least studied crops for high density planting, but remains a strong candidate with continued development in dwarfing selections (Bors, 2005) and high-density training systems (Hrotko et al., 2008).

High-density tart cherry systems are being developed in Utah in response to growers' concerns about production efficiency and fruit quality. Because tart cherries

from Utah are primarily dried, they may particularly benefit from the increase in dry matter content (i.e., sugar) that occurs when cherries are grown in high-density systems (Rowley, 2013). High-density tart cherry trials remain in early stages, but existing commercial orchards of various age and size can be used to gain important insights into favorable tree training and management strategies that will result in the highest production efficiency and fruit quality.

We explored the effect of tree age and size on light distribution, yield and fruit sugar content in Utah commercial tart cherry orchards. A gradient of tree ages and size, expressed as trunk cross sectional area (TCSA), branch characteristics, and canopy dimensions, was established to explore the impact of training and management on production efficiency and fruit sugar content. We then used those relationships to identify current growing methods contributing to high yield and fruit quality and conclude with information for the continued development of high-density tart cherry systems.

Materials and Methods

Data Collection. The research was conducted in Utah Co., UT in commercial tart cherry orchards (*Prunus cerasus* 'Montmorency', *P. mahaleb*) representative of the region. Six to nine orchard blocks for each of five growers were sampled for tree size and canopy shape in May 2014, representing blocks between 5 and 30 years old. Growers represent various management strategies such as tree spacing, fertilization, irrigation, pruning, and crop load, which were analyzed primarily aggregated at the orchard level. Five individual trees were selected per orchard along a diagonal transect in the interior of the orchard for sampling in 38 blocks for a total of 190 trees. Each tree was measured for

trunk diameter (*trunk cross sectional area* = π * [*diameter* / 2] ^{2}), scaffold count, scaffold branch diameter, scaffold branch length, and scaffold branch angle. The cumulative scaffold branch cross sectional area (BCSA) was calculated as the sum of scaffold branch cross sectional areas.

Canopy volume measurements were taken from each major cardinal direction traveling diagonal to the row direction. In other words, if the tree rows are N-S, the first major cardinal direction chosen would be NE. For each direction, three points were measured as the distance from the trunk and height from the ground at the top curve, bottom curve, and maximum spread. Two more points were measured at the bottom and top of the canopy in line with the trunk. Volume was calculated as the sum of four vertically stacked geometric volume estimations, two cones and two frustums. The average distance from the trunk to canopy edge (*radius*) for the bottom tier of measurements and the average distance from the bottom canopy measurement and the inner canopy measurement at the trunk (*height*) were estimated as one cone (*volume* = *height* * π/3 * *radius*^{2}). The second cone was calculated similarly for the top tier of measurements and the top canopy measurement at the trunk. The inner sections of the tree canopy were estimated as frustums, or the volume between two ellipses. Each frustum is characterized by a top and bottom ellipse, with their area determined by a set of N-S and E-W diameters (d_1d_2, d_3d_4), and the average height between them.

$$volume = height * π/12 * (d_1d_2 + d_3d_4 + [d_1d_2d_3d_4]^{1/2})$$

For a subset of three orchard blocks per grower, the same five trees were visited in July 2014 consecutively throughout the day (08:00-18:00) over two days to measure light interception and fruit sugar content. Light intensity ($μmol\ m^{-2}\ s^{-1}$) was measured

using an Apogee Instruments MQ-306 quantum light meter with six sensors. Two tiers of light readings were taken at the base of the canopy and halfway to the top. For each reading, the light meter was inserted under or into the canopy the length of the meter (50 cm) directly towards the trunk and level to gravity. Readings were taken at each major cardinal direction and midway between [N, NE, E, SE, etc.]. Two additional readings were taken at the trunk (one at each tier) for a total of 18 readings per tree. A 'full sun' reading was taken as a baseline approximately every tree or more as needed if the 'full sun' level changed. 'Full sun' readings ranged greatly from mid-day clear sky (2400 μmol m^{-2} s^{-1}) to stormy overcast (100 μmol m^{-2} s^{-1}) during the two-day sampling period. To account for various light conditions throughout the sampling period, percent light absorbed was calculated as:

absorbed light = (full sun - light at canopy position) / full sun

Fruit sugar content was estimated by measuring fruit soluble solid concentration (^{O}Brix), using a standard handheld refractometer. Fruit samples were gathered for each major cardinal direction and at the trunk, for a total of five samples per tree. Five representative fruits were gathered within an arm's reach around the canopy and within an arm's reach into the canopy from each major cardinal direction position at the edge of the canopy to match the light sampling. The fruit were inserted into a large syringe with a filter. The syringe was squeezed upside-down and shaken to extract and mix the fruit liquids. A sample of liquid was placed on the glass slide of the refractometer and read for soluble solid concentration.

Yield per tree for growers 1-4 was reported by the regional processing and distribution facility for 2012-2015, estimated from the total yield per each block.

Data Analysis. Correlation among tree size measurements, yield, fruit sugar content, and light absorption were determined by simple ordinary least squares regression in R (lm(); Warton et al., 2006). In some cases, a polynomial function returned a higher r^2 than the linear function and was chosen as the best-fit model. Data were analyzed at multiple scales: within canopy, individual tree, block, and grower levels. Results are similar across scales and are reported primarily at the block level with blocks identified by grower.

Results and Discussion

The gradient in tree age and size was useful for exploring patterns in branch and canopy dimensions. Tree size consistently increased with age until about 20 years when canopy dimensions saturate and decline (Fig. 4-1). Tree size and age are strongly correlated, particularly for the age and TCSA relationship (Fig. 4-1A). The non-linear relationship of tree age and size revealed multiple stages in growth described by a linear establishment phase (0-15 years), a stable optimal phase (15-25), and a declining senescent phase (>25; Fig. 4-1B-D). Canopies fill available space towards the end of the establishment phase between 11-15 years (Fig. 4-1C). The multi-stage growth is not as evident in the age and TCSA relationship, which only showed a slow saturation following the establishment phase.

Tree size emerged as a superior indicator of structure and function than age when comparing orchard systems, confirming earlier claims for the study of grafted systems (Hinkley et al., 2011). Strong relationships were found among TCSA and canopy dimensions (Fig. 4-2). These relationships showed asymptotes around 300 cm^2 TCSA as
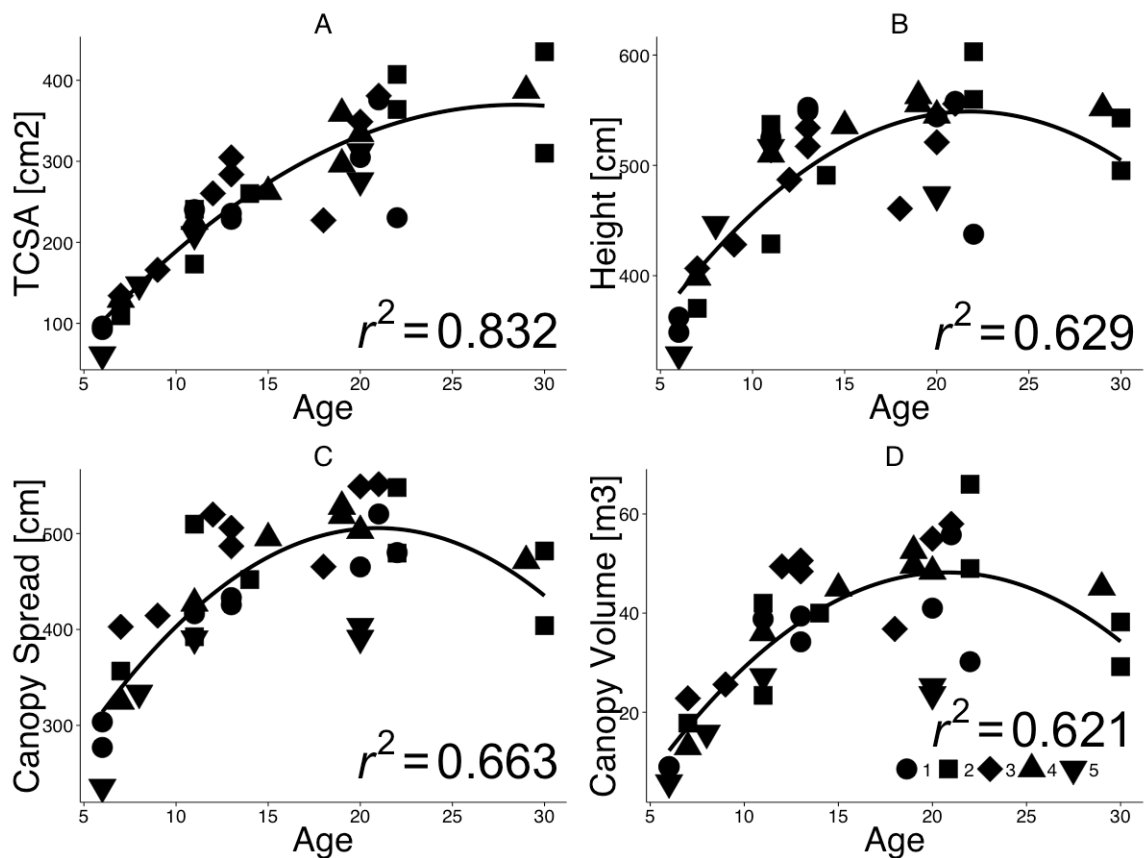
Fig. 4-1. The non-linear relationship of tree age with A) trunk cross sectional area (TCSA), B) height, C) canopy spread, and D) canopy volume at a block level for 'Montmorency' tart cherries on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2).
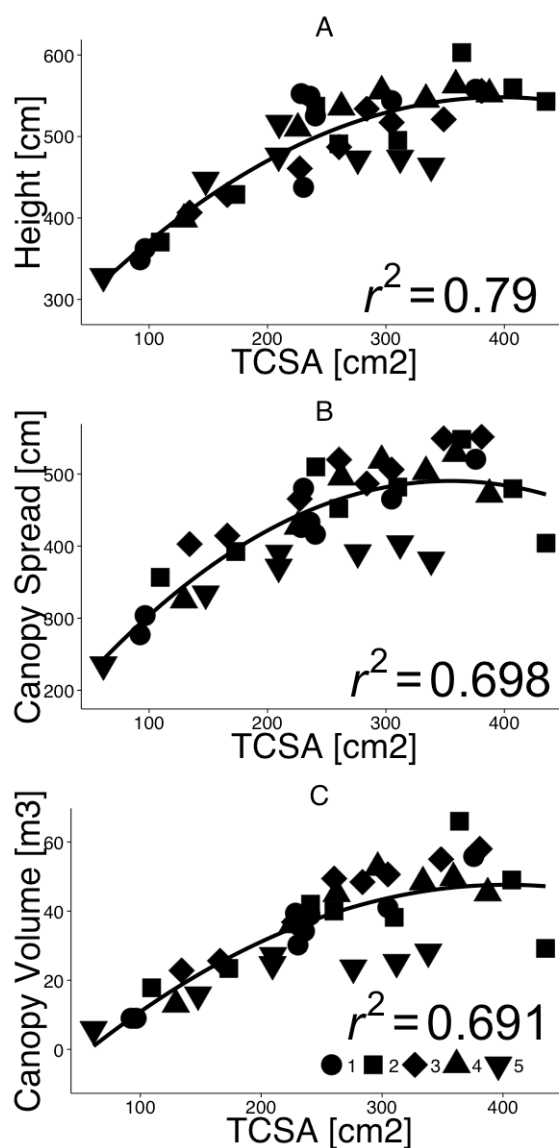
Fig. 4-2. The non-linear relationship of trunk cross sectional area (TCSA) with A) height, B) canopy spread, and C) canopy volume at a block level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2).

canopies meet spacing limits, but did not show any major declines following saturation. Other relationships related to tree size and branching structure, such as TCSA with BCSA and canopy height with scaffold length, were strongly correlated and largely invariant with tree size (Fig. C-1). Such strong relationships in tree size reveal patterns in branch architecture conserved with age and orchard system.

Yield and fruit sugar content declined with tree size and age (Fig. 4-3). Crop load and yields were at record highs across the region in the year sampled (Fig. C-2) with 23,000 metric tons harvested for the State of Utah, while average yields for Utah range from 11,000-14,000 metric tons (USDA, 2015). Tree size was not significantly correlated with yield per tree (Fig. 4-3A). Only minor declines in yield with tree size were observed, but crop load sharply declined with tree size. Senescent orchards declined in canopy size and were observed to include trees with diseased, dead, or removed scaffold branches, which may explain the overall decline in yield and average crop load. TCSA was inversely related to fruit sugar content saturating between 200 - 300 cm^2 (Fig. 4-3B). Height demonstrated a strong indirect relationship, while canopy spread and canopy volume also emerged as important factors related to fruit sugar content (Fig. C-3), suggesting canopy dimensions represent a more important influence on fruit sugar content than branch architecture. Yield increased weakly with TCSA expressed per age, though sugar content remained indirectly related (Fig. 4-3C,D). Individuals that are optimally managed for size may improve yields, but consequences of size in regards to fruit sugar content remain.

Tree size and canopy dimensions interact to affect fruit sugar content (Fig. 4-4). Yield, canopy height, and canopy spread expressed per TCSA were positively related
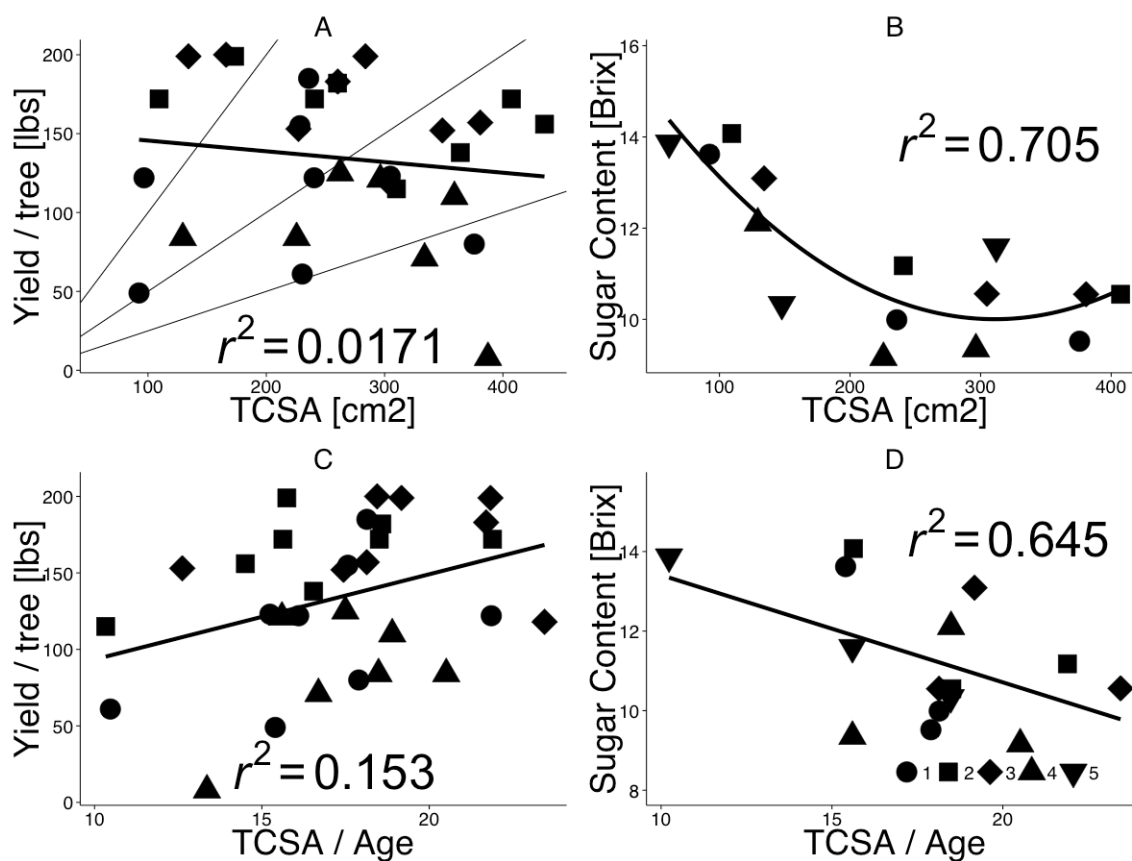
Fig. 4-3. The relationship of yield / tree and sugar content by tree size, as represented by trunk cross sectional area, and tree size standardized by age for 'Montmorency' tart cherries on Mahaleb seedling rootstocks for various growers in Utah Co. Each data point represents average values of five randomly selected individuals for each sampled block with yield data represented by the per tree average value of the total yield harvested for the block in 2014. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2). For subplot A, crop load isoclines (1, 0.5, and 0.25) are represented by thin lines.
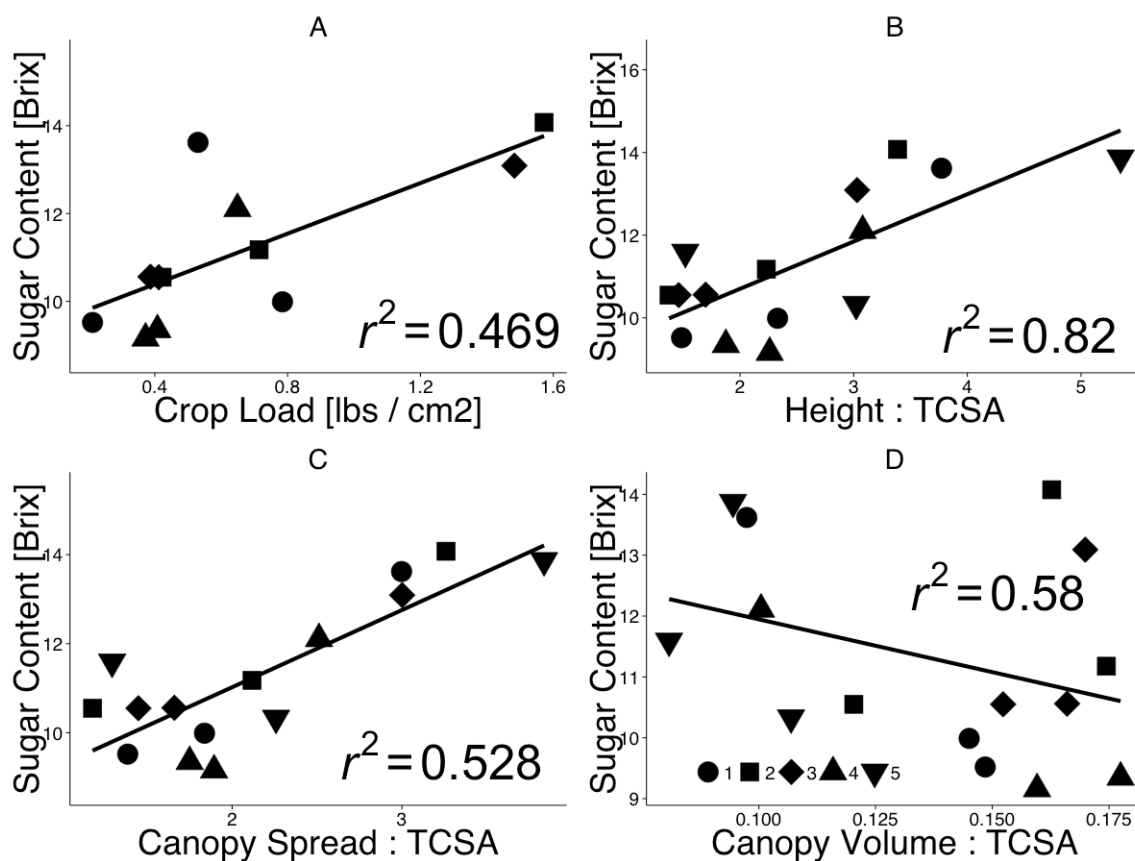
Figure 4-4. Drivers of fruit sugar content standardized by trunk cross sectional area (TCSA) at a block level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals with yield data represented by the per tree average value of the total yield harvested for the block in 2014. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2).

with fruit sugar content. In other words, individuals with higher crop load facilitated by a taller or wider canopy produce fruit with higher sugar content. These individuals may also express slimmer or younger branching structures driving increased crop load. Canopy volume per TCSA remained indirectly related to fruit sugar content (Fig 4-4D). It may be possible that the height and spread canopy dimensions contribute to improved light capture driving fruit sugar content, while overall increases in canopy volume contribute more interior shading than light capture potential. Larger canopies may produce a higher quantity of fruit, but quality tends to decline with increased fruit number and shading (Naschitz et al., 2010). High quality fruit has been demonstrated to grow on young branches (Hrotko et al., 2008). For optimum yield and fruit sugar content, management should focus on developing trees with more open canopy structures with less volume that have high light exposure and turnover of fruiting branches.

