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CROWN IDEOTYPES FOR GENETICALLY IMPROVED BLACK WALNUT (JUGLANS NIGRA L.) CLONES UNDER AN INTENSIVE MANAGEMENT REGIME IN INDIANA, USA

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Approved by: Linda S. Lee 10/15/2014

Head of the Department Graduate Program Date

CROWN IDEOTYPES FOR GENETICALLY IMPROVED BLACK WALNUT (*JUGLANS NIGRA* L.) CLONES UNDER AN INTENSIVE MANAGEMENT REGIME IN INDIANA, USA

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ABSTRACT

Pang, Kejia. Ph.D., Purdue University, December 2014. Crown Ideotypes for Genetically Improved Black Walnut (*Juglans nigra* L.) Clones under an Intensive Management Regime. Major Professor: Charles Michler.

Developing crown ideotypes is important for more efficiently producing timber from black walnut (*Juglans nigra* L.), a valuable hardwood species that mainly grow in the Central Hardwood Region, US. To develop black walnut crown ideotypes for timber growth under an intensive management regime in North-Central Indiana, the following investigations were conducted:

1. Leaf area is strongly correlated to light interception and growth. Mixed effects, allometric models for leaf area and mass at both branch- and tree-level were developed for some genetically improved black walnut clones. Mixed effects branch-level models were built for nine clones. Branch-level model indicated that branches in the top and the base of the live crown grew more leaf mass and area than similar sized branches in the middle of the live crown. Tree-level models were then developed for 25 clones by summing branch-level estimates. Models with crown radius and diameter at breast height (DBH) predicted whole-tree leaf area and mass better than models using DBH alone. Further, there were strong clonal differences in total leaf area, stem volume increment, leaf area index, foliar density index, and growth efficiency. These differences together with the allometirc models demonstrated that some genotypes were more growth efficient in producing bolewood than others.

2. Branching pattern and dynamics are key determinants of tree growth and wood quality. Multi-level, linear mixed effects models of a list of branch attributes were

developed for 25 black walnut clones. Branch attributes that were models included: 1) maximum branch diameter in a segment; 2) relative branch diameter in a segment; 3) one-year radial growth of branches; 4) branch insertion angle; 5) first – order branch length; 6) branch frequency; 7) branch basal area per meter of stem. Branch and segment position within a crown were major predictors for branch characteristics, while branch angle also influenced branch allometry. DBH was the most useful tree-level predictor for branch attributes. Desirable characteristics were shown: some clones had small branches or small branch basal area per meter of stem when assuming a same DBH; some clones had large branch angle given a same branch diameter; variance also existed in branch length and branch frequency. These clone variance that captured by the branch allometric models indicated that some black walnut clones had better balance between fast growth and good wood quality, and this balance may also be enhanced through further breeding programs.

3. Estimation of genetic parameters can help improving the efficiency of genotype evaluation and selection process in plant breeding programs. The genetic variation and inheritance of a number of traits in phenology, morphology, physiology, and the genetic correlations among them were investigated for 25 black walnut clones.

4. Microsatellite markers were useful in fingerprinting cultivars and determine genetic relatedness among them. A set of eight microsatellite markers was used to genotype 25 black walnut clones. The identity of 212 ramets was verified, and a few trees among them were found mislabeled. A genetic dendrogram was constructed to show genetic relatedness among clones. In addition to verifying known pedigrees, new discoveries were: clone C55 and C702 were closely related, as well as C705 and C728. Two more dendrograms, one based on crown architecture traits, and the other on tree size and form traits, were also built to compare with the genetic dendrogram. The genetic dendrogram showed that these eight molecular markers had the ability to distinguish genetically related clones from less related ones. Crown architecture traits and tree size and form traits also were able to group genetically related clones together.

Based on the investigations on foliage models, crown architecture pattern, and the clonal repeatabilities of, and the genotypic correlations among different traits, a crown ideotype for black walnut grown for timber and another for nuts were developed.

CHAPTER 1. INTRODUCTION

1.1 The Concept of Ideotype

Plant breeding has traditionally been conducted using two major approaches: one is defect elimination, such as disease resistance breeding that incorporates a better immune response into a weak variety that is prone to the disease; the second is selection for yield, aiming at yield improvement solely without trait incorporation (Donald, 1968). However, while some new varieties from traditional breeding programs succeed, the biological mechanisms underlying their improved survival, yield, or quality often remain poorly understood. This is why single trait selection to enhance yield can sometimes fail, as warned by Way et al (1983). Donald (1968) doubted that selection for yield could ever reach the asymptote of yield because the best combination of plant traits is never sought and may be achieved only by chance. Hence, it seems desirable to devise a more holistic approach to model plants by examining a set of traits, rather than one, where each of these traits is directly or indirectly associated with the breeding goal. Ideotype, referring to a form denoting an idea, was first defined as a model plant that has multiple desired characteristics that grows and behaves in an expected manner in a certain type of environment (Donald, 1968). Arguably a combination of traits leading to improved yield may be a result of natural or artificial selection pressure (Simmonds, 1985; Dickmann et al., 1994), and a comprehensive breeding approach aimed at an ideotype would not completely eliminate the uncertainty of success in breeding. It would be good, still, to better understand the biological basis of successful new genotypes, such as a better understanding of yield- and quality-related traits, and use this understanding of yield components to guide the selection of elite parents and progeny more effectively (Dickmann et al., 1994; Donald, 1968). Donald (1968) defined crop ideotype as model crops that are expected to have a better quality or quantity of a useful product when planted as a cultivar, and proposed an ideotype for wheat (1968) and one for barley (1979). Since then, many plant breeders have explored ideotypes for a wide range of species (Table 1-1), aiming for their own particular environment and culture regimes. At the beginning, ideotype breeding was mostly applied to agronomic crop species. Later, breeders extended ideotypes to fruit, timber, and biomass tree species, albeit with fewer species and on a less advanced level due to perennials' longer growing period and more complex physical structure.

1.2 Past research about ideotypes

1.2.1 What traits compose crop ideotypes?

With a view of "taking the whole plant into consideration" (Rasmusson, 1987), plant breeders have investigated many traits, including but not limited to morphology, physiology, biochemistry, and ecology, to draw clearer pictures for ideotypes for a variety of plant species.

The most basic and probably the most important traits are morphological traits. Selection based on morphological traits is traditional in crop breeding, since high yield or quality is usually associated with certain morphological features. Some growth traits, such as size- or shape-related characteristics, height, diameter, and fruit or seed weight, are morphological traits per se. Morphological features are generally easy to measure, thus they have made fast screening of hundreds of thousands of progeny possible. Plant morphological characteristics are displayed at multiple levels: whole-plant level, organ level, and the interactions among individual organs. These features at different levels determine how plants acquire resources, condition their internal environment, and subsequently grow (Ford, 1992). Therefore, a set of morphological traits are often the first step when plant breeders start to explicitly describe an ideotype. Physiological and ecological characteristics have also been examined and listed as ideotype components as well. For instance, being a weak competitor was considered as an ecological feature for *Populus* spp. ideotype (Dickmann, 1985; Dickmann and Keathley, 1996), wind-firm and tolerant of heavy snow loads as ecological characteristics for Scandinavian conifers (Kärki and Tigerstedt, 1985), and high leaf photosynthetic rate was regarded as a common feature for many tree ideotypes no matter what the end product is (Dickmann et al., 1994). Morphology, physiology, and ecology are closely related and mutually affect one another. Certain plant forms indicate specific physiological mechanisms, and morphology and physiology may adapt to environmental changes.

1.2.2 Examples of ideotypes

1.2.2.1 Agronomic crop ideotypes

Agronomic crops were the first species group where ideotype was studied. Based on experimental findings and physiological considerations, Donald (1968) outlined the morphological characteristics of a wheat ideotype densely planted in fertile soil as follows: a strong and short stem; few, erect and small leaves; a large and erect ear; presence of awns, and a single culm. Upright leaves were included in this wheat ideotype because upright leaves were believed to have higher light interception than horizontal and drooping leaves and therefore higher photosynthetic rates (Donald, 1968). After comparing these traits in *Limnanthes alba* and five varieties of *Limnanthes douglasii*., Jain and Abuelgasim (1981) concluded that a meadowfoam ideotype (*Limnanthes spp.*) can be defined according to the traits (mostly morphological) of *Limnanthes douglasii* var. *nivea*: taller plant stature, lower seed shattering, earlier flowering, and higher seed yield. A common bean ideotype (Brothers and Kelley, 1993) was specified as: acute branch angles, an upright growth habit, intermediate seed weight, and a low number of seeds per pod and pods per plant. Virk et al. (2004) specified a rice ideotype (New Plant Type – between indica and japonica NPT-IJs) which had the following morphological traits: higher panicle density (number· m^{-2}), increased grain-filling percentage, larger panicles with more spikelets, improved harvest index, and greater biomass.

Specifying the ecological features for an ideotype is important, because plants growing in different environments may have adapted to have different physiological characteristics. Molina-Cano et al. (1990) defined a barley ideotype for a typical Mediterranean environment, which is quite different from the climate conditions in Northern Europe that are ideal for barley. The barley cultivar which had the best performance in a Mediterranean environment has the following morphological characteristics: later heading, shorter straw, denser spikes than the two-rowed barley variety Beka, which was well adapted the growing conditions in Spain; and these physiological features: higher inverse of leaf area rate and grain, increased leaf area ratio, lower leaf senescence rate, and shorter grain filling period than the original variety.

Different crop species have different products of economic interest. Therefore, for some species with special uses, biochemical traits are used in the development of an ideotype. Because smooth bromegrass (*Bromus inermis* Leyss.) is an important forage species with high nutrition, the traits selected for ideotype were all related to forage yield and cell wall constituents. The proposed bromegrass ideotype featured reduced lignin and cellulose, increased hemicelluloses, but without change in cell wall content (Casler et al., 1989). In addition, the aforementioned experiment showed that ideotype breeding (multiple-trait selection) was more effective than single-trait selection because multiple-trait selection all had desirable responses.

1.2.2.2 Tree ideotypes

Among many morphological features, tree crown architecture, i.e., branching pattern, such as branch size, branch angle, branch length, number of branches, self-pruning, is the most important set of characteristics for determining both growth and quality of harvest products. A crown is the carbon factory aboveground. Therefore, tree ideotypes are often named crown ideotype for species with all types of uses: fruit, timber, and biomass, etc.

1.2.2.2.1 Fruit tree ideotypes

Lauri and Costes (2003) modeled a low-input regular-bearing apple ideotype by employing a whole-tree architectural analysis for an apple cultivar in France. They found that fruiting pattern and production efficiency was largely determined by the length, frequency, and spatial distribution of laterals (long shoot, spur) in one-year-old apple trees. Wit et al. (2004) sought an apple ideotype by separating crown structural groups based on morphological characteristics such as number, length, and position of the branches of both one-year-old and two-year-old apple seedlings, but they suggested that further investigation on older apple trees may be needed since it is difficult to predict the future architecture of apple trees based on young seedlings. Cilas et al. (2006) specified a coffee ideotype based on their highly inheritable architectural traits. By using an analysis of the genetic correlations between architectural parameters and the yield of coffee trees, they found that the proportion of fruiting nodes at plagiotropic level 15 starting at the top of the tree may be a good predictor for yield over two fruiting cycles (Cilas et al., 2006).

1.2.2.2.2 Timber tree ideotypes

Some crown ideotypes for timber species have been explored as well. A Norway spruce ideotype for high density stands was proposed to have a narrow crown, thin and hanging branches, and a high harvest index (Kärki, 1985; Kärki and Tigerstedt, 1985). A narrow crown is considered to be closely related to a high harvest index (Kuuluvainen, 1988). In the northern hemisphere, a narrow crown is more efficient in light interception than a broad one (Pulkkinen and Pöykkö, 1990). The notion of narrow crown is essential for high density stands, because it will lead to high stemwood production per unit ground area, and consequently high stand productivity, although individual trees may not be excellent (Cannell, 1982).

1.2.2.2.3 Biomass tree ideotypes

For high biomass production from trees, Tharakan et al. (2005) suggested that rather than one single ideotype, multiple ideotypes should be applied for willow (*Salix spp.*), and they developed two distinct willow ideotypes that both lead to high biomass production. The first willow ideotype was characterized by more small-diameter stems, lower specific leaf area and leaf area index, high wood specific gravity, and foliage nitrogen, while the other ideotype featured a relatively small quantity of large-diameter stems, high specific leaf area, high leaf area index, low wood specific gravity, and low foliage nitrogen.

Forest tree breeders have integrated biochemical, physiological, ecological, phenological, and wood properties into ideotype breeding. Martin et al. (2001) summed the poplar ideotype developed by Dickmann (1985) and Dickmann and Keathley (1996), and a Scandinavian conifer ideotype described by Kärki and Tigerstedt (1985). Dickman et al. (1994) specified a general ideotype for forest tree crops grown for stemwood in a high – density, unirrigated, and intensive culture regime.

1.3 Moving towards black walnut ideotypes

Ideotype breeding is still in its infancy in most forest tree improvement programs. Most research has been conducted with species grown primarily on short rotations (3-25 years) for aboveground biomass (e.g., *Populus* and *Salix*; Tharakan et al., 2005) or pulpwood (e.g., *Pinus* sp., Emhart et al., 2007). However, little research has been done for those grown for fine hardwood timber and veneer over longer periods (30-60 years), such as black walnut (*Juglans nigra*), a valuable hardwood species planted widely in the Central Hardwood Region, USA. Developing black walnut ideotypes for timber production would greatly benefit its genetic improvement program as well as the timber industry.

1.3.1 The origin, history, and biology of black walnut

Walnut (referring to *Juglans regia* L.) is written as “walhnutu” in old English, and it refers to the nut of the walnut tree. The name literally means “foreign nut” (wealh + hnutu = “foreign” + “nut”), because it was brought to the British isles from Gaul and Italy (Online Etymology Dictionary, 2013, http://www.etymonline.com/index.php?term=walnut&allowed_in_frame=0), although the species more likely originated from central Asia (Foroni et al., 2007). In Latin, *nigra* means black, referring to the dark color of the heartwood of *Juglans nigra*. Black walnut is native to North America, ranging from the southern part of three Canadian provinces: Ontario, Quebec, and Manitoba, to Florida in the southern United States, and to eastern North Dakota, eastern Utah, and northern Texas as their western frontier (USDA Plants Database, http://plants.usda.gov/core/profile?symbol=JUNI&mapType=nativity). Black walnut is often clustered in small groups or scattered in several mixed mesophytic forest types: yellow-poplar, sugar maple, beech - sugar maple, yellow poplar - northern red oak - white oak, and American elm - silver maple, but rarely growing in pure stands (Williams, 1990). Black walnut grows naturally in coves, bottom lands in riparian regions, abandoned agricultural fields, and fertile woodlands, because the soil type of these sites is usually deep, moist, well-drained, and loamy or silty loamy soil – the best for black walnut (Williams, 1990; Michler et al., 2007).

Black walnut is an allogamous, monoecious, and anemophilous woody species. Although staminate and pistillate flowers grow on the same tree, it is dichogamous: male flowers usually do not shed pollen when female flowers of the same tree are receptive (Cecich, 1998). If pollen shedding happens before the female flowers become receptive, it is called protandry, but if it happens after the females are receptive, it is named as protogyny (Cecich, 1998). Woody plants usually do not flower for some number of years due to their long juvenile period. The juvenile period for stand-grown black walnut is usually about 20 years. The black walnut trees used in this study, however, were grafted clones, so the juvenile period of these trees was shortened and they flowered earlier than wild black walnut.

1.3.2 Economic Significance of Black walnut

Black walnut is one of the most valuable fine hardwood species, with both edible nuts and quality timber as its products. First, its nuts are an important food source for wild animals, and they are also harvested and consumed fresh by humans or used in baking (cakes, cookies, pies, and etc.) and ice cream. Second, its wood is often used as furniture, flooring, veneer, cabinets, and gunstocks, etc. Although the native range of black walnut covers 42 states and provinces (39 in the USA and 3 in Canada), growing stock volume is concentrated in 11 states, including Missouri, Ohio, Iowa, Indiana, Illinois, Tennessee, West Virginia, Kansas, Pennsylvania, Virginia, and Michigan (Shifley, 2004). Black walnut plantations (about 13,800 ac as of 2004) produce about 1% of the total black walnut volume (ft^3) in America (Shifley, 2004). Considering the high economic value of black walnut veneer, growing black walnut in plantations under good management can be a profitable investment.

1.3.3 The advantages of using clone materials to explore ideotype

Clonal forestry is becoming more and more popular, not only because it can increase economic gain by duplicating good genetics from elite genotypes, but also because it makes breeding programs more promising. Use of clonal material decreases the complexity and heterogeneity of mature tree canopies, and makes it possible to link rotation-age yield with traditionally measured parameters of growth used in genetic trials (Dickmann and Keathley, 1996). Genetic correlations between traits that develop over time are determined with greatest power when within-group variance is minimal relative to among-group variance, a situation best achieved by using clonally propagated genotypes (Callister et al., 2007). For instance, crown characteristics of conifers were found to be highly heritable (Kärki, 1985; Pulkkinen and Pöykkö, 1990), thus, the same crown architecture of a naturally grown tree can be copied in plantations through vegetative propagation (Dickmann et al., 1994). The black walnut trees in this study were propagated by grafting, a method commonly practiced on a commercial scale.

1.3.4 Genetics of black walnut

Most published studies of black walnut were based on progeny of open-pollinated trees either in natural stands or grafted clonal banks (Michler et al., 2007). Narrow sense heritability (h^2) of height growth was estimated as 0.41 based on a 13-year old progeny test (Rink and Clausen, 1989) and about 0.40 in a study of twinned seedlings of black walnut (Kung et al., 1974). Similar or slightly lower values were reported by Beineke (1989) and others (Beineke, 1974; Rink, 1984; Rink et al., 1995). Estimates of the heritability of diameter growth of black walnut range from 0.35 to 0.65 based on studies on twins (Kung et al., 1974), clones (Beineke et al., 1991), and open – pollinated families (Rink et al., 1995), although a lower heritability estimate of 0.28 was reported from a 35-year-old progeny test (Woeste, 2002). As is typical of most tree species, the heritability of diameter growth in black walnut seedlings increased in the first ten years from the time of outplanting and did not stabilize until age 15 (Hammitt, 1997; Rink, 1997).

Tree form is a more complex trait to measure than diameter or height, but reported heritability estimates of this trait were moderate, ranging from 0.40 (Beineke, 1989) to 0.50 (Beineke et al., 1991), indicating potential genetic gain with this trait through selection. The heritability estimates of other less-studied traits include branch angle (0.20), number of crooks (0.24), sweep (0.32), branch number (0.41), defoliation date (0.73) and foliation date (0.92) (Beineke, 1974). Heritability of leaf drop date (0.13, different from that reported by Beineke 1974), multiple stems (0.18), insect damage (0.27), and leaf angle (0.32) were reported by Bey (1970). Anthracnose resistance, which may be important in lengthening the growing season, was reported to be highly inheritable (Funk et al., 1981; Woeste and Beineke, 2001); however, significant correlations between growth and anthracnose resistance were not found (Todhunter and Beineke, 1984).

Wood quality traits (heartwood color, heartwood formation, and wound occlusion) are generally expensive to evaluate because they require destructive sampling (Michler et al., 2007). Nonetheless, heritability of heartwood area was reported to be moderate to high (>0.40) (Nelson, 1976; Rink, 1987a; Woeste, 2002), and it is possible that this trait is related to tree vigor (Woeste, 2002).

1.4 Defining black walnut crown ideotypes for timber production

Ideotypes may be designed differently for different environments, and there may be more than one ideotype for the same environment and culture regime (Simmonds, 1985; Tharakan et al., 2005). There are countless traits related to yield or quality, so the description of even a simple ideotype for a particular environment is complex. It is neither impossible to investigate every trait for an ideotype for one environment, nor every possible ideotypes in all possible production environments due to limited time, budget, and knowledge. Particularly for tree species (perennials), some traits present in the current high yield genotype may not be associated with high yield in the future due to both genetic and environment effects. Therefore, every ideotype that has been published was an incomplete ideotype. Nevertheless, an incomplete ideotype may be useful, if it captures the key traits that affect yield and quality, and these traits possess moderate to high heritability.

1.4.1 Important traits that may be included in the design of black walnut timber ideotypes

Growth rate is critical for timber species due to their longer rotation cycle than annual agronomic crops and fruit tree species. Thus, fast growth is one important component for a black walnut ideotype. Height and diameter growth are two basic traits measured in this project to determine growth rate due to the ease with which they are measured and also because they are good measures of tree vigor.

Although tree crown is not part of the end product of timber species, the architecture of crown is essential for crown ideotype as it greatly affects growth and quality for timber species. Crown width is important in terms of narrow crown ideoype, if can be obtained, will help increase stand productivity by increasing the number of narrow but efficient genotypes planted in a limited space. In addition to ground space efficiency, it is also important to evaluate the efficiency of various crown architectural parts within the 3-D crown space so that the balance between fast growth (e.g. more branches) and good quality (e.g. fewer knots and smaller knot size) can be found, i.e. a 'sparse – moderate but efficient crown ideotype' may be designed. In order to achieve this, the following work was done. First, leaf area was modeled at branch- level and tree- level, and thus whole tree leaf area was estimated, clonal growth efficiency (the ratio of stem volume increment to total leaf area) was calculated and compared, and clonal variations in correlations between tree – level dimensions (DBH and crown radius) and tree leaf area were revealed (Chapter 2). Second, branch characteristics - branch diameter, branch angle, branch length, branch growth, branch frequency, and branch basal area per meter of stem were explicitly modeled to examine genotypic differences in architectural traits and the allometric relationships among branch attributes and tree – level parameters (Chapter 3). Besides crown architecture, there are other various traits that may be related to growth. To obtain more evidence as to what traits may be included in black walnut crown ideotypes, a number of traits in phenology (leaf flush, pistillate bloom date, and pollen shed date), physiology (photosynthetic rate, foliar nitrogen and carbon concentration, and specific leaf area, etc.), and fruit production (number of fruits produced, size and dry weight of fruits and seeds) were analyzed on their variance, broad sensed heritability, and the correlation between them and tree growth and form (Chapter 4). Microsatellite molecular markers were deployed to characterize the black walnut clones genetically, and the relations between their genetic identity and clonal crown architecture was examined (Chapter 5). A preliminary list of traits that may be useful in defining a black walnut timber ideotype, including morphological, physiological, ecological and growth-related traits were listed in Table 1-2.

1.4.2 Limitations to ideotype breeding and this study

Although many years have passed since Donald (1968) first proposed the concept of ideotype, its application in forest tree crops are still in its infancy. There are some limitations to ideotype tree breeding and its application in timber crop trees. First, ideotype breeding integrates multiple components (morphology, physiology, biochemistry, genetics, and ecology, etc.) into a selection model, which considerably increases the complexity of selecting those traits and validating them as good predictors. Breeders usually select traits empirically because it is impossible to obtain complete knowledge of the connections between physiology and genetics for a particular species. On the other hand, at fixed selection intensity, the efficiency of selection decreases as more traits are added. As a complex trait closely associated with fitness, a complete ideotype can be expected to have low heritability. Viewing an ideotype as a single quantitative trait and using clones rather than progeny may be one solution to help offset the limitation that low heritability places on gain (Dickmann et al., 1994). With limited information at hand, we can work towards a working ideotype instead of a complete ideotype. We must adjust the details of the working ideotypes when new circumstances arise.

Trees have a much longer lifespan than annual plants. Therefore, tree crop ideotype breeding may focus on a short number of years early in the rotation cycle instead of the whole lifespan of trees. But if we do so, we need to keep in mind that early traits and the correlations among them may change later in the rotation cycle because genes that underlie those traits may have different phenotypic effects at different developmental stages. Models can be used to predict future trends; however, there will always be discrepancies between a model and what occurs in reality, which means it takes a long time to validate proposed tree ideotypes.

A limitation of the current study, which had the goal of designing crown ideotypes for black walnut grown for timber, was that destructive sampling was not allowed. No biomass or dimension measurements of the bark or roots were possible, woody anatomical properties could not be evaluated, and biomass or volume estimation of branches and stems could only be predicted by models and not actually measured. The time span of this study was limited to three years (the 7th to the 10th year from planting), far from the plantation's harvest time at age 30 or even later. Thus, the working ideotype of black walnut timber trees I present will need to be validated at harvest.

1.5 Description of the study site

This study was conducted in a 40.5 ha, even-aged black walnut plantation in West Point, Tippecanoe County, Indiana, US (40.22° N, 87.01° W, Figure 1-1). The local annual average temperature is 11.1°C, and the annual average precipitation is 92.2 cm (U.S. Climate Data http://www.usclimatedata.com/climate.php?location=USIN0707). The soil type is well drained Elston loam (Web Soil Survey, http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx); site index is approximately 29 m on a 50 year basis (Zellers et al., 2012). Before planting, site preparation made the plantation as homogeneous as possible. In 2002, the site was planted with grafted and genetically improved black walnut clones on a wide spacing of 4.57 m × 6.10 m (Figure 1-2). The management regime for these black walnut trees was intense. First, fertigation was applied every other day throughout each growing season. Second, pre- and post-emergent herbicide was applied during the first few years after planting to enhance the establishment of black walnut trees, and continued later to ensure higher nutrient availability. Third, walnut leaf anthracnose caused by *Gnomonia leptostyla* (Fr.) Ces. and de N. was treated with azoxystrobin (Zellers et al., 2012) to delay early leaf abscission, and narrow range oil was applied as needed to treat walnut scale (*Quadraspidiotus juglansregiae*). Lastly, structured pruning was implemented every winter after 2003.