Surprisingly, there was no significant correlation with light ($r^2 < 0.2$) for any factor or scale tested, including fruit sugar content. The light environment was highly variable during sampling and may have contributed to the poor relationships with light. This is in contrast to a well-established positive relationship between light availability and fruit quality (Corelli-Grappadelli and Lakso, 2004). The expected positive relationship between light and fruit sugar content emerged when subsetting the data for relatively low light conditions ('full sun' < 1,000 μmol m^{-2} s^{-1}; Fig C-4). Light sampling during periods of diffuse light (i.e., dawn, dusk, overcast) may improve overall effectiveness of light readings and representation of canopy density because diffuse light is a better indicator of canopy leaf area that is not biased by the intensity of direct light (Anderson, 1964). Despite variable light conditions, only 6.4% (85 / 1,332) of light

measurements in the whole study were greater than the 30% light absorbance threshold established as a minimum for apple fruit production (Heinike, 1966; Forshey et al., 1992). This may indicate that tart cherry canopies are very quickly too dense for adequate light penetration to the canopy interior. We observed a high proportion of fruits at the canopy periphery suggesting suitable conditions for fruit set are restricted to the canopy periphery. Alternately, seasonal shifts in leaf development may impact our understanding of the canopy light distribution. Most fruit development occurs during early stages of growth when the surrounding leaf area is small and more light reaches the canopy interior (Kappes and Flore, 1986). Further evaluation of the canopy light distribution is needed throughout the season under optimal conditions to address the lack of any strong relationship between light and fruit sugar content.

Only minor differences in tree size and canopy dimensions were driven by differences in management among the growers sampled (Fig. C-5). Tree size and canopy dimensions were largely invariant with respect to grower, except for the maintenance of smaller canopy spread and volume in older individuals by grower 5 (Fig. 4-1C,D). These differences were less apparent with respect to TCSA (Fig. 4-2). Although not significant, growers may be stratified across a relative size gradient with a high proportion of grower 2 and grower 3 blocks represented by data points above the regression lines and grower 4 and grower 5 blocks represented by data points below the lines. Tree size in grower 1 blocks are scattered throughout. The stratification may indicate more or less aggressive fertilization and irrigation management strategies, with growers 2 and 3 managing most aggressively. The stratification of growers also emerged with respect to yield and sugar quality (Fig. 4-3, C-3, C-6), suggesting optimal growth leading up to maturity can

establish a high potential for yield and fruit quality (Rowley, 2013). In a soil amendment study with a partially similar group of growers, Rowley (2013) found that some orchards are already functioning at maximum fruit production and aggressive fertility treatments only improved fruit production for growers with deficient soil nutrients. Other direct factors of management were explored that did not contribute significantly to yield or fruit quality at the orchard system level, but contribute to driving factors related to tree size and canopy dimensions. For instance, scaffold branch angle may contribute to canopy spread and tree spacing may affect canopy development and light capture (Fig. C-7). Tree spacing may also impact yields per acre as growers transition to orchard systems that manage smaller trees in higher density (Fig. C-8). Overwhelmingly, orchard system-level factors of tree size drive yield and fruit quality. Management should focus on efficient early growth to quickly reach maturity and maintain canopy height and spread to improve light capture, yield, and fruit sugar content.

Conclusions

Tree size and canopy dimension drives yield and fruit quality in tart cherry. Yield and fruit quality decline with tree size and age. Small trees with open canopies facilitated by canopy height and spread are yield efficient and produce high quality fruit. Higher crop load and fruit quality in smaller tart cherry trees are consistent with physiological patterns in tree size and fruit quality established for other crops suited to high-density systems driven by physiological efficiency of small tree size with more open space and better light penetration (Fideghelli et al., 2003; Lauri and Claverie, 2008). Tart cherry

may be particularly well suited to a high-density system due to its growth habit to wide

branch angles (Chapter II). Growing tart cherry in a high-density system will require

maintenance of open canopies, including renewal pruning of two to four year-old

branches (Hrotko et al., 2008). In high-density planting, canopies should be designed to

facilitate growth in two-dimensions, such as height and spread, but not the third

dimension so as to limit shading from canopy volume. Establishment growth should be

facilitated to fill the available space quickly with a high number of slender branches. For

orchards with ~427 trees/ha, optimal space filling occurs at 14 years or 250 cm^2 TCSA.

Branches should be renewed in a pattern that maintains young fruiting wood and high

light availability. Tart cherry remains a strong candidate for high-density planting with

growing evidence and trials evaluating effective management strategies. Evidence from

current commercial low-density systems supports better pruning to open up the canopy

and improve light penetration as fruit sugar content increases with smaller canopy

dimensions. Future plantings may shift to facilitate more effective canopy structures with

a transition to smaller tree size in high-density systems.

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CHAPTER V

CONCLUSION

Smaller trees are more physiologically and production efficient in orchard systems. In orchard systems, smaller trees are maintained primarily using dwarfing rootstocks and pruning that facilitate younger and slenderer growth with higher metabolic activity. Relative to their size measured by branch and canopy dimensions, smaller trees tend to partition more available resources to reproductive output than structural materials. As such, high-density management systems that facilitate small trees improve production efficiency by facilitating an increase in physiological efficiency towards fruit development (Fideghelli et al., 2003). High-density systems are also well suited for mechanization, which can improve resource use, labor requirements, and economic efficiency (Lang, 2005). With the management of small trees in high-density systems, physiological efficiency, production efficiency, and economic efficiencies are improved together.

This dissertation research supports the continued development of orchard systems that maintain small trees to improve physiological and production efficiency. Orchard tree growth and production was explored using a physiologically-driven modeling approach combining empirical observation within a theoretical context derived from the study of wild plants, called allometry. Tree size, architecture, and biomass of apple (*Malus* spp., 'Golden Delicious') and tart cherry (*Prunus cerasus*, *mahaleb*) followed strong allometric patterns that were broadly consistent among the two orchard tree species and the theoretical expectations derived from wild plants (Chapter II). The most consistent relationship was the trunk diameter (or trunk cross sectional area) ~ stem

biomass relationship, which broadly followed the 8/3-power law (Niklas and Spatz, 2004). Branch and canopy dimensions that include a measure of length, such as branch length and canopy height, revealed an architecture indicative of high water efficiency and metabolic activity that is relieved from the biomechanical constrains of weight bearing (Price et al, *preprint*). Differences in production efficiency were found for a tree size gradient of 'Golden Delicious' apple rootstocks with individuals that express small branch and canopy dimensions producing a higher proportion of fruit relative to tree size (Chapter III). In commercial tart cherry orchards, smaller individuals with relatively larger canopy height and spread were found to express higher fruit quality (Chapter IV). This dissertation improves scientific understanding of physiological and production efficiency and supports continued development of dwarfing rootstocks and orchard management strategies for small tree size across orchard species and systems.

The study of physiological and production efficiency among orchard species and management systems reveals general patterns that may emerge universally for plant growth and reproduction. Such an understanding of commonalities among tree fruit, or all extant tree species, is an important step in horticulture research. Modern advancements in computationally intensive analysis have facilitated deeper understanding into general plant function and crop production. Efforts in computer simulation, empirical modeling, and theoretical formulations improve prediction of tree architecture, biomass partitioning, and fruit production (Niklas and Enquist, 2003; Allen et al., 2005; Lang and Lang, 2008). As data acquisition and analytical techniques advance, horticultural research will benefit through the understanding of physiological drivers of plant growth and reproduction and the mechanisms underlying orchard system improvement. These advanced data

acquisition and analytical efforts may then bridge biological and economic scales to link physiological, agroecosystem, and food system levels.

While improvements in physiological and production efficiency from small tree size support the development of more intense high-density orchard systems, system-wide health may not be correlated with such intensification. Other consequences arise from the intensification and mechanization of these systems that can have negative impacts on other aspects of plant function, such as over-cropping, and can have broader implications for plant health and agroecosystem function, such as disease incidence. Trees that are managed for small size tend to overproduce and require application of plant hormones and growth regulators that control fruit set (Patracek et al., 2003). Other agricultural chemicals are also used to increase fruit size, synchronize ripening, and aid in mechanical harvest. Orchard systems that use small trees plant individuals in high-density monoculture, which increases the incidence of disease and pest outbreaks (Vandermeer, 2011). These issues quickly become high priorities for research and management to maintain fruit production, fruit quality and economic stability for which agricultural chemicals supply a quick and readily available solution. Physiological and production efficiency are important goals for orchard system development that must be balanced with other outcomes of intensive cropping to ensure plant health, economic security, and sustainability of fruit production. As research and management continues working to balance biological and economic efficiency, cultural solutions that improve the physiological and ecological properties of the system should be priories for long-term solutions.

Factors contributing to physiological, agroecosystem, and food system level

health are important considerations in determining the overall efficiency, resilience,

and sustainability of orchard systems. Ecologically minded solutions for sustainability in

agriculture and fruit production are gaining credibility and adoption to complement

improved efficiency in plant physiology (National Research Council, 2010). USDA

National Institute of Food and Agriculture operates under a definition of 'sustainable

agriculture' that has recently experienced widespread adoption. Sustainability in

agriculture seeks to: "Satisfy human food and fiber needs; Enhance environmental quality

and the natural resource base upon which the agriculture economy depends; Make the

most efficient use of nonrenewable resources and on-farm resources and integrate, where

appropriate, natural biological cycles and controls; Sustain the economic viability of farm

operations; and, Enhance the quality of life for farmers and society as a whole" (U.S.

Code Title 7, Section 3103). Innovative growers and research programs provide

continued support for adoption of management strategies that facilitate sustainability and

ecological principles, such as resilience and biodiversity, in agriculture (Palmer and

Wunsche, 2004; Brym and Reeve, 2016). 'Integrated' solutions are also important

contributions to fruit production that aid the transition from chemically-driven

management strategies to alternate sustainable solutions (Avilla and Riedl, 2003).

Available knowledge and technologies should be used to maintain fruit production and

agroecosystem health, while long-term systems-driven research in orchard management

should promote overall sustainability in fruit production.

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APPENDICES

Appendix A. Additional figures for Chapter II
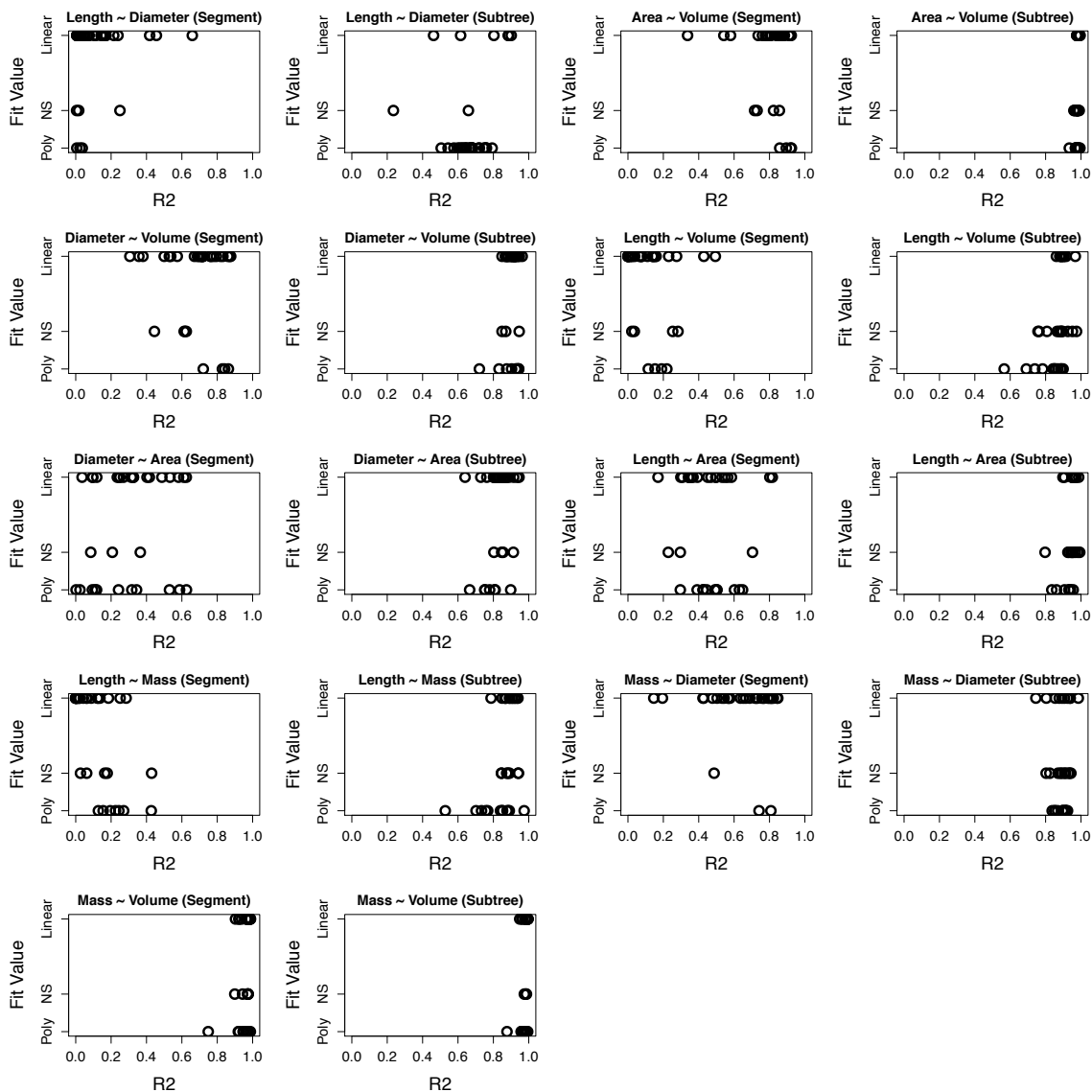
Figure A-1-1. Detailed summary of strongest model fitted and the r^2 of the linear model. The linear or polynomial (Poly) model with the lower AIC was determined to be the best fit. The polynomial model was further determined to be not significant (NS) if the 2*standard error of the polynomial term overlapped with 0.
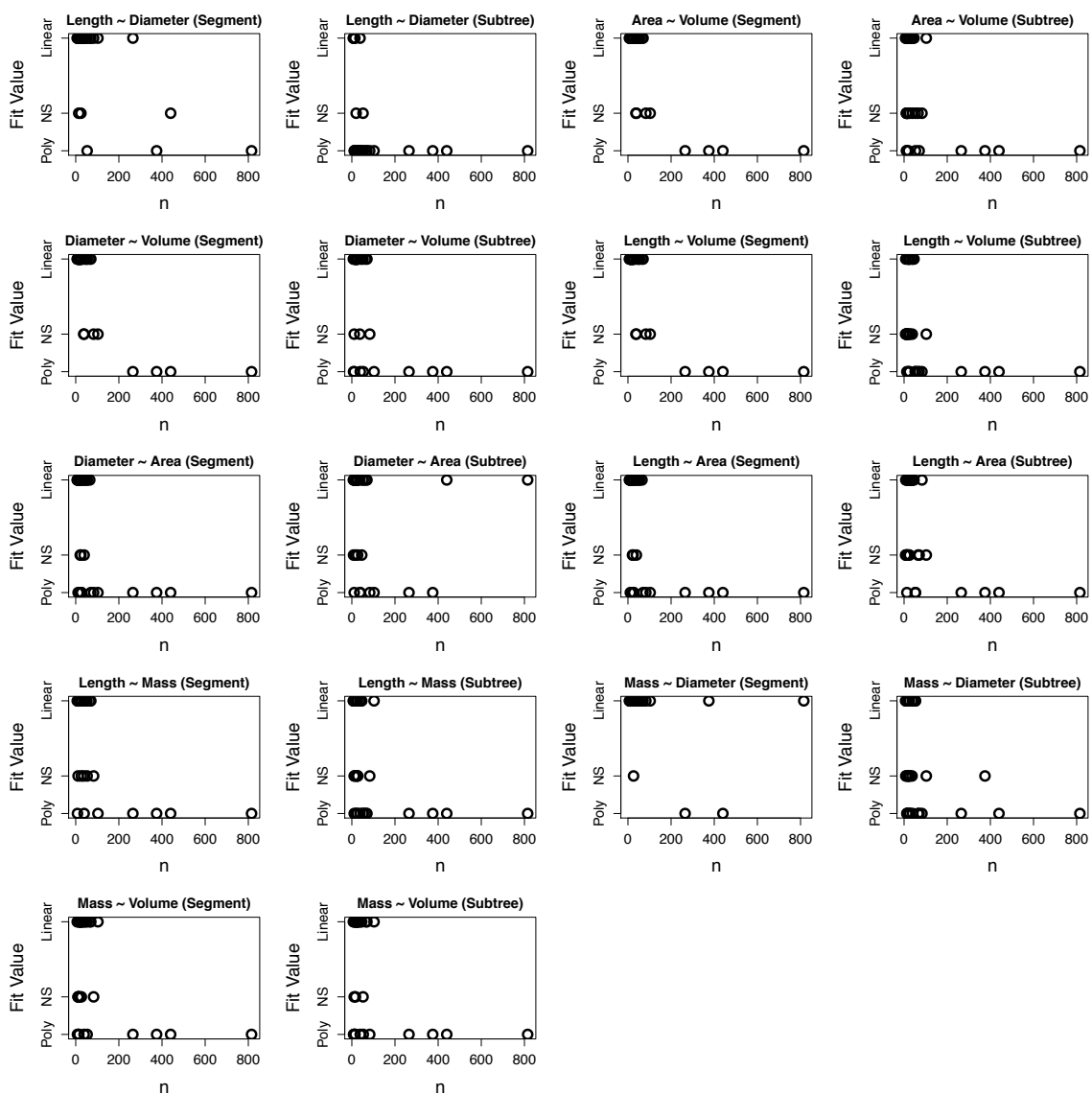
Figure A-1-2. Detailed summary of strongest model fitted and the group sample size (n). The linear or polynomial (Poly) model with the lower AIC was determined to be the best fit. The polynomial model was further determined to be not significant (NS) if the 2*standard error of the polynomial term overlapped with 0.
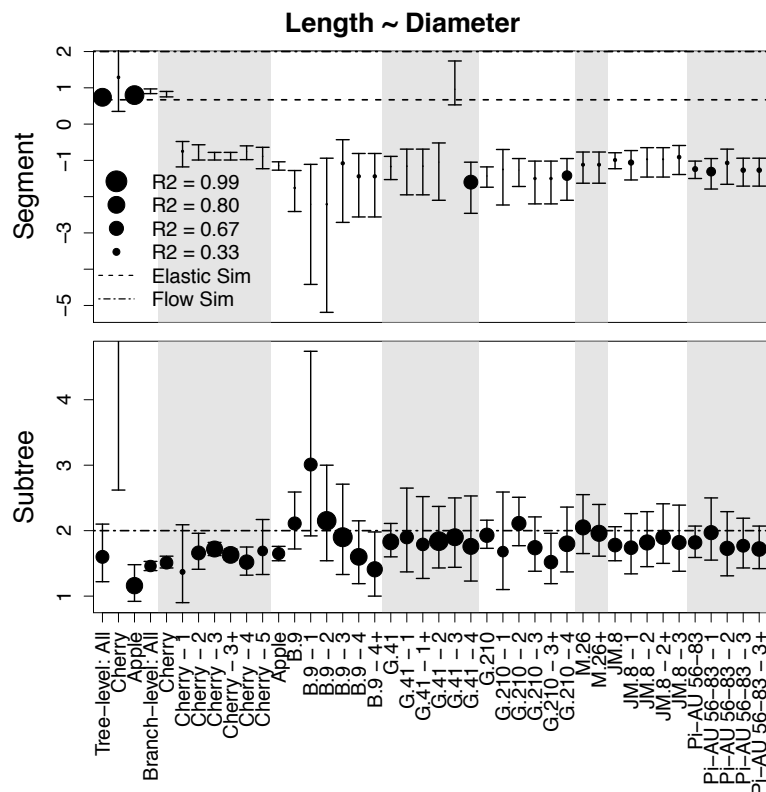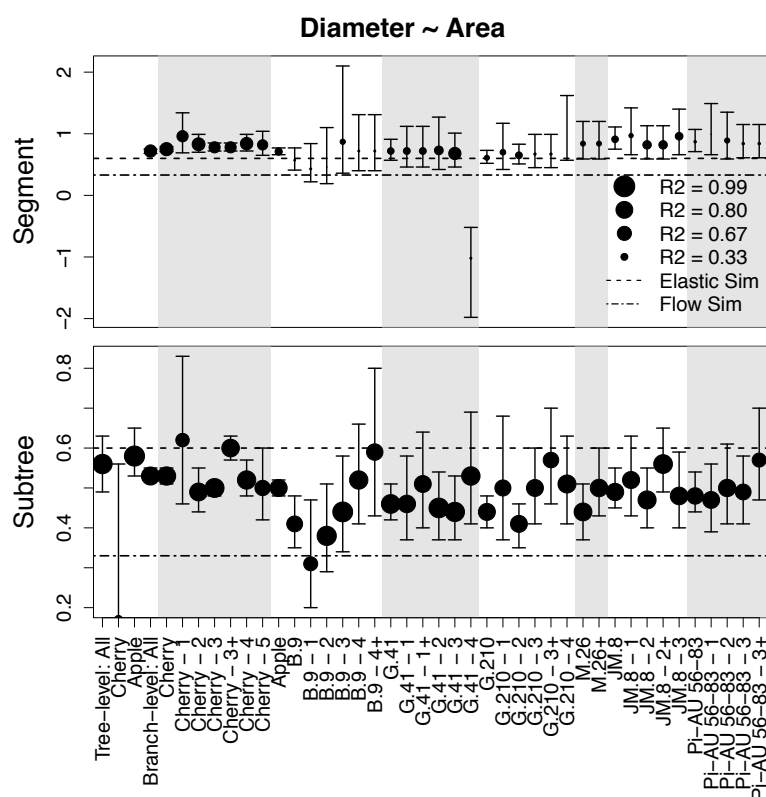
Figure A-2-1. Estimates of allometric exponent (*a*) and 95% confidence intervals for five

24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden

Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for

each branch-level classification: segment and subtree. The groups are organized roughly

by shaded region. The first group (white space) are the tree-level data, except for the 'all-

branch' group for all branches collected in the dataset. The remaining groups are branch-

level data broken down by species (tart cherry, apple) and the rootstock abbreviations for

apples. Individuals are identified by a hyphen and an individual number. The addition of

the '+' indicates the individuals that were sampled in more detail and include twig length

and mass data noted by a '+'. The predicted *a* from the process-bases models are marked

as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a

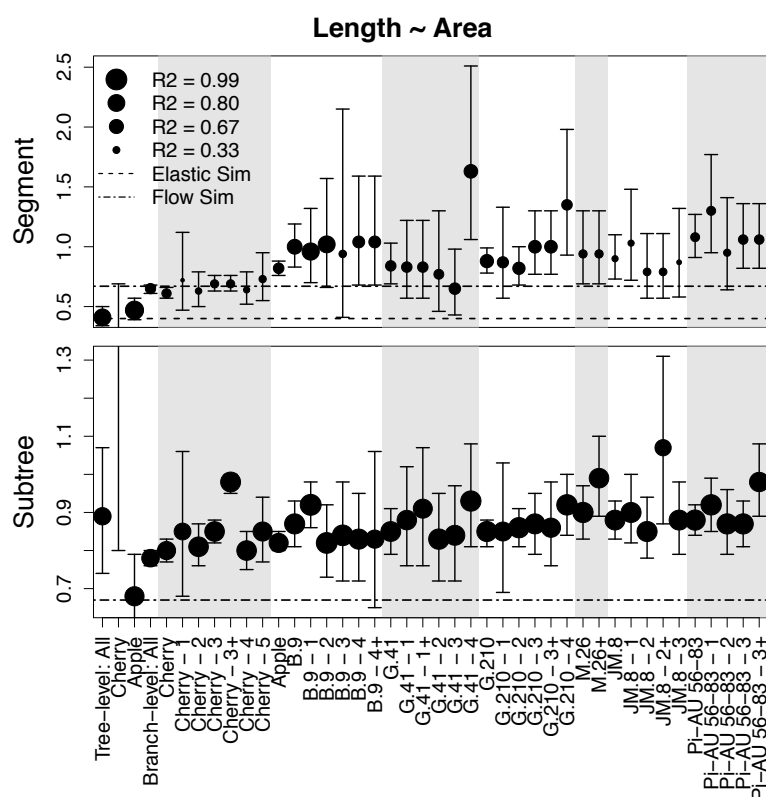dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.

Figure A-2-2. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for each branch-level classification: segment and subtree. The groups are organized roughly by shaded region. The first group (white space) are the tree-level data, except for the 'all-branch' group for all branches collected in the dataset. The remaining groups are branch-level data broken down by species (tart cherry, apple) and the rootstock abbreviations for apples. Individuals are identified by a hyphen and an individual number. The addition of the '+' indicates the individuals that were sampled in more detail and include twig length and mass data noted by a '+'. The predicted *a* from the process-bases models are marked as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.
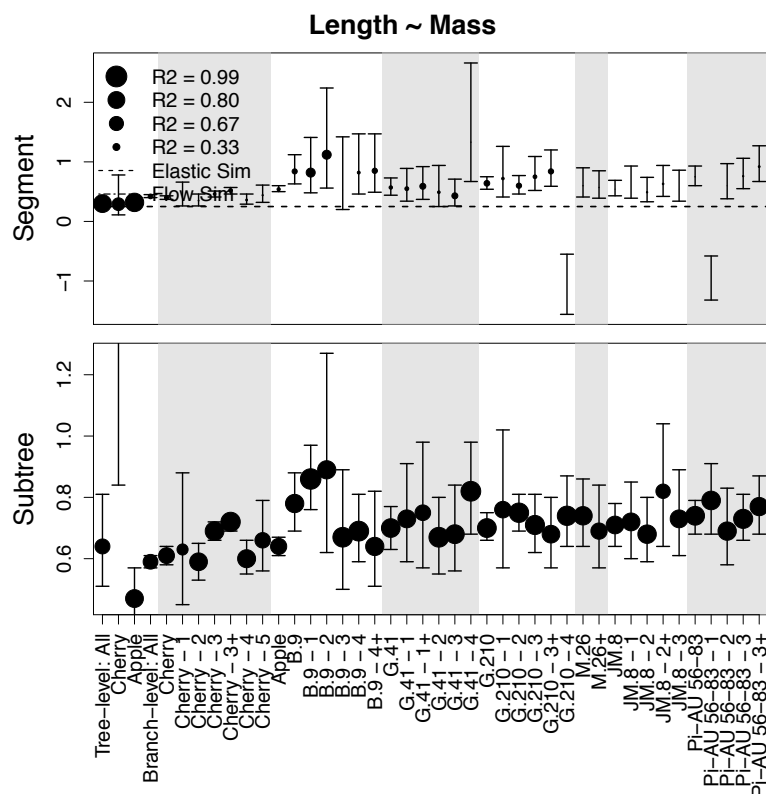
Figure A-2-3. Estimates of allometric exponent (*a*) and 95% confidence intervals for five

24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden

Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for

each branch-level classification: segment and subtree. The groups are organized roughly

by shaded region. The first group (white space) are the tree-level data, except for the 'all-

branch' group for all branches collected in the dataset. The remaining groups are branch-

level data broken down by species (tart cherry, apple) and the rootstock abbreviations for

apples. Individuals are identified by a hyphen and an individual number. The addition of

the '+' indicates the individuals that were sampled in more detail and include twig length

and mass data noted by a '+'. The predicted *a* from the process-bases models are marked

as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a

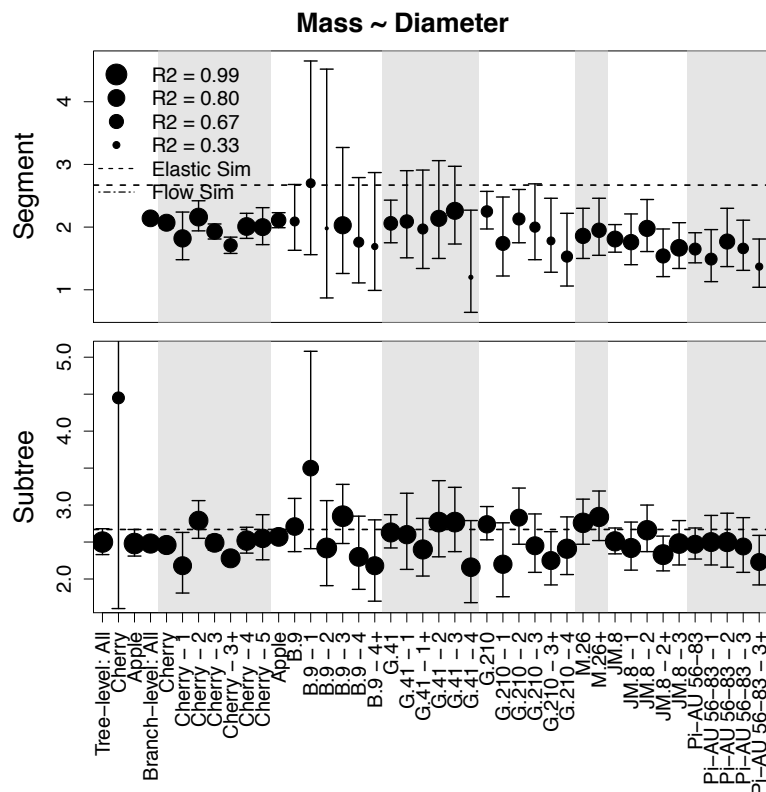dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.