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1.7 Tables

Table 1-1 Ideotype developed for plants, including annual crops, fruit tree crops, biomass tree crops, and timber tree crops

Crop groups	Species	References
Annual crops		
wheat	*Triticum* spp.	Donald, 1968
barley	*Hordeum vulgare*	Donald, 1979; Rasmusson, 1987, 1991
maize	*Zea mays*	Mock and Pearce, 1975
bromegrass	*Bromus inermis*	Walton and Murchison, 1979
dry beans	*Phaseolus vulgaris*	Adams, 1982; Kelly and Adams, 1987; Brothers and Kelley, 1993
soybean	*Glycine* spp.	Mehrotra and Chaudhary, 1980; Kokubun, 1988
pea	*Pisum sativum*	Heath and Hebblethwaite, 1984; Hovinen, 1988
chickpea	*Cicer arietinum*	Bahl and Jain, 1977; Siddique et al., 1984
cotton	*Gossypium* spp.	Coffey and Davis, 1985
spring rape	*Brassica napus*	Thurling, 1991
meadowfoam	*Limnanthes* spp.	Jain and Abuelgasim, 1981
Fruit tree crops		
banana	*Musa* spp.	Stover, 1982
mango	*Mangifera indica*	Tyagi, 1986
apple	*Malus* spp.	Dickmann et al., 1994
coffee	*Coffea canephora*	Cilas et al., 2006
Timber crops		
Scots pine	*Pinus sylvestris*	Kärki, 1985; Pöykkö, 1993
Norway spruce	*Picea abies*	Pöykkö and Pulkkinen, 1990; Pulkkinen and Pöykkö, 1990
Biomass crops		
willow	*Salix* spp.	Tharakan et al., 2005
poplar	*Populus* spp.	Dickmann, 1985; Dickmann and Keathley, 1996

Table 1-2 A proposed crown ideotype for black walnut (Juglans nigra) grown for stemwood in a low density plantation, irrigated, intensive silvicultural system

Traits	Description
Stem growth and nut production	Rapid height and diameter growth
	High growth efficiency
	Few nuts (few flowers)
Phenology	Late leaf flushing to avoid frost damage
Physiology	High photosynthetic rate
	High specific leaf area (SLA)
	High foliar nitrogen concentration
	Intermediate total leaf area
	Intermediate to high foliar nitrogen concentration
Morphology	Sparse crown: low branch frequency and low foliar density
	Small branches or low branch basal area per meter of stem
	Intermediate to wide crown
	Intermediate to large average branch angle
	High portion of biomass (volume) allocation to stem
	Straight stem
Roots*	Large and strong root system
	Large surface area of fine roots
	Even spatial distribution in each direction

* Root characteristics were not investigated in this study.

1.8 Figures

Figure 1-1 Location of the study site: West Point, IN (40.22° N, 87.01° W)

Figure 1-2 Plantation spacing 4.57 m × 6.10 m (Left picture was taken in 2009 spring, right in 2011 winter)

CHAPTER 2. MODELING LEAF AREA AND MASS, AND ESTIMATING GROWTH EFFICIENCY FOR PLANTATION-GROWN BLACK WALNUT (*JUGLANS NIGRA* L.) CLONES IN INDIANA, USA

2.1 Introduction

Light absorption and light use efficiency determine the productivity of a tree; light absorption of a tree is linearly correlated to its leaf area (Binkley et al., 2013). Therefore, leaf area is an essential metric of tree growth, and modeling leaf area of tree species has become a particular interest to many physiologists and ecologists. Direct measurements of leaf area or mass from mature trees through destructive sampling is logistically difficult, labor-intensive, impractical (Medhurst et al., 1999), and not feasible for long-term studies (Laubhann et al., 2010). Thus, many researchers have relied upon non-destructive methods, one of which is allometric modeling of more easily measured tree attributes such as stem diameter, tree height, crown length, crown radius, basal area, and sapwood area. These allometric models have been developed in the past several decades for a variety of economically important tree species, of which most were conifers (Gilmore et al., 1996; Maguire and Bennett, 1996; Maguire et al., 1998; Kenefic and Seymour, 1999; Monserud and Marshall, 1999; DeRose and Seymour, 2009; Weiskittel et al., 2009; Hofmeyer et al., 2010), but allometric models for some hardwood species have been published too (Helgerson et al., 1988; Korsmo, 1995; Vertessy et al., 1995; Bartelink, 1997; Meadows and Hodges, 2002; Zianis and Mencuccini, 2003; Calvo-Alvarado et al., 2008; Zellers et al., 2012).

Branch allometric models generally rely on only branch diameter to predict branch leaf area and mass. However, position of individual branches in the crown plays a significant role in the amount of leaf area and mass displayed (Maguire and Bennett, 1996). Branch leaf mass and area will monotonically increase as branch diameter increases; however, light levels usually decrease from the periphery of a tree crown towards its interior. This would result in foliage recession where branches come out of the stem, particularly in the lower crown where self-shading is pronounced. It is therefore unrealistic to model foliage area or mass using a simple monotonically increasing relationship between branch diameter and branch leaf area or mass (Kershaw and Maguire, 1995). Instead, adding variables that define branch position within the live crown such as relative depth into crown (RDINC) to the branch-level leaf area and mass models yields more precise models for some conifers (Maguire and Bennett, 1996; Kenefic and Seymour, 1999; DeRose and Seymour, 2009).

Most recently-developed allometric leaf area and mass models are based on the pipe model theory (Shinozaki et al., 1964; Long et al., 1981), which postulates that one unit of conducting xylem (sapwood) tissue physiologically supports one unit of leaf area. Hence, sapwood area at any point of the main stem or a branch is proportional to the leaf area distal to that point. These sapwood-area based models are more accurate compared to simpler diameter-based models (Waring et al., 1982; Gilmore et al., 1996; Kenefic and Seymour, 1999), but they require estimation of sapwood area through destructive sampling of the trees or significant increment coring of the boles. This can limit the development of sapwood-based models using trees in hardwood plantations that are producing high quality timber or veneer. Diameter-based allometric models for branch- and whole-tree leaf area and mass could be applied with the caveat that the end user avoid severe extrapolation beyond the range of the data used to develop the model (Waring et al., 1982). Diameter-based allometric relationships still explained over 80% of the variation in sapwood area, total leaf area, or biomass of other tree parts in several temperate hardwood species (Vertessy et al., 1995; Bartelink, 1997; Ter-Mikaelian and Korzukhin, 1997; Santa Regina and Tarazona, 2001; Zianis and Mencuccini, 2003), and are nearly as accurate as sapwood area in predicting whole tree foliar mass and area for some tropical species (Calvo-Alvarado et al., 2008).

In hardwoods, including a variable that represents branch angle (ϑ) from vertical may improve branch-level models, as branches with different angles differ both in leaf area display and mechanical support. Conifers generally are geomorphic, have strong apical dominance and, therefore, produce lateral branches with low angles (nearly perpendicular to stem) on a single straight stem. Many hardwood species, on the other hand, are more strongly photomorphic, lack strong apical dominance, and often have multiple leaders developed from lateral branches with acute angles (Oliver and Larson, 1990; Zellers et al., 2012; Nelson et al., 2014). This difference between conifers and hardwoods shows that angles of lateral branches may be an indicator of not only the strength of apical dominance, but also of a branches' growth potential; that is, the acuter the angle of a branch, the greater the release it gets from its own gravity moment, and the larger the opportunity to capture light, grow leaves, and potentially become a co-dominant leader. Branch angle was used to predict branch diameter in Scots pine (*Pinus sylvestris* L.) (Mäkinen and Colin, 1998) and was correlated to tree diameter of *Eucalyptus nitens* (Deane and Maiden) Maiden (Medhurst and Beadle, 2001); branch angle was predicted by stem diameter in Norway spruce (*Picea abies* (L.) Karst.) (Mäkinen et al., 2003b) and silver birch (*Betula pendula* Roth.) (Mäkinen et al., 2003a). Therefore, branch geometry can strongly influence tree growth and allometry through alterations of leaf area display.

Growth efficiency was defined as the ratio of stem volume increment to tree leaf area and was regarded as an indicator of tree vigor and stand productivity (Waring et al., 1980). Stemwood production was related to the amount, vertical distribution, and density of foliage in *Pinus contorta* Var. *Latifolia* (Smith and Long, 1989). Dense crowns may reduce light penetration and therefore lower growth efficiency, while sparse crowns may be a mechanism that enables trees to have optimal growth performance in a variety of environments (Mäkelä and Vanninen, 1998). The general trend in conifers was that stem volume increment increases as tree and crown size increase, which are typically measured by total leaf area, but growth efficiency declines as total leaf area increases (Smith and Long, 1989; Maguire et al., 1998; DeRose and Seymour, 2009; Hofmeyer et al., 2010). Studies of tree leaf area, crown structure, and stem growth efficiency have been rare in hardwood species.

The objectives of this study were to develop clone-specific branch- and tree-level allometric models for black walnut (*Juglans nigra* L.) leaf area and mass and then test for differences in stemwood-based growth efficiency among clones. We hypothesized that: 1) branch position and branch angle would dynamically affect branch leaf area and mass for black walnut trees; 2) tree-level leaf area and mass could be predicted well with DBH alone; 3) there would be strong differences among clones in both branch- and tree-level models; and 4) absolute stem volume growth would reach highest with highest foliage area and foliage density (largest tree leaf area per unit of ground area), however, growth efficiency would be maximized in clones with intermediate foliage area and density.

2.2 Materials and Methods

2.2.1 Materials

This study is part of a larger project determining crown ideotypes for 25 black walnut clones. The black walnut clones used in this study were part of the black walnut genetic improvement program, which started at Purdue University in 1967. The goals of the program were to preserve selected, high quality timber genotypes, and establish clone banks for clonal forestry (Beineke, 1989). Different methods were applied: controlled pollination to produce new genotypes, grafting to preserve already-existing and tested superior genotypes, and selecting excellent new genotypes on multiple traits from the progeny (Beineke, 1983). The 25 clones were grafted onto seedling rootstocks and then planted in 2002 in a plantation with a homogeneous soil type and management regime. Considerable variance in growth and crown structure was observed (Table 2-2 & 2-3). Therefore, this was a unique opportunity to explore if the observed variance in growth was due to clonal differences in amount of foliage and foliage related characteristics.

2.2.2 Data Collection

From this ideotype project, branches were destructively sampled from a subset of nine clones that represented the broad range of size and crown characteristics of the larger project (Table 2-3). Originally five to ten trees were selected from each clone, but in summer 2010 and 2011, strong winds caused crown damage to some of these trees. These damaged individuals were excluded from further analysis because the crowns could not be reconstructed. Further, clonal identity of every tree was verified by microsatellite markers and mislabeled trees were removed from further analysis.

2.2.2.1 Specific leaf area

Specific leaf area (SLA) for broadleaved species is the ratio of one-sided leaf area to the dry weight of a leaf. SLA varies within a crown as the vertical position of the foliage changes, i.e., leaves in the upper crown are thicker and tend to have lower SLA in order to reduce water stress in high light conditions, while leaves in the lower crown are thinner and have a higher SLA in order to capture more light in low light conditions (Kershaw Jr. and Maguire, 1995; Meadows and Hodges, 2002). SLA was measured in July 2010. Tree crowns were divided into two parts for sampling, the lower third and the middle-upper two thirds, assuming that the upper third and middle third crown were exposed to the same light environment due to the wide spacing among trees in the plantation. From each clone, three to five trees were randomly selected, and from each tree, five fully developed leaves were randomly selected within each of the two crown positions. Leaves were removed by hand or with a pole-pruner, then put into paper bags and stored in a 4 °C cooler to keep them from drying. An Epson® Expression 10000 XL scanned the leaves at a resolution of 300 dpi, and then WinFolia™ 2009a software (Régent Instruments, Québec, Canada) determined the one-sided leaf area to the nearest 0.0001 cm^2. Leaves were then oven-dried at 65°C for 72 hours and weighed to the nearest 0.01 g. Clonal SLAs were determined by dividing sampled leaf areas by the sampled leaf dry weights of each leaf, then averaging for each crown position.

2.2.2.2 Branch leaf mass and area

Branches were sampled in late July and early August of 2011 using a stratified approach that referenced individual branch measurements taken from October 2010 to March 2011 in the same plantation. Branches were first categorized into five branch diameter (BD) size groups for each clone: 0 – 1.27cm, 1.28 – 2.54 cm, 2.55 – 3.81 cm, 3.82 – 5.08 cm, and larger than 5.08 cm. As each size group is distributed non-randomly within the crown (e.g., large branches are found only in middle and bottom portions of the crown, whereas small branches are found throughout, albeit mostly concentrated in the upper crown), multiple randomizations of branch selections were conducted to assure samples would be collected from throughout the range of branch height positions observed for the size group on each clone. If selected branches were broken or pruned, then a nearby, similarly sized branch was chosen. Fifteen to 16 branches were selected across the eight to ten trees in each clone for a total of 138 branches from 79 trees of nine clones (Table 2-3). An Altec® lift was utilized to reach branches. All leaves from each branch were stripped and put into paper bags. They were stored in a 4 °C walk-in cooler, then oven-dried at 65°C for 72 hours, and finally weighed to the nearest 0.01 g. Individual branch leaf areas were calculated by multiplying branch leaf mass by its positional SLAs accordingly: lower crown SLA was used for the branches of which the relative depth into crown of branch tips (tRDINC) were below 0.67 (see 2.3.1 for how tRDINC was estimated), otherwise mid-upper crown SLA was used.

2.2.2.3 Other branch and tree parameters

Several tree and crown architectural attributes were measured during the dormant season from October 2010 to March 2011 on 179 sample trees across all 25 clones. Tree attributes included: diameter at breast height (DBH; 1.37 m above ground), total tree height (Ht), crown radii (CR) in four cardinal directions, and height to live crown base (HCB). DBH was measured by a digital caliper (Haglöf Sweden, Inc.) in two perpendicular directions (North to South, and West to East) with the position marked on the bark for consistency, to the nearest 0.25 cm. Total tree height (Ht) and HCB were determined by a laser (Impulse 200, Laser Technology Inc.) to the nearest 0.3 m and was verified by a height pole when necessary. Crown radii were measured by tape to the nearest 0.25 cm.

For each tree, BD above basal swelling was measured for every branch; for branches of which BD was larger than 1.27 cm: branch height (BHt, where branches originated from the stem) and branch angle (ϑ) from vertical were also measured. For top branches above the reach of the lift, we measured the stem diameter immediately above the highest branch we could reach and treated the remaining stem as a terminal branch. Branch Diameter (BD) was measured by a digital caliper to the nearest 0.025 cm, BHt was measured with a height pole to the nearest 0.25 cm, and branch angle ϑ was measured with a digital protractor (General®, UltraTech™ Tool System) to the nearest 0.5 degree. Diameter at breast height (DBH), Ht, HCB, and BD were measured again in July and August 2011 while collecting branch leaf samples for mass and area modeling.

2.2.3 Data Analysis

2.2.3.1 Branch-level models

Branch diameter is the primary predictor for branch leaf area and mass in both hardwood species, including black walnut (Zellers et al., 2012), and conifer species as well (Kershaw Jr. and Maguire, 1995; Maguire et al., 1998; Kenefic and Seymour, 1999; Monserud and Marshall, 1999). Therefore, we began with a basic, mixed-effects branch-level model of:

$$\ln Y = (a_0 + c_{0j}) + (a_1 + c_{1j}) \ln BD + \varepsilon, \qquad [1]$$

where Y is either branch leaf area (BLA, cm) or branch leaf mass (BLM, g), BD is branch diameter, a_i's are the fixed parameter estimates, c_{ij}'s are the random parameter estimates associated with the jth clone with $c_{0j} \sim^{idd} N(0, \sigma_{0j}^2)$, and ε is the error term with $\varepsilon \sim^{idd} N(0, \sigma^2)$.

As foliage mass and area on a given-sized branch has been found to decrease towards the top and bottom of the live crown (Maguire and Bennett, 1996), many researchers have included positional variables that can describe foliage amount in a dynamic way through the crown. One of the simplest modeling approaches was to use relative depth into crown (bRDINC) (e.g., Kenefic and Seymour, 1999). In my exploratory analysis, this approach did not capture the strong nonlinearity of the relationship; therefore, we used the variable allometric ratio modeling approach (Ruark et al., 1987), which was demonstrated for leaf area modeling by Maguire et al. (1998) and DeRose and Seymour (2009). The model was expressed as:

$$\ln Y = (a_0 + c_{0j}) + (a_1 + c_{1j}) \ln BD + (a_2 + c_{2j}) \ln bRDINC + (a_3 + c_{3j}) bRDINC \ + \varepsilon, \qquad [2]$$

where *Y*, *BD*, b_i, c_{ij} and ε are as defined for eq. [1] and b*RDINC* is defined as (Kenefic and Seymour, 1999):

$$bRDINC = (Ht - BHt)/(Ht - HtCB) \qquad [3]$$

where *Ht* is tree height, *BHt* is branch basal height, and *HCB* is height of crown base.

Conifer branches usually form at flat angles, being nearly perpendicular to the stem. Thus, bRDINC adequately represents the social position of each branch in the crown of conifers. However, bRDINC may not work well for many hardwoods, particularly those with weak epinastic control, as branches grow more acutely to the terminal seeking light. Thus, Nelson et al. (2014) argued that bRDINC does not represent the social positions of hardwood branches and introduced a “relative height of branch tip” variable to address this perceived shortcoming. We tested the Nelson et al. (2014) method for black walnut using two model forms:

$$\ln Y = (a_0 + c_{0j}) + (a_1 + c_{1j}) \ln BD + (a_2 + c_{2j}) \ln tRDINC + (a_3 + c_{3j}) bRDINC \ + \varepsilon, \qquad [4]$$

$$\ln Y = (a_0 + c_{0j}) + (a_1 + c_{1j}) \ln BD + (a_2 + c_{2j}) \ln tRDINC + (a_3 + c_{3j}) tRDINC + \varepsilon \qquad [5]$$

where *Y*, *BD*, *b$_i$*, *c$_{ij}$* and *ε* are as defined for eq. [1] and *tRDINC* is relative depth into crown of the tip height of the first order branch (BtHt) calculated similarly to bRDINC using BtHt in place of BHt in eq. [3]. BtHt was estimated as:

$$BtHt = BHt + BL * cos\vartheta, \qquad [6]$$

where ϑ is the branch angle from vertical and BL is estimated branch length. Branch length (BL) was predicted by branch diameter using an allometric equation predicting first-order branch length developed from the same 25 black walnut clones (see chapter 3 for more details) since it was too difficult to measure BL from the lift.

Inclusion of branch angle (ϑ) may serve as an alternative to tRDINC for capturing social position differences in foliage amount within a hardwood crown, and would not require measurement of BL, which can be difficult to determine in large trees. Branch angle is a trade-off between maximizing light reception in individual branch's micro environment and minimizing the mechanical support for the branch's weight, i.e., the smaller the ϑ, the larger the release from its gravity moment, and therefore, more growth potential gained. Exploratory analysis suggested that for a given-sized branch, the influence of ϑ on foliage amount did not monotonically change. Hence, we tested inclusion of ϑ by:

$$\ln Y = (a_0 + c_{0j}) + (a_1 + c_{1j}) \ln BD + (a_2 + c_{2j}) \ln(\cos\theta + 1) + (a_3 + c_{3j}) \cos\theta + \varepsilon \qquad [7]$$

where *Y*, *BD*, *b$_i$*, *c$_{ij}$* and ε are as defined for eq. [1], and ϑ is the branch angle from vertical in radians, with the constant 1 added to cosϑ to better linearize the relationship and avoid undefined values of $\cos\theta$ for $\theta \geq \pi/2$.

Complex modeling forms may reduce the efficiency and power of a model, therefore, model simplification is often needed. We explored the correlation between clone and other variables including intercept (effects of clone) in each corresponding equation. We first attempted to use the full covariance matrix structure with correlated random effects, but most models did not converge. Therefore, we assumed random effects were not correlated and used a diagonal covariance structure. Further simplification determined that clone had insignificant influence on all parameter estimates (i.e., all random effects were nearly 0), except for the intercept of each equation (c_{0j}'s). Inclusion of these random effects led to significant ($p < 0.05$) or marginally significant ($p < 0.06$) improvement to models. Therefore, my models simplified to:

$$\ln Y = (a_0 + c_{0j}) + a_1 \ln BD + \varepsilon \qquad [8]$$

$$\ln Y = \left(a_0 + c_{0j}\right) + a_1 \ln BD + a_2 \ln bRDINC + a_3 bRDINC \ + \varepsilon \qquad [9]$$

$$\ln Y = \left(a_0 + c_{0j}\right) + a_1 \ln BD + a_2 \ln tRDINC + a_3 bRDINC \ + \varepsilon \qquad [10]$$

$$\ln Y = \left(a_0 + c_{0j}\right) + a_1 \ln BD + a_2 \ln tRDINC + a_3 tRDINC \ + \varepsilon \qquad [11]$$

$$\ln Y = (a_0 + c_{0j}) + a_1 \ln BD + a_2 \ln(\cos\theta + 1) + a_3 \cos\theta + \varepsilon \qquad [12]$$

with all variables defined as in eq. [1], [2], [4], [5],and [7], respectively.

Log bias of these models was calculated via the method developed by Snowdon (1991). Model performance was evaluated using -2 REML log-likelihood values, and the Akaike information criterion (AIC). Goodness of fit was evaluated with coefficient of determination (R^2) proposed for linear mixed effect models (Nakagawa and Schielzeth, 2013). Residual plots were used to assess the model heteroscedasticity.

2.2.3.2 Tree-level models

Tree-level leaf area (TLA) and mass (TLM) of the 25 clones were calculated using the branch summation method (Loomis et al., 1966; Whittaker and Marks, 1975; Monserud and Marshall, 1999). We first chose the best branch-level equations according to their AIC, -2 Log-likelihood value, and R^2, then calculated clone-specific, branch-level leaf area and mass using either the calculated c_{0j}'s for the clones used for branch-level modeling or setting $c_{0j} = 0$ for the clones not used. After applying branch-level equations to all measured branches, we then back-transformed the predicted values to the original scale, multiplied the log-bias correction factors, then finally summed the BLA or BLM to get a predicted total TLA or TLM. Two tree-level leaf models were tested:

$$\ln Z = (d_0 + g_{0j}) + (d_1 + g_{1j}) \ln DBH + \varepsilon \qquad [13]$$

$$\ln Z = (d_0 + g_{0j}) + (d_1 + g_{1j}) \ln DBH + (d_2 + g_{2j}) \ln CR + \varepsilon \qquad [14]$$

where Z represents either TLM (g) or TLA (cm), DBH is diameter at breast height in cm, CR is crown radius in m, d_i are the fixed parameter estimates, g_{ij} are the random parameter estimates associated with the *j*th clone with $g_{0j} \sim^{idd} N(0, \sigma_{0j}^2)$, and ε is the error term with $\varepsilon \sim^{idd} N(0, \sigma^2)$. Model performance was evaluated using -2 REML log-likelihood, and AIC. Goodness of fit was evaluated by R^2, and residual plots were used to assess the model heteroscedasticity.

2.2.3.3 Standing volume increment and growth efficiency

As trees could not be destructively sampled or cored, standing bole volume increment in the season of 2010 was estimated by subtracting the 2009 year-end volume from the 2010 year-end volume using the paraboloid equation: V =1/2* A_b*Ht (Husch et al., 2002), where A_b is the cross sectional area at breast height including bark, and Ht is tree height. We assumed that bark thickness did not appreciably change across the years this project was conducted. Growth efficiency was calculated as standing stem volume increment divided by predicted TLA. Leaf area index (LAI) was calculated as TLA divided by projected crown area. To better characterize crown density, we then calculated a foliar density index (FDI), as LAI divided by crown length, to indicate how many layers of leaves were displayed within each unit of crown length. Relationships among growth efficiency, LAI and FDI were explored. Clonal differences for stemwood production and growth efficiency were tested using Tukey's Studentized Range (HSD) multiple comparison test. All analyses were conducted using SAS 9.3 (SAS Institute Inc., 2011). A criterion of α= 0.05 was used for all formal tests.

2.3 Results

2.3.1 Branch-level models

Across all nine clones, specific leaf area (SLA) in the lower crown was significantly larger than that of mid-upper crown ($p < 0.0001$) (Table 2-4). Most clones did not differ significantly in SLA at either crown position (all p's ≥ 0.0774); clone 717 was, however, significantly larger than all others at both crown positions (lower crown SLA: 183.65 ± 16.79 $cm^2 \cdot g^{-1}$ [mean± standard deviation], p=0.0002; mid-upper crown SLA: 160.62 ± 30.80 $cm^2 \cdot g^{-1}$, p=0.0009). Albeit minor, these differences indicate that clone-specific SLAs would be more accurate when expanding branch foliage weights to leaf area for subsequent modeling.

Among all branch-level models (Table 2-5), the basic BD model (eq. [8]) performed well having high R^2s (0.9767 for BLM and 0.9731 for BLA), but the AIC, and -2 REML log-likelihood value for the basic BD model were the highest among all models. Models [9] (position of branch base bRDINC used), [10] (positions of branch tip tRDINC and base bRDINC used), [11] (position of branch tip tRDINC used), and [12] (branch angle variable cosθ used) performed better than the basic model eq. [8] with higher R^2, lower AIC, and -2 REML log-likelihood values, indicating they were better than basic model eq. [8]. Among models in which branch position variables or angle variables were added (eq. [9] to [12]), eq. [12] (model with branch angle variables) was the worst. Equations [10] (position of both branch tip and base involved) and [11] (position of branch tip involved) had very similar information criterion and R^2, indicating they performed almost equivalently. Equation [9] (position of branch base involved) had the lowest AIC, -2 REML log likelihood values, and the highest R^{2}'s; it was therefore used later to develop tree-level models. These results indicated that adding positional variables or angular variables to the basic model all improved the model performance, but positional variables performed better than angular variables, with bRDINC as the best.

Regarding genetic differences, clones C708, C712, C717, and C726 held greater leaf area and mass at a given RDINC than the population average, while clones C130, C55, C710, C714, and C715 were lower than the population average (Figure 2-1 and 2-2). For the BLM model, random parameters for clones C717 and C710 were significantly different from zero ($p = 0.0015$ and 0.0175, respectively). As for the BLA model [10] (Figure 2-2), clones C712, C717, and C726 had higher intercept than the population average, and clones C55, C710, C714, and C715 had lower intercept than the population average, indicating with a same-sized branch diameter located at the same relative position, high intercept clones produced more foliage than low intercept clones. However, random parameters were significant only for C710 and C717 ($p = 0.0179$ and <0.0001, respectively). Clone C714's random parameters were marginally significant ($p=0.067$). According to Figure 2-1 and 2-1, a same sized branch grew more leaves, both in terms of leaf mass and area, if located in the upper crown. As for eq. [12], it seems both smaller angled branches and larger angled branches held more foliage as well (Figure 2-3 and 2-4). This was in accordance with the vertical distribution of branch angle (Figure 2-5), i.e., more small angled branches were located in the upper crown, while most large angled branches were located in lower crown.

2.3.2 Tree-level models

A DBH-only tree-level model, Eq. [13], explained 62.48% of the variance for TLM and 63.88% for TLA. Including CR in the model (Eq. [14]) increased precision as indicated by lower AIC, -2 log-likelihood values, and higher R^2 values (Table 2-6).

For the TLM model, Clones C708, C710, C712, C717, and C726 had higher intercepts than the population average (fixed effects portion estimates, Table 2-6), while Clones 130, C55, C714, and C715 had lower intercepts (Figure 2-6 and 2-8). For the TLA model (Figure 2-7 and 2-9), Clone C708, C717, and C726 had larger intercepts than the population average (fixed effects portion estimates, Table 2-6). Clone C712 almost overlapped with the population average, and C130, C55, C710, C714, and C715 had smaller intercepts. These estimates mean that when crown radii was held constant at the average 2.77 m, clones located lower than the population average line had less foliage than the ones that had higher intercepts (Figure 2-6 and 2-7). When DBH was held constant at the average 14.68 cm, clones located lower than the population average line held less foliage than the clones above the population average (Figure 2-8 and 2-9). In other words, given a fixed amount of foliage, clones with lower intercepts grew to larger sizes in terms of DBH or crown radii.

2.3.3 Standing volume increment and growth efficiency

Among the 25 clones observed, total leaf area (TLA), total leaf mass (TLM), standing volume increment (SVI) in 2010, growth efficiency (GE), leaf area index (LAI), and foliage density index (FDI) varied widely. Estimated average TLA ranged from 81.50 m^2 in clone C729 (DBH: 9.91 cm) to 205.87 m^2 in clone C777 (DBH: 15.24 cm); estimated average TLM ranged from 6.05 kg in clone C729 to 15.56 kg in clone C777 (Table 2-6). The mean SVI in 2010 ranged from 45.95 dm^3 (clone C729) to 15.91 dm^3 (clone C714, DBH: 16.29±0.83 cm), average GE extended from 0.31 $dm^3 \cdot m^{-2}$ (clone C717) to 1.12 $dm^3 \cdot m^{-2}$ (clone C714), mean LAI varied from 4.08 $m^2 \cdot m^{-2}$ (clone C729) to 8.09 $m^2 \cdot m^{-2}$ (clone C702, DBH: 14.88±0.66 cm), and FDI from 0.57 $m^2 \cdot m^{-2} \cdot m^{-1}$ (clone 720, DBH: 14.01±1.26 cm) to 1.33 $m^2 \cdot m^{-2} \cdot m^{-1}$ (clone C717).

Standing volume increment increased monotonically with increasing tree leaf area (Figure 2-10), but growth efficiency decreased with increasing leaf area (Figure 2-11). There were strong clonal differences in growth efficiency (Figure 2-11, 2-12, and 2-13). For example, Clone C714 had the highest estimated standing stem volume increment, but smaller foliage area than most clones other than clone C55, indicating high growth efficiency in comparison to other clones. Clone 717, on the other hand, was inefficient because it displayed the largest amount of leaf area, but this did not lead to higher stem volume Increment. Growth efficiency also declined as LAI and FDI increased (Figure 2-12 and 2-13), but a few clones with medium LAI and FDI had higher efficiency than others.

Clone C714, C55, and C710 all had sparse crowns (low FDI and LAI), but high growth efficiency. Clone C714 stood out because it showed both high absolute standing volume growth and high growth efficiency.

2.4 Discussion

2.4.1 Branch-level models

My analysis showed that SLA increased with crown depth (Table 2-4), a result in accordance with the vertical pattern of SLA in other species (Kershaw Jr. and Maguire, 1995; Bartelink, 1996, 1997; Nelson et al., 2014). Several authors have found that the vertical position of branches is a reliable and useful predictor of leaf area and mass (Maguire and Bennett, 1996; Hofmeyer et al., 2010; Nelson et al., 2014). This was also the case for black walnut in this study. The models I fit for black walnut produced results that different from those of previous studies, however. Maguire & Bennett (1996) and Weiskittel et al. (2009) graphed the vertical distribution of foliage amount (area and mass) of several conifer species based on their branch-level equations. They showed that for a fixed sized branch, leaf mass and area generally peaked in the bottom of the middle third or top of the bottom third of the live crown. In my results, no peaks were observed, but the leaf area and mass reached a trough in the middle crown (an bRDINC value of 0.72 for BLM and 0.61 for BLA), and more foliage was located on branches that originated in the upper and lower crown than the middle (Figure 2-1 & 2-2). We believe that both distribution patterns are due to the genetics of black walnut, light environment, and culture regime. An important difference between the growth habit of conifers and hardwoods is that middle branches of conifers usually have multiple years of foliage, but new branches at top of crown only have foliage of the most recent year. Because branches of many conifer species can grow needles without any branch diameter growth for up to ten years (Reukema, 1959; Kershaw Jr. et al., 1990; Fujimori, 1993), it is reasonable that the middle branches of conifers might hold more foliage than a same-sized young branch found higher in the crown or branch that is dying at the bottom of the crown. For deciduous hardwoods, however, branches do not accumulate foliage from previous years, so for a given-size branch, leaf area may not peak at middle crown, as shown by the leaf area models developed for red maple, paper birch, grey birch, and several hybrid poplar clones in Maine (Nelson et al., 2014). Second, hardwoods generally have weaker apical dominance than conifers, and are much more phototrohic, therefore, hardwood branches often emerge from the stem at acute angles. Thus, acute branches that originate from lower crown positions may grow into higher crown positions, or in some cases, branches emerged horizontally but curved up more acutely later, gaining access to higher levels of light. In this study, the large amount of foliage in the upper crown of hardwoods, as compared to conifers, was probably the result of the high light environment in the black walnut plantation and because continuous fertigation allowed the trees to keep growing throughout the season. When comes to application, we do not suggest to extrapolate model [9] to branches of which the bRDINC is between 0 and 0.2, which is beyond the data range in this study.

The negative correlation between branch angle and branch length (Figure 2-14) may help explain the observed correlation between branch angle and branch leaf mass and area, because it indicates that branch angle affects branch leaf mass and branch length in a similar fashion. Same-sized branches with smaller branch angles have the potential to support greater weight, because more upright branches have less torque on the center of gravity of the branch than branches that emerge more horizontally from the stem (Figure 2-15; Morgan and Cannell, 1988). In other words, smaller angled branches may have been released to an extent from the burden of supporting their weight, therefore they grow thicker and longer than larger angled branches. One example of this is the co-dominant leaders commonly seen in hardwood species. These branches had more growth potential due to the small angle of their insertion into the stem. As for the larger-angled branches that held more foliage mass and area than branches with moderate angles, although these branches displayed a large angle at the origin, they most likely curved up later and thus acquired the advantage of smaller angled branches.

Most acute-angled branches originated in the upper crown, and horizontal-angled branches in the lower crown (Figure 2-5). Thus branch angle may have substituted for vertical position and predicted foliage mass and area as well as the position variables (bRDINC and tRDINC) did.

Although adding both bRDINC and tRDINC (eq [10]), or tRDINC only (eq. [11]) predicted branch foliage mass and area satisfactorily, there are drawbacks to using these variables in models. Direct measurement of height of a branch tip is difficult; even estimation through branch angle and length may be impossible when the tree sizes are large and trees cannot be destructively sampled. Further, branch basal heights are stable and do not change like tip heights do, so tip heights would have to be remeasured to monitor the yearly changes of branch leaf area. Because new tree heights need to be re-measured to calculate new bRDINC, both tree heights and new tip heights of branches need to be measured again as well.

Clones with lower intercepts in eq. [9] grew less leaf mass (Clone C130, C55, C710, C714, and C715) and area (Clone C130, C55, C708,C710, C714, and C715) given a fixed branch diameter, indicating these clones may have a leaf arrangement along branches that enables better light penetration. Clones with large amounts of foliage per unit of branch diameter may increase mutual shading among branches; thus some of the foliage may be wasted. Among all nine clones, the one with highest intercepts in branch-level models was C717, meaning given a fixed diameter, its branch grew more leaf area and the leaf arrangement may be denser than the clones with low intercepts.

2.4.2 Tree-level models

Some clones had low coefficients in tree-level equations (for example, clone C55 and C714 in eq. 15), indicating that for a given crown radius, less foliage was grown. This means that for these clones, there was more space between adjacent leaves on average, implying a leaf arrangement that may have enabled deeper light penetration through the crown. Thus, the tree-level models were also in agreement with results from branch-level modelling that the same clones had a more efficient leaf arrangement at branch-level. “Narrow crown” ideotype was defined for Norway spruce (Kärki and Tigerstedt, 1985) thus high stand productivity can be achieved by dense plantings, it is also possible to breed black walnut toward a narrow crown ideotype if aiming at the negative deviation from the regression between crown radius and stem growth. Actually, narrow crown ideotype indeed is a balance between high harvest index and high total stem production (Sheppard and Ford, 1986).

The model fit statistic (R^2) of my tree-level models was not as good as that from other research, possibly because of the particular features of the study site and the sampling methods I used. My study was conducted at an even-age site, while Zellers et al. (2012) sampled trees of three different ages and thus different tree sizes. The other reason might be that SLA and leaf mass were sampled in two years, not in one, and leaves used for estimating SLA were not sampled from each branch but instead we resampled from two crown positions.

One possible reason that clone C717 may have grown more leaf area and had higher leaf mass because of a fertilizer leak that was observed around its planting area. Research has shown that extra nitrogen can stimulate trees to put on more leaves and grow higher SLA (Knops and Reinhart, 2000).

2.4.3 Standing volume increment and growth efficiency

In this study, more foliage led to higher stem volume increment. This was in agreement with the report that *Picea sitchensis* (Sikta spruce) with more needle tissue yielded more wood and grew the tallest (Cannell, 1974). With regard to the trend that growth efficiency declined as LAI and FDI increased, this result was in agreement with previous studies of some conifer species (Maguire et al., 1998; DeRose and Seymour, 2009; Hofmeyer et al., 2010), and may be explained by Kuuluvainen’s hypothesis (1988) that more foliage packed within a short vertical distance would lower the light penetration and impede gas exchange, leading to slower growth. Clone C55, C710, and C714 had low

FDIs but high growth efficiency. Because clone C55 is believed to be a parent of C710 and C714, it seems likely that crown sparseness may be inheritable and worth further genetic investigation. C714 had both high growth efficiency and high absolute growth, indicating that it may be superior to its parent clone (C55) and half sibling clone (C710).

In the future, black walnut breeders should consider incorporating growth efficiency and foliar density as selection criteria; more foliage does not make a better tree, on the contrary, a sparse crown of foliage uses the light and space more efficiently. Thus, the variation in leaf area allometry and growth efficiency made it possible for “sparse-moderate” crown ideotype to be realized, i.e., genotypes with low crown foliar density but high growth efficiency.

2.4.4 Conclusion

The branch position variable bRDINC predicted branch-level leaf area and mass the best. Branch angle can be used to predict branch leaf area and mass; however, it may not produce estimates as accurate as models that include bRDINC. DBH together with crown radii predicted tree leaf area and mass better than DBH alone. Clone C714 best meets the ideal of a fast growing, highly efficient, and high quality genotype. Because it was difficult to tease out the effect of pruning on the light environment of individual branches; it may be helpful to devise a study to quantify it in the future, for instance, to compare intensively managed black walnut to the naturally grown trees.

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2.6 Tables

Table 2-1 Explanations and units of symbols used in chapter 2

Symbol	Explanation	Units
THt	Total tree height	m
BHt	Branch basal height from ground	m
BtHt	Height of branch tip	m
HCB	Height of the crown base (the lowest living branch)	m
bRDINC	Relative depth into crown of branches: (THt - BHt)/CL	-
BD	Branch diameter	cm
BL	Branch length	cm
tRDINC	Relative depth into crown of the centers in each one-meter stem segment: (THt - height of each segment center)/CL	-
CL	Crown length:(THt – HCB)	m
CR	Crown radius, the mean of crown radii in four cardinal directions	m
DBH	Diameter at breast height (1.37 m)	cm
SLA	Specific leaf area (leaf area/leaf mass)	-
BLA	Branch leaf area	cm^2
BLM	Branch leaf mass	g
TLA	Total leaf area	cm^2
TLM	Total leaf mass	g
a, d	Fixed parameters	-
c, g	Random parameters	-
ε	Random error	-
ϑ	Branch insertion angle (from the vertical)	°

Table 2-2 Tree attributes of the 25 clones and 172 trees used in this study. Diameter at breast height (DBH), total tree height (THt) and crown radius (CR) were measured at end of growing season in 2010. Branch density (Bden) is the ratio of the total number of living branches to crown length. Total leaf mass (TLM) and leaf area (TLA) are estimated from models developed in this paper. Clones used in the branch-level modeling are shown with an asterisk (*).

clone	N	DBH(cm)		THt (m)		CR (m)		Bden (m^{-1})		TLA(m^2)		TLM(kg)	
		Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
C55*	9	14.55±1.01	12.95-16.00	10.09±0.52	9.4-10.72	2.70±0.17	2.34-2.95	7.82±1.89	5.55-10.36	113.35±14.10	90.47-128.14	8.98±1.20	7.10-10.23
C130*	8	15.37±1.00	13.46-16.64	8.87±0.41	8.32-9.70	2.86±0.20	2.62-3.13	8.70±0.86	7.49-9.90	155.43±21.24	129.33-181.80	11.33±1.44	9.50-13.12
C700	4	13.11±0.94	12.07-14.35	9.02±0.86	7.79-9.65	2.70±0.37	2.18-3.06	10.13±2.54	6.88-12.55	124.48±10.91	111.08-134.96	9.59±0.74	8.69-10.24
C701	6	12.95±0.53	12.32-13.84	9.09±0.24	8.83-9.48	2.73±0.27	2.26-3.03	6.22±1.15	5.02-8.14	116.06±20.70	83.08-138.75	8.90±1.48	6.48-10.49
C702	7	14.88±0.66	13.72-15.62	9.86±0.41	9.5-10.41	2.47±0.28	2.03-2.99	8.93±2.24	5.78-11.86	149.17±9.43	139.60-167.03	11.26±0.74	10.56-12.60
C703	8	14.84±0.75	13.59-16.13	9.06±0.66	7.68-9.69	2.68±0.22	2.26-2.93	7.07±1.80	5.12-9.91	141.43±13.32	120.96-164.97	11.00±1.10	9.48-13.18
C705	9	13.26±1.08	11.56-14.86	9.25±0.90	7.7-10.36	2.99±0.34	2.30-3.52	7.51±1.70	4.84-10.16	132.67±35.02	70.88-181.81	10.16±2.74	5.24-13.99
C707	12	14.30±1.15	12.70-16.51	9.52±0.78	8.08-10.71	2.54±0.32	2.02-2.98	8.70±2.26	4.94-11.51	123.40±17.45	92.53-153.41	9.33±1.34	7.18-11.69
C708*	13	15.03±0.78	13.21-16.00	9.81±0.50	8.83-10.51	2.70±0.24	2.37-3.01	10.25±2.64	5.39-13.20	160.40±26.77	119.61-200.38	13.23±2.18	9.85-16.70
C709	5	13.39±0.45	12.70-13.84	9.21±0.08	9.16-9.36	2.50±0.14	2.36-2.74	9.24±1.32	7.49-10.58	136.83±24.02	97.52-158.15	10.38±1.73	7.46-11.67
C710*	10	14.69±0.34	14.35-15.37	10.2±0.48	9.19-10.66	2.88±0.21	2.60-3.14	7.87±1.17	6.47-9.66	142.97±15.21	122.16-165.39	11.56±1.17	9.83-13.27
C712*	8	15.65±0.92	14.48-17.15	9.68±1.09	7.68-10.78	2.75±0.10	2.60-2.83	6.71±1.91	4.27-10.21	161.81±27.60	127.87-195.83	12.14±2.07	9.60-14.57
C713	8	15.51±1.12	14.48-17.91	9.74±0.63	9.02-10.91	2.88±0.32	2.46-3.47	7.44±1.31	5.34-9.00	159.47±20.55	133.10-193.85	12.09±1.50	10.37-14.63
C714*	8	16.29±0.83	15.11-17.15	10.96±0.42	10.16-11.33	2.96±0.23	2.65-3.41	7.60±1.97	4.95-10.07	142.75±18.60	122.28-179.80	11.49±1.58	9.77-14.69
C715*	20	16.27±1.13	14.48-18.92	9.10±0.59	8.08-10.75	2.87±0.25	2.20-3.19	10.03±1.62	5.77-12.15	156.23±35.72	88.55-233.63	12.28±2.68	6.74-18.14
C716	5	13.51±0.60	12.83-14.22	8.98±1.02	7.56-9.94	2.63±0.18	2.32-2.78	9.85±1.96	7.83-12.38	124.90±20.95	97.87-152.50	9.56±1.60	7.67-11.79
C717*	4	13.94±0.42	13.34-14.22	7.82±0.51	7.11-8.32	2.89±0.20	2.61-3.10	8.46±1.03	7.22-9.72	203.32±39.85	163.25-253.53	12.35±2.44	9.87-15.47
C718	5	15.47±0.24	15.11-15.75	10.32±0.29	9.97-10.76	2.62±0.18	2.38-2.86	7.96±0.85	6.93-8.98	168.48±16.04	150.08-191.16	12.82±1.26	11.18-14.53
C719	2	13.02±0.63	12.57-13.46	7.47±0.37	7.21-7.73	2.65±0.35	2.40-2.90	8.61±2.24	7.03-10.2	129.00±39.45	101.10-156.90	9.82±3.21	7.55-12.09
C720	6	14.01±1.26	11.68-15.11	9.25±0.72	8.42-10.39	3.09±0.28	2.78-3.50	7.19±1.28	5.76-8.80	124.97±18.69	101.66-154.26	9.54±1.41	7.69-11.68
C726*	8	13.32±0.53	12.57-14.10	8.86±0.24	8.53-9.25	2.77±0.23	2.47-3.15	5.21±1.27	3.73-7.75	145.88±17.19	123.41-170.90	11.07±1.30	9.64-12.97
C728	1	12.32	12.32	8.27	8.27	2.49	2.49	8.84	8.84	109.82	109.82	8.47	8.47
C729	1	9.91	9.91	7.29	7.29	2.52	2.52	6.87	6.87	81.50	81.50	6.05	6.05
C730	4	14.45±0.52	13.84-15.11	8.89±0.21	8.71-9.19	2.64±0.08	2.56-2.72	9.31±1.77	7.45-11.61	151.69±40.93	114.54-192.03	11.42±2.78	9.02-14.43
C777	1	15.24	15.24	9.15	9.15	3.42	3.42	11.5	11.5	205.87	205.87	15.56	15.56

Table 2-3 Branch attributes of the 138 branches used in branch leaf area and mass model development. Branch angle θ (°) and branch height (BHt) were measured at end of growing season in 2010. Branch diameter (BD) and branch leaf mass (BLM) were measured in 2011 July, branch leaf area (BLA) was calculated by multiplying BLM and specific leaf area (Table 4) of each clone at the same time.

Clone	N	BD (cm)		θ(°)		BHt (m)		bRDINC		tRDINC		BLA (m^2)		BLM (kg)	
		Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
C55	16	3.54±1.39	1.50-5.98	57.00±17.85	18-84	5.10±1.77	2.46-8.30	0.72±0.21	0.35-0.99	0.53±0.26	0.05-0.89	5.53±3.87	0.56-14.10	0.43±0.30	0.05-0.95
C130	16	3.17±1.85	0.51-7.40	69.19±23.45	26-110	4.98±1.40	3.50-8.30	0.71±0.21	0.20-0.94	0.56±0.29	0.02-0.92	6.01±6.96	0.05-26.78	0.43±0.51	0.00-1.96
C708	15	3.34±2.09	0.86-6.91	62.73±16.36	27-90	4.55±1.83	2.47-9.15	0.77±0.22	0.23-1.00	0.63±0.22	0.09-1.00	6.67±6.95	0.13-19.47	0.54±0.56	0.01-1.56
C710	16	3.82±2.02	0.84-7.66	54.75±15.11	33-82	4.68±1.13	2.22-6.55	0.76±0.13	0.55-1.00	0.54±0.21	0.12-0.96	7.25±8.51	0.14-31.60	0.58±0.69	0.01-2.55
C712	15	3.67±1.71	1.24-6.16	71.20±14.36	50-90	4.77±1.56	2.54-7.32	0.76±0.17	0.49-1.00	0.64±0.22	0.18-1.00	7.35±5.70	0.41-16.47	0.54±0.43	0.03-1.31
C714	15	3.47±2.16	0.86-7.34	69.00±18.73	24-90	5.49±1.72	2.49-7.95	0.72±0.17	0.41-1.00	0.59±0.23	0.07-0.96	6.37±6.86	0.14-20.18	0.50±0.55	0.01-1.39
C715	15	3.60±2.03	1.22-7.21	55.80±16.77	21-90	4.11±1.32	2.35-6.03	0.81±0.16	0.58-1.00	0.57±0.26	0.07-0.96	6.64±6.89	0.36-21.46	0.54±0.58	0.03-1.79
C717	15	3.16±1.51	1.04-5.56	68.53±21.89	25-102	4.64±1.67	2.60-8.00	0.74±0.22	0.29-1.00	0.59±0.29	0.02-1.06	8.64±9.22	0.53-30.98	0.49±0.51	0.03-1.69
C726	15	3.67±2.18	1.04-7.81	70.37±10.78	45-90	4.37±1.29	2.20-6.26	0.77±0.17	0.51-1.00	0.63±0.17	0.28-0.85	8.17±9.05	0.36-28.46	0.59±0.64	0.03-1.96

Table 2-4 Specific leaf area (mean ± standard deviation, cm2•g-1) at two different crown positions of nine *Juglans nigra* L. clones. Specific leaf area is the ratio of leaf mass to one-sided leaf area. N: number of trees.

Clone	N	Mid-Upper Crown		N	Lower Crown	
		Mean±SD	Range		Mean±SD	Range
C55	4	118.28±13.28	102.65-129.84	4	148.78±10.27	138.67-158.40
C130	5	136.74±31.18	112.10-191.14	5	158.12±7.73	146.38-166.87
C708	10	116.64±12.14	103.55-140.24	9	145.67±19.05	126.59-178.84
C710	4	124.01±15.36	102.92-139.76	3	144.83±32.33	115.61-179.56
C712	5	125.66±13.04	110.31-138.99	5	161.79±8.46	152.62-172.19
C714	5	116.44±7.49	109.90-128.29	5	148.92±8.08	140.69-161.52
C715	10	119.57±12.99	100.06-142.98	10	149.76±12.42	119.96-161.68
C717	5	160.62±30.80	139.57-214.92	5	183.65±16.79	162.96-202.72
C726	5	122.52±2.71	119.75-126.59	5	145.00±10.16	131.34-156.87

Table 2-5 Parameter estimates of fixed effects and fit statistics of branch-level models for 9 *Juglans nigra* L. clones (parameter estimates in first row, standard errors in second row, and p-value in third).