Figure A-2-4. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for each branch-level classification: segment and subtree. The groups are organized roughly by shaded region. The first group (white space) are the tree-level data, except for the 'all-branch' group for all branches collected in the dataset. The remaining groups are branch-level data broken down by species (tart cherry, apple) and the rootstock abbreviations for apples. Individuals are identified by a hyphen and an individual number. The addition of the '+' indicates the individuals that were sampled in more detail and include twig length and mass data noted by a '+'. The predicted *a* from the process-bases models are marked as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.
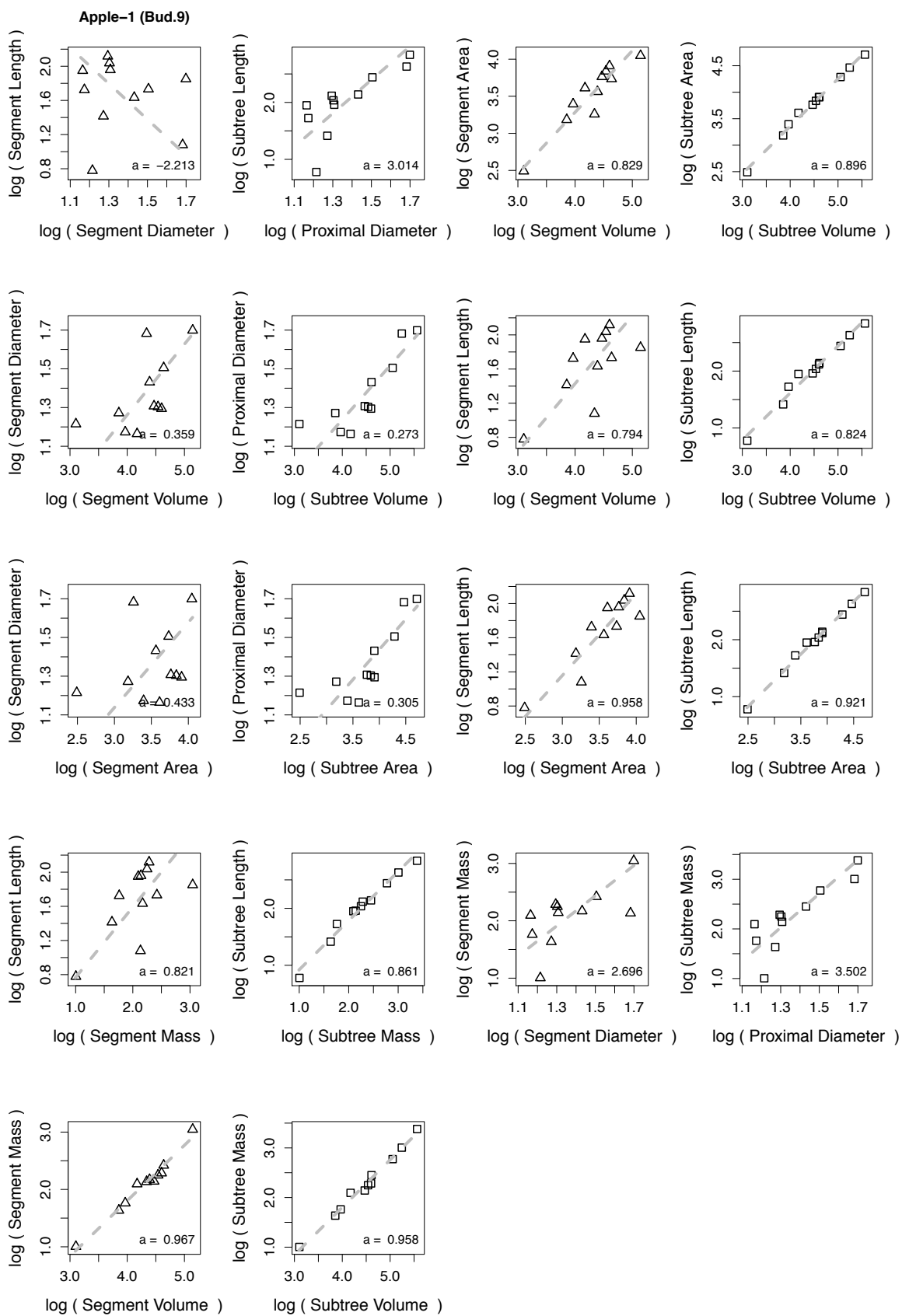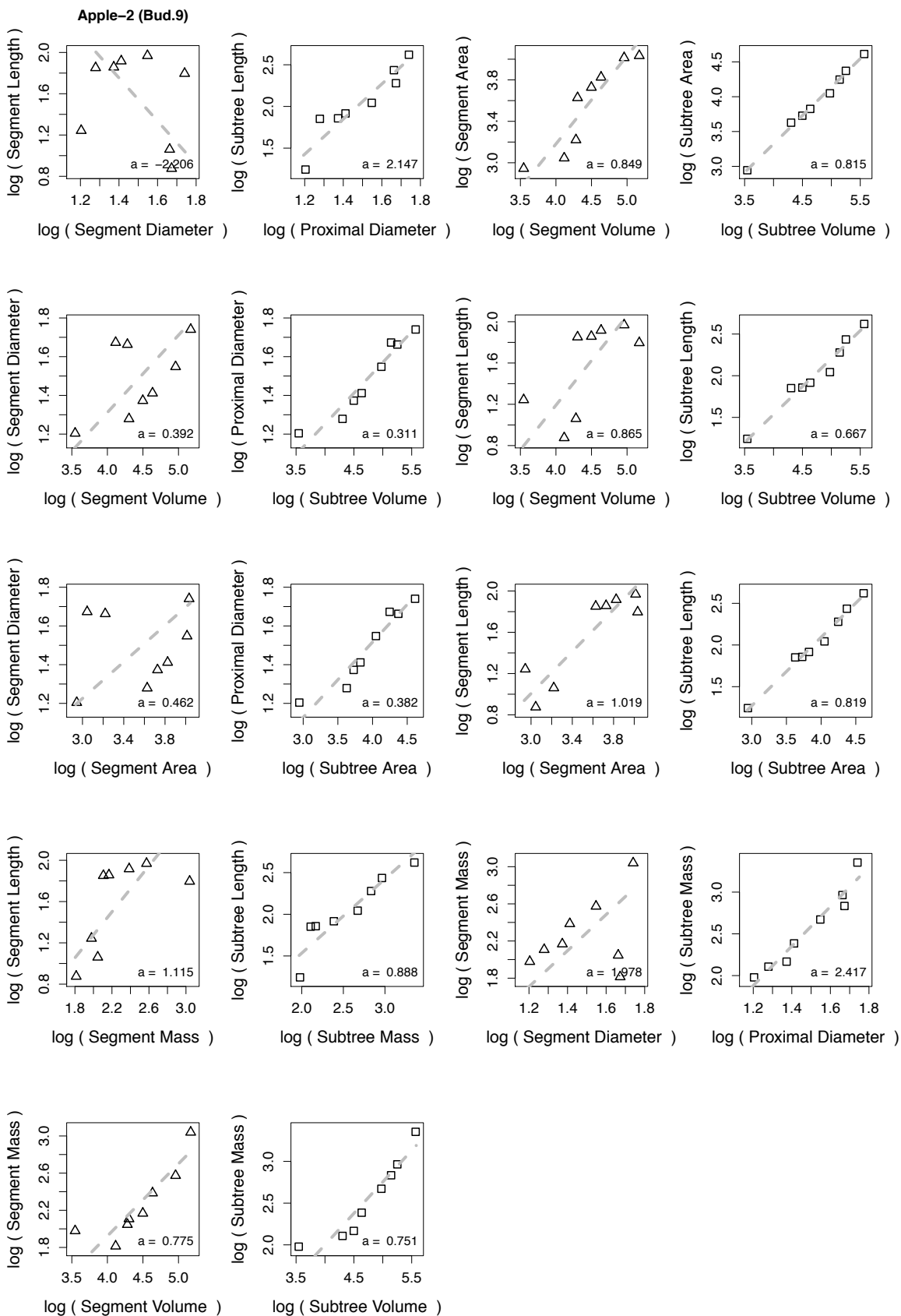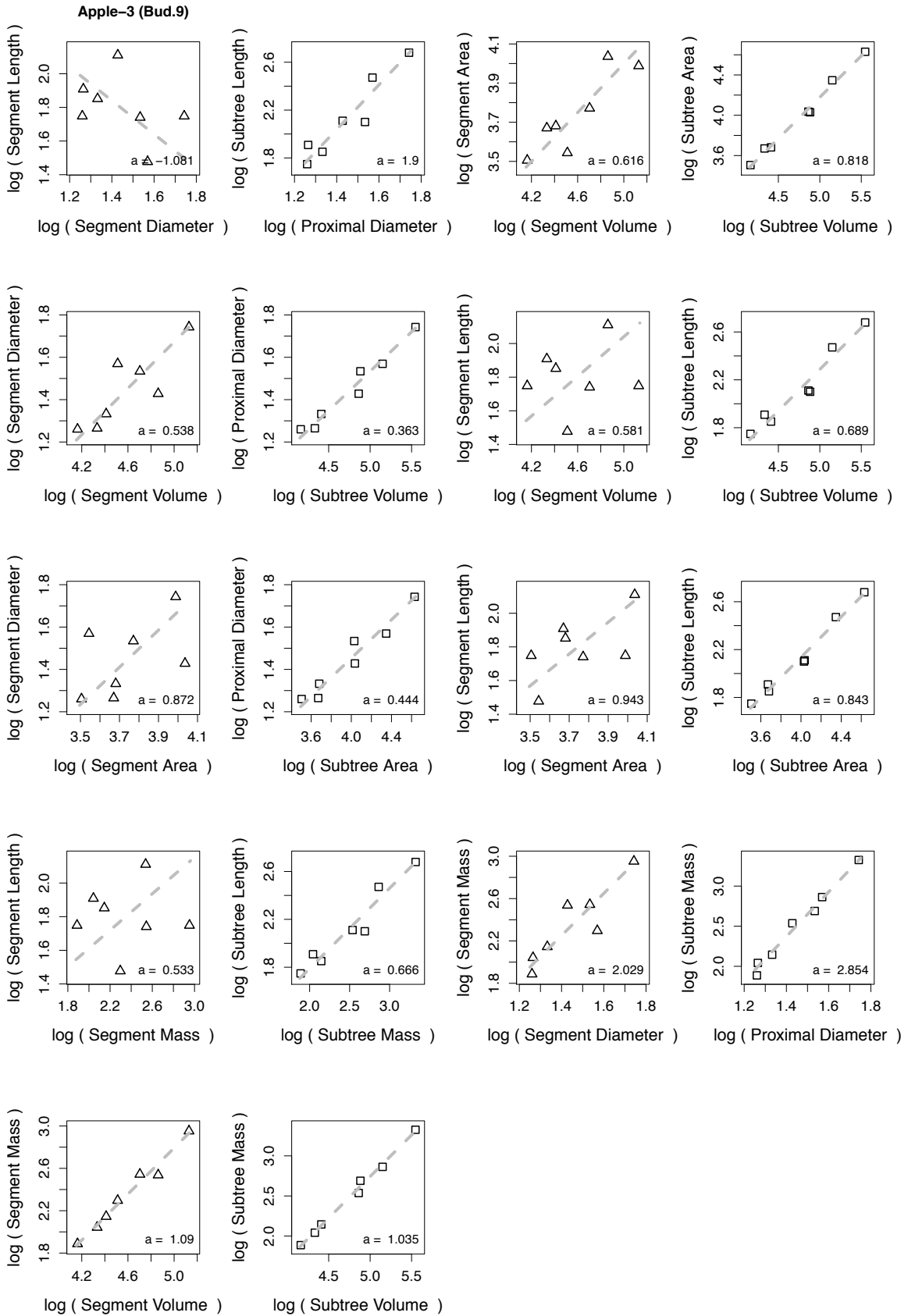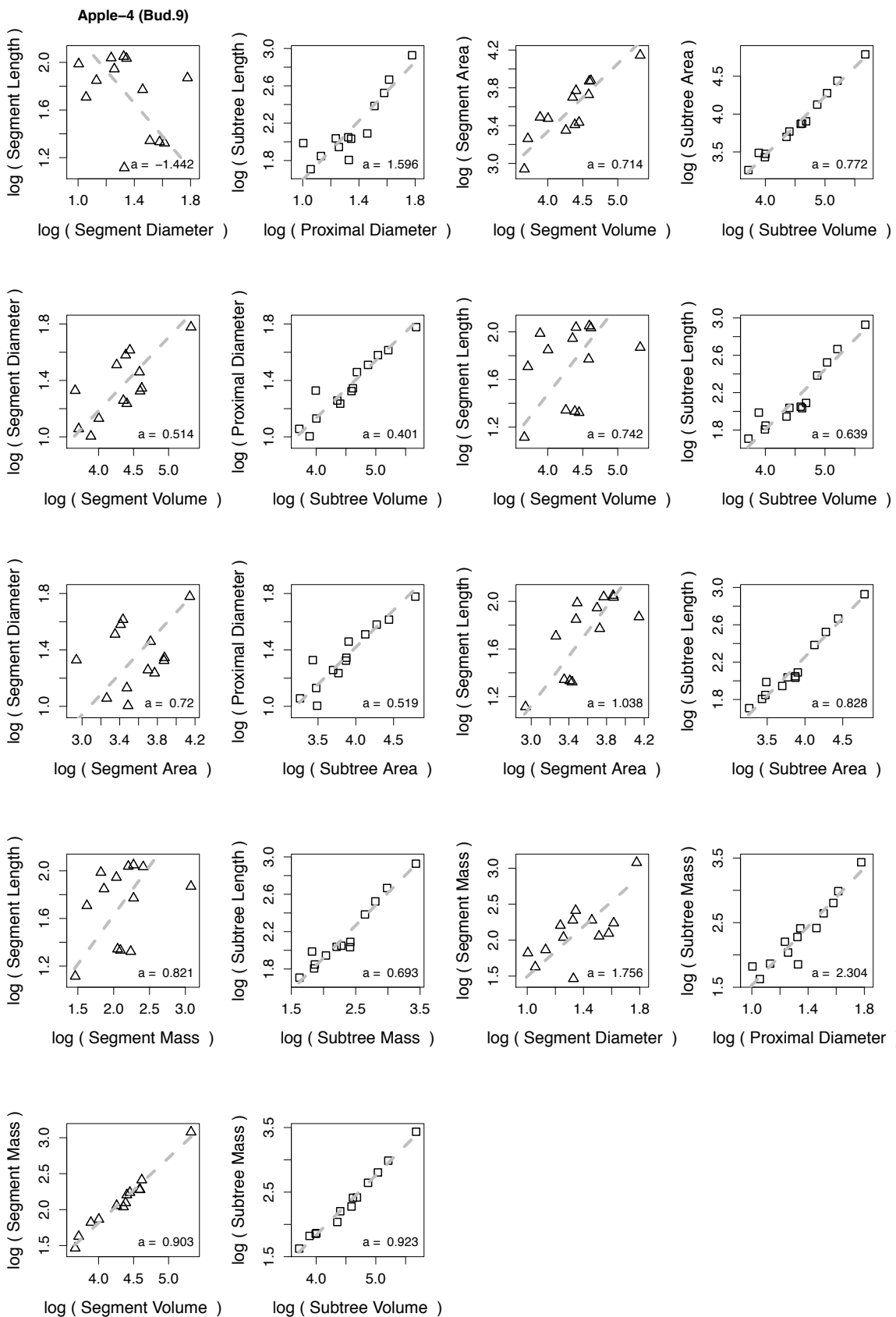
Figure A-2-5. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for each branch-level classification: segment and subtree. The groups are organized roughly by shaded region. The first group (white space) are the tree-level data, except for the 'all-branch' group for all branches collected in the dataset. The remaining groups are branch-level data broken down by species (tart cherry, apple) and the rootstock abbreviations for apples. Individuals are identified by a hyphen and an individual number. The addition of the '+' indicates the individuals that were sampled in more detail and include twig length and mass data noted by a '+'. The predicted *a* from the process-bases models are marked as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.

Figure A-2-6. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for each branch-level classification: segment and subtree. The groups are organized roughly by shaded region. The first group (white space) are the tree-level data, except for the 'all-branch' group for all branches collected in the dataset. The remaining groups are branch-level data broken down by species (tart cherry, apple) and the rootstock abbreviations for apples. Individuals are identified by a hyphen and an individual number. The addition of the '+' indicates the individuals that were sampled in more detail and include twig length and mass data noted by a '+'. The predicted *a* from the process-bases models are marked as horizontal lines. The predicted *a* from the FS model: elastic similarity is marked by a dashed line and flow similarity by a dot-dash line. R^2 is shown by scaled dot size.

Figure A-2-7. Estimates of allometric exponent (*a*) and 95% confidence intervals for five 24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for each branch-level classification: segment and subtree. The groups are organized roughly by shaded region. The first group (white space) are the tree-level data, except for the 'all-branch' group for all branches collected in the dataset. The remaining groups are branch-level data broken down by species (tart cherry, apple) and the rootstock abbreviations for apples. Individuals are identified by a hyphen and an individual number. The addition of the '+' indicates the individuals that were sampled in more detail and include twig length and mass data noted by a '+'. The predicted *a* from the process-bases models are marked as horizontal lines. The predicted *a* from the WBE model is marked by a dashed line. R^2 is shown by scaled dot size.

Figure A-2-8. Estimates of allometric exponent (*a*) and 95% confidence intervals for five

24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden

Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for

each branch-level classification: segment and subtree. The groups are organized roughly

by shaded region. The first group (white space) are the tree-level data, except for the 'all-

branch' group for all branches collected in the dataset. The remaining groups are branch-

level data broken down by species (tart cherry, apple) and the rootstock abbreviations for

apples. Individuals are identified by a hyphen and an individual number. The addition of

the '+' indicates the individuals that were sampled in more detail and include twig length

and mass data noted by a '+'. The predicted *a* from the process-bases models are marked

as horizontal lines. The predicted *a* from the WBE model is marked by a dashed line. R^2

is shown by scaled dot size.

Figure A-2-9. Estimates of allometric exponent (*a*) and 95% confidence intervals for five

24-year-old tart cherry (*Prunus cerasus*; *P.* mahaleb) and nineteen 10-year-old 'Golden

Delicious' apple (*Malus spp.*; various rootstocks) at an individual and group level for

each branch-level classification: segment and subtree. The groups are organized roughly

by shaded region. The first group (white space) are the tree-level data, except for the 'all-

branch' group for all branches collected in the dataset. The remaining groups are branch-

level data broken down by species (tart cherry, apple) and the rootstock abbreviations for

apples. Individuals are identified by a hyphen and an individual number. The addition of

the '+' indicates the individuals that were sampled in more detail and include twig length

and mass data noted by a '+'. R^2 is shown by scaled dot size.

Figure A-3. Data visualization for each allometric relationship at an individual level. Each individual in the data set (19 apple; 5 tart cherry) are depicted in order of trunk diameter per page. Each apple is identified by its rootstock noted in parentheses. Data points correspond to branches at each branch-level classification. Segment level estimates are marked by triangles and subtree by squares. Dashed lines mark the estimated exponent (a) displayed on the figure.

Apple−1 (Bud.9)

Apple–2 (Bud.9)

Apple–3 (Bud.9)

Apple−4 (Bud.9)

Apple–5 (G.41)

Apple–6 (G.41)

Apple−7 (G.41)

Apple–8 (G.41)

Apple–9 (G.210)

Apple−10 (G.210)

Apple–11 (G.210)

Apple−12 (G.210)

Apple−13 (M.26)

Apple−14 (JM.8)

Apple−15 (JM.8)

log (Segment Length) vs log (Segment Diameter), a = 0.972

log (Subtree Length) vs log (Proximal Diameter), a = 1.824

log (Segment Area) vs log (Segment Volume), a = 0.608

log (Subtree Area) vs log (Subtree Volume), a = 0.793

log (Segment Diameter) vs log (Segment Volume), a = 0.497

log (Proximal Diameter) vs log (Subtree Volume), a = 0.372

log (Segment Length) vs log (Segment Volume), a = 0.482

log (Subtree Length) vs log (Subtree Volume), a = 0.678

log (Segment Diameter) vs log (Segment Area), a = 0.817

log (Proximal Diameter) vs log (Subtree Area), a = 0.468

log (Segment Length) vs log (Segment Area), a = 0.793

log (Subtree Length) vs log (Subtree Area), a = 0.854

log (Segment Length) vs log (Segment Mass), a = 0.49

log (Subtree Length) vs log (Subtree Mass), a = 0.685

log (Segment Mass) vs log (Segment Diameter), a = 1.982

log (Subtree Mass) vs log (Proximal Diameter), a = 2.664

log (Segment Mass) vs log (Segment Volume), a = 0.984

log (Subtree Mass) vs log (Subtree Volume), a = 0.99

Apple−16 (JM.8)

Apple−17 (PiAu.5683)

Apple−18 (PiAu.5683)

Apple−19 (PiAu.5683)