Model	a_0	a_1	a_2	a_3	AIC	-2 Log Likelihood	R^2-fixed	R^2-fixed+random	RMSE	Log bias Correction Factor
Branch Leaf Mass (BLM)										
[8]	3.0475	2.2859	---	---	-2.5	-6.5	0.970	0.9767	0.0059	0.9961
	0.0545	0.0305								
	<0.0001	*<0.0001*								
[9]	1.1088	2.3048	-1.4060	1.9486	-34.1	-30.1	0.9755	0.9812	0.0048	0.9979
	0.4041	0.0285	0.2652	0.4244						
	0.0253	*<0.0001*	*<0.0001*	*<0.0001*						
[10]	2.6317	2.2088	-0.2102	0.4716	-20.1	-24.1	0.973	0.9806	0.0050	0.9904
	0.1521	0.0360	0.0462	0.1850						
	<0.0001	*<0.0001*	*<0.0001*	*0.0120*						
[11]	2.6331	2.2762	-0.2406	0.4401	-20.3	-24.3	0.9738	0.9805	0.0050	0.9957
	0.1469	0.0286	0.0553	0.1673						
	<0.0001	*<0.0001*	*<0.0001*	*0.0096*						
[12]	3.0277	2.2615	-1.8732	1.5947	-16.1	-20.1	0.971	0.9793	0.0053	0.9917
	0.0591	0.0337	0.6683	0.4910						
	<0.0001	*<0.0001*	*0.0059*	*0.0015*						
Branch Leaf Area (BLA)										
[8]	7.9854	2.2639	---	---	22.7	18.7	0.9547	0.9731	0.0068	0.9973
	0.0761	0.0328								
	<0.0001	*<0.0001*								
[9]	5.1901	2.2499	-1.8038	2.9666	-13.2	-17.2	0.9632	0.9796	0.0052	0.9948
	0.4233	0.0296	0.2761	0.4418						
	<0.0001	*<0.0001*	*<0.0001*	*<0.0001*						
[10]	7.1411	2.1262	-0.2703	1.0754	0.1	-3.9	0.9594	0.9783	0.00C55	0.9895
	0.1681	0.0381	0.0490	0.1960						
	<0.0001	*<0.0001*	*<0.0001*	*<0.0001*						
[11]	7.0909	2.2813	-0.3593	1.0690	-6.3	-10.3	0.9636	0.9790	0.0053	1.0006
	0.1579	0.0295	0.0573	0.1731						
	<0.0001	*<0.0001*	*<0.0001*	*<0.0001*						

Table 2-5 continued

[12]	8.0108	2.2843	-1.8842	1.3751	18.2	14.2		0.9562	0.9738		0.0067	0.9922
	0.0775	0.0378	0.7510	0.5517								
	<0.0001	*<0.0001*	*0.0134*	*0.0140*								

AIC: Akaike information criterion; RMSE: Root-mean-square deviation.

Table 2-6 Estimates of fixed effects and fit statistics of tree-level models for 25 *Juglans nigra* L. clones (parameter estimates in first row, standard errors in second row, and p-value in third).

Model	d_0	d_1	d_2	AIC	-2 Log Likelihood	R^2-fixed	R^2-fixed+random	RMSE	Log Bias Correction Factor
Tree Leaf Mass(TLM)									
	4.9746	1.6150							
[13]	0.3896	0.1461	---	-159.4	-163.4	0.4852	0.6248	0.0021	1.0109
	<0.0001	*<0.0001*							
	2.1543	1.4808	0.5662						
[14]	0.6490	0.1416	0.1094	-181.5	-185.5	0.5380	0.6884	0.0018	1.0090
	0.0029	*<0.0001*	*<0.0001*						
Tree Leaf Area(TLA)									
	9.9260	1.5876							
[13]	0.4272	0.1603	---	-137.3	-141.3	0.4164	0.6388	0.0023	1.0096
	<0.0001	*<0.0001*							
	6.8600	1.4312	0.6205						
[14]	0.6877	0.1535	0.1151	-161.5	-165.5	0.4733	0.7012	0.0020	1.0083
	<0.0001	*<0.0001*	*<0.0001*						

AIC: Akaike information criterion; RMSE: Root-mean-square deviation.

Table 2-7 TLA (tree leaf area), GE (growth efficiency), LAI (leaf area index), FDI (foliage density index), and VI (stem volume increment) of nine selected clones. GE: VI/TLA, LAI: TLA/projected crown area on the ground, FDI: LAI/projected crown area on the ground. Clones with different letters were significantly different at level of a=0.05. N: number of trees.

Clone	N	TLA (m^2)		GE ($dm^3 \cdot m^{-2}$)		LAI ($m^2 \cdot m^{-2}$)		FDI ($m^2 \cdot m^{-2} \cdot m^{-1}$)		VI (dm^3)	
C714	8	142.75±18.60	BC	1.12±0.11	A	5.23±0.80	CD	0.60±0.09	C	159.11±16.27	A
C55	9	113.35±14.10	C	1.06±0.21	AB	5.03±1.02	D	0.64±0.13	C	119.92±28.26	AB
C710	10	142.97±15.21	BC	0.87±0.11	AB	5.52±0.62	BCD	0.71±0.11	BC	123.08±13.86	A
C715	20	156.23±35.72	B	0.87±0.17	AB	6.04±1.16	BCD	0.88±0.13	B	131.87±28.14	A
C726	8	145.88±17.19	BC	0.57±0.10	C	6.13±1.02	ABCD	0.88±0.15	B	81.54±11.74	BC
C708	13	160.40±26.77	B	0.89±0.13	AB	7.01±1.05	AB	0.90±0.15	B	141.84±24.28	A
C130	8	155.43±21.24	B	1.06±0.21	B	6.09±0.99	BCD	0.91±0.17	B	129.13±21.24	A
C712	8	161.81±27.60	B	0.87±0.26	AB	6.81±1.26	ABC	0.94±0.22	B	139.29±44.71	A
C717	4	203.32±39.85	A	0.31±0.13	C	7.75±1.23	A	1.33±0.22	A	62.90±27.43	C

2.7 Figures

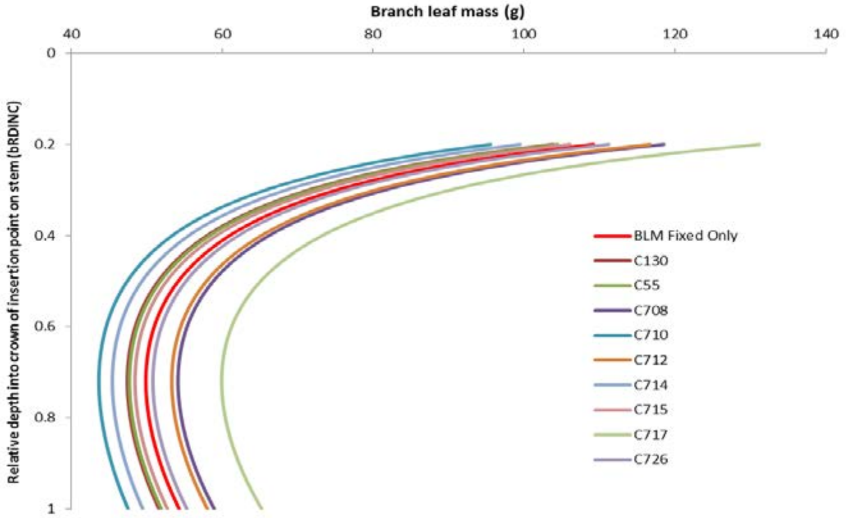


Figure 2-1 Branch leaf mass estimated from eq. [9] for selected black walnut (*Juglans nigra* L.) clones: how branch leaf mass changes when bRDINC changes (branch size held constant at 1.5 cm). For Y axis, 0 is top of a crown, 1 is the bottom of it. Clonal curves were graphed based on random effect estimates in eq. [9].

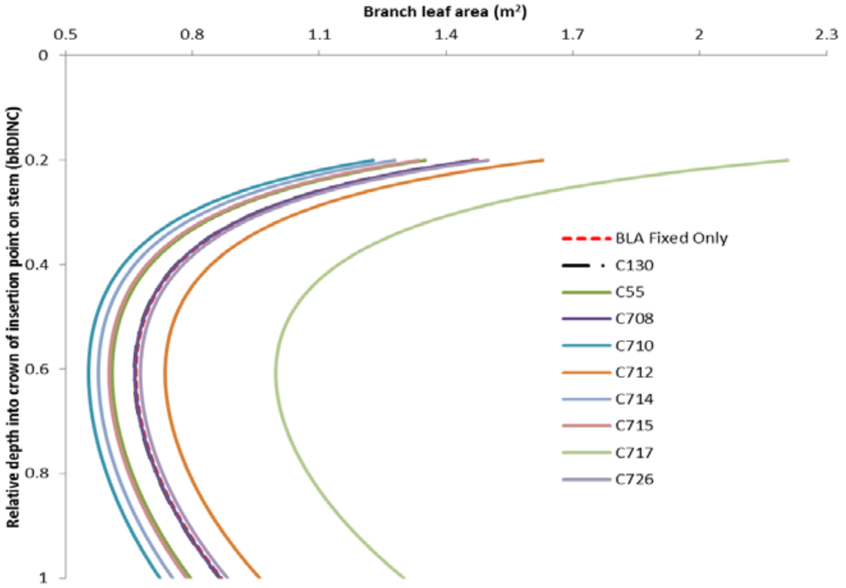


Figure 2-2 Branch leaf area estimated from eq. [9] for selected black walnut (*Juglans nigra* L.) clones: how branch leaf area behaves when bRDINC changes (branch size held constant at 1.5 cm). For Y axis, 0 is top of a crown, 1 is the bottom of it. Clonal curves were graphed based on random effect estimates in eq. [9].

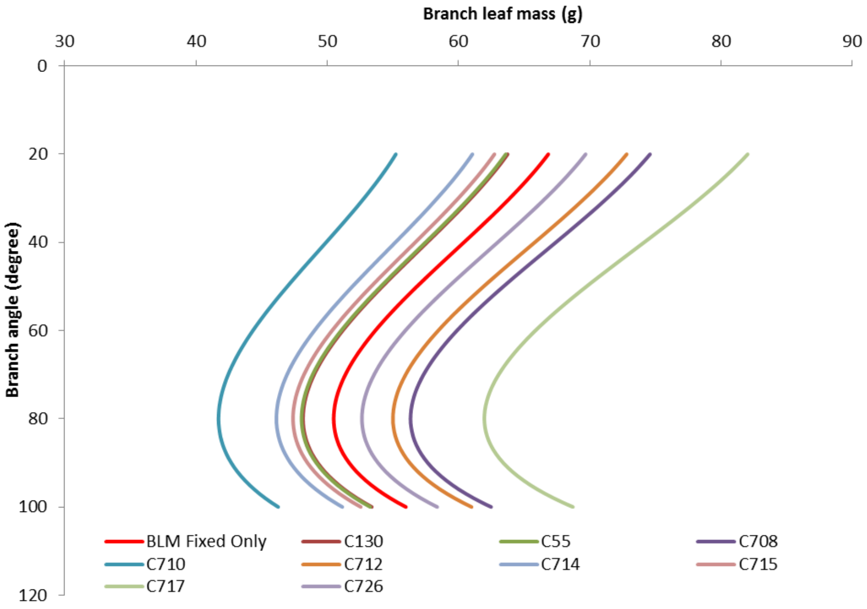


Figure 2-3 Branch leaf mass estimated from eq. [12] for selected black walnut (*Juglans nigra* L.) clones: how branch leaf mass behaves when branch angle changes (branch size held constant at 1.5 cm). Clonal curves were graphed based on random effect estimates in eq. [12].

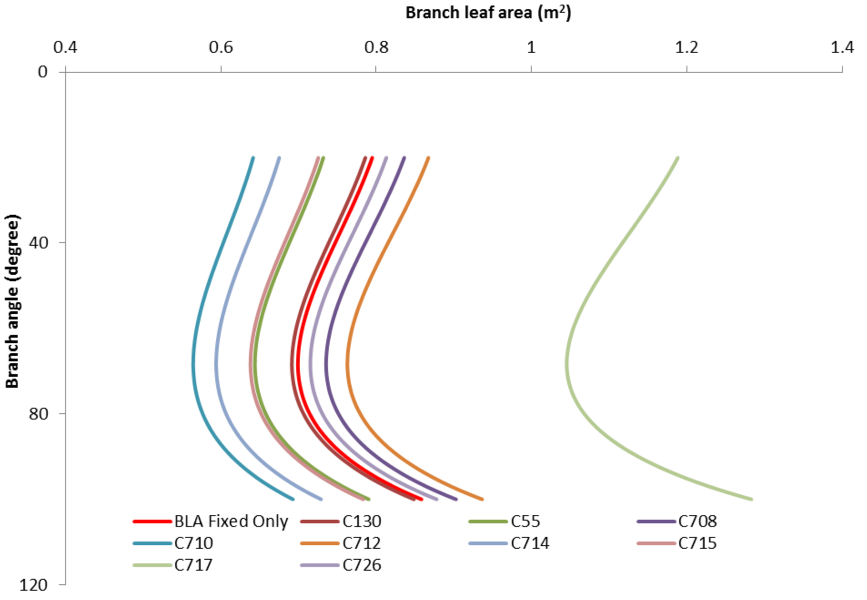
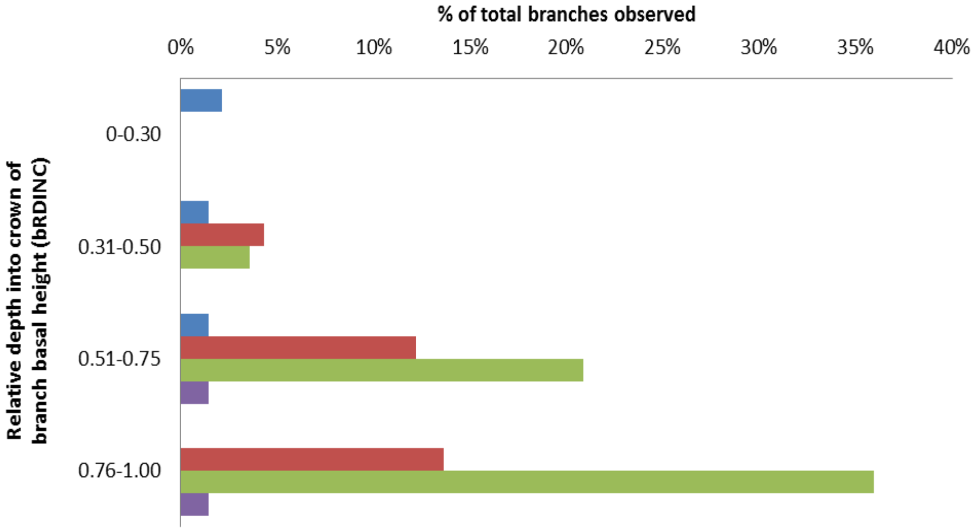


Figure 2-4 Branch leaf area estimated from eq. [12] for selected black walnut (*Juglans nigra* L.) clones: how branch leaf area behaves when branch angle changes (branch size held constant at 1.5 cm). Clonal curves were graphed based on random effect estimates in eq. [12].



	0.76-1.00	0.51-0.75	0.31-0.50	0-0.30
🟦 <30°	0.00%	1.44%	1.44%	2.16%
🟥 30°- 60°	13.67%	12.23%	4.32%	0.00%
🟩 60°- 90°	35.97%	20.86%	3.60%	0.00%
🟪 >90°	1.44%	1.44%	0.00%	0.00%

Figure 2-5 Vertical distribution of branch angle in 25 black walnut (*Juglans nigra* L.) clones.

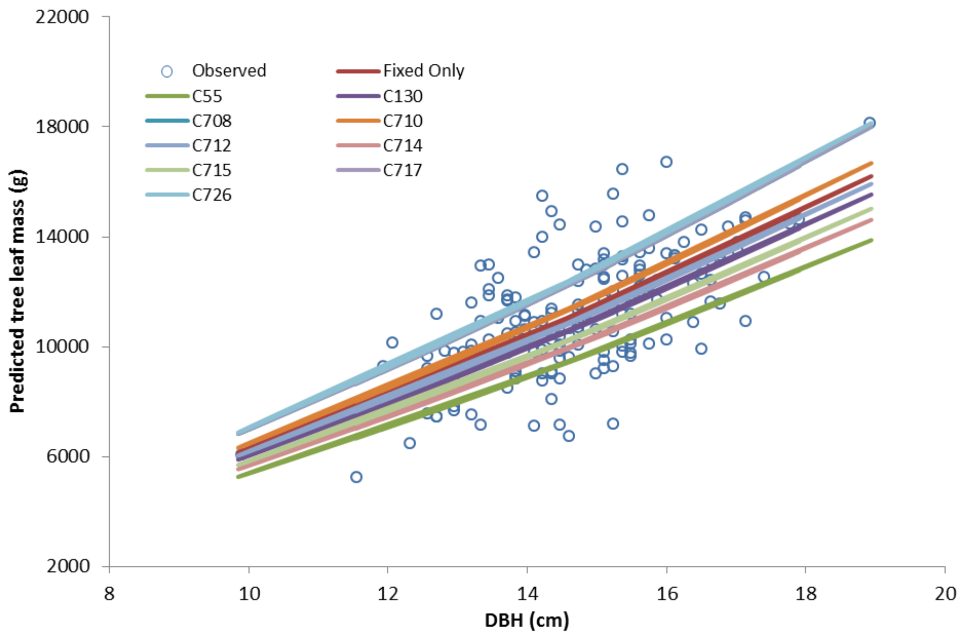


Figure 2-6 Tree-level leaf mass models (eq. [14]) for selected black walnut (*Juglans nigra* L.) clones (when crown radius was held constant at the average 2.77 m). Clonal curves were graphed based on random effect estimates in eq. [14].

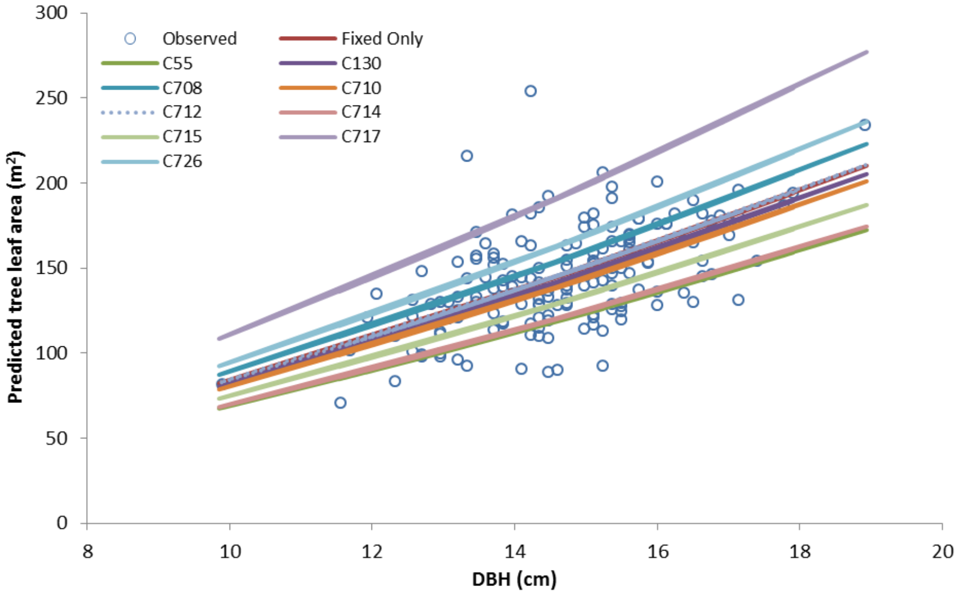


Figure 2-7 Tree-level leaf area models (eq. [14]) for selected black walnut (*Juglans nigra* L.) clones (when crown radius was held constant at the average 2.77 m). Clonal curves were graphed based on random effect estimates in eq. [14].

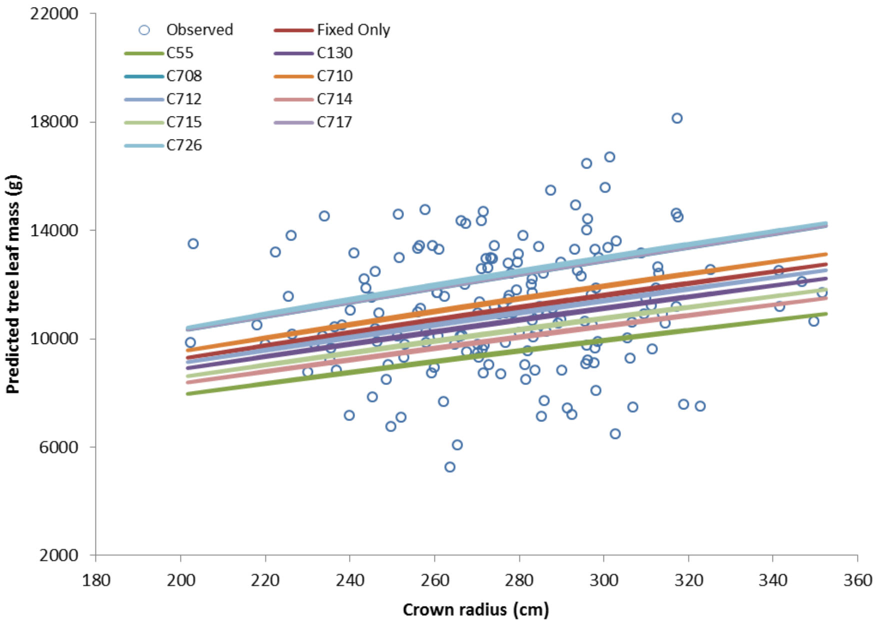


Figure 2-8 Tree-level leaf mass models (eq. [14]) for selected black walnut (*Juglans nigra* L.) clones (when DBH was held constant at the average 14.68 cm). Clonal curves were graphed based on random effect estimates in eq. [14].

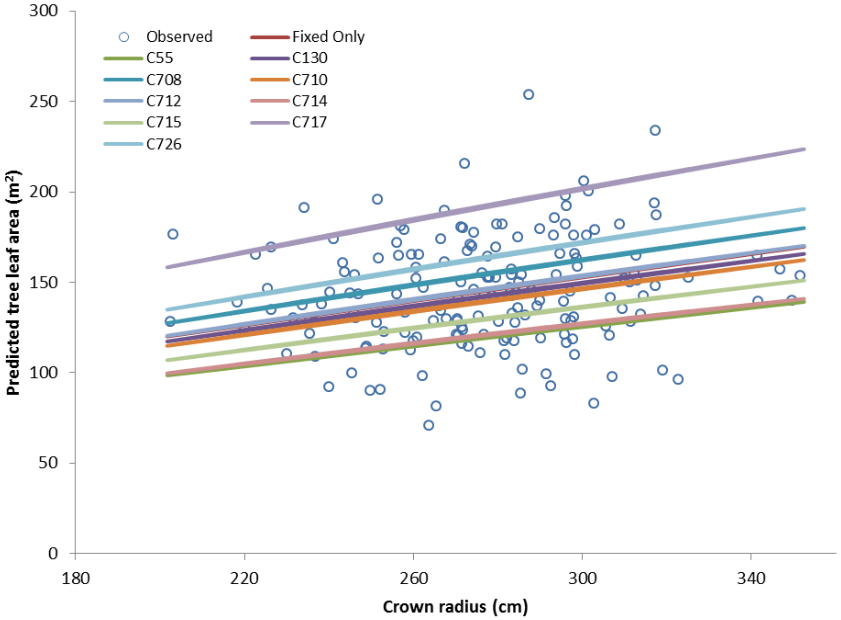


Figure 2-9 Tree-level leaf area models (eq. [14]) for selected black walnut (*Juglans nigra* L.) clones (when DBH was held constant at the average 14.68 cm). Clonal curves were graphed based on random effect estimates in eq. [14].

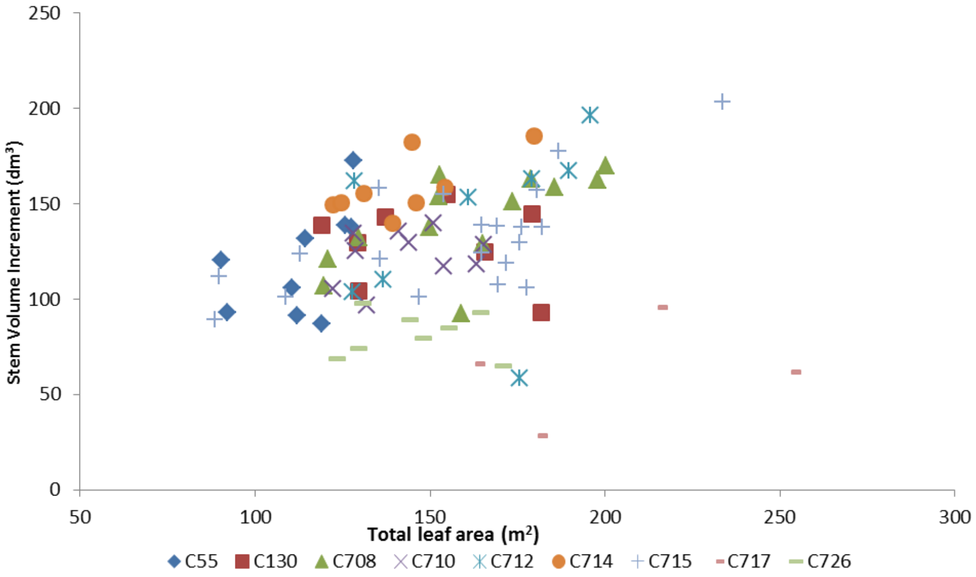


Figure 2-10 Estimated stem volume increment when total leaf area (TLA) increased.

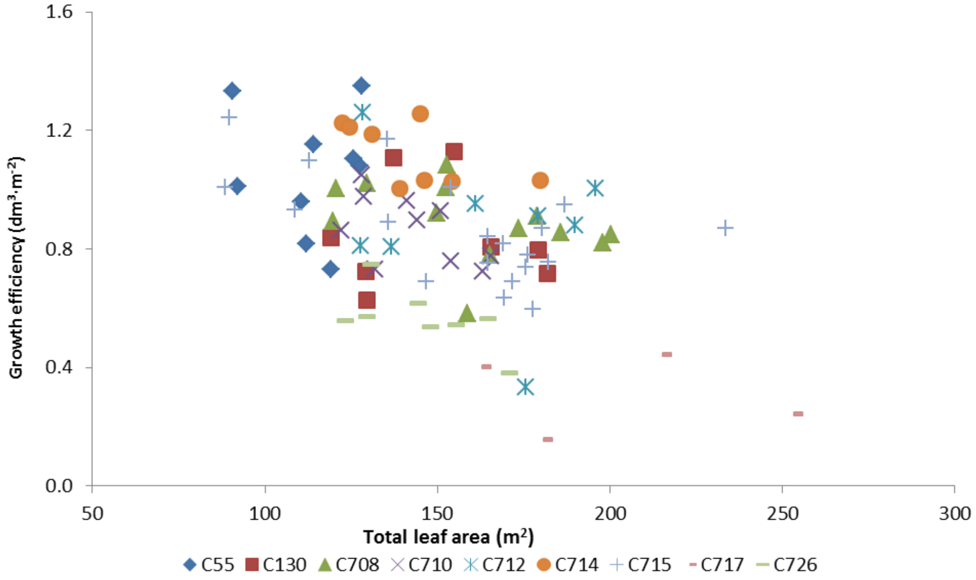


Figure 2-11 Growth efficiency of black walnut (*Juglans nigra* L.) clones when total leaf area (TLA) varied.

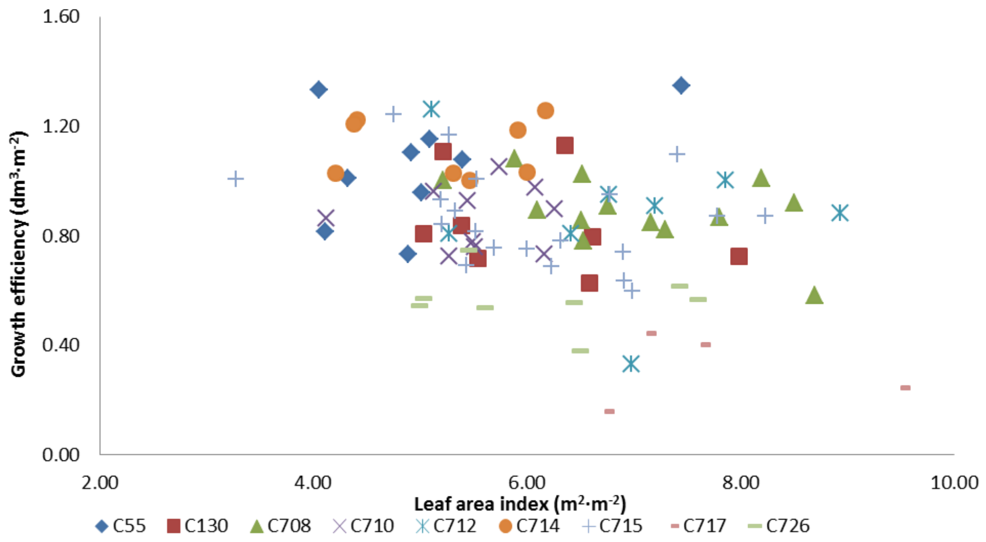


Figure 2-12 Growth efficiency of black walnut (*Juglans nigra* L.) clones when leaf area index (LAI) changed.

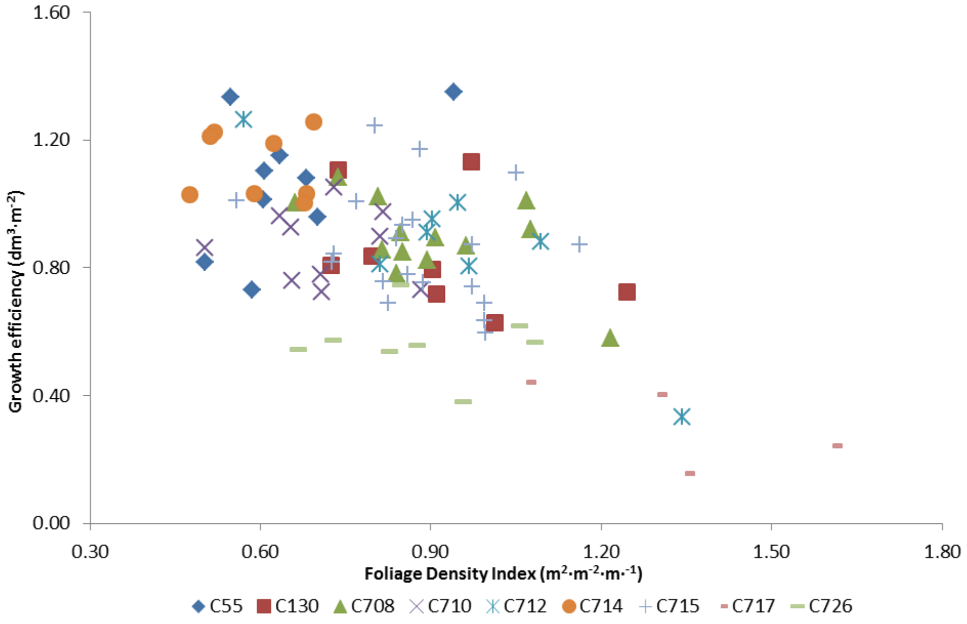


Figure 2-13 Growth efficiency of selected black walnut (*Juglans nigra* L.) clones when foliage density index (FDI) increased.

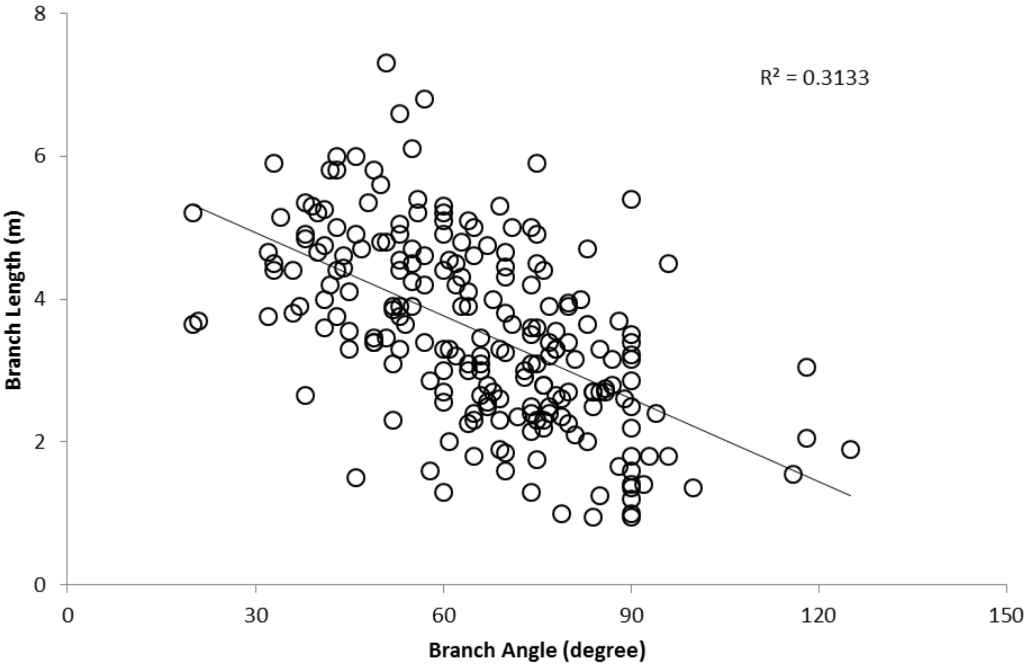


Figure 2-14 Branches with smaller angles in black walnut (*Juglans nigra* L.) tended to be longer than branches with larger angles.

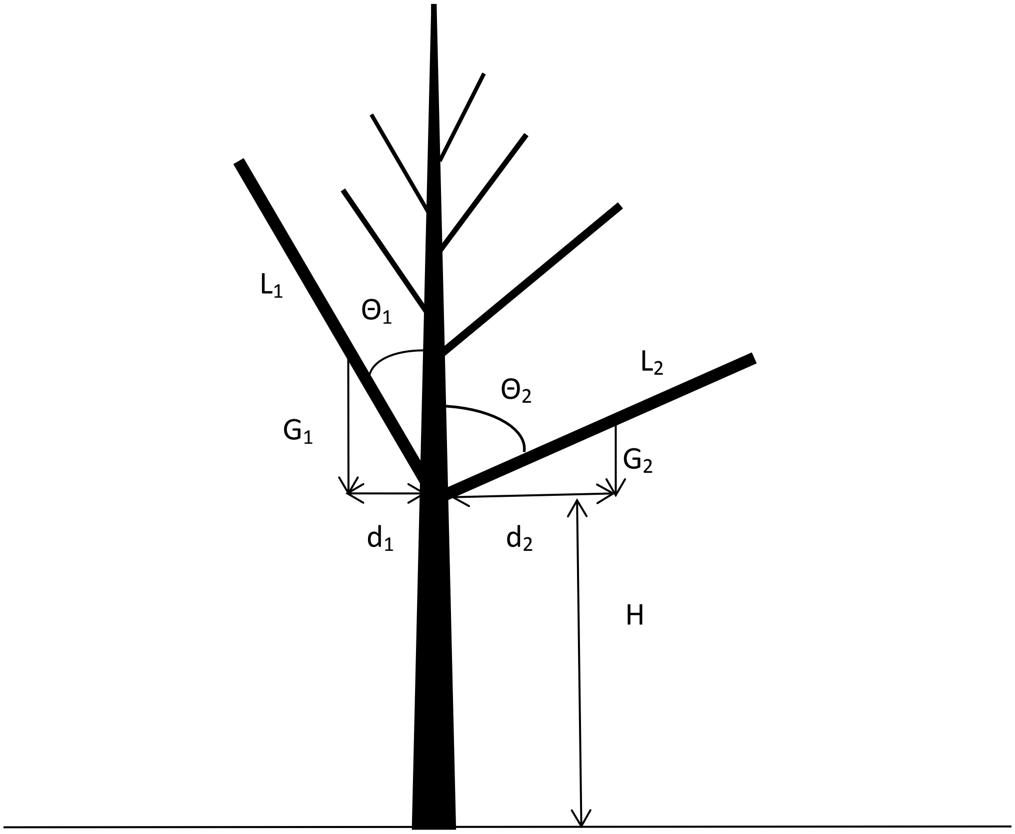


Figure 2-15 Smaller angled branches were released compared to larger angled branches. All the branches attached to the stem are at their equilibrium, indicating that the principle of moments can be applied. At height H, the tree stem offers a counter clock-wise moment M1 to support branch L1, and clock-wise moment M2 for L2. So M1= G1d1, M2=G2d2. Assume branch L1 and L2 have the same weight (G1=G2) and branch diameter, and given that M1 and M2 have a threshold (upper limit, at a certain height of the tree stem, the support to the branch at that point is limited to a threshold), because branch L1 has a smaller angle Θ1, therefore, the torque d1 of G1 is smaller than d2 of G2. Thus, branch L1 has more growth potential – it can grow longer than L2.

CHAPTER 3. MODELING BRANCH CHARACTERISTICS OF WIDELY SPACED BLACK WALNUT (*JUGLANS NIGRA* L.) CLONES UNDER AN INTENSIVE MANAGEMENT REGIME IN INDIANA, USA

3.1 Introduction

Crown architecture is a major determinant of tree growth (Assman, 1970) due to its influence on photosynthesis. Crown architecture is the confluence of branching pattern (i.e., the diameter, angle, frequency, length, and spatial distribution of branches) and branch dynamics (i.e., the initiation, growth, death, and self-pruning of branches). These processes affect not only tree growth, but also wood quality through impacts on structural strength and appearance of wood products (Uusvaara, 1985; Maguire et al., 1994; Mäkinen and Hein, 2006).

Silvicultural practices exert strong influence on timber value by regulating branch attributes. Past silvicultural regimes for both conifers and hardwoods mostly focused on natural regeneration and high density plantings, because dense planting promotes self-pruning and reduces branch (primordia) initiation, and thus helps trees form branch-free boles to a desirable height (6 – 8 m for hardwoods) at early ages. Management of some species, including black walnut, is now shifting to more widely spaced and intensively managed plantations in order to shorten rotation length and increase economic return (Senft et al., 1985; Ballard and Long, 1988; Clark III and Saucier, 1989; Barbour and Kellogg, 1990; Mäkinen and Colin, 1998; Bohanek and Groninger, 2003). These wide spacings increase tree growth rate, but reduce timber quality by increasing stem taper, the proportion of juvenile core, the frequency of large branches, and average branch size in both conifers and hardwoods (Merkel, 1967; Phelps and Chen, 1989; Deans and Milne, 1999; Macdonald and Hubert, 2002; Bohanek and Groninger, 2003; Seifert et al., 2003;

Seeling et al., 2004). Therefore, it has become necessary to balance fast growth and the end-product quality (Ballard and Long, 1988; Mäkinen and Colin, 1998). One way to achieve this is clonal forestry – by propagating ideotypes that meet the balance between rapid growth and great quality to maximize economic gain. Ideotype was defined by Donald (Donald, 1968) as a model plant that produce high yield or quality of end products in a predictable manner under a certain environment and management. Such crown ideotypes may be realized in the current populations by examining the genetic variations in the key branching patterns that determine growth and quality, or through breeding programs by hybridizing potential genotypes toward such as balance.

Modeling branch characteristics is an explicit way to quantitatively characterize crown architecture. Allometric models can reveal the relationships among different tree structures, therefore, may help define desirable crown ideotypes. For instance, branch diameter is generally positively correlated with tree diameter as reflected by some allometric equations (Mäkinen and Colin, 1998; Harri Mäkinen et al., 2003b; Weiskittel et al., 2010). However, genetic variance may exist in the populations that some of the genotypes tend to grow smaller branches while achieve a larger DBH. Similar approaches can be applied for other branch attributes, such as branch angle, branch length, etc. These genotypes, if exist, will be the ideotypes we are seeking, or can be used in breeding programs for further improvement. There have been a number of branch attribute models developed for conifers, such as Scots pine (*Pinus sylvestris*) (Uusvaara, 1985; Mäkinen and Colin, 1998), Norway spruce (*Picea abies*) (Houllier et al., 1995; Harri Mäkinen et al., 2003b; Mäkinen and Hein, 2006), Douglas-fir (*Pseudotsuga menziesii*) (Maguire et al., 1994; Weiskittel et al., 2007a), radiata pine (*Pinus radiata* (D.) Don.) (Woollons et al., 2002), Sitka spruce (*Pinus sitchensis* (Bong.) Carr.) (Achim et al., 2006), loblolly pine (*Pinus taeda*) (Doruska and Burkhart, 1994), balsam fir (*Abies balsamea* (L.) Mill) (Weiskittel et al., 2010), Eastern hemlock (*Tsuga Canadensis* (L.) Carr.) (Weiskittel et al., 2010), northern white-cedar (*Thuja occidentalis* (L.)) (Weiskittel et al., 2010), red spruce (*Picea rubens* (Sarg.)) (Weiskittel et al., 2010), eastern white pine (*Pinus strobus*

(L.)) (Weiskittel et al., 2010), and other species, but there have been only limited studies of hardwoods such as silver birch (*Betula pendula* Roth.) (Niemistö, 1995; Harri Mäkinen et al., 2003a). Past studies on wood quality of hardwoods have focused on stem form (Beineke et al., 1991; Bohanek and Groninger, 2003; Saha et al., 2012) and heartwood coloration (Szopa et al., 1980; Phelps and McGinnes, 1983; Phelps et al., 1983). Black walnut (*Juglans nigra* L.) is a hardwood species renowned for its valuable veneer. It is planted widely across the Central Hardwoods Region. The general standard for its quality is that the fewer and smaller the defects (mostly branch knots but also color variation and consistency of grain pattern), the higher the quality and value. In a study of how planting densities influence the bole quality of black walnut, Bohanek and Groninger (2003) examined the defects caused by branches in both butt and upper logs, but no models of branch properties have been built for black walnut.

To meet this challenge for black walnut, multiple genetically improved black walnut clones (Beineke, 1983, 1989) may be used. The homogeneous environment and management in the study site offered us an excellent opportunity to explore genetic variation in branching pattern in black walnut clones. The objectives of this study were to develop prediction models for maximum branch diameter and relative branch diameter in a segment along the stem, one-year branch radial growth, branch insertion angle, branch length, branch frequency, and branch basal area per meter of stem of 25 black walnut clones, and determine if the clones differed based on these models.

3.2 Materials and Methods

3.2.1 Data Collection

Diameter at breast height (1.37m, DBH), tree height, crown width, and height to the crown base were measured in the fall of 2010 and 2011 on 172 trees across the 25 black walnut clones. For each tree, branches were accessed with an Altec lift, and attributes were measured between October 2010 and March 2011. Branch diameter just above the branch collar was measured on every branch (Branch diameters for previously pruned branches were estimated by measuring the diameter of pruning scars). Orientation of all branches (including scars) was recorded as one of four cardinal directions (N, S, E, and W) or four intermediate directions (NW, SW, SE, and NE). Branch height on the stem was measured on all living branches larger than 1.27 cm and all pruning scars regardless of size. Branch insertion angle (from vertical) was measured using a digital protractor on living branches larger than 1.27 cm and all vigorous growing branches (less than 1.27 cm, thinner bark) to the nearest 0.5 degree. Small-diameter branches in the upper crown were not excluded from angle and height measurement because they were vigorously growing, contributed a relatively large amount of leaf area, and their growth had not been influenced by shade.

Three to four trees were selected from each clone and the diameter of all the living branches was measured again between November 2011 and February 2012 to determine their one-year radial growth. First – order branch length was measured on a subset of branches pruned in February 2012. For these branches, we also measured branch diameter and branch height.

Tree- and branch-level attributes varied considerably among clones (Table 3-2 and 3-3). Because not all attributes could be measured on every branch, multiple branch datasets were used to accommodate different modeling purposes. Below is a brief description of these datasets:

1. Dataset I: the largest dataset, n_t =168, n_b =15,309 (t: trees, b: branches). Branches included all living branches, dead branches, and pruned branches (scars) of the intact sample trees. Branch direction and diameter were available for all branches, while branch height and/or branch angle were unavailable for some unpruned branches due to their small sizes. This dataset was used to model branch frequency and branch basal area per meter of stem.

2. Dataset II: second largest dataset, n_t =168, n_b=9236, was a subset of Dataset I. Branch direction, diameter, and height were available for all branches, but not all

insertion angles were available. This dataset was used to model maximum branch diameter and relative branch diameter (scars included).

3. Dataset III: n_t =168, n_b= 5741. This dataset included only unpruned branches. Branch direction, diameter, height, and insertion angle were measured for all branches, except four branches that were pruned incorrectly and therefore their insertion angles were missing. This dataset was used to model maximum branch diameter and relative branch diameter for unpruned branches. Dataset III was a subset of Dataset II.

4. Dataset IV: n_t =172, n_b= 5929, included only unpruned branches. Branch direction, diameter, height, and insertion angle were measured for all branches in this dataset. This dataset was used to model branch angle for unpruned branches. Dataset IV was almost identical to Dataset III, except that data for four more trees of C708 were added.

5. Dataset V: n_t =69, n_b= 1750, included branches the diameter of which was recorded for both 2010 and 2011. Branch direction, diameter, height, and insertion angle were measured for all branches in this dataset. This dataset was used to model branch diameter growth.

6. Dataset VI: n_t =244, n_b=794. Branch diameter and branch length were measured for all branches in this dataset. This dataset was used to model first-order branch length.

3.2.2 Data analysis

The datasets in this study have a hierarchical structure: multiple measurements were made at both branch- and tree- level, with branches nested within annual shoots, annual shoots within trees, and trees within clones. Hence, a multi-level linear mixed effects model approach was employed to take the mutual dependence of the measurements into account.

The data reflected both temporal and spatial structure because the branches initiated in different years. First, branches of new annual shoot form above the older shoot. Second, higher branches cast shade on lower branches and consequently may slow their growth, and there is also a spatial order for branches at different heights to intercept water and nutrients transported from below. The whorls in many conifers (a proxy for branch age, i.e., the chronological order of lateral buds initiation) are such structures. However, black walnut arranges branches alternately on the stem, and the vertical scope of annual shoots was difficult to recognize for these nine-year-old trees. Thus, stems were divided into one-meter segments to approximately account for branch age (temporal) and the vertical (spatial) structure along the stem.

We wanted to determine if clones differed in their branch characteristics, so clone was treated as a fixed effect in the models. Stem segments and trees were considered random effects. The first-order autoregressive covariance structure [AR (1)] was applied at the segment level in models when appropriate. Either a diagonal covariance structure (no correlations exist among random covariance estimates) or an unstructured covariance structure (correlations were calculated among all variables) was applied within individual segments.

The overall performance of each model was evaluated using Akaike's information criterion (AIC), and -2 Log-likelihood value. Generalized R^2 at the original data scale for both fixed factors and the full model (fixed plus random factors) were calculated to examine the goodness of fit of each model. The performance of the fixed part was also evaluated by mean error E, mean absolute error $|E|$, and mean squared error E^2 at the original data scale (Hein et al., 2008). Parameters that were biologically sound and statistically significant at α=0.05 were selected. Residual plots were checked for heteroskedasticity and bias.

3.2.3 Maximum branch diameter

Branch diameter was modeled in two stages: the diameter of the thickest branch in each one-meter stem segment was predicted first, then the diameter of the smaller branches within that same segment. Maximum branch diameter was modeled for two datasets II (including scars) and III (unpruned branches only), respectively. The reasons and purposes of doing so were: 1) including pruning scars in the model was necessary to account for the full range of maximum branch diameter; 2) to test if adding branch angle improves the model (using dataset III), since branch angle could not be measured for pruning scars in dataset II and branch angle could only be determined for unpruned branches.

3.2.3.1 Maximum branch diameter in a segment (pruned branches included)

A total of 1,184 branches, including pruned branches, were extracted from dataset II as the thickest from individual segments. $BDMax_{cts}$ was related to the relative location of their segment within the crown (C_RDINC_{ctb}) and tree diameter (DBH_{ct}). After preliminary analysis and model selection, a random coefficient, log-link model with a normally distributed response variable modified from Mäkinen et al. (2003b) and Hein et al. (2008) was used. Random effects were found with $\ln C\_RDINC_{cts}$ and C_RDINC_{cts} at segment level.

$$\ln BDMax_{cts} = a_0 + a_1 DBH_{ct} + (a_2 + \alpha_{cts2}) \ln C_{RDINC_{cts}} + (a_3 + \alpha_{cts3}) C_{RDINC_{cts}} + a_{5i} Clone + \alpha_{ct} + \alpha_{ctsb} \qquad [1a]$$

In which,

$$\begin{pmatrix} \alpha_{cts2} \\ \alpha_{cts3} \end{pmatrix} \sim iid\ N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix} \sigma^2{}_{\alpha_{cts2}} & 0 \\ 0 & \sigma^2{}_{\alpha_{cts3}} \end{bmatrix}, \alpha_{ctsb} \sim iid(0, \sigma^2{}_1).$$

3.2.3.2 Maximum branch diameter in a segment (unpruned branches only)

A total of 983 unpruned branches were extracted from dataset III as the thickest from individual segments. The form of model [1a] was also applied to dataset III, and it will be referred as model [1b] in the following text. In addition, model [2] which included cosine of branch angle ($Cos\theta_{ctsb}$) was also used. Again, random effects were found with $\ln C\_RDINC_{cts}$, C_RDINC_{cts}, and $Cos\theta_{ctsb}$.

$$\ln BDMax_{cts} = a_0 + a_1 DBH_{ct} + (a_2 + \alpha_{cts2}) \ln C_{RDINC_{cts}} + (a_3 + \alpha_{cts3}) C_{RDINC_{cts}} + (a_4 + \alpha_{cts4}) Cos\theta_{ctsb} + a_{5i} Clone + \alpha_{ct} + \alpha_{ctsb} \quad [2]$$

In which

$$\begin{pmatrix}\alpha_{cts2}\\ \alpha_{cts3}\\ \alpha_{cts4}\end{pmatrix} \sim iid\ N\left[\begin{pmatrix}0\\0\end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix} {\sigma^2}_{\alpha_{cts2}} & {\sigma^2}_{\alpha_{cts2}\alpha_{cts3}} & {\sigma^2}_{\alpha_{cts2}\alpha_{cts4}} \\ {\sigma^2}_{\alpha_{cts2}\alpha_{cts3}} & {\sigma^2}_{\alpha_{cts3}} & {\sigma^2}_{\alpha_{cts3}\alpha_{cts4}} \\ {\sigma^2}_{\alpha_{cts2}\alpha_{cts4}} & {\sigma^2}_{\alpha_{cts3}\alpha_{cts4}} & {\sigma^2}_{\alpha_{cts4}} \end{bmatrix},$$

$\alpha_{ctsb} \sim iid(0, {\sigma^2}_2)$.

3.2.4 Relative branch diameter

Branches in each segment were ranked according to their diameter from largest to smallest (the thickest branch was ranked as 1, the second largest was ranked as 2, and so on). Same as maximum branch models, relative branch diameter models were developed for dataset II and III, respectively. A logit link model with a binomial distribution, modified from Hein et al (2008) was used. Relative branch diameter was closely related to its rank within the segment and the number of branches in each whorl or segment (Hein et al., 2008; H. Mäkinen et al., 2003). Because branch height for many small sized branches (<1.27cm) in middle and lower crown were not recorded, number of branches in each segment was not available, thus not included in the model.