Cherry-1

Cherry-2

Cherry-3

Cherry–4

Cherry–5
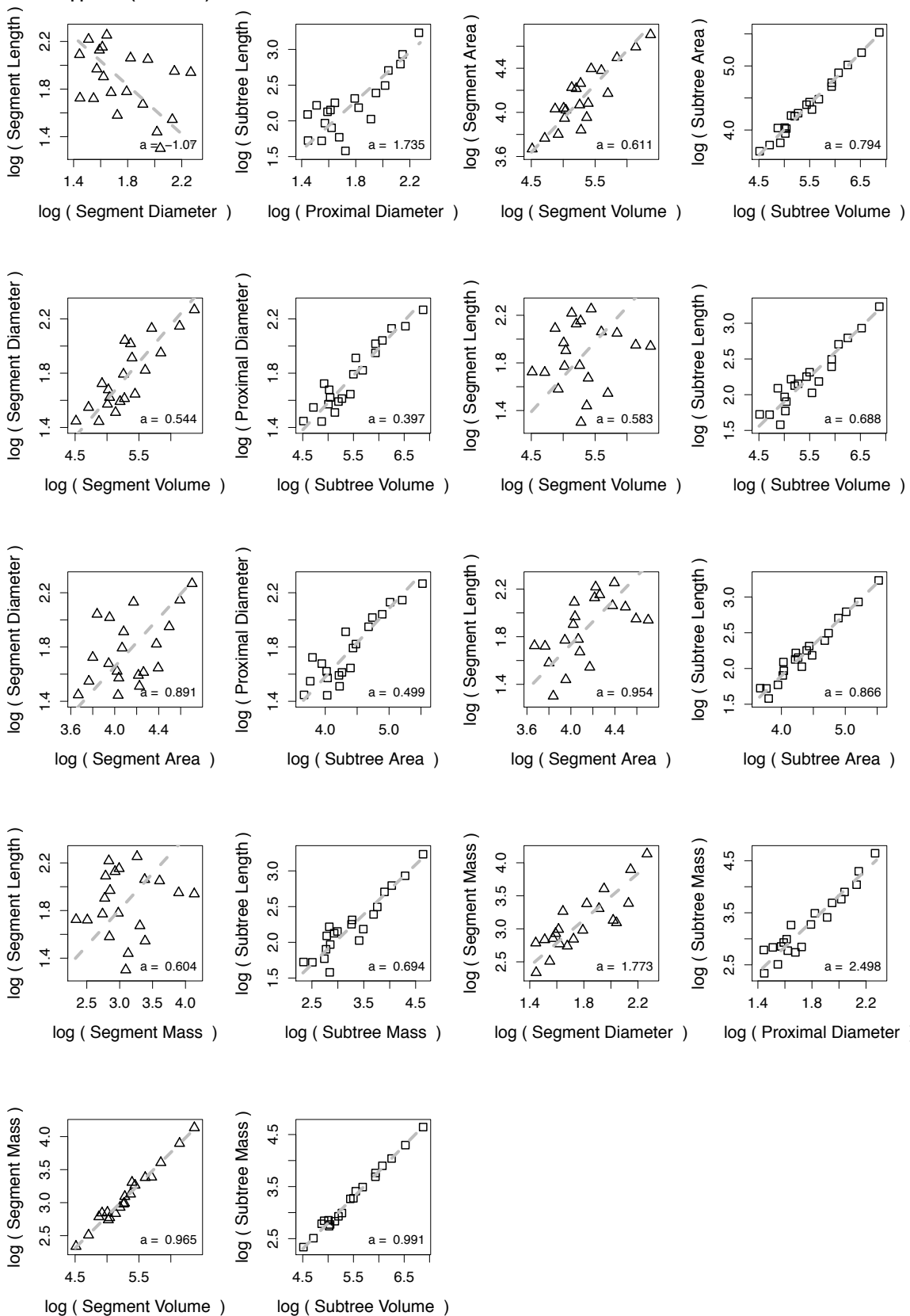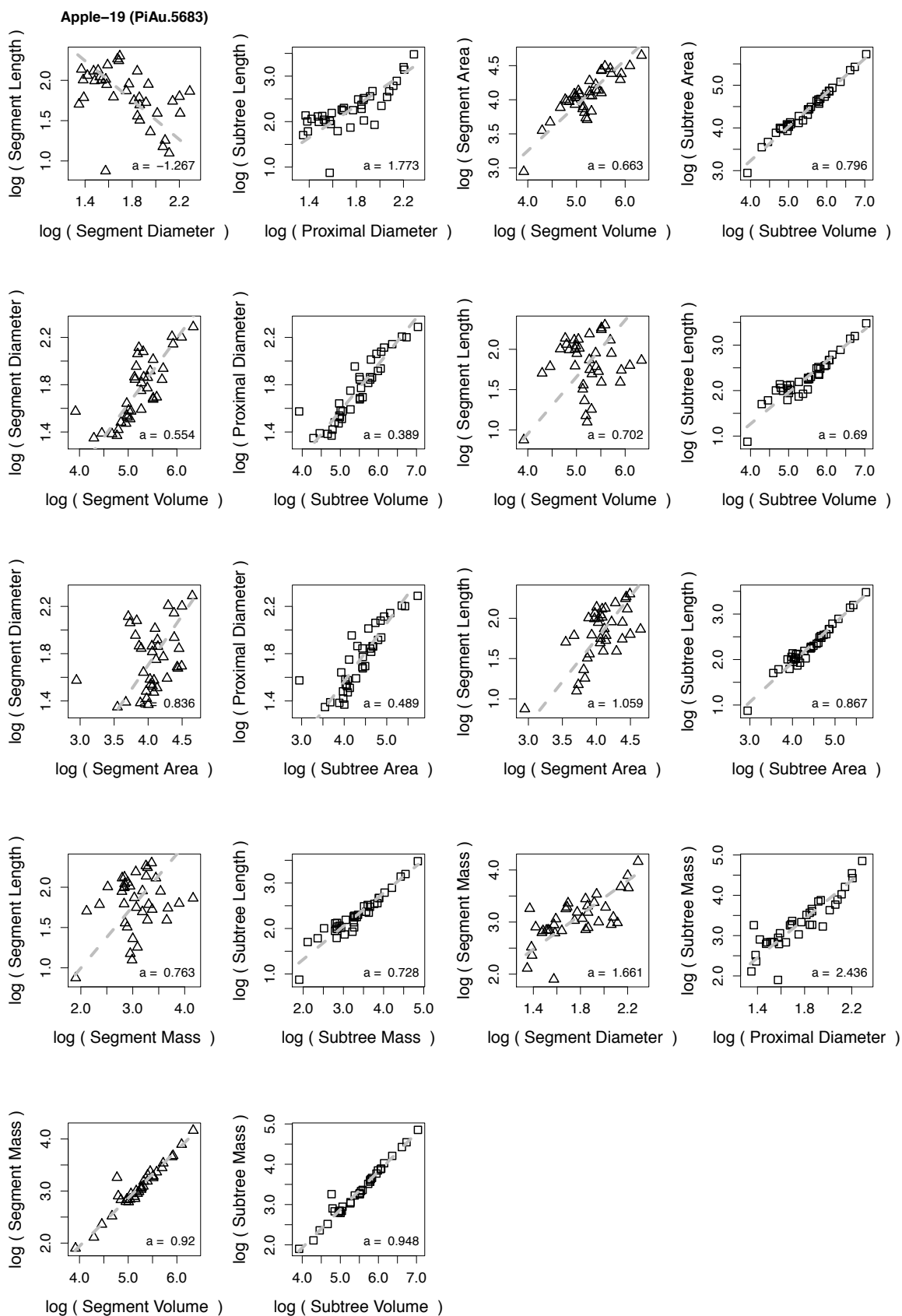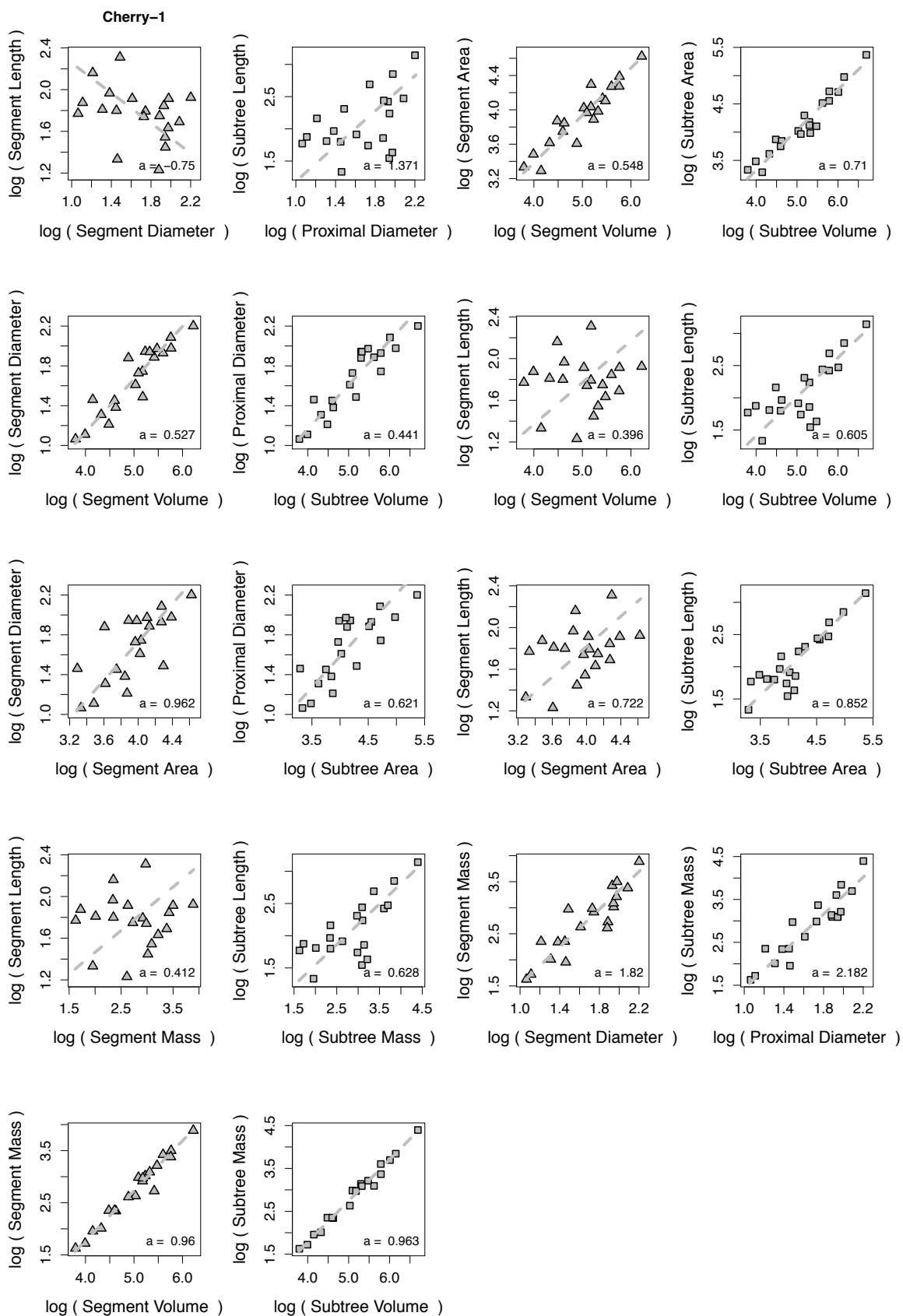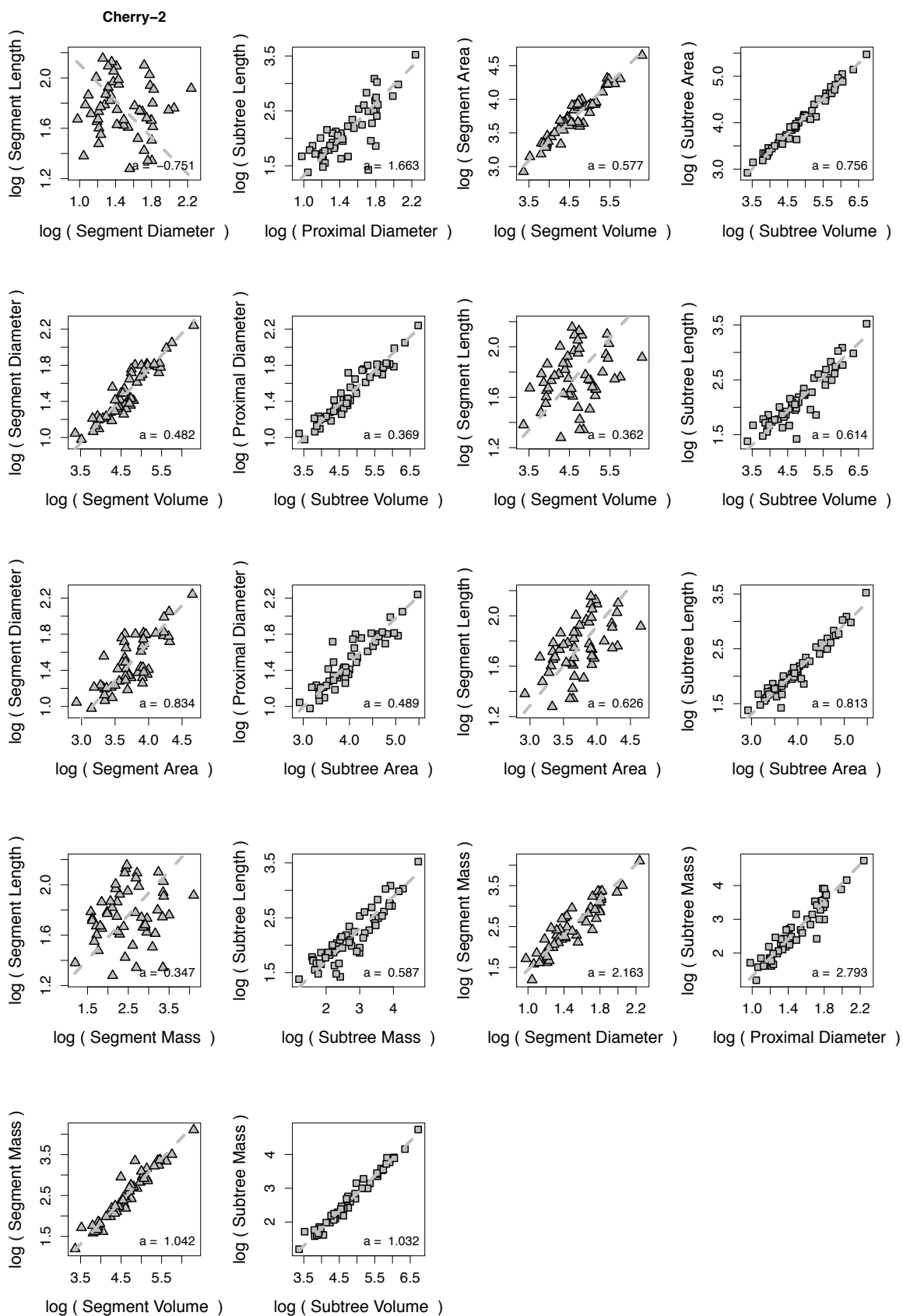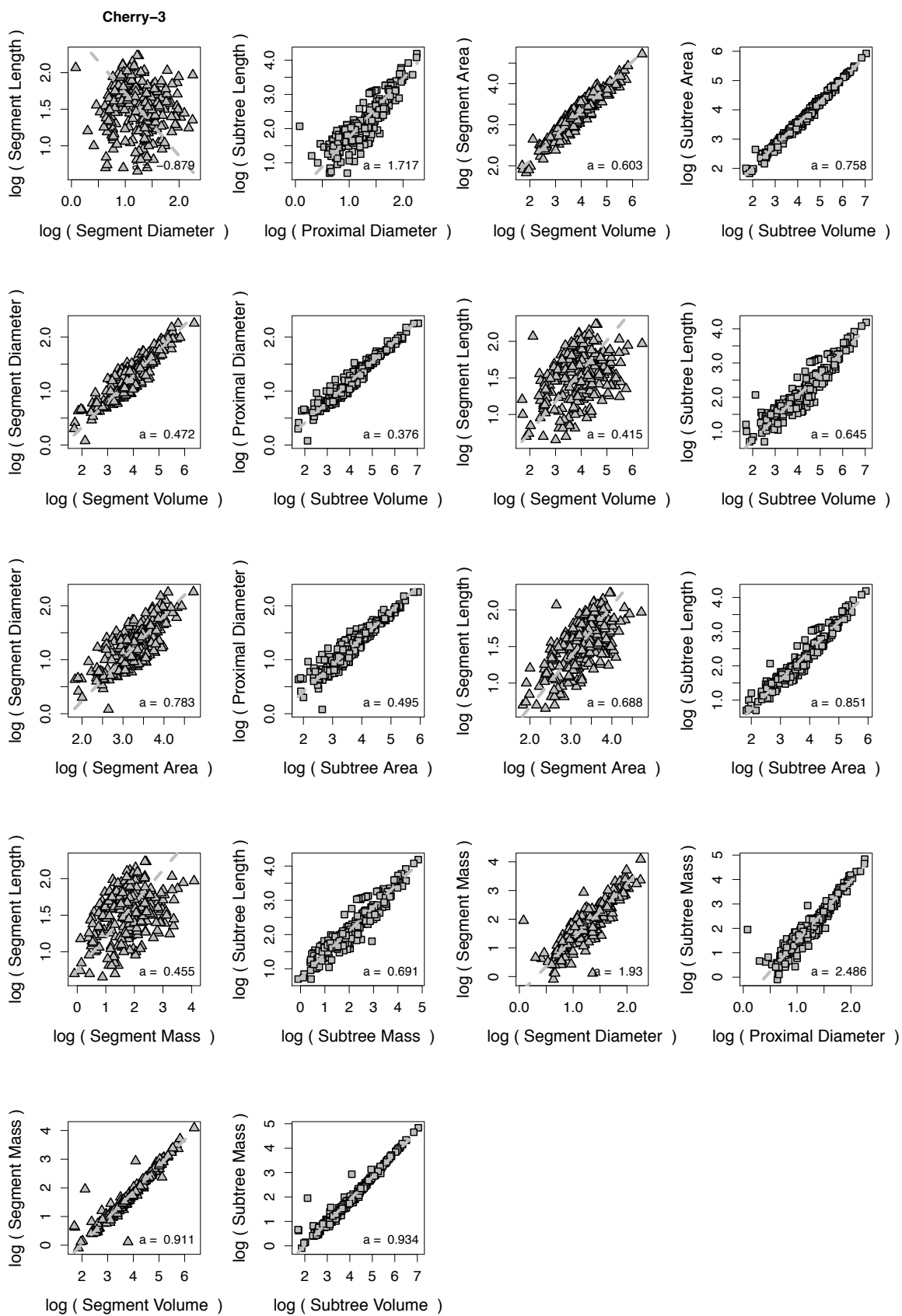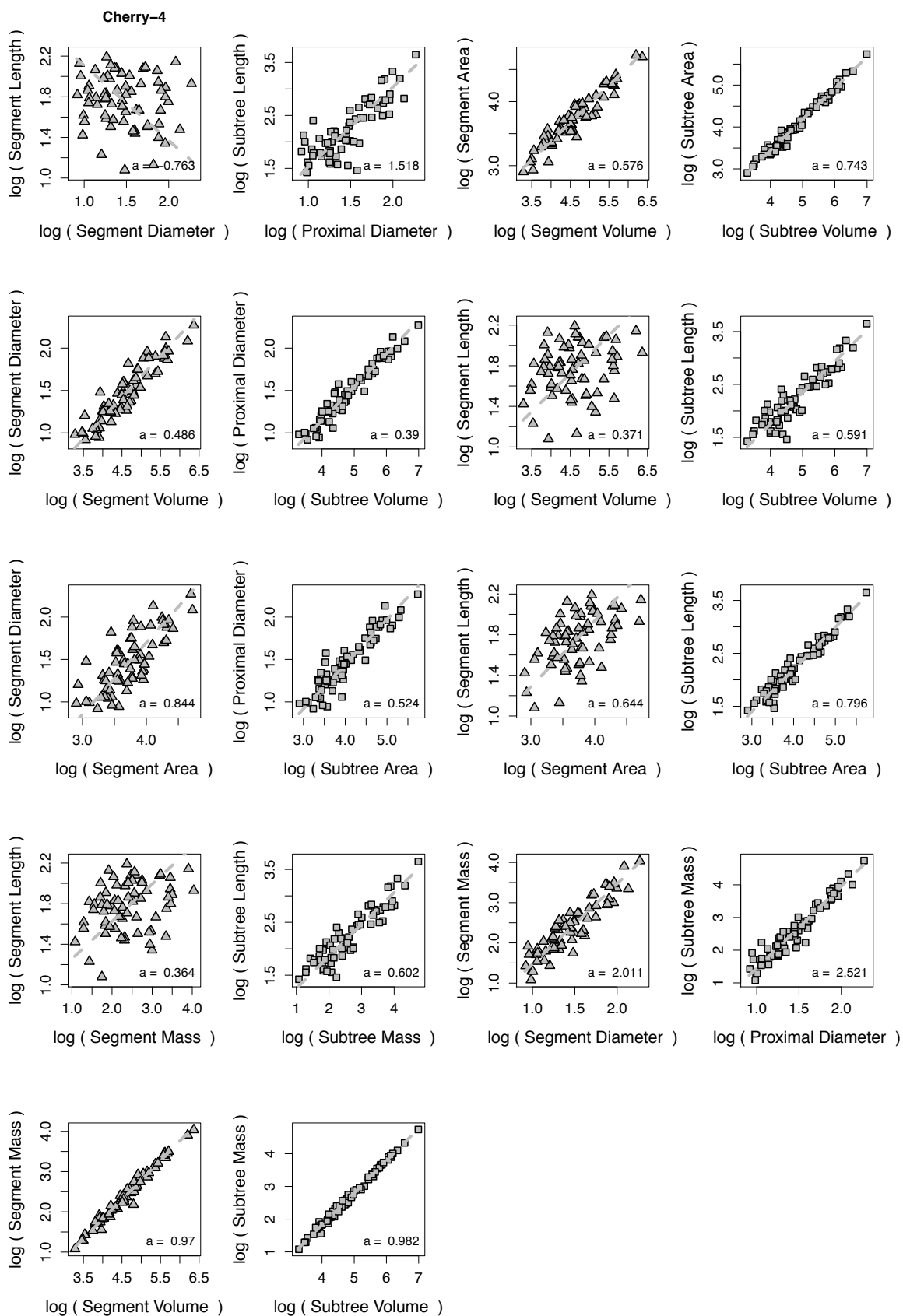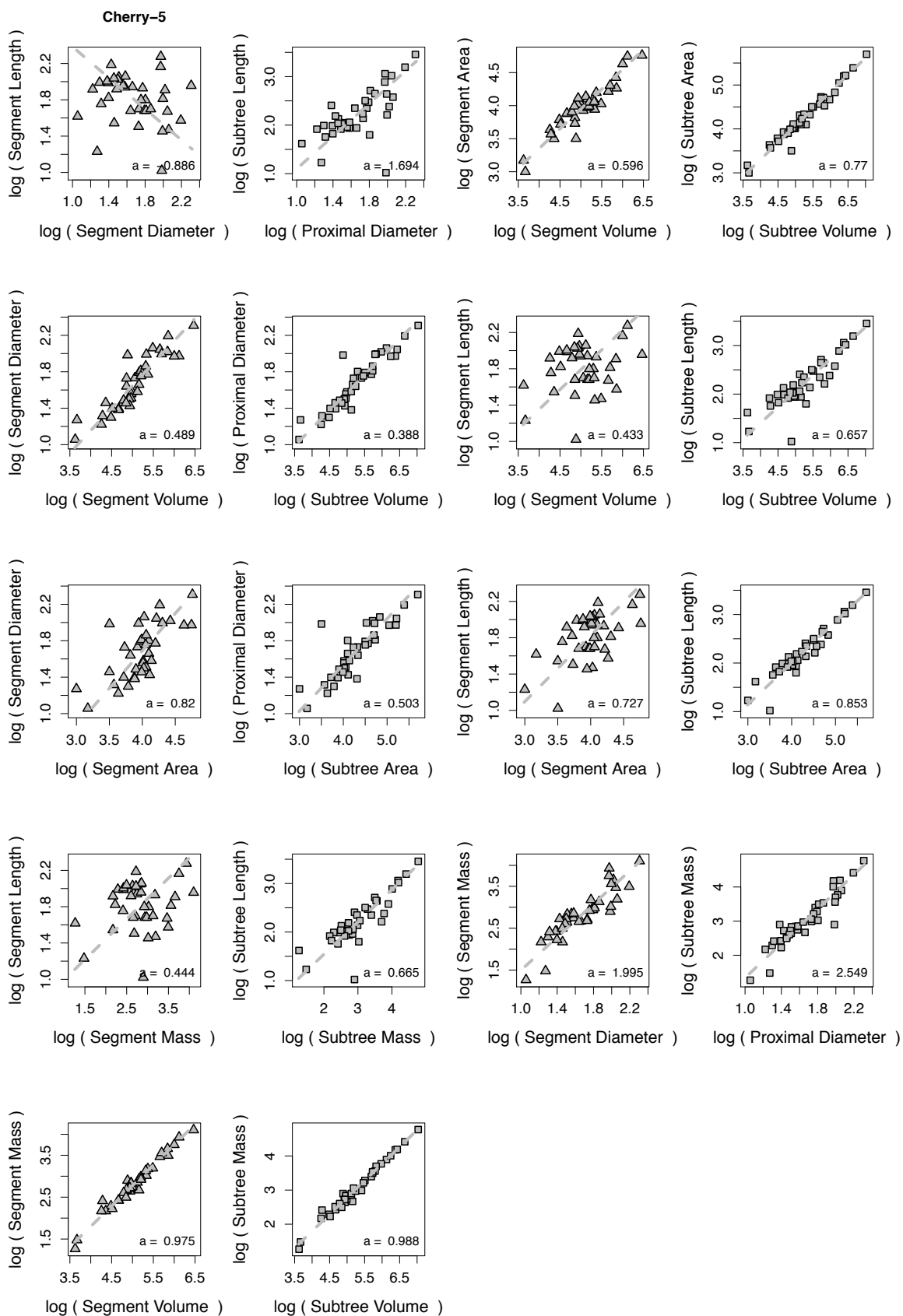
Figure A-4. Data visualization for each allometric relationship at a species level. Data points correspond to branches at each branch-level classification. Segment level estimates are marked by triangles and subtree by squares with tart cherry shaded and apple open symbol. Dashed lines mark the estimated exponent (a) of the group. Dotted lines mark the estimated a of the species.
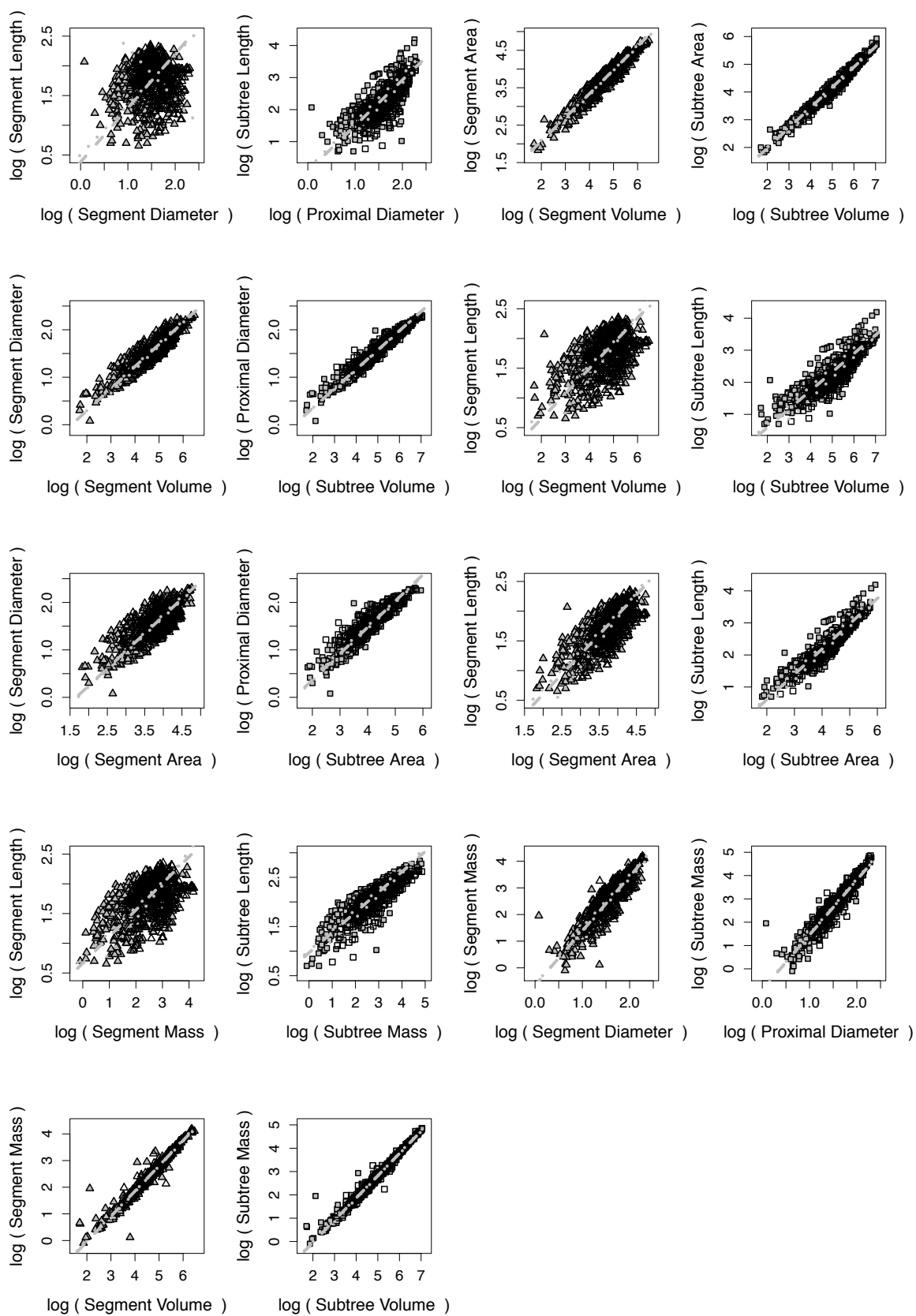
Appendix B. Additional tables and figures for Chapter III

Table B-1. Summary of branch angles for 10-year-old 'Golden Delicious' on various rootstocks.

	B.9	G.41	G.210	M.26	JM.8	Pi-AU 56-83
No. Horizontal	1	7	15	4	4	7
No. Vertical	5	4	7	5	6	9
No. Between	7	6	4	18	15	21
Horiz. : Vert.	0.20	1.75	2.14	0.80	0.67	0.78
Avg Angle	45.8	57.9	64.4	57.2	54.0	54.9
SD Angle	39	40	40	35	33	36
Avg Between Angle	72.1	56.7	76.2	62.5	66	65.5
SD Between Angle	11	27	8	18	11	17
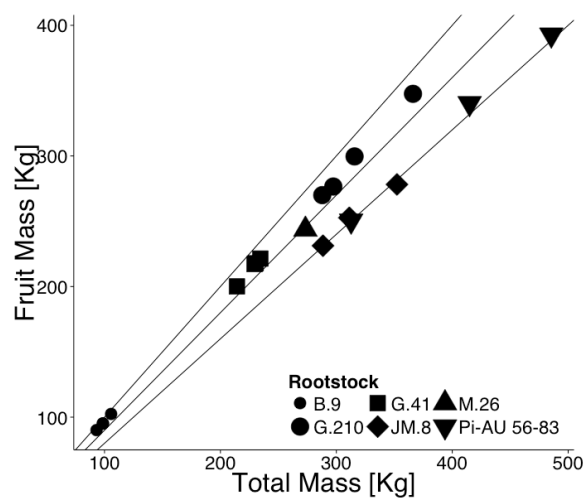
Figure B-1. The 'Harvest Index' relationship of fruit mass (cumulative yield) with total mass for 10-year-old 'Golden Delicious' individuals on various rootstocks. Total represents the sum of dry weight of aboveground woody biomass and cumulative yield. Harvest index isoclines (1, 0.9, and 0.8) are represented by the thin lines.
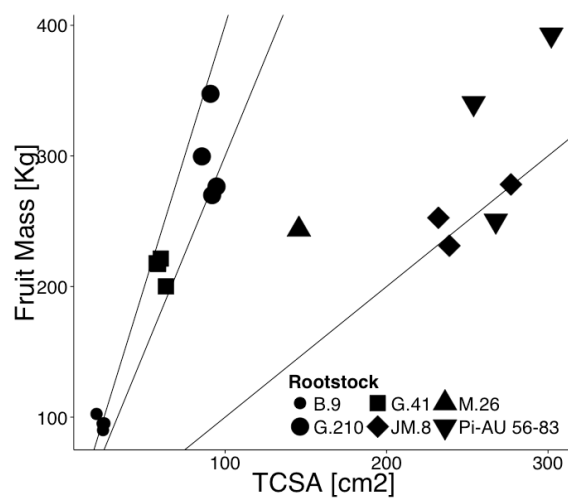
Figure B-2. The 'Yield Efficiency' relationship of fruit mass (cumulative yield) with trunk cross sectional area (TCSA) for 10-year-old 'Golden Delicious' individuals on various rootstocks. Yield efficiency isoclines (4, 3, and 1) are represented by the thin lines.

Appendix C. Additional figures for Chapter IV
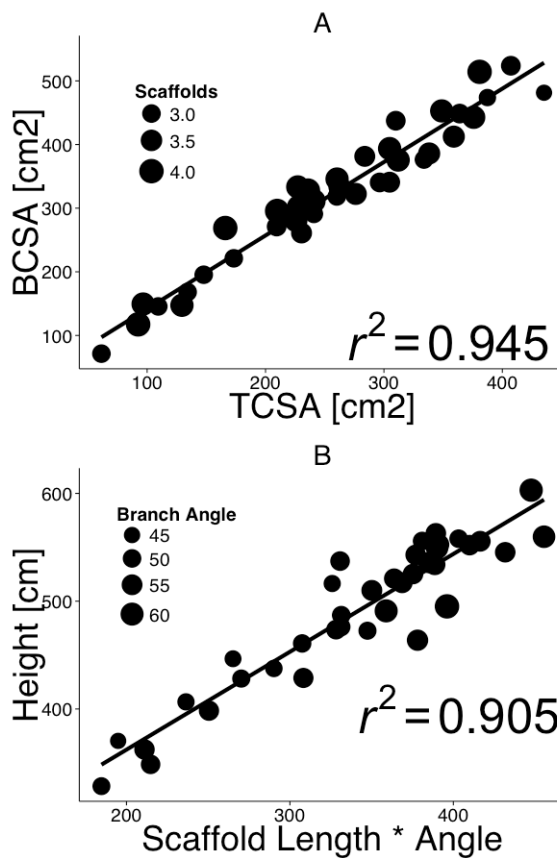
Figure C-1. The linear relationship of averaged tree size measurements at a block level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks in Utah Co., including A) trunk cross sectional area (TCSA) and cumulative scaffold branch cross sectional area (BCSA), B) height and scaffold length. Each block is represented by the average values of five randomly selected individuals with a symbol summarizing a related management practice: A) number of scaffolds, B) scaffold branch angle.