3.2.4.1 Relative branch diameter (pruned branches included)

A total of 8,035 branches were extracted from dataset II as the smaller branches in individual segments.

$$\ln\left(\frac{{}^{BD_{ctsb}}/_{BDMax_{cts}}}{1 - {}^{BD_{ctsb}}/_{BDMax_{cts}}}\right) = (b_0 + \beta_{cts0}) + (b_1 + \beta_{cts1}) \ln R_{ctsb} + \beta_{ct} + \beta_{ctsb} \quad [3a]$$

In which,

$$\begin{pmatrix}\beta_{cts0}\\ \beta_{cts1}\end{pmatrix} \sim iid\ N\left[\begin{pmatrix}0\\0\end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix} {\sigma^2}_{\beta_{cts0}} & {\sigma^2}_{\beta_{cts0}\beta_{cts1}} \\ {\sigma^2}_{\beta_{cts0}\beta_{cts1}} & {\sigma^2}_{\beta_{cts1}} \end{bmatrix}, \beta_{ctsb} \sim iid(0, {\sigma^2}_3).$$

3.2.4.2 Relative branch diameter (unpruned branches only)

A total of 4,744 branches were extracted from dataset III as the smaller branches in individual segments. The form of model [3a] was also applied to dataset III, and it will be referred as model [3b] in the following text. In addition, model [4] which included $Cos\theta_{ctsb}$ of unpruned branches was also used.

$$\ln\left(\frac{{}^{BD_{ctsb}}/_{BDMax_{cts}}}{1-{}^{BD_{ctsb}}/_{BDMax_{cts}}}\right) = (b_0+\beta_{cts0}) + (b_1+\beta_{cts1})\ln R_{ctsb} + (b_2+\beta_{cts2})Cos\theta_{ctsb} + \beta_{ct}+\beta_{ctsb} \qquad [4]$$

$$\begin{pmatrix}\beta_{cts0}\\ \beta_{cts1}\\ \beta_{cts2}\end{pmatrix} \sim iid\ N\left[\begin{pmatrix}0\\0\\0\end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix}{\sigma^2}_{\beta_{cts0}} & {\sigma^2}_{\beta_{cts0}\beta_{cts1}} & {\sigma^2}_{\beta_{cts0}\beta_{cts2}}\\ {\sigma^2}_{\beta_{cts0}\beta_{cts1}} & {\sigma^2}_{\beta_{cts1}} & {\sigma^2}_{\beta_{cts1}\beta_{cts2}}\\ {\sigma^2}_{\beta_{cts0}\beta_{cts2}} & {\sigma^2}_{\beta_{cts1}\beta_{cts2}} & {\sigma^2}_{\beta_{cts2}}\end{bmatrix},$$

$\beta_{ctsb} \sim iid(0, {\sigma^2}_4)$.

3.2.5 Branch radial growth (one year: 2011-2012)

Branch radial growth was related to its original diameter and its relative depth within the crown.

$$\ln(BDG+1)_{ctsb} = (c_0+\gamma_{cts0}) + (c_1+\gamma_{cts1})\ln BD_{ctsb} + (c_2+\gamma_{cts2})\ln B_{RDINC_{ctsb}} + c_{4i}Clone + \gamma_{ct}+\gamma_{ctsb} \qquad [5]$$

In which,

$$\begin{pmatrix}\gamma_{cts0}\\ \gamma_{cts1}\\ \gamma_{cts2}\end{pmatrix} \sim iid\ N\left[\begin{pmatrix}0\\0\\0\end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix}{\sigma^2}_{\gamma_{cts0}} & {\sigma^2}_{\gamma_{cts0}\gamma_{cts1}} & {\sigma^2}_{\gamma_{cts0}\gamma_{cts2}}\\ {\sigma^2}_{\gamma_{cts0}\gamma_{cts1}} & {\sigma^2}_{\gamma_{cts1}} & {\sigma^2}_{\gamma_{cts1}\gamma_{cts2}}\\ {\sigma^2}_{\gamma_{cts0}\gamma_{cts2}} & {\sigma^2}_{\gamma_{cts1}\gamma_{cts2}} & {\sigma^2}_{\gamma_{cts2}}\end{bmatrix},$$

$\gamma_{ctsb} \sim iid(0, {\sigma^2}_5)$.

Branch diameter growth was also related to $Cos\theta$ besides its original diameter.

$$\ln(BDG+1)_{ctsb} = c_0 + (c_1 + \gamma_{cts1}) \ln BD_{ctsb} + (c_3 + \gamma_{cts3}) Cos\theta_{ctsb} + c_{4i} Clone + \gamma_{ct} + \gamma_{ctsb} \qquad [6]$$

In which,

$$\begin{pmatrix} \gamma_{cts1} \\ \gamma_{cts3} \end{pmatrix} \sim iid\ N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix} \sigma^2{}_{\gamma_{cts1}} & 0 \\ 0 & \sigma^2{}_{\gamma_{cts3}} \end{bmatrix}, \gamma_{ctsb} \sim iid(0, \sigma^2{}_6).$$

3.2.6 Branch angle

The insertion angle of a branch can be predicted by its relative position within the crown and/or its own diameter.

$$\ln \vartheta_{ctsb} = d_0 + d_2 B\_RDINC_{ctsb} + d_{3i} Clone + \delta_{ct} + \delta_{cts} + \delta_{ctsb} \qquad [7]$$

In which,

$$\delta_{ct} \sim iid(0, \sigma^2{}_{ct}), \delta_{cts} \sim iid(0, \sigma^2{}_{cts}), \delta_{ctsb} \sim iid(0, \sigma^2{}_7).$$

$$\ln \vartheta_{ctsb} = d_0 + (d_1 + \delta_{cts1}) \ln BD_{ctsb} + (d_2 + \delta_{cts2}) B\_RDINC_{ctsb} + d_{3i} Clone + \delta_{ct} + \delta_{ctsb} \qquad [8]$$

In which,

$$\begin{pmatrix} \delta_{cts1} \\ \delta_{cts2} \end{pmatrix} \sim iid\ N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \varphi_{cts}\right], \varphi_{cts} = \begin{bmatrix} \sigma^2{}_{\delta_{cts1}} & \sigma^2{}_{\delta_{cts1}\delta_{cts2}} \\ \sigma^2{}_{\delta_{cts1}\delta_{cts2}} & \sigma^2{}_{\delta_{cts2}} \end{bmatrix}, \delta_{ctsb} \sim iid(0, \sigma^2{}_8).$$

3.2.7 Branch length

Branch length was related to branch diameter.

$$\ln BL = (e_0 + \varepsilon_{cb0}) + (e_1 + \varepsilon_{cb1}) \ln BD + e_{2i} Clone + \varepsilon_{cb} \qquad [9]$$

In which,

$$\begin{pmatrix} \varepsilon_{cb0} \\ \varepsilon_{cb1} \end{pmatrix} \sim iid\ N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \varphi_{cb}\right], \varphi_{cts} = \begin{bmatrix} \sigma^2{}_{\varepsilon_{cb0}} & \sigma^2{}_{\varepsilon_{cb0}\varepsilon_{cb1}} \\ \sigma^2{}_{\varepsilon_{cb0}\varepsilon_{cb1}} & \sigma^2{}_{\varepsilon_{cb1}} \end{bmatrix}, \ \varepsilon_{ctb} \sim iid(0, \sigma^2{}_9).$$

3.2.8 Branch frequency and branch basal area per meter of stem

Because not all branch heights were recorded, number of branches and accumulated branch basal area in a segment along the stem could not be modeled such as maximum branch diameter and relative branch diameter. Instead, branch frequency (NBM, number of branches per meter of effective stem length, Table 3-1) and branch basal area per meter of stem (BAM, Table 3-1) were modeled. Two fixed effects models were developed for they were specific enough and mixed effects models were unnecessary.

Branch frequency was best predicted by clone:

$$\ln NBM = f_0 + f_{1i} Clone +_{\tau} \qquad [10]$$

Branch basal area per meter of stem was best predicted by DBH and clone:

$$\ln BAM = g_0 + g_1 DBH + g_{2i} Clone +_{\omega} \qquad [11]$$

3.3 Results

3.3.1 Branch diameter

3.3.1.1 Maximum branch diameter in a segment

Model [1a] and [1b], in the same form, were developed for datasets II and III. Model [1b], based on unpruned branches, predicted the maximum branch diameter within individual segments to be smaller than model [1a], especially for branches in middle and lower crown, but predicted maximum branch diameter in the upper crown to be larger than model [1a] (Figure 3-1). The fixed portion of model [1a] and [1b] captured 42.15%, and 38.22% of the variation for dataset II and III, respectively, while the two full models explained near 100% of the variation in both datasets, respectively (Table 3-4).

Model [1b] and [2] were both built for the dataset III, except that model [2] had three branches missing branch angle. Model [2] contained one more variable than model [1b]: $Cos\theta_{ctsb}$. The results showed that model [2] was superior to [1b] due to its lower

AIC and -2 Log-likelihood value, E, |E|, E^2, and a larger proportion of variation was explained by the fixed part of the model: 48.02% (Table 3-4).

The clonal difference predicted by model [1a] and [1b] were similar: the maximum branch diameter in a segment of clone C715 ($p = 0.0166$ in [1a], $p = 0.0116$ in [1b]) and C730 ($p = 0.0107$ in [1a] and $= 0.0029$ in [1b]) were significantly lower than reference clone C130, while other clones were not significantly different from C130 ($p > 0.0947$ in [1a] and > 0.1999 in [1b]). After taking account of branch angle, model [2] explained more clonal variation in maximum branch diameter. It predicted that besides C715 and C730, the maximum branch diameter of clone C55, C702, C707, C710, and C713 were also significantly smaller than that of C130.

Maximum branch diameter increased as DBH increased, but it changed curvilinearly over the relative position of stem segments. Model [1a] and [1b] predicted that for a given DBH, maximum branch diameter peaked at around 0.8 of the crown from stem apex (Figure 3-1), while model [2] predicted that for a given DBH and a fixed branch angle, the maximum branch diameter peaked near the bottom of the crown (Figure 3-2). That is, maximum branch diameter peaked when the segment center was located at either 0.8 or 1.0 of the crown, there, the position of the thickest branch would be within ± 0.5 m from the segment center. Although model [1b] and [2] predicted slightly different trends of maximum branch diameter in the lower half crown, they showed the same overall trend: maximum branch diameter increased most across segments in the upper half of the crown, and in the lower half of the crown segments differed relatively little for maximum branch diameter. When DBH and C_RDINC were held constant, maximum branch diameter was predicted by model [2] to decrease as branch angle increased (Figure 3-3).

3.3.1.2 Relative branch diameter

Relative branch diameter was negatively correlated with the size rank of each branch within a one - meter stem unit. Model [3a] and [3b] were developed for datasets II and III using the same form. Model [3b], which was based on unpruned branches only, predicted the diameter of smaller branches in the same segment in the lower crown to be smaller than model [3a] did, while it predicted the diameter of smaller branches in the same segment in the upper crown to be larger than model [3a] (Figure 3-4). For the diameter of smaller branches, model [3a] captured 62% (fixed part) and 88.36% (full model) of the variation in dataset II, while model [3b] explained 56.1% (fixed part) and 89.69% (full model) of the variation in dataset III. Relative branch diameter was predicted to share the same dynamic trends as the maximum branch diameter (Figure 3-4 & 3-5), as relative branch diameter was modeled based on maximum branch diameter. While the rank of smaller branches within one segment was the major predictor for their diameter, as shown in model [3b], model [4] performed slightly better than [3b] for the same dataset after adding cosine of branch angle. Model [4] had lower AIC, -2 loglikelihood value, E, |E|, E^2, and a larger proportion of variation explained: 58.01% (fixed part) and 90.39% (full model, Table 3-5). The diameter of the smaller branches increased as the branch angle decreased (Figure 3-6), similar to maximum branch diameter.

All three models ([3a], [3b], and [4]) predicted that for clones C701, C707, C708, and C720, if given a fixed maximum branch diameter in one segment, the rest of the branches in the same segment were significantly smaller than those of C130 [i.e., for C701, C707, C708, and C720 the difference in diameter between the thickest branch and other (smaller) branches were larger]. By contrast, branches of C715 and C730 were larger (i.e., the difference in size between the thickest branch and other smaller branches was smaller) (Table 3-5). These results indicated that among all the clones, the difference in branch sizes of C701, C707, C708, and C720 was relatively large, while clones C715 and C730 had more even sized branches within segments. The same two clones (C715 and C730) tended to have smaller maximum branch diameter than C130.

3.3.1.3 Branch radial growth in one year

Branch radial growth could be predicted by BD and B_RDINC (model [5]), or BD and cosθ (model [6]), respectively. Model [5] was superior to model [6] based on its (lower) AIC, -2 log likelihood, |E|, and E^2, although E was slightly higher for model 5 (Table 3-6). Model [5] explained 45.79% (fixed part) and 59.53 % (full model) of the variation, which was better than model [6], which captured 27.44% (fixed part) and 57.12% (full model) of the variation.

Model [5] and [6] had clonal differences. In model [5], Clone C712 was predicted to have significantly less branch radial growth from 2010 to 2011 than C130, and C700 significantly higher. In model [6], besides C712, Clones C55, C702, C705, C707, C710, C713, C714, C715, and C720 were also predicted to have significantly less branch radial growth. Model [6] predicted that the smaller the branch angle, the faster the radial growth, while model [5] indicated that the higher the position within a crown, the more a branch grows radially (Figure 3-7 and 3-8). Both models predicted that branches which were smaller than 0.7 cm did not grow, especially if located in the lower crown. As the initial BD gets larger, for a given relative position or a constant angle, the larger the initial branch diameter, the more it grows.

3.3.2 Branch angle

Model [7] captured 27.14% (fixed portion only) and 38.05% (mixed) of the variation in branch angle (Table 3-7). Adding branch diameter improved the predicting power, as model [8] explained 42.09% (fixed portion only) and 52.64% (mixed) of the variation (Table 3-7). Both models predicted the following clones had significantly lower branch angle than C130: C55, C701, C702, C707, C708, C710, C713, C714, C715, and C716. Branch angle increased as its relative position in the crown lowered (Figure 3-9 and 3-10), and/or as its diameter decreased. As shown in a preliminary model that does not involve clone factors, branch angle was also negatively correlated with DBH, i.e., smaller branch angles were associated with larger DBH. However, DBH was not significant after adding clone into the model. The fact that the clones listed above were at the upper end of the DBH distribution may help explain this, or it may be due to the relatively small range of the DBH data of these even-aged trees.

3.3.3 Branch length

Branch diameter was the best predictor of first-order branch length. Model [9] explained 88.73% (fixed) and 91.06% (mixed) of the variation (Table 3-8). Clone C708, C710, C712, and C714 tended to have longer first-order branch length when branch diameter was held constant (Figure 3-11).

3.3.4 Branch frequency and branch basal area per meter of stem

Branch frequency was well predicted by clone itself - 69.02% of the variation in average branch frequency was captured by model [10] (Table 3-9). Clone C702, C703, C707, C708, C713, C714, C715, and C716 had significantly higher branch frequency than C130, while C726 had significantly lower branch frequency.

Branch basal area per meter of stem was predicted by DBH and clone. Model [11] explained 61.57% of the variation (Table 3-10). Branch basal area per meter increased as DBH increased, and Clone C55, C702, C707, C709, and C714 were predicted to have significantly lower branch basal area per meter of stem when DBH was held constant.

3.4 Discussion

3.4.1 Branch- and tree- level variables in the models

Branch position within a crown was an important predictor of branch diameter, branch radial growth, branch angle, and other branch attributes for a number of species with different stand densities (Colin and Houllier, 1992; Mäkinen and Colin, 1998; Mäkinen et al., 2003a, 2003b; Weiskittel et al., 2007a; Hein et al., 2008), including stands that had not reached crown closure (Garber and Maguire, 2005). This was because branch position variables integrated several effects exerted synergistically by branch age, light level, hormone, and competition from adjacent branches and trees (Weiskittel et al., 2007a). The position variables of branch or stem segment were also shown to be good predictors for these branch characteristics in my black walnut models, demonstrating their importance in tree allometry.

Besides position variables, the results showed that branch angle was an important predictor of the diameter and one-year radial growth of the thickest and other smaller branches in individual segments. In my models, adding branch angle increased the prediction power over using position variables only (model [2] vs. [1b] and model [3b] vs. [4]), and was also useful for predicting branch radial growth without position variables (model [6]). These results indicated that branch angle influences branch diameter and its radial growth. Branch angle can be seen as an indicator of apical dominance and control. For instance, conifers, which display stronger apical dominance than hardwoods, commonly have a strong central leader with small and flat branches attached to it, while many hardwoods often develop several large co-leaders with acute angles. Branch angle influences the dynamic relationship between branches and the central leader. The growth of branches with smaller angles is considered to be less constrained by gravity, and branches that emerge at small angles (upright branches) have a better chance to survive and grow than large angled (flat) branches (see chapter 2).

As is commonly seen in tree allometry, branch size, in addition to position variables and branch angle, was strongly related to tree-level parameters such as DBH, tree height, crown length, and height: diameter (H:D) ratio. HD ratio was used to represent the social class of Douglas fir trees, for it was considered an indicator for available resources to individual trees (Hein et al., 2008). However, neither H:D ratio nor tree height was statistically significant in my mixed effects models. This may be because the black walnut clones in my experiment were the same (young) age, thus no forest strata had formed yet. Also because of the wide spacing in the plantation, competition among trees was still minimal. DBH was shown to be an efficient predictor for maximum branch diameter

(Colin and Houllier, 1992), and it was significant in my maximum branch diameter model as well.

3.4.2 Branch diameter and its growth

3.4.2.1 Branch diameter in a segment

The negative correlation between branch angle and diameter indicated by Model [2] was in accordance with the finding of Mäkinen and Colin (1998). The stagnant trend (little increase or even a decrease) of maximum branch diameter profile in the lower crown that we observed was also seen in other species (Weiskittel et al., 2007a; Hein et al., 2008). This phenomenon was likely caused by self-shading and shading from neighboring trees (Garber and Maguire, 2005). The positive relation between DBH and maximum branch diameter predicted by model [2] was also seen in previous studies (Mäkinen and Colin, 1998; Hein et al., 2008). It was in accordance with the finding that silvicultural treatments, such as fertilizer, wide spacing, and vegetation control, promote branch diameter growth as well as stem diameter growth (Weiskittel et al., 2007b).

For a given DBH, clones C55, C702, C707, C710, C713, C715, and C730 tended to have smaller maximum branch diameters than the clones at the lower end of the DBH distribution. Clones C710 and C730 were half siblings of maternal clone C55, thus it was not surprising that these three clones all had lower intercepts in model [2], assuming maximum branch diameter is under some degree of genetic control.

3.4.2.2 Branch radial growth

Modeling branch radial growth is desirable because it may help estimate carbon partitioning between branches and stem. Among a collection of factors which influence branch growth: light availability, water, nutrients, respiration, and gravity, light availability is the primary driving force (Mäkinen, 2002). Thus, branch position within the crown naturally serves as a good predictor for branch growth because it represents the light level well. This was corroborated by my branch radial growth model. More specifically, branches in the upper crown grew more than the branches in the lower crown (Figure 3-7), and this was in accordance with some previous findings (Mäkinen, 1999, 2002; Weiskittel et al., 2007b). Branch growth of silver birch was best predicted by branch age (Mäkinen, 2002), but branch position within the crown is a good surrogate of branch age, as position is highly correlated with age. Generally branches in the upper crown have more growth flushes than branches in the lower crown (Kozlowski, 1964). We also found that branches in upper crown grew more foliage than the ones in lower crown (see chapter 2); this helped explain the rapid radial growth of upper branches in model [5].

Upright branches (with smaller branch angles) grew faster than larger angled branches (Figure 3-8) as predicted by model [6]. This was in agreement with the predictions from model [2] and [4] that larger branches tended to have smaller angles. Stem diameter increment was found to be a tree – level predictor for branch radial growth in silver birch (Mäkinen, 2002) and Douglas-fir (Weiskittel et al., 2007b), however, it was not significant in predicting branch radial growth for black walnut at their 9th year in my study. This may be explained by the finding of Mäkinen (2002) that no clear connection between branch radial increment variation and tree characteristics of silver birch after some years.

3.4.3 Branch angle

The initial angle of an emerging branch is determined by the angle of the lateral bud, then it will orient towards light, subject to gravity and dominance control from the stem (Weiskittel et al., 2007a). Thus, branch angles typically increase from upper crown to lower crown, due to growth regulator gradients decreasing with distance from the tree top, more light interception at crown periphery, and increasing foliage and woody mass in branches from upper to lower crown (Roeh and Maguire, 1997).

No tree-level parameter was significant in predicting branch angle. DBH and branch position were used to predict branch angle of Scots pine (Mäkinen and Colin, 1998) and silver birch (Harri Mäkinen et al., 2003a), and both models revealed that trees with larger DBH tended to have branches with smaller angle. Colin and Houllier (1992) also reported that Norway spruce in France that grew faster in height tended to have smaller branch angles. In walnut, however, DBH was negatively correlated with branch angle (r_{ij}=-0.5911, p=0.0056, Chapter 4). Neither DBH nor tree height were significant predictors for branch angle in mixed effects model [7] and [8]. This might be due to the fact that most clones that were predicted to have smaller angles were at the upper end of DBH distribution, or the range in tree- level characteristics was limited.

Including branch diameter to model [8] strongly improved the predicting power to predict branch angle. This was in accordance with the report that branch angle was a function of its location and size (Weiskittel et al., 2007a). Although my result that larger branches tended to have smaller angles was in contrast with the findings of Weiskittel et al (2007a) and Hein et al. (2008), it was in agreement with other studies (King et al., 1992; Mäkinen and Colin, 1998; Mäkinen et al., 2003a, 2003b).

Although selecting clones with small branch angles may increase branch and DBH growth, it may also lower wood quality for two reasons. First, branches with acute angles disturb a higher volume of stem wood than flat angled branches, increasing size of defects caused by branches and reducing stem value (Colin and Houllier, 1992). Second, acute angled branches have a higher possibility of becoming a co-leader to compete with the main stem, and are very likely to worsen the stem form in the future. Flat (large) branch angle was considered a desirable branch characteristic for timber quality in coastal Douglas fir (King et al., 1992). Among all the clones that had low intercepts in model [8], clones C702, C710, C713, and C715 had particularly small branch angles, while C55, C701, C707, C708, C709, C714, C716, C720, and C730 had moderate branch angles.

Average branch angle was under moderate genetic control in the black walnut populations in this study (clone repeatability: 0.59 ±0.11, see Chapter 4). Previous studies showed that branch angle in Douglas-fir was under weak genetic control

(Weiskittel et al., 2007a), however, branches of young age expressed stronger genetic effect (St. Clair, 1994), and others have reported moderate heritability of branch angle (Velling, 1988; Haapanen et al., 1997), and high heritability (King et al., 1992) for the same trait.

3.4.4 Branch length

Branch diameter was the strongest predictor of branch length, although clones also differed significantly for this trait ($p<0.0001$). Clones C708, C710, C712, and C714 had longer branches than all other clones. In addition to comparing clones for first-order branch length, model [9] may be used to estimate branch volume for different clones.

Branch length could have been modeled more systematically using branch position, angle, and tree-level variables. However, due to the physical difficulties of measuring their length while they were still attached to the stem, first-order branch length was measured on pruned branches only. A refined model can be developed by using a more systematic sampling procedure in the future.

3.4.5 Branch frequency and branch basal area per meter of stem

Spacing between trees strongly influences the number of branches on the stem, because light intensity was positively related to primordium initiation in black spruce and white spruce: reduced light level led to reduced primordium frequency that varied depending on provenances (Pollard and Logan, 1979). My experimental setting-uniform wide spacing and management regime-was ideal for determining the genotypic effect of black walnut clones on branch frequency. It was also reported that branch frequency is subject to moderate genetic control (Velling, 1988; Vestøl et al., 1999). My results showed that clone had a strong effect on branch frequency in black walnut as well - 69.02% of the variation in this trait was explained by clone.

It was reported that the amount of stemwood produced in *Pinus contorta* and *Picea sitchensis* was controlled by annual height growth and number of lateral branches produced per unit shoot length (Cannell, 1974). Larger Douglas – fir trees had higher branch densities per unit length of annual segment (Weiskittel et al., 2007a), which indicated that high branch frequency was positively correlated with growth. We also found this relationship (model [10]): clones C702, C703, C707, C708, C713, C714, C715, and C716 at the upper end of DBH distribution had significantly higher branch frequency than C726, a slower growing clone.

Branch basal area per meter of stem may serve as a better indicator of crown sparseness than branch frequency. According to model [11], given a fixed DBH, clones C55, C702, C707, C709, and C714 tended to have significantly lower branch basal area per meter of stem. Lower branch basal area per meter of stem means a smaller volume of branch wood, and clones with low branch basal area per meter of stem can be regarded as having a sparse crown type. Clone C55 and C714 had higher growth efficiency (see chapter 2), and this was in agreement with the finding that sparse branching was associated with high stemwood production efficiency in Sitka spruce (Cannell et al., 1983). Trees with less branch wood need less structural support from the stem. Thus, a sparse crown is also mechanically economical.

3.4.6 Limitations, applications and future directions

Although branch diameters were measured on every branch, branch height and angle were mainly recorded for branches larger than 1.27 cm plus some vigorous branches smaller than 1.27 cm. Thus, except model [9], [10], and [11], models in this study were not applied to all branches. The fully occluded pruning scars on the stem near the ground were invisible and were therefore not included in my dataset. Although model [7] was better than [8], model [8] required less measurement to predict branch angle, so it can be used if higher accuracy was not demanded.

To understand branch dynamics over time in an even-aged and intensively managed plantation, branch characteristics will need to be modeled multiple times over several stages of growth, including seedlings. My models were only a snapshot of the long growing process of the black walnut clones, even the branch radial growth model was only based on one-year’s growth data. Thus, these models may not be able to reveal functional relationships. The goal of these analyses should be the determination of relationships between branching, tree growth, and stem quality. These allometric models would likely improve the efficiency of early selection.