A

B
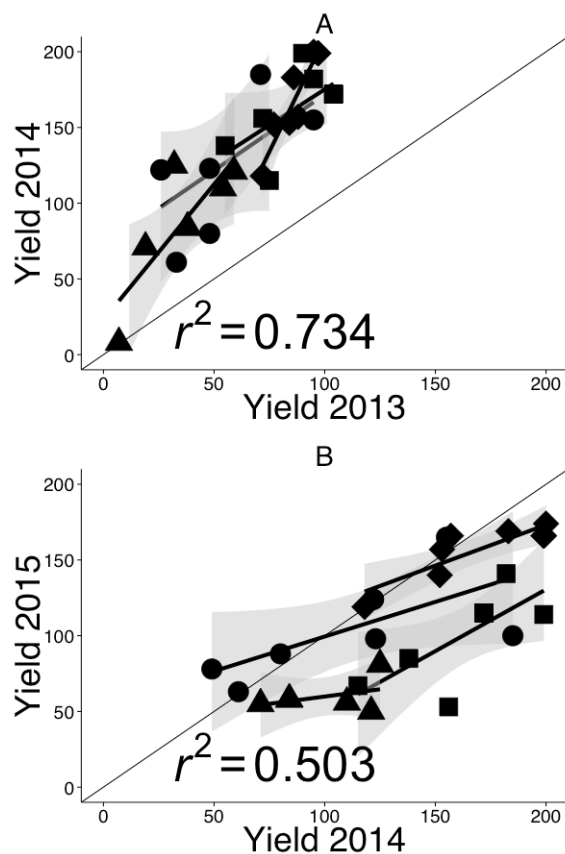
Figure C-2. Shifts in yield / tree for years adjacent to the year of the study (2014) for 'Montmorency' tart cherries on Mahaleb seedling rootstocks for various growers in Utah Co. Each block in the study is represented by the per tree average value of the total yield harvested for the block in 2013-2015. The bold lines represent the regression line and shaded 95% confidence interval for each grower. The reported correlation (r^2) represents the regression of the aggregated data among growers.
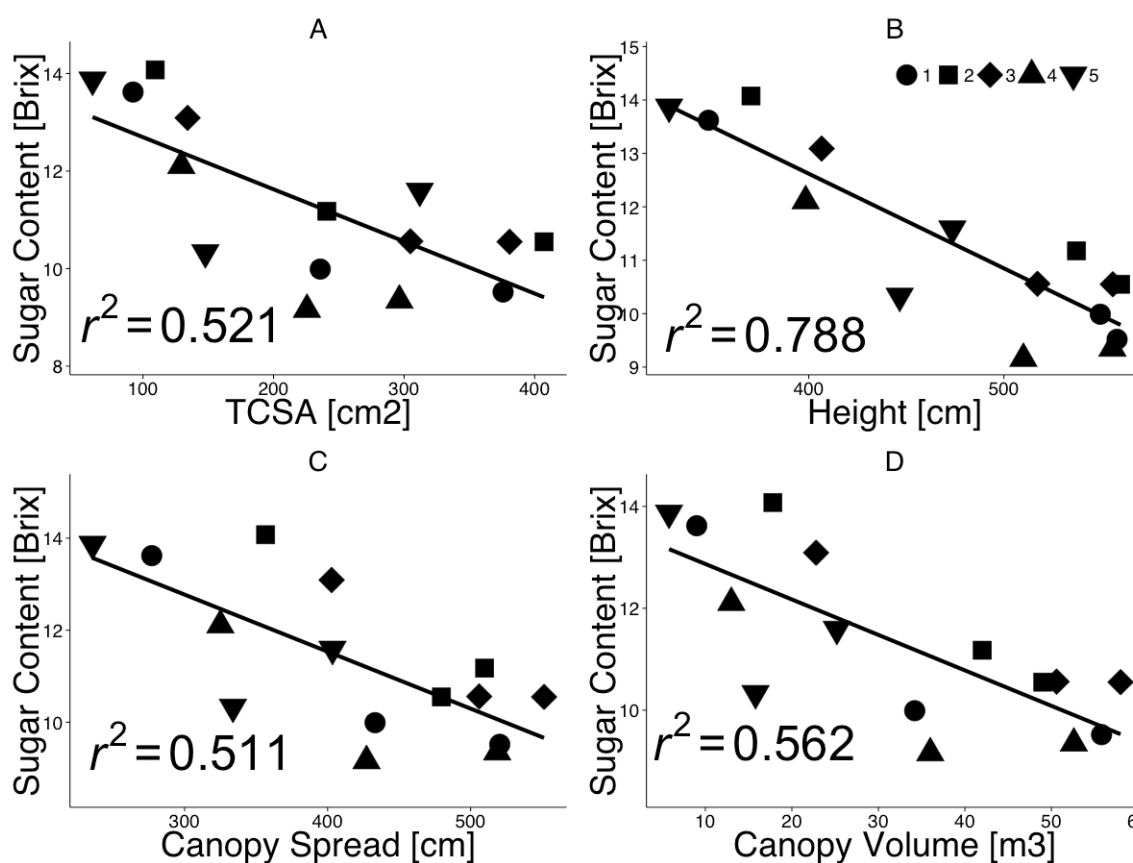
Figure C-3. The indirect relationship of A) trunk cross sectional area (TCSA), B) height, C) canopy spread and C) canopy volume with fruit sugar content at a block level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2).
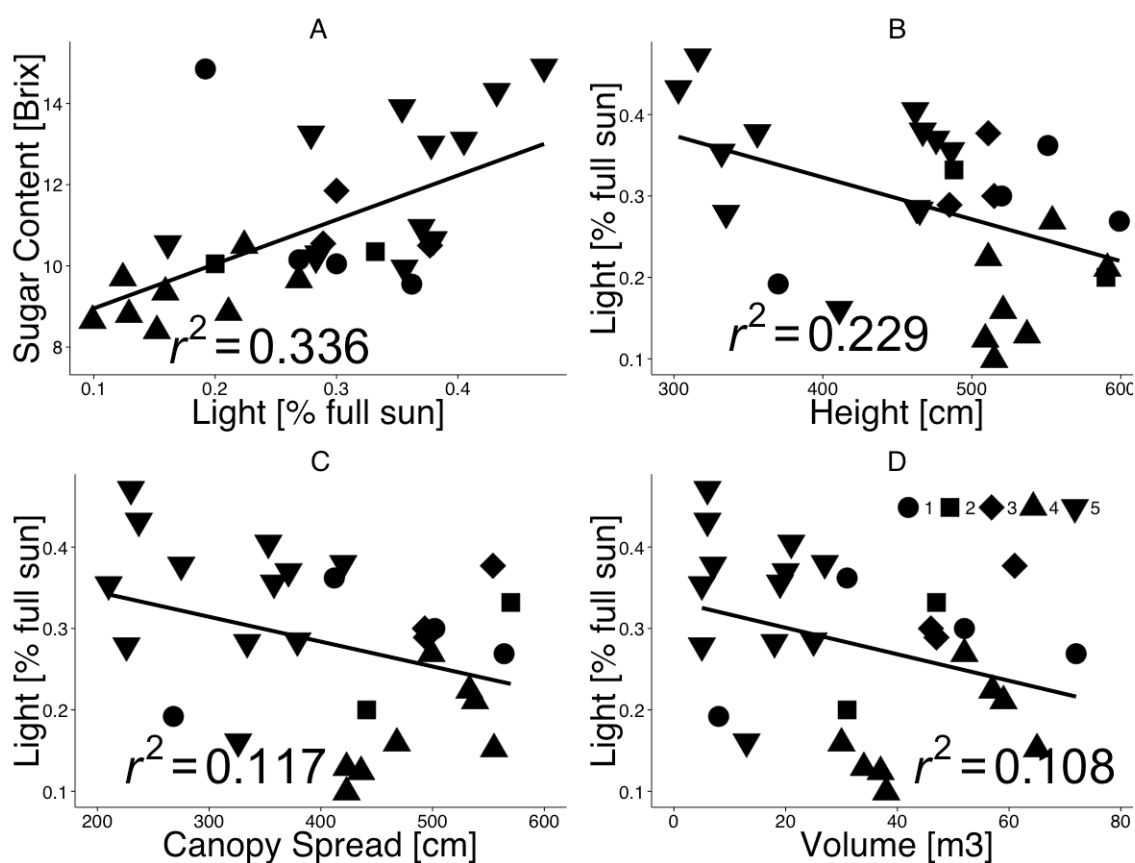
Figure C-4. The relationship of canopy light absorption with A) sugar content, B) height, C) canopy spread, and D) canopy volume at a block level for 'Montmorency' tart cherries on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2). A subset of light measurements are reported for instances where full sun was below 1000 μmol m^{-2} s^{-1}.

Figure C-5. Boxplots of tree size, canopy dimensions, yield, and sugar content separated by tree age (young vs. old) and grower.