3.5 Reference

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3.6 Tables

Table 3-1 Explanations and units of symbols used in chapter 3

Symbol	Explanation	Units
THt	Total tree height	m
BHt	Branch height from ground	m
HCB	Height of the crown base (the lowest living branch)	m
CL	Crown length: THt - HCB	m
B_RDINC	Relative depth into crown of branches: (THt - BHt)/CL	-
ESL	Effective stem length: stem length between the lowest branch (including scar) and the highest branch measured in a tree	m
BAM	total branch basal area m^{-1} of stem: total branch basal area/ESL	m^{2}·m^{-1}
BD	Branch diameter	cm
BDG	Branch radial growth: BD of 2011 – BD of 2010	cm
BDMax	Branch diameter of the largest branch in every one-meter segment of the stem	cm
BL	Branch length	cm
C_RDINC	Relative depth into crown of the centers in each one-meter stem segment: (THt - height of each segment center)/CL	-
CW	Crown width, the mean of crown radii in four cardinal directions	m
DBH	Diameter at breast height (1.37 m)	cm
HD	THt (m) × 100 / DBH (cm)	-
NBM	Branch frequency (number of branches m^{-1} of stem): number of branches measured in a tree/ESL	m^{-1}
NST	Number of segments in a tree	-
PSM	Percentage of stem length measured: BHt of the highest branch measured/THt	%
R	Rank of a branch in a segment, from largest to smallest in diameter	-
RelBD	Relative branch diameter of branches in each segment other than the largest branch (BD/BDmax)	-
S	One-meter segment within tree stems	-
E, |E|, E^{2}	Mean error, mean absolute error, mean squared error	-
a, b ,c, d, e, f, g	Fixed parameters	-
c, t, s, b	Subscripts for clone, tree, segment, and branch, respectively	-
$\alpha, \beta, \gamma, \delta, \rho, \psi, \omega$	Random parameters (variance components)	-
ϑ	Branch insertion angle (from the vertical)	°

Table 3-2 Tree-level and segment-level attributes of 25 black walnut (*Juglans nigra* L.) clones

		DBH (cm)		THt (m)		HCB (m)		CL (m)		CW (m)		PSM (%)	
Clone	N_t	Mean±SD	Min- Max	Mean±SD	Min- Max	Mean±SD	Min- Max	Mean±SD	Min- Max	Mean±SD	Min- Max	Mean±SD	Min- Max
C55	9	14.55±1.01	12.95-16.00	10.09±0.52	9.4-10.72	1.04±0.10	0.87-1.17	9.04±0.51	8.30-9.65	2.70±0.17	2.34-2.95	74±6	68-84
C700	4	13.11±0.94	12.07-14.35	9.02±0.86	7.79-9.65	0.98±0.12	0.80-1.05	8.04±0.74	6.99-8.61	2.69±0.37	2.18-3.06	83±9	72-91
C701	6	12.95±0.53	12.32-13.84	9.09±0.24	8.83-9.48	1.05±0.12	0.92-1.21	8.04±0.28	7.71-8.50	2.73±0.27	2.26-3.03	78±4	74-84
C702	7	14.88±0.66	13.72-15.62	9.86±0.41	9.50-10.41	0.86±0.29	0.29-1.05	9.00±0.49	8.45-9.75	2.47±0.28	2.03-2.99	78±9	63-86
C703	7	14.7±0.87	13.59-16.13	9.36±0.30	8.78-9.69	1.00±0.16	0.66-1.14	8.36±0.34	7.77-8.80	2.63±0.26	2.26-2.93	70±10	58-82
C705	7	13.52±1.00	11.94-14.86	9.63±0.53	8.85-10.36	1.08±0.09	0.94-1.21	8.55±0.52	7.76-9.24	3.08±0.25	2.77-3.52	78±11	60-88
C707	12	14.3±1.15	12.7-16.51	9.52±0.78	8.08-10.71	0.94±0.25	0.34-1.39	8.59±0.79	7.26-9.67	2.54±0.32	2.02-2.98	76±10	61-88
C708	14	15.02±0.83	13.21-16.26	10.02±0.31	9.52-10.51	1.01±0.06	0.90-1.12	9.01±0.32	8.51-9.61	2.72±0.23	2.29-3.01	76±9	58-85
C709	5	13.39±0.45	12.7-13.84	9.21±0.09	9.16-9.36	1.06±0.06	1.01-1.16	8.15±0.12	7.99-8.32	2.50±0.15	2.36-2.74	85±9	72-95
C710	10	14.69±0.34	14.35-15.37	10.20±0.48	9.19-10.66	0.99±0.18	0.68-1.34	9.21±0.40	8.52-9.72	2.88±0.21	2.60-3.14	76±5	70-82
C712	8	15.45±0.98	14.48-17.15	10±0.73	8.74-10.78	1.06±0.08	0.95-1.18	8.94±0.72	7.79-9.68	2.76±0.10	2.60-2.85	66±8	57-77
C713	9	15.41±1.09	14.48-17.91	9.72±0.60	9.02-10.91	1.15±0.08	1.01-1.23	8.57±0.58	7.91-9.68	2.85±0.32	2.46-3.47	72±8	62-81
C714	9	16.4±0.84	15.11-17.27	10.98±0.40	10.16-11.33	0.99±0.07	0.88-1.09	9.99±0.39	9.14-10.33	2.98±0.23	2.65-3.41	72±10	57-82
C715	19	16.24±1.16	14.48-18.92	9.11±0.60	8.08-10.75	1.03±0.14	0.60-1.27	8.08±0.62	6.88-9.73	2.85±0.24	2.20-3.19	80±4	70-87
C716	6	14.22±0.93	12.95-15.37	9.55±0.68	8.24-10.02	0.95±0.13	0.72-1.09	8.61±0.72	7.22-9.22	2.71±0.26	2.32-3.12	76±7	69-87
C717	3	13.97±0.55	13.34-14.35	7.80±0.56	7.21-8.32	1.00±0.09	0.91-1.09	6.80±0.60	6.22-7.41	2.88±0.25	2.61-3.10	83±3	80-87
C718	5	15.47±0.24	15.11-15.75	10.32±0.29	9.97-10.76	0.99±0.08	0.91-1.07	9.33±0.26	8.97-9.68	2.62±0.18	2.38-2.86	80±8	67-87
C719	2	13.02±0.63	12.57-13.46	7.47±0.37	7.21-7.73	1.04±0.03	1.01-1.06	6.43±0.34	6.19-6.68	2.65±0.35	2.40-2.90	81±1	80-82
C720	6	14.08±1.29	11.68-15.11	9.42±0.60	8.55-10.39	1.02±0.07	0.94-1.12	8.40±0.56	7.55-9.27	3.03±0.27	2.78-3.50	76±4	72-81
C726	8	13.32±0.53	12.57-14.10	8.86±0.24	8.53-9.25	1.09±0.10	1.01-1.27	7.77±0.23	7.53-8.20	2.77±0.23	2.47-3.15	74±2	71-77
C728	1	14.48	14.48	8.67	8.67	0.98	0.98	7.68	7.68	2.64	2.64	74	74
C729	1	9.91	9.91	7.29	7.29	1.12	1.12	6.17	6.17	2.52	2.52	74	74
C730	5	14±0.94	12.57-15.11	8.93±0.16	8.8-9.19	1.07±0.17	0.84-1.30	7.86±0.19	7.70-8.15	2.58±0.13	2.45-2.72	83±3	79-87
C777	1	15.24	15.24	9.15	9.15	1.01	1.01	8.14	8.14	3.42	3.42	86	86
C130	8	15.37±1	13.46-16.64	8.87±0.41	8.32-9.70	0.97±0.08	0.89-1.09	7.9±0.42	7.38-8.77	2.86±0.2	2.62-3.13	80±3	75-82

Table 3-2 continued

		NBM (m^{-1})		BAM (m^2·m^{-1})			C_RDINC		NST	
Clone	Nt	Mean±SD	Min- Max	Mean±SD	Min- Max	Ns	Mean±SD	Min- Max	Mean±SD	Min- Max
C55	9	14.63±2.53	11.67-18.15	57.24±11.56	41.68-74.00	64	0.75±0.27	0.27-1.25	4.73±2.12	1-8
C700	4	13.14±1.80	11.69-15.62	55.08±7.23	46.7-62.57	26	0.74±0.30	0.08-1.22	4.38±2.19	1-9
C701	6	11.91±1.83	9.25-14.20	61.48±7.61	53.86-74.28	39	0.72±0.28	0.21-1.20	4.33±2.06	1-8
C702	7	16.89±1.67	14.83-19.02	63.32±7.09	51.00-71.33	52	0.73±0.30	0.12-1.28	4.87±2.33	1-10
C703	7	16.16±1.78	14.34-19.63	79.58±12.28	61.70-92.05	44	0.75±0.27	0.26-1.25	4.41±1.96	1-8
C705	7	13.77±1.35	12.00-15.47	70.86±15.41	57.54-102.66	52	0.69±0.30	0.14-1.23	4.98±2.28	1-9
C707	12	15.16±1.67	12.40-18.11	62.93±15.23	49.34-105.73	84	0.75±0.30	0.17-1.31	4.54±2.13	1-9
C708	14	18.36±1.14	16.62-20.06	71.94±10.74	58.13-99.11	73	0.70±0.29	0.17-1.19	4.90±2.33	1-9
C709	5	13.76±0.61	13.05-14.3	54.31±9.88	44.59-69.01	36	0.61±0.29	0.09-1.06	5.14±2.15	2-9
C710	10	13.74±1.49	11.65-15.91	75.17±9.56	60.72-87.99	76	0.77±0.29	0.23-1.31	4.72±2.28	1-9
C712	8	13.07±1.63	9.54-14.23	76.52±12.12	57.42-93.58	50	0.78±0.26	0.24-1.27	4.48±1.96	1-8
C713	9	14.58±1.01	13.21-16.57	88.92±11.30	72.20-104.28	58	0.74±0.27	0.22-1.23	4.78±1.95	2-9
C714	9	15.46±1.22	13.31-17.14	73.99±17.27	52.57-106.86	71	0.76±0.28	0.19-1.23	4.87±2.47	1-10
C715	19	16.47±1.90	13.36-20.41	81.86±12.59	63.05-112.14	135	0.72±0.31	0.21-1.40	4.69±2.10	1-9
C716	6	15.28±1.45	13.13-17.29	65.51±11.67	48.88-77.87	45	0.78±0.32	0.16-1.30	4.47±2.29	1-9
C717	3	13.09±0.99	12.03-13.98	80.81±16.09	67.70-98.77	19	0.72±0.31	0.23-1.23	4.00±1.91	1-7
C718	5	13.35±1.30	11.93-14.82	69.05±11.31	60.46-88.20	43	0.70±0.31	0.19-1.23	5.19±2.52	1-9
C719	2	12.19±3.05	10.04-14.35	66.65±22.89	50.46-82.84	11	0.68±0.31	0.21-1.16	4.27±1.68	2-7
C720	6	12.60±1.49	10.43-14.61	66.24±9.65	49.82-78.37	43	0.73±0.29	0.26-1.30	4.58±2.13	1-8
C726	8	8.89±1.11	7.76-10.97	74.26±7.99	63.36-84.16	49	0.70±0.26	0.23-1.13	4.57±1.78	2-8
C728	1	14.51	14.51-14.51	70.88	70.88-70.88	7	0.79±0.33	0.33-1.24	4.00±2.16	1-7
C729	1	12.56	12.56-12.56	55.17	55.17-55.17	5	0.72±0.30	0.34-1.10	4.00±1.58	2-6
C730	5	14.45±1.18	12.85-15.56	66.23±7.31	54.20-73.15	37	0.78±0.37	0.20-1.47	4.59±2.19	1-8
C777	1	15.98	15.98-15.98	94.60	94.60	7	0.69±0.32	0.24-1.13	5.00±2.16	2-8
C130	8	13.03±1.31	11.37-15.53	79.03±10.81	64.91-101.87	58	0.74±0.32	0.17-1.29	4.38±2.14	1-8

Table 3-3 Branch attributes of 25 black walnut (*Juglans nigra* L.) clones

		B_RDINC			MaxBD (cm)			R			RelBD			θ (°)	
Clone	Nb	Mean±SD	Min- Max	Nb	Mean±SD	Min- Max	Nb	Mean±SD	Min- Max	Nb	Mean±SD	Min- Max	Nb	Mean±SD	Min- Max
C55	489	0.79±0.25	0.20-1.22	64	4.28±1.05	1.57-6.20	489	5.23±3.42	1-17	425	0.51±0.23	0.12-1.00	332	65.48±15.97	24-123
C700	176	0.78±0.25	0.12-1.27	26	4.31±1.49	1.12-6.25	176	5.23±3.79	1-19	150	0.51±0.26	0.14-0.98	118	70.60±20.94	10-125
C701	252	0.75±0.24	0.21-1.14	39	4.56±1.43	1.64-7.26	252	4.72±3.18	1-16	213	0.53±0.25	0.12-0.98	155	65.40±19.46	20-138
C702	452	0.81±0.27	0.18-1.26	52	4.16±1.61	0.91-7.86	452	6.15±4.33	1-23	398	0.52±0.22	0.06-0.99	263	55.47±15.89	14-99
C703	386	0.79±0.23	0.24-1.23	44	4.98±1.48	2.11-7.96	386	5.91±3.99	1-21	341	0.48±0.23	0.08-1.00	231	70.32±17.36	26-118
C705	389	0.77±0.26	0.15-1.23	52	4.37±1.51	1.42-7.54	389	5.15±3.28	1-16	337	0.55±0.23	0.08-0.99	247	65.84±15.31	16-103
C707	596	0.81±0.26	0.20-1.26	84	4.42±1.45	1.57-7.48	596	5.07±3.42	1-19	512	0.50±0.24	0.06-0.99	370	61.81±17.19	15-131
C708	497	0.79±0.25	0.22-1.18	73	4.62±1.87	1.27-8.45	497	5.23±3.73	1-21	424	0.50±0.25	0.05-0.99	459	66.57±17.44	5-113
C709	301	0.68±0.26	0.08-1.12	36	4.06±1.39	1.22-6.34	301	5.77±3.89	1-20	265	0.48±0.24	0.05-1.00	228	66.00±17.45	23-115
C710	619	0.77±0.25	0.23-1.26	76	4.46±1.58	1.27-7.40	619	5.81±4.01	1-21	540	0.55±0.23	0.08-0.99	431	57.78±17.25	18-109
C712	364	0.82±0.22	0.31-1.20	50	4.84±1.49	1.07-6.76	364	5.35±3.58	1-16	314	0.52±0.23	0.12-1.00	245	68.40±16.26	20-105
C713	550	0.82±0.24	0.26-1.28	58	5.07±1.46	1.70-8.43	550	6.27±4.07	1-18	490	0.49±0.23	0.05-1.00	326	53.25±16.67	10-120
C714	497	0.84±0.24	0.23-1.17	71	4.72±1.60	1.14-7.72	497	5.40±3.70	1-16	425	0.50±0.23	0.09-0.99	296	66.66±16.54	17-115
C715	1280	0.78±0.27	0.20-1.32	135	4.35±1.66	0.86-9.02	1280	6.55±4.41	1-23	1143	0.55±0.22	0.04-1.00	770	57.12±17.96	12-129
C716	310	0.83±0.26	0.18-1.25	45	4.25±1.60	0.71-7.16	310	4.98±3.18	1-16	265	0.50±0.23	0.10-0.99	193	67.27±20.36	17-125
C717	161	0.72±0.25	0.18-1.15	19	4.36±1.68	0.76-7.01	161	5.72±3.53	1-15	142	0.55±0.21	0.14-0.99	97	65.70±17.59	20-113
C718	266	0.76±0.27	0.17-1.18	43	4.47±1.47	1.78-7.95	266	4.77±3.18	1-14	222	0.54±0.24	0.11-0.99	154	70.27±19.53	30-120
C719	91	0.74±0.28	0.23-1.26	11	3.96±1.45	1.61-6.30	91	5.38±3.57	1-16	80	0.59±0.23	0.14-0.99	61	67.49±11.64	37-90
C720	270	0.80±0.24	0.24-1.23	43	4.67±1.65	1.46-7.67	270	5.14±3.94	1-19	227	0.50±0.22	0.11-0.99	149	60.56±18.17	11-100
C726	370	0.72±0.24	0.29-1.21	49	4.69±1.63	1.04-7.94	370	5.27±3.62	1-20	319	0.52±0.25	0.08-1.00	234	70.12±14.98	20-115
C728	47	0.76±0.25	0.34-1.18	7	4.68±0.74	3.89-5.77	47	4.43±2.64	1-10	40	0.55±0.23	0.13-0.99	31	67.74±17.34	24-90
C729	41	0.78±0.22	0.43-1.18	5	3.81±1.16	2.24-5.28	41	5.85±3.55	1-13	36	0.53±0.19	0.20-0.94	27	79.56±17.32	52-116
C730	304	0.80±0.30	0.16-1.39	37	3.94±1.90	1.75-9.91	304	5.72±3.83	1-18	265	0.57±0.22	0.11-0.99	192	61.67±11.59	35-90
C777	74	0.76±0.29	0.19-1.20	7	4.98±2.04	2.21-7.92	74	7.34±5.80	1-24	66	0.51±0.22	0.13-0.98	44	66.41±16.66	34-102
T130	454	0.76±0.27	0.24-1.21	58	4.67±1.61	2.16-9.55	454	5.65±3.87	1-19	396	0.53±0.26	0.07-0.99	276	70.00±15.89	36-120

Table 3-3 continued

	BDG (cm)			BL (cm)		
Clone	N_b	Mean±SD	Min- Max	N_b	Mean±SD	Min- Max
C55	90	0.34±0.40	0-2.04	38	285.39±103.85	130-570
C700	51	0.77±0.51	0-2.03	12	363.33±88.35	200-520
C701	53	0.73±0.61	0-2.41	13	451.46±88.49	325-600
C702	78	0.52±0.50	0-2.30	50	328.94±105.81	140-540
C703	81	0.47±0.49	0-1.85	37	299.59±120.67	90-570
C705	99	0.47±0.48	0-1.85	34	368.53±115.10	130-590
C707	84	0.38±0.46	0-2.67	17	345.00±128.54	100-575
C708	63	0.57±0.51	0-1.77	40	424.63±195.16	95-730
C709	82	0.44±0.39	0-1.60	15	283.67±133.11	120-500
C710	89	0.50±0.56	0-3.37	35	397.29±103.02	210-650
C712	76	0.27±0.41	0-2.08	45	382.93±146.87	120-625
C713	97	0.48±0.55	0-2.30	46	368.37±106.71	140-545
C714	86	0.37±0.40	0-1.57	59	325.15±113.00	95-640
C715	199	0.56±0.51	0-2.32	100	328.42±103.89	95-580
C716	77	0.47±0.49	0-2.18	42	300.71±135.39	95-550
C717	60	0.71±0.66	0-2.40	22	362.27±78.43	240-530
C718	63	0.64±0.40	0-1.64	22	348.50±103.65	210-580
C719	39	0.81±0.69	0-3.18	21	300.24±103.30	140-475
C720	38	0.41±0.39	0-1.59	19	366.16±157.46	130-585
C726	68	0.47±0.47	0-1.85	30	376.43±128.65	143-560
C728	22	0.82±0.74	0.03-2.96	11	330.00±137.26	160-575
C729	17	0.44±0.44	0-1.46	14	308.93±55.58	185-370
C730	85	0.51±0.52	0-2.18	36	263.33±118.73	100-600
C777				6	345.00±139.36	155-540
T130	53	0.80±0.76	0-3.05	30	303.50±131.93	100-610

Table 3-4 Parameter estimates and fit statistics of model [1a], [1b], and [2] for maximum branch diameter in a segment for dataset II & III, n_t = 168

		1a					1b							2
		n_b=1184					n_b=983							n_b=980, 3 branches missing angles
Parameters	Estimates	SE	t-Value	p > t		Estiamtes	SE	t-Value	p > t		Estiamtes	SE	t-Value	p > t
Fixed														
a_0	3.31570	0.2117	15.66	<.0001		3.0877	0.2564	12.04	<.0001		2.1212	0.2216	9.57	<.0001
a_1	0.04338	0.01013	4.28	<.0001		0.04192	0.01151	3.64	0.0004		0.04195	0.0096	4.37	<.0001
a_2	1.87230	0.08762	21.37	<.0001		1.6748	0.1053	15.90	<.0001		1.3588	0.08802	15.44	<.0001
a_3	-2.3511	0.1415	-16.61	<.0001		-2.1652	0.1938	-11.17	<.0001		-1.3508	0.1682	-8.03	<.0001
a_4	-	-	-	-		-	-	-	-		0.5991	0.0518	11.57	<.0001
$a_{5\text{-}C55}$	-0.0914	0.05434	-1.68	0.0947		-0.08034	0.06238	-1.29	0.1999		-0.145	0.05569	-2.60	0.0102
$a_{5\text{-}C700}$	0.02677	0.07394	0.36	0.7179		-0.02015	0.08418	-0.24	0.8112		-0.012	0.07715	-0.16	0.8764
$a_{5\text{-}C701}$	0.05676	0.06573	0.86	0.3893		-0.03785	0.07405	-0.51	0.6101		-0.1243	0.06482	-1.92	0.0571
$a_{5\text{-}C702}$	-0.08120	0.0572	-1.42	0.1581		-0.07814	0.06533	-1.20	0.2337		-0.183	0.05707	-3.21	0.0017
$a_{5\text{-}C703}$	0.06703	0.05925	1.13	0.2598		0.03211	0.06837	0.47	0.6394		0.05795	0.06338	0.91	0.3621
$a_{5\text{-}C705}$	0.03616	0.0598	0.60	0.5464		0.04441	0.06786	0.65	0.5138		0.03288	0.06212	0.53	0.5974
$a_{5\text{-}C707}$	-0.0368	0.05216	-0.70	0.482		-0.06913	0.05991	-1.15	0.2505		-0.1428	0.05418	-2.64	0.0093
$a_{5\text{-}C708}$	-0.0294	0.05237	-0.56	0.5751		-0.05784	0.05969	-0.97	0.3343		-0.106	0.05424	-1.95	0.0527
$a_{5\text{-}C709}$	0.0396	0.06601	0.60	0.5496		-0.03458	0.0730	-0.47	0.6364		-0.0513	0.06471	-0.79	0.4292
$a_{5\text{-}C710}$	-0.0652	0.05241	-1.24	0.2154		-0.05277	0.06033	-0.87	0.3832		-0.1472	0.05378	-2.74	0.0070
$a_{5\text{-}C712}$	-0.0435	0.05692	-0.76	0.4466		-0.07698	0.06591	-1.17	0.2448		-0.0621	0.06089	-1.02	0.3098
$a_{5\text{-}C713}$	0.00767	0.05489	0.14	0.8891		-0.01786	0.06294	-0.28	0.777		-0.1539	0.05494	-2.80	0.0058
$a_{5\text{-}C714}$	-0.0653	0.05363	-1.22	0.2257		-0.05586	0.06175	-0.90	0.3672		-0.0935	0.05701	-1.64	0.1033
$a_{5\text{-}C715}$	-0.1159	0.04783	-2.42	0.0166		-0.1397	0.05458	-2.56	0.0116		-0.2615	0.05015	-5.21	<.0001
$a_{5\text{-}C716}$	-0.0568	0.06085	-0.93	0.3523		-0.02743	0.07047	-0.39	0.6977		-0.098	0.06199	-1.58	0.1163
$a_{5\text{-}C717}$	-0.0118	0.08004	-0.15	0.8833		0.00724	0.09122	0.08	0.9369		-0.0213	0.08247	-0.26	0.7963
$a_{5\text{-}C718}$	-0.0161	0.06017	-0.27	0.7893		0.03397	0.06878	0.49	0.6222		0.00482	0.06313	0.08	0.9392
$a_{5\text{-}C719}$	-0.0726	0.1001	-0.73	0.4695		-0.09556	0.1112	-0.86	0.3914		-0.0252	0.1120	-0.22	0.8224
$a_{5\text{-}C720}$	-0.0031	0.06083	-0.05	0.9589		-0.0052	0.06932	-0.08	0.9403		-0.1029	0.06076	-1.69	0.0927
$a_{5\text{-}C726}$	0.02023	0.06043	0.33	0.7383		0.0243	0.06873	0.35	0.7242		0.04104	0.06409	0.64	0.5230
$a_{5\text{-}C728}$	0.06039	0.1200	0.50	0.6156		0.1152	0.1407	0.82	0.4146		0.1019	0.1401	0.73	0.4683
$a_{5\text{-}C729}$	-0.0084	0.1462	-0.06	0.9543		-0.01301	0.1673	-0.08	0.9381		-0.0294	0.1638	-0.18	0.8580
$a_{5\text{-}C730}$	-0.1701	0.06578	-2.59	0.0107		-0.2286	0.07553	-3.03	0.0029		-0.2771	0.06676	-4.15	<.0001
$a_{5\text{-}C777}$	0.04951	0.1183	0.42	0.6761		0.02117	0.1322	0.16	0.8731		-0.0136	0.1215	-0.11	0.9109
Random														
α_{ct}	0	.	.	.	α_{ct}	0	.	.	.	α_{ct}	0	.	.	.
α_{cts}	.	.	.	.	α_{cts}	0	.	.	.	$\sigma^2{}_{\alpha_{cts2}}$	0.108	0.02408	4.49	<.0001
$\boldsymbol{\sigma^2}{}_{\boldsymbol{\alpha_{cts2}}}$	0.06163	0.00706	8.73	<.0001	$\sigma^2{}_{\alpha_{cts2}}$	0.04383	0.01243	3.53	0.0002	$\sigma^2{}_{\alpha_{cts2}\alpha_{cts3}}$	-0.1925	0.02615	-7.36	<.0001
$\boldsymbol{\sigma^2}{}_{\boldsymbol{\alpha_{cts3}}}$	0.1208	0.0069	17.5	<.0001	$\sigma^2{}_{\alpha_{cts3}}$	0.1649	0.02403	6.86	<.0001	$\sigma^2{}_{\alpha_{cts3}}$	0.2735	0.035	7.81	<.0001