Young (<15 yrs) **Old (> 15 yrs)**

Young (<15 yrs)   **Old (> 15 yrs)**

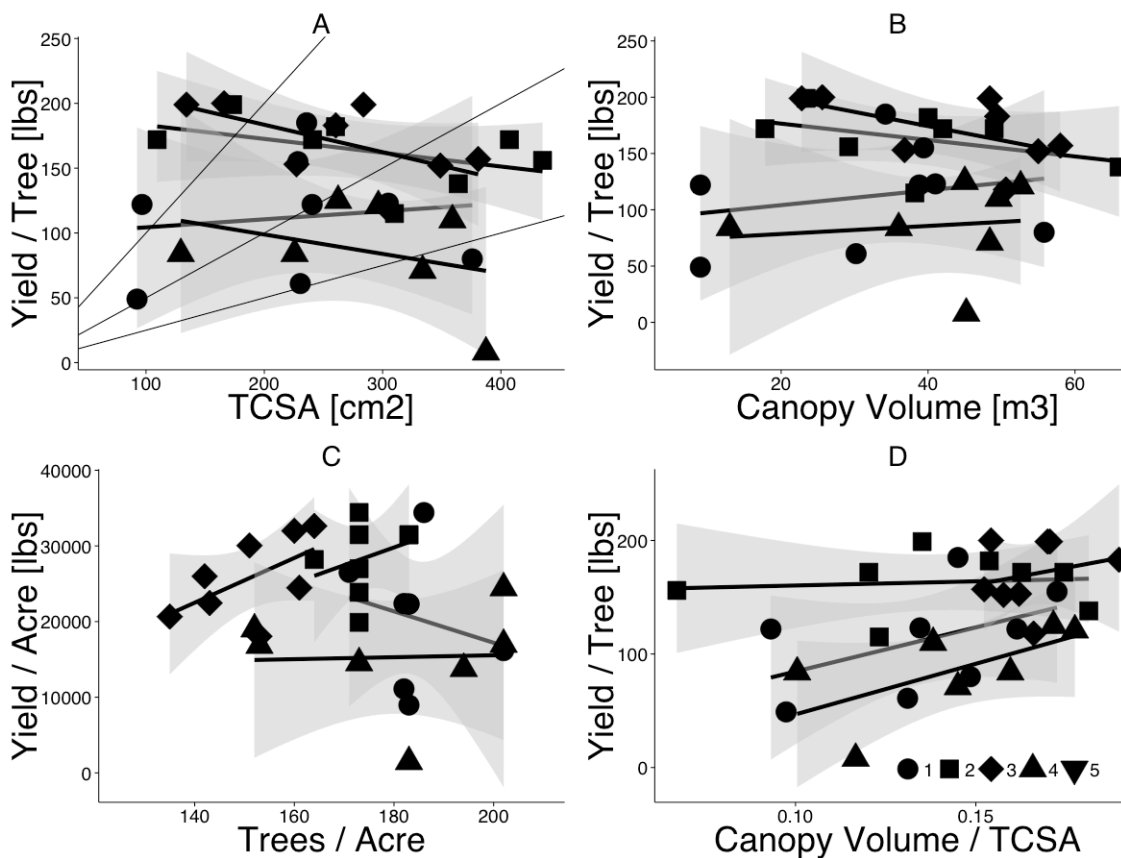**Young (<15 yrs)** — **Old (> 15 yrs)**
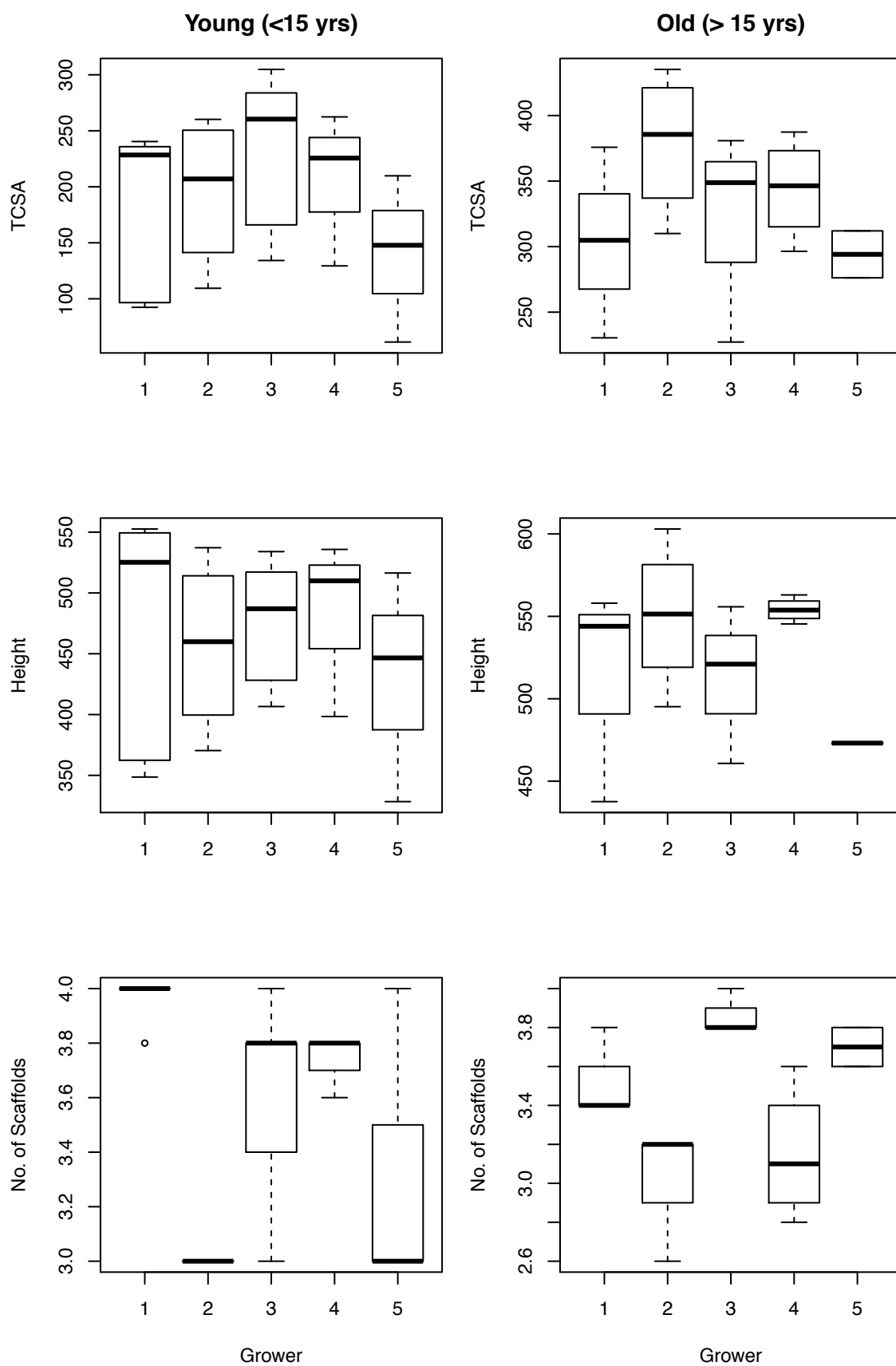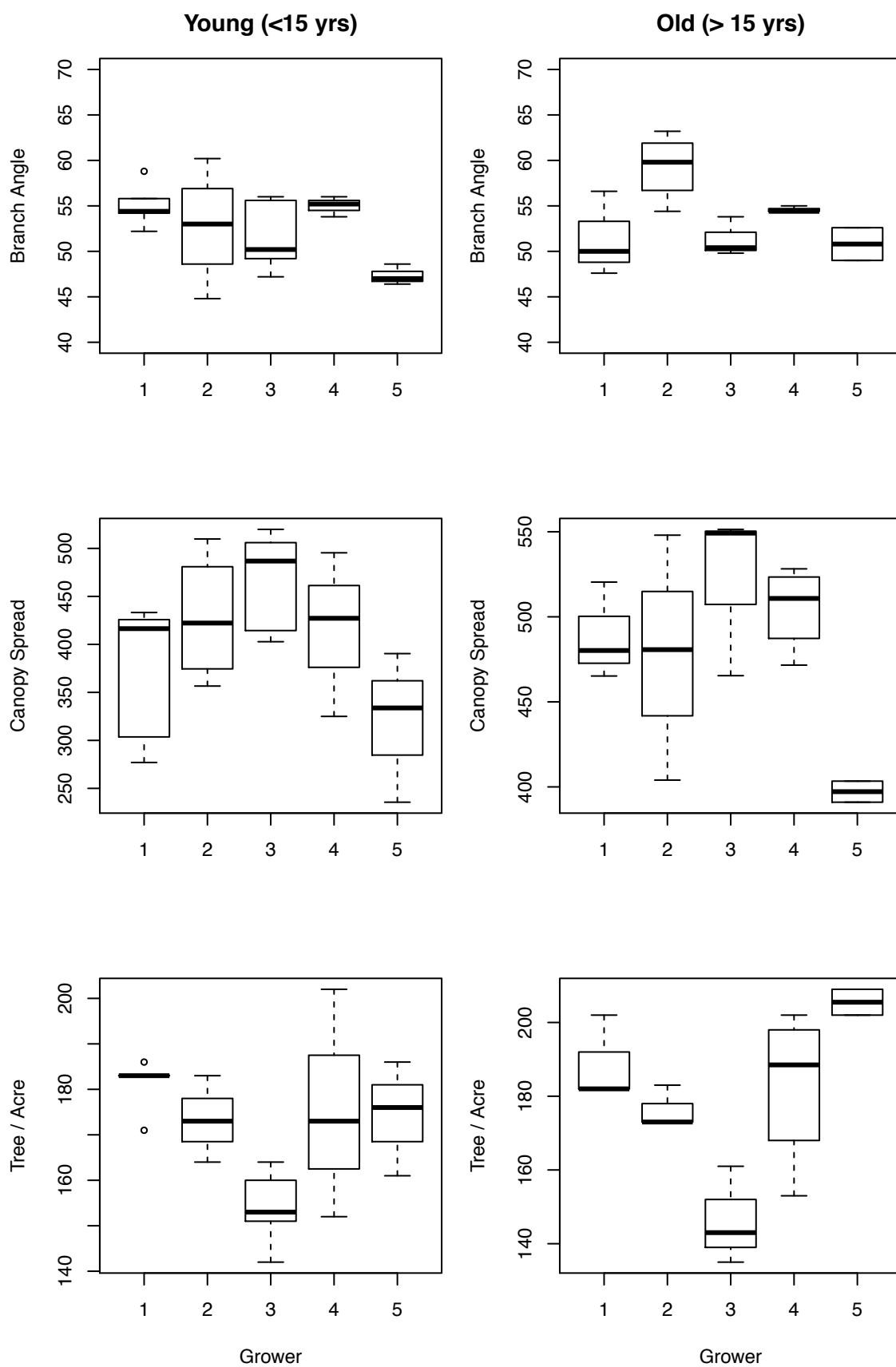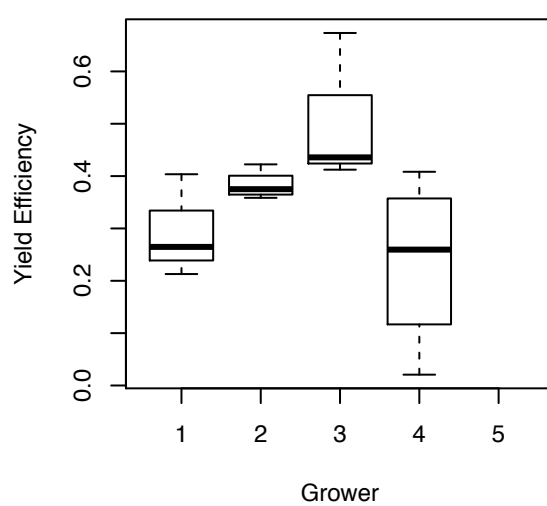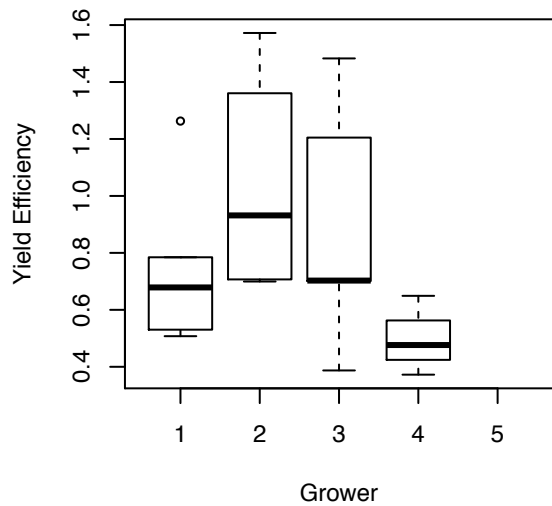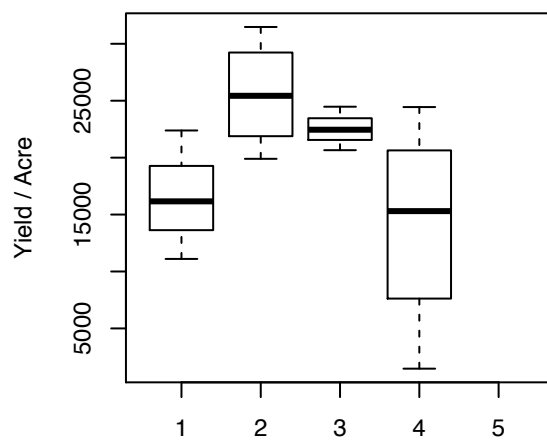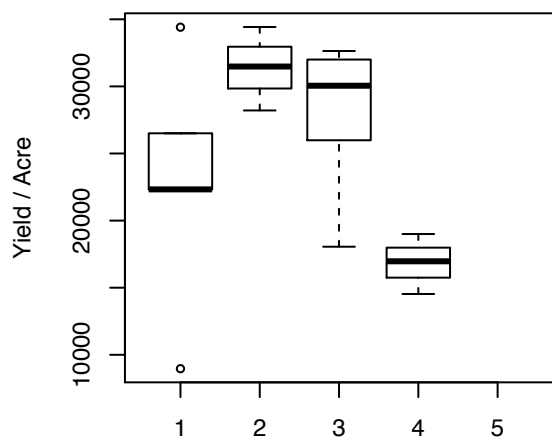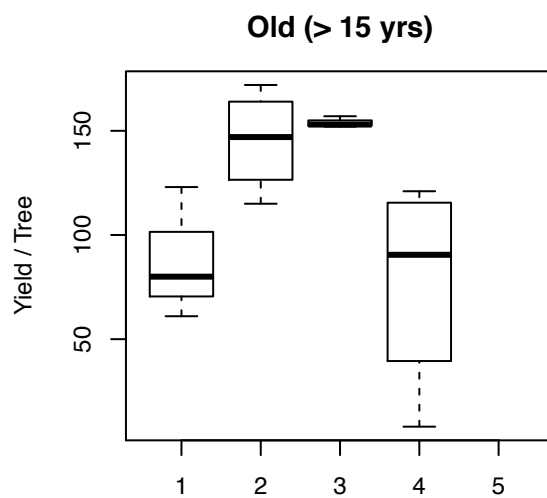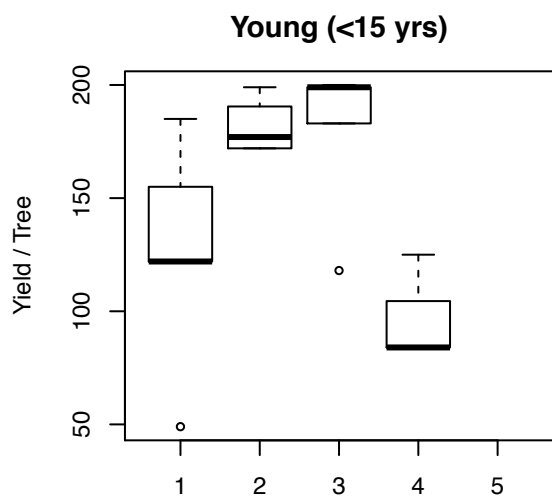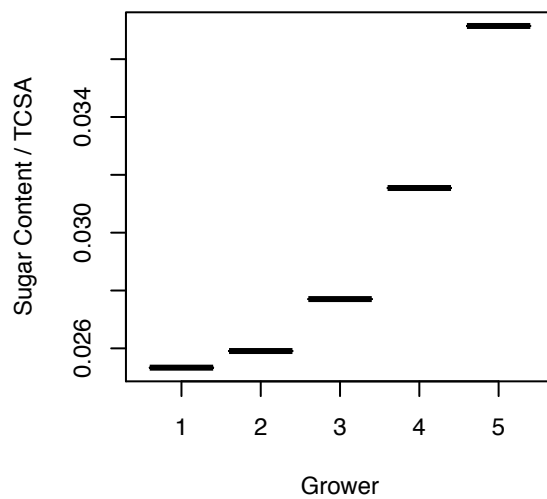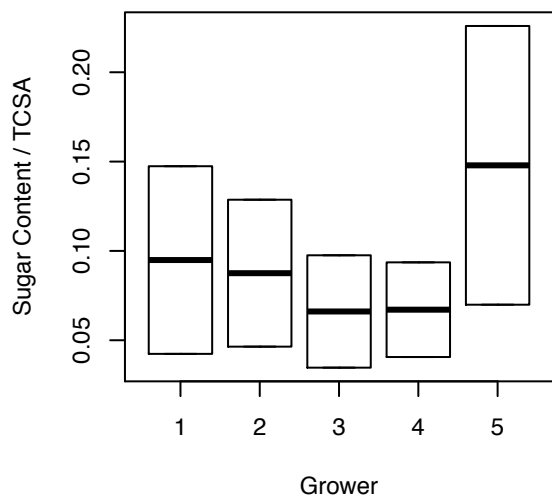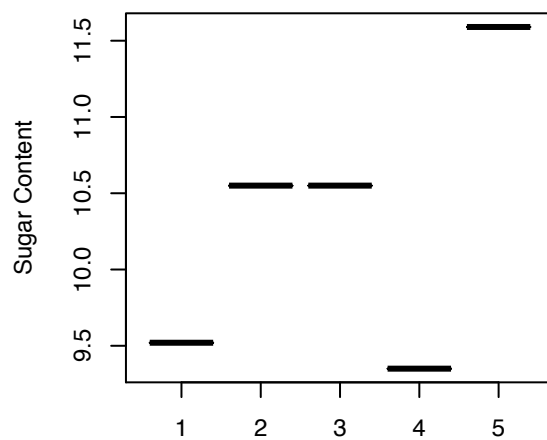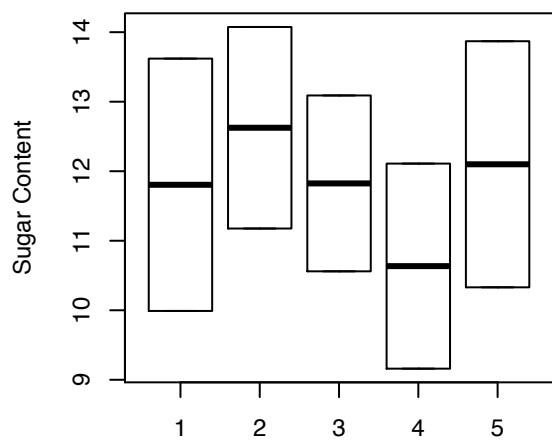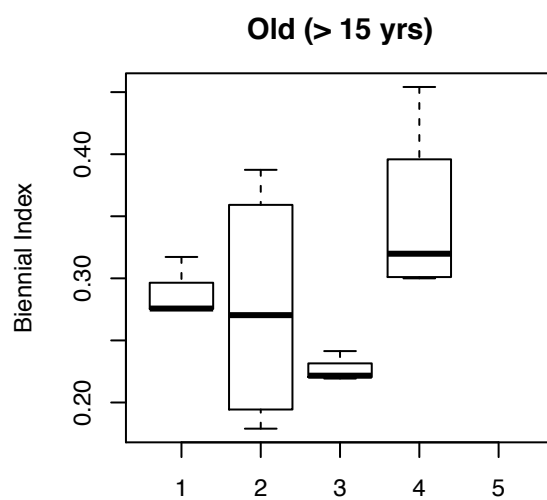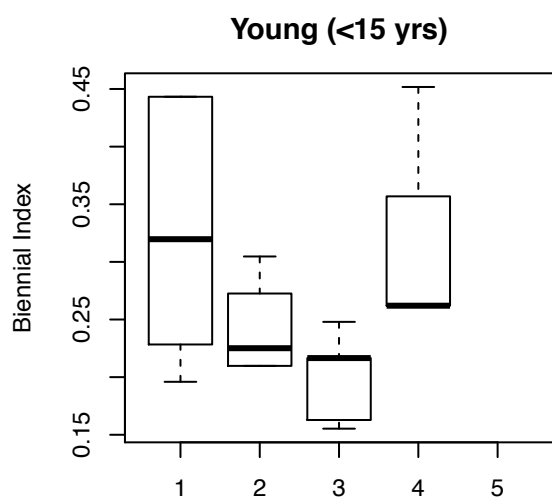
Figure C-6. The relationship of A) trunk cross sectional area (TCSA), B) canopy volume, C) trees per acre and D) canopy volume / TCSA with yield per tree at a block level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals and the per tree average value of the total yield harvested for the block in 2014. Growers are distinguished by symbol. The bold lines represent the regression line and shaded 95% confidence interval for each grower. For subplot A, crop load isoclines (1, 0.5, and 0.25) are represented by thin lines.
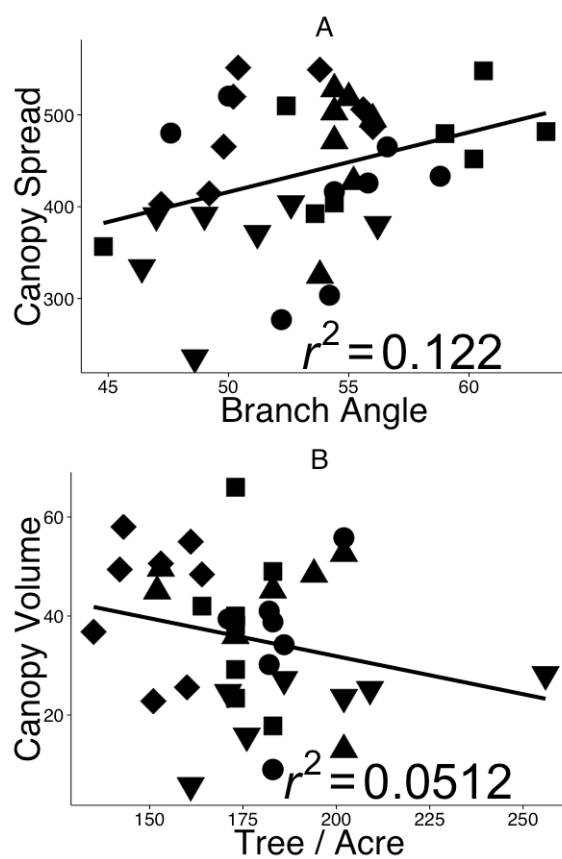
Figure C-7. The relationship of A) branch angle with canopy spread and B) trees per acre with canopy volume for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. The bold lines represent the regression line corresponding to the reported correlation (r^2). The median block spacing was 14×18 ft for an average of (176 +/- 22 trees/acre).
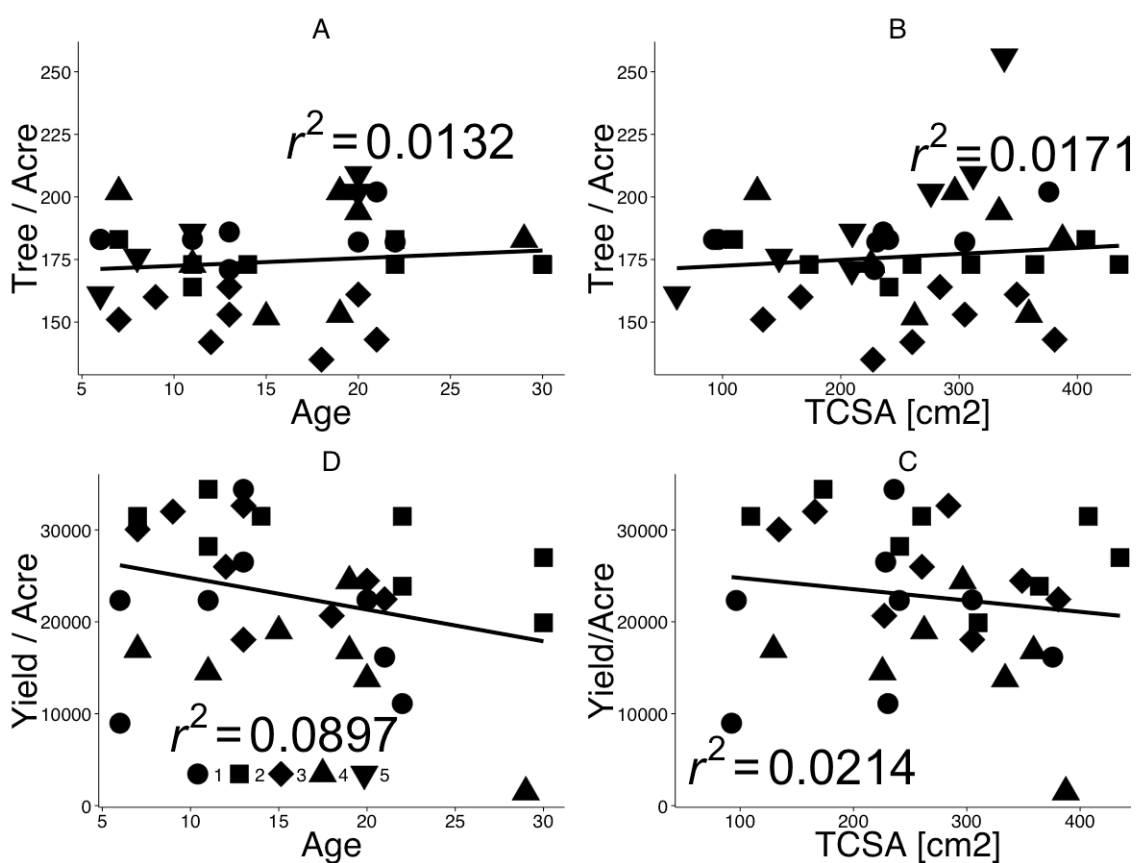
Figure C-8. The relationship of age and trunk cross sectional area with number of trees per acre and yield per acre level for 'Montmorency' tart cherries of various ages on Mahaleb seedling rootstocks for various growers in Utah Co. Each block is represented by the average values of five randomly selected individuals and the per tree average value of the total yield harvested for the block in 2014. Growers are distinguished by symbol. The bold lines represent the regression line corresponding to the reported correlation (r^2).

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Education

Institution	Major/Area	Degree and Year
Utah State University	Biology / Ecology	PhD, *expected* Apr 2016
University of Michigan	Forest Ecology	MS, Apr 2011
University of Michigan	Ecology	BS, Dec 2008

Published Manuscripts

Brym ZT, Reeve J. **2016**. Agroecological principles from a bibliographic analysis of the term agroecology. *Sustainable Agriculture Reviews*, 19: *in press*.

Susko, AQ., **Brym ZT**. **2016**. An Introduction to R Statistical Computing in Horticultural Science. *HortTechnology*, *accepted with revision*.

Brym ZT, Allen D, Ibanez I. **2014**. Community control on growth and survival of an exotic shrub. *Biological Invasions*, 16(12), 2529-2541.

White EP, Baldridge E, **Brym ZT**, Locey KJ, McGlinn D, Supp SR. **2013**. Nine simple ways to make it easier to (re)use your data. *Ideas in Ecology and Evolution*, 6(2).

Brym ZT, Lake JK, Allen D, Ostling A. **2011**. Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. *Journal of Applied Ecology*, 48, 1098-1106.

Blue JD, Armstrong M, **Brym Z**, Chandler J, Cheluitte C, Coole C, Farinas S, Koch JB. **2009**. Synthesis and the future of ecology. *Bulletin of the Ecological Society of America*, 90(3), 283-285.

Grants and Awards

Dec **2013**; Utah State University Office of Research and Graduate Studies Doctoral Dissertation Improvement Grant; Using an Agroecological Approach to Evaluate Influences of Canopy Shape and Branch Architecture on Yield of Tree Fruit; **$8,679**

Jul **2012**; Utah State University Ecology Center Graduate Research Fellowship; Developing an Agroecological Approach to Biomass Scaling and Branching Architecture Using Orchard Trees; **$9,500**

Dec **2011**; Utah State University Graduate Student Senate Research Award; **$1,000**

Aug **2010**; Ecological Society of America Strategies for Ecology Education, Diversity and Sustainability Outstanding Leadership Recognition

Apr **2010**; University of Michigan School of Natural Resources and Environment William D. Drake Prize; **$2,000**

Sep **2009**; University of Michigan Marching Band Shepherd Graduate Fellowship; **$10,000**

May **2009**, **2011**; NSF Graduate Research Fellowship Program; Honorable Mention

Grants and Awards (Cont.)   **Zachary T. Brym**

Apr **2009**; Ecological Society of America Strategies for Ecology Education, Diversity and Sustainability Special Project Grant; National Chapter BioBlitz; **$5,000**

Jun **2008**; University of Michigan Undergraduate Research Opportunities Program Summer Research Fellowship; **$5,000**

Jun **2008**; Garden Club of America Summer Scholarship in Field Botany; **$1,500**

Teaching

Jan **2015 - Present**; WIS 6934 Data Carpentry for Biologists; Utah State University / University of Florida; Teaching Materials and Website Developer; www.datacarpentry.org/semester-biology

Sep **2012**, **2013**, **2014**; BIOL 4400 Plant Physiology; Utah State University; Teaching Assistant and Guest Lecturer

Jan **2011**, **2012**, **2014**; BIOL 1620 Biology II Lab; Utah State University; Teaching Assistant

Sep **2011**, **2014**; BIOL 1610 Biology I Lab; Utah State University; Teaching Assistant

Sep **2010**; NRE 547 Forest Ecology in a Changing World; University of Michigan; Teaching Assistant and Lab Curriculum Developer

May **2007**; Kellogg Environmental Center, CT Department of Environmental Protection; Curriculum Developer, Park Interpreter, and Activities Coordinator

Leadership and Administrative Duties

Aug **2014** - Aug **2015**; American Society for Horticultural Science GRAD Working Group; Chair

Jul **2012** - May **2014**; Utah State University Department of Biology Graduate Programs Committee; Graduate Student Representative

Jun **2008** - Apr **2011**; Ecological Society of America, Strategies for Ecology Education, Diversity and Sustainability, Michigan Chapter; Chair

Outreach and Synergy

Oct **2015**; National Ecological Observatory Network and Data Carpentry; Spatio-temporal Data Teaching Materials Hackathon

Aug **2015**; American Society for Horticultural Science Annual Meeting; An Introduction to Advanced Computing in Science Workshop

Mar **2014**; Utah State University Ecology Center; Science Communication Workshop

Nov **2013**; Intermountain Bioneers Conference Seminar; The Rudiments of Pruning Fruit Trees

Oct **2013**; Association for Ecosystem Research Centers and American Institute of Biological Science; Media and Policy Communication Workshop, Congressional Briefing re: Food Security, Ecosystem Science, And Science Funding

Sep **2013**; Science Magazine Dance Your PhD Contest Entry; Prune to Wild

Aug **2010**; Ecological Society of America Annual Meeting; Diversity and Inclusiveness Workshop