Table 3-4 continued

α_{ctsb}	2.34E-07	4.7E-05	0.01	0.498	α_{ctsb}	0.00441	0.01412	0.31	0.3775	$\boldsymbol{\sigma^2}_{\boldsymbol{\alpha_{cts2}\alpha_{cts4}}}$	0.1927	0.04247	4.54	<.0001
	-	-	-	-		-	-	-	-	$\sigma^2_{\alpha_{cts3}\alpha_{cts4}}$	-0.2642	0.05225	-5.06	<.0001
	-	-	-	-		-	-	-	-	$\sigma^2_{\alpha_{cts4}}$	0.3322	0.08342	3.98	<.0001
	-	-	-	-		-	-	-	-	α_{ctsb}	9.53E-06	0.00202	0	0.4981
AR(1)	-	-	-	-	AR(1)	-	-	-	-	AR(1)	-	-	-	-
Fit Statistics														
-2 log-likelihood	637.6					597.1					352.3			
AIC	643.6					603.1					366.3			
R^2(fixed)	0.42152					0.3822					0.4802			
R^2(fixed+random)	1					0.9987					1			
E	0.1753					0.1812					0.1378			
|E|	0.9171					0.9431					0.8580			
E^2	1.4270					1.4645					1.2158			

Table 3-5 Parameter estimates and fit statistics of model [3a], [3b], and [4] for Relative branch diameters in a segment for dataset II & III, n_t=168

	3a				3b				4			
	n_b=8035				n_b=4744				n_b=4743 (one branch angle missing)			
Parameters	Estimate	SE	t-Value	p > t	Estimate	SE	t-Value	p > t	Estimate	SE	t-Value	p > t
Fixed												
b_0	3.372	0.1012	33.33	<.0001	3.1385	0.1142	27.47	<.0001	2.9630	0.1123	26.37	<.0001
b_1	-1.9923	0.02837	-70.23	<.0001	-2.056	0.03595	-57.19	<.0001	-2.0024	0.03491	-57.36	<.0001
b_2	-	-	-	-	-	-	-	-	0.3146	0.03217	9.78	<.0001
$b_{3\text{-}C55}$	-0.1961	0.1213	-1.62	0.1083	-0.0574	0.1361	-0.42	0.6737	-0.0703	0.1336	-0.53	0.5996
$b_{3\text{-}C700}$	-0.1259	0.1652	-0.76	0.4471	0.06429	0.1856	0.35	0.7296	0.07129	0.1827	0.39	0.697
$b_{3\text{-}C701}$	-0.3065	0.1438	-2.13	0.0348	-0.4167	0.1639	-2.54	0.0121	-0.4241	0.1613	-2.63	0.0095
$b_{3\text{-}C702}$	0.1064	0.1262	0.84	0.4007	0.02691	0.1434	0.19	0.8514	-0.0375	0.1403	-0.27	0.7898
$b_{3\text{-}C703}$	-0.2008	0.1309	-1.53	0.1274	-0.2158	0.1484	-1.45	0.1483	-0.2300	0.1461	-1.57	0.1177
$b_{3\text{-}C705}$	0.06071	0.1286	0.47	0.6376	0.00345	0.1454	0.02	0.9811	-0.0151	0.1428	-0.11	0.9161
$b_{3\text{-}C707}$	-0.3025	0.1159	-2.61	0.01	-0.2567	0.1311	-1.96	0.0522	-0.2883	0.1287	-2.24	0.0266
$b_{3\text{-}C708}$	-0.3018	0.1212	-2.49	0.0139	-0.2905	0.1366	-2.13	0.0351	-0.313	0.1342	-2.33	0.021
$b_{3\text{-}C709}$	-0.0555	0.1403	-0.40	0.6929	0.08909	0.1541	0.58	0.5641	0.05832	0.1511	0.39	0.7
$b_{3\text{-}C710}$	0.09201	0.1165	0.79	0.4311	0.2027	0.1312	1.54	0.1246	0.1566	0.1285	1.22	0.2251
$b_{3\text{-}C712}$	-0.1564	0.1317	-1.19	0.2369	-0.085	0.1489	-0.57	0.569	-0.1016	0.1463	-0.69	0.4884
$b_{3\text{-}C713}$	0.00808	0.1208	0.07	0.9468	-0.0267	0.1367	-0.20	0.8454	-0.0884	0.1338	-0.66	0.51
$b_{3\text{-}C714}$	-0.1763	0.122	-1.45	0.1505	-0.1376	0.1381	-1.00	0.3209	-0.1483	0.1359	-1.09	0.2772
$b_{3\text{-}C715}$	0.3487	0.104	3.35	0.001	0.329	0.1178	2.79	0.0059	0.2828	0.1156	2.45	0.0156
$b_{3\text{-}C716}$	-0.2362	0.1367	-1.73	0.0862	-0.1023	0.1563	-0.65	0.5139	-0.1200	0.1538	-0.78	0.4365
$b_{3\text{-}C717}$	0.2244	0.1736	1.29	0.1983	0.1247	0.1972	0.63	0.5281	0.09278	0.1936	0.48	0.6324
$b_{3\text{-}C718}$	-0.1686	0.1424	-1.18	0.2381	-0.2146	0.1633	-1.31	0.1909	-0.1805	0.1609	-1.12	0.264
$b_{3\text{-}C719}$	0.288	0.2125	1.35	0.1776	0.4424	0.2392	1.85	0.0665	0.4309	0.2341	1.84	0.0678
$b_{3\text{-}C720}$	-0.3823	0.1425	-2.68	0.0082	-0.4243	0.1635	-2.59	0.0105	-0.4578	0.1609	-2.85	0.0051
$b_{3\text{-}C726}$	-0.1109	0.1302	-0.85	0.3954	-0.0796	0.1481	-0.54	0.5921	-0.1022	0.1459	-0.70	0.4849
$b_{3\text{-}C728}$	-0.3523	0.2728	-1.29	0.1987	-0.2481	0.3032	-0.82	0.4146	-0.2376	0.2979	-0.80	0.4264
$b_{3\text{-}C729}$	0.2715	0.3152	0.86	0.3904	0.2382	0.3548	0.67	0.5031	0.2908	0.3538	0.82	0.4125
$b_{3\text{-}C730}$	0.2754	0.1396	1.97	0.0505	0.4498	0.1593	2.82	0.0054	0.4076	0.1559	2.61	0.0099
$b_{3\text{-}C777}$	0.1656	0.2468	0.67	0.5035	0.268	0.2731	0.98	0.3281	0.2336	0.2677	0.87	0.3843

Table 3-5 continued

Random														
β_{ct}	0	.	.	.	β_{ct}	0	.	.	.	β_{ct}	0	.	.	.
$\sigma^2{}_{\beta_{cts0}}$	2.4719	0.137	18.04	<.0001	$\sigma^2{}_{\beta_{cts0}}$	2.4551	0.1527	16.08	<.0001	$\sigma^2{}_{\beta_{cts0}}$	2.1743	0.1503	14.47	<.0001
$\sigma^2{}_{\beta_{cts0}\beta_{cts1}}$	-1.1843	0.07223	-16.4	<.0001	$\sigma^2{}_{\beta_{cts0}\beta_{cts1}}$	-1.3129	0.09196	-14.28	<.0001	$\sigma^2{}_{\beta_{cts0}\beta_{cts1}}$	-1.1714	0.0878	-13.34	<.0001
$\sigma^2{}_{\beta_{cts1}}$	0.6248	0.04127	15.14	<.0001	$\sigma^2{}_{\beta_{cts1}}$	0.7899	0.06039	13.08	<.0001	$\sigma^2{}_{\beta_{cts1}}$	0.7297	0.05677	12.85	<.0001
	-	-	-	-		-	-	-	-	$\sigma^2{}_{\beta_{cts0}\beta_{cts2}}$	0.2029	0.05607	3.62	0.0003
	-	-	-	-		-	-	-	-	$\sigma^2{}_{\beta_{cts1}\beta_{cts2}}$	-0.1524	0.03511	-4.34	<.0001
	-	-	-	-		-	-	-	-	$\sigma^2{}_{\beta_{cts2}}$	0.04049	0.03732	1.08	0.1390
β_{ctsb}	0.2836	0.01879	15.09	<.0001	β_{ctsb}	0.2378	0.01694	14.04	<.0001	β_{ctsb}	0.2244	0.0152	14.76	<.0001
AR(1)	0.6733	0.02162	31.15	<.0001	AR(1)	0.487	0.03585	13.58	<.0001	AR(1)	0.4696	0.03559	13.2	<.0001
Fit Statistics														
-2 log-likelihood	11149.7					8007.2					7890.8			
AIC	11159.7					8017.2					7906.8			
R^2(fixed)	0.6200					0.5610					0.5801			
R^2(fixed+random)	0.8837					0.8969					0.9040			
E	0.0835					0.0105					0.0109			
|E|	0.5801					0.5729					0.5600			
E^2	0.5745					0.5603					0.5354			

Table 3-6 Parameter estimates and fit statistics of model [5] and [6] for branch radial growth for dataset V, $n_t = 69$

	5					6			
	n=1750					n=1734			
Parameters	**Estimate**	**SE**	**t-Value**	**p > t**		**Estimate**	**SE**	**t-Value**	**p > t**
Fixed									
c_0	-0.242	0.04997	-4.84	<.0001		-	-	-	-
c_1	0.4337	0.0151	28.73	<.0001		0.3592	0.01516	23.69	<.0001
c_2	-0.4279	0.01809	-23.66	<.0001		-	-	-	-
c_3	-	-	-	-		0.2456	0.03061	8.02	<.0001
$c_{4\text{-}C55}$	-0.0617	0.06041	-1.02	0.3129		-0.1305	0.03767	-3.46	0.0012
$c_{4\text{-}C700}$	0.1593	0.06385	2.50	0.0163		0.09342	0.04878	1.91	0.0619
$c_{4\text{-}C701}$	0.1014	0.0638	1.59	0.1189		0.06261	0.04726	1.32	0.1919
$c_{4\text{-}C702}$	-0.0274	0.06189	-0.44	0.6603		-0.1524	0.05026	-3.03	0.0040
$c_{4\text{-}C703}$	-0.0108	0.0616	-0.17	0.8623		-0.0677	0.0383	-1.77	0.0838
$c_{4\text{-}C705}$	-0.1079	0.06127	-1.76	0.0849		-0.1027	0.03757	-2.73	0.0089
$c_{4\text{-}C707}$	-0.0713	0.06107	-1.17	0.2495		-0.1076	0.03904	-2.76	0.0084
$c_{4\text{-}C708}$	-0.0292	0.06305	-0.46	0.6454		-0.0847	0.04636	-1.83	0.0745
$c_{4\text{-}C709}$	-0.084	0.06213	-1.35	0.183		-0.0574	0.03962	-1.45	0.1541
$c_{4\text{-}C710}$	-0.0329	0.06069	-0.54	0.590		-0.1383	0.04637	-2.98	0.0046
$c_{4\text{-}C712}$	-0.1544	0.06153	-2.51	0.0158		-0.2025	0.03933	-5.15	<.0001
$c_{4\text{-}C713}$	-0.0227	0.06073	-0.37	0.7098		-0.1327	0.04468	-2.97	0.0048
$c_{4\text{-}C714}$	-0.0982	0.06138	-1.60	0.1166		-0.131	0.03776	-3.47	0.0012
$c_{4\text{-}C715}$	-0.0223	0.05418	-0.41	0.6831		-0.077	0.03187	-2.42	0.0198
$c_{4\text{-}C716}$	-0.0043	0.06168	-0.07	0.945		-0.0384	0.04126	-0.93	0.3574
$c_{4\text{-}C717}$	0.0971	0.06269	1.55	0.1284		0.08791	0.04556	1.93	0.0600
$c_{4\text{-}C718}$	-0.0021	0.06362	-0.03	0.9741		0.04094	0.04073	1.01	0.3202
$c_{4\text{-}C719}$	0.1272	0.07046	1.81	0.0776		0.1273	0.05548	2.29	0.0265
$c_{4\text{-}C720}$	-0.0682	0.07031	-0.97	0.3374		-0.1295	0.0585	-2.21	0.0319
$c_{4\text{-}C726}$	0.01952	0.06256	0.31	0.7565		-0.0056	0.03943	-0.14	0.8871
$c_{4\text{-}C728}$	0.1703	0.08633	1.97	0.0547		0.1715	0.06939	2.47	0.0173
$c_{4\text{-}C729}$	0.04384	0.08843	0.50	0.6225		-0.0205	0.0676	-0.3	0.7626
$c_{4\text{-}C730}$	0.06204	0.0618	1.00	0.3208		-0.0442	0.04481	-0.99	0.3288
$c_{4\text{-}C130}$	0	.	.	.		0.03228	0.04601	0.7	0.4866
Random									
γ_{ct}	0.00337	0.00118	2.86	0.0021	γ_{ct}	0	.	.	.
$\sigma^2_{\gamma_{cts0}}$	0.02853	0.00949	3.01	0.0013	$\sigma^2_{\gamma_{cts1}}$	0.00692	0.00276	2.5	0.0061
$\sigma^2_{\gamma_{cts0}\gamma_{cts1}}$	-0.0243	0.00695	-3.49	0.0005	$\sigma^2_{\gamma_{cts3}}$	0.07456	0.01235	6.04	<.0001
$\sigma^2_{\gamma_{cts1}}$	0.02231	0.00581	3.84	<.0001		-	-	-	-
$\sigma^2_{\gamma_{cts0}\gamma_{cts2}}$	0.01921	0.009	2.14	0.0327		-	-	-	-
$\sigma^2_{\gamma_{cts1}\gamma_{cts2}}$	-0.0094	0.0059	-1.6	0.1101		-	-	-	-
$\sigma^2_{\gamma_{cts2}}$	0.02703	0.01091	2.48	0.0066		-	-	-	-
γ_{ctsb}	0.04079	0.00167	24.38	<.0001	γ_{ctsb}	0.04466	0.00188	23.81	<.0001
AR(1)	-	-	-	-		-	-	-	-
Fit statistics									
-2 log-likelihood	-276					92.3			
AIC	-260					98.3			
R^2(fixed)	0.4579					0.2744			
R^2(fixed+random)	0.5953					0.5712			
E	0.0505					0.0482			
|E|	0.2695					0.3187			
E^2	0.1484					0.1974			

Table 3-7 Parameter estimates and fit statistics of model [7] and [8] for branch angle for dataset IV, n_t =172

	7					8			
	n=5929					n=5929			
Parameters	Estimate	SE	t-Value	p > t		Estimate	SE	t-Value	p > t
Fixed									
d_0	3.8261	0.03087	123.95	<.0001		4.0083	0.02886	138.9	<.0001
$d_{1\ BD}$	-	-	-	-		-0.08539	0.00271	-31.51	<.0001
$d_{2\ B\_RDINC}$	0.6064	0.02159	28.09	<.0001		0.6951	0.01911	36.38	<.0001
$d_{3\text{-}C55}$	-0.0941	0.0376	-2.50	0.0134		-0.1157	0.03493	-3.31	0.0012
$d_{3\text{-}C700}$	-0.067	0.04915	-1.36	0.1750		-0.08173	0.04589	-1.78	0.0770
$d_{3\text{-}C701}$	-0.1169	0.0437	-2.68	0.0083		-0.1221	0.04068	-3.00	0.0032
$d_{3\text{-}C702}$	-0.2658	0.03983	-6.67	<.0001		-0.2861	0.03705	-7.72	<.0001
$d_{3\text{-}C703}$	-0.0205	0.04078	-0.50	0.6154		-0.02778	0.03791	-0.73	0.4648
$d_{3\text{-}C705}$	-0.0658	0.04003	-1.64	0.1023		-0.06608	0.03743	-1.77	0.0795
$d_{3\text{-}C707}$	-0.1469	0.03599	-4.08	<.0001		-0.1577	0.03349	-4.71	<.0001
$d_{3\text{-}C708}$	-0.0944	0.03469	-2.72	0.0073		-0.09517	0.03239	-2.94	0.0038
$d_{3\text{-}C709}$	-0.0604	0.04265	-1.42	0.159		-0.094	0.03983	-2.36	0.0196
$d_{3\text{-}C710}$	-0.2308	0.03625	-6.37	<.0001		-0.2313	0.03381	-6.84	<.0001
$d_{3\text{-}C712}$	-0.0701	0.03992	-1.76	0.0811		-0.06677	0.03707	-1.80	0.0737
$d_{3\text{-}C713}$	-0.3229	0.03776	-8.55	<.0001		-0.3224	0.03517	-9.17	<.0001
$d_{3\text{-}C714}$	-0.0993	0.03792	-2.62	0.0098		-0.08245	0.03557	-2.32	0.0218
$d_{3\text{-}C715}$	-0.2252	0.03254	-6.92	<.0001		-0.2152	0.03036	-7.09	<.0001
$d_{3\text{-}C716}$	-0.0993	0.04257	-2.33	0.0210		-0.09848	0.03972	-2.48	0.0143
$d_{3\text{-}C717}$	-0.0762	0.05362	-1.42	0.1572		-0.08544	0.04972	-1.72	0.0878
$d_{3\text{-}C718}$	0.00592	0.04465	0.13	0.8946		0.03615	0.04214	0.86	0.3924
$d_{3\text{-}C719}$	0.00496	0.06389	0.08	0.9383		-0.02223	0.05904	-0.38	0.7071
$d_{3\text{-}C720}$	-0.1839	0.04389	-4.19	<.0001		-0.1715	0.04095	-4.19	<.0001
$d_{3\text{-}C726}$	-0.0166	0.03989	-0.42	0.6775		-0.01432	0.03703	-0.39	0.6995
$d_{3\text{-}C728}$	-0.0379	0.08468	-0.45	0.6555		-0.0338	0.07874	-0.43	0.6684
$d_{3\text{-}C729}$	0.08951	0.08997	0.99	0.3214		0.05749	0.08104	0.71	0.4792
$d_{3\text{-}C730}$	-0.1131	0.04383	-2.58	0.0108		-0.1626	0.04062	-4.00	<.0001
$d_{3\text{-}C130}$	-0.0381	0.07827	-0.49	0.6273		-0.02563	0.0734	-0.35	0.7274
$d_{3\text{-}C55}$	0	.	.	.		0	.	.	.
Random									
δ_{ct}	0.00228	0.00073	3.13	0.0009	δ_{ct}	0.00243	0.00064	3.83	<.0001
δ_{cts}	0.00467	0.00132	3.55	0.0002	$\sigma^2{}_{\delta_{cts1}}$	0.001606	0.00029	5.60	<.0001
	-	-	-	-	$\sigma^2{}_{\delta_{cts1}\delta_{cts2}}$	-0.00492	0.00116	-4.23	<.0001
	-	-	-	-	$\sigma^2{}_{\delta_{cts2}}$	0.01724	0.0051	3.38	0.0004
δ_{ctsb}	0.06663	0.00167	40.03	<.0001	δ_{ctsb}	0.05235	0.00138	37.98	<.0001
AR(1)	0.238	0.01885	12.62	<.0001	AR(1)	0.2722	0.01906	14.28	<.0001
Fit statistics									
log-likelihood	907.3				log-likelihood	-414.7			
AIC	915.3				AIC	-402.7			
R^2(fixed)	0.2714				R^2(fixed)	0.4209			
R^2(fixed+random)	0.3805				R^2(fixed+random)	0.5264			
E	2.3355				E	1.7555			
|E|	12.2057				|E|	10.6495			
E^2	232.6906				E^2	184.8070			

Table 3-8 Parameter estimates and fit statistics of model 9 for branch length for dataset VI, n_t= 244

Parameters	n_b=794 Estimates	SE	t-Value	p > t
Fixed				
$e_{0\ int}$	4.6875	0.03544	132.28	<.0001
$e_{1\ LnBD}$	0.7970	0.01371	58.16	<.0001
$e_{4\text{-}C55}$	-0.0343	0.03965	-0.86	0.3883
$e_{4\text{-}C700}$	-0.0474	0.04812	-0.99	0.3253
$e_{4\text{-}C701}$	0.0079	0.04529	0.17	0.8617
$e_{4\text{-}C702}$	-0.0155	0.03669	-0.42	0.6722
$e_{4\text{-}C703}$	-0.0152	0.03952	-0.38	0.7017
$e_{4\text{-}C705}$	0.01425	0.03865	0.37	0.7128
$e_{4\text{-}C707}$	0.00698	0.04479	0.16	0.8764
$e_{4\text{-}C708}$	0.08649	0.03626	2.39	0.0179
$e_{4\text{-}C709}$	-0.0159	0.05142	-0.31	0.7572
$e_{4\text{-}C710}$	0.08334	0.0379	2.20	0.0289
$e_{4\text{-}C712}$	0.09244	0.03663	2.52	0.0123
$e_{4\text{-}C713}$	-0.0262	0.03578	-0.73	0.4644
$e_{4\text{-}C714}$	0.1030	0.0370	2.78	0.0058
$e_{4\text{-}C715}$	-0.0015	0.03329	-0.05	0.9632
$e_{4\text{-}C716}$	0.02117	0.03887	0.54	0.5867
$e_{4\text{-}C717}$	0.03171	0.04131	0.77	0.4435
$e_{4\text{-}C718}$	-0.0288	0.04173	-0.69	0.4908
$e_{4\text{-}C719}$	0.07791	0.04725	1.65	0.1006
$e_{4\text{-}C720}$	0.05405	0.04366	1.24	0.2171
$e_{4\text{-}C726}$	-0.0697	0.03809	-1.83	0.0685
$e_{4\text{-}C728}$	-0.0584	0.0529	-1.10	0.2707
$e_{4\text{-}C729}$	-0.2266	0.04566	-4.96	<.0001
$e_{4\text{-}C730}$	-0.0527	0.0406	-1.30	0.1957
$e_{4\text{-}C777}$	-0.1510	0.06201	-2.43	0.0157
$e_{4\text{-}C130}$	0	.	.	.
Random				
${\sigma^2}_{\varepsilon_{cb0}}$	0.04217	0.00853	4.95	<.0001
${\sigma^2}_{\varepsilon_{cb0}\varepsilon_{cb1}}$	-0.0236	0.0052	-4.54	<.0001
${\sigma^2}_{\varepsilon_{cb1}}$	0.01333	0.00333	4.01	<.0001
ε_{cb}	0.01435	0.00092	15.53	<.0001
Fit statistics				
log-likelihood	-828.10			
AIC	-820.10			
R^2(fixed)	0.8873			
R^2(fixed+random)	0.9106			
E	2.3250			
|E|	32.7858			
E^2	1800.76			

Table 3-9 Parameter estimates and fit statistics of model 10 for branch frequency for dataset I, n_t= 168

Parameters	Estimates	SE	t Value	Pr > |t|
$f_{0\ int}$	2.563	0.03939	65.07	<.0001
$f_{4\text{-}C55}$	0.1067	0.05413	1.97	0.0507
$f_{4\text{-}C700}$	0.005875	0.06822	0.09	0.9315
$f_{4\text{-}C701}$	-0.09551	0.06016	-1.59	0.1146
$f_{4\text{-}C702}$	0.2596	0.05766	4.50	<.0001
$f_{4\text{-}C703}$	0.2147	0.05766	3.72	0.0003
$f_{4\text{-}C705}$	0.05558	0.05766	0.96	0.3367
$f_{4\text{-}C707}$	0.1500	0.05085	2.95	0.0037
$f_{4\text{-}C708}$	0.3555	0.05284	6.73	<.0001
$f_{4\text{-}C709}$	0.05788	0.06351	0.91	0.3637
$f_{4\text{-}C710}$	0.05209	0.05284	0.99	0.326
$f_{4\text{-}C712}$	-0.00019	0.0557	0	0.9973
$f_{4\text{-}C713}$	0.1149	0.05413	2.12	0.0356
$f_{4\text{-}C714}$	0.1724	0.05413	3.18	0.0018
$f_{4\text{-}C715}$	0.2321	0.04695	4.94	<.0001
$f_{4\text{-}C716}$	0.1597	0.06016	2.65	0.0088
$f_{4\text{-}C717}$	0.006561	0.07542	0.09	0.9308
$f_{4\text{-}C718}$	0.02471	0.06351	0.39	0.6978
$f_{4\text{-}C719}$	-0.07801	0.08807	-0.89	0.3773
$f_{4\text{-}C720}$	-0.03564	0.06016	-0.59	0.5545
$f_{4\text{-}C726}$	-0.3842	0.0557	-6.90	<.0001
$f_{4\text{-}C728}$	0.1119	0.1182	0.95	0.3451
$f_{4\text{-}C729}$	-0.03285	0.1182	-0.28	0.7814
$f_{4\text{-}C730}$	0.1046	0.06351	1.65	0.1019
$f_{4\text{-}C777}$	0.2085	0.1182	1.76	0.0798
$f_{4\text{-}C130}$	0	.	.	.
Fit statistics				
τ (residual)	0.01241	0.00147	8.46	<.0001
R^2	0.6902			

Table 3-10 Parameter estimates and fit statistics of model 11 for branch basal area per meter of stem for dataset I, n_t= 168

Parameters	Estimate	SE	t Value	Pr > |t|
$g_{0\ int}$	2.8084	0.1965	14.29	<.0001
$g_{1\ DBH}$	0.1014	0.01236	8.20	<.0001
$g_{4\text{-}C55}$	-0.2541	0.06907	-3.68	0.0003
$g_{4\text{-}C700}$	-0.1353	0.0894	-1.51	0.1323
$g_{4\text{-}C701}$	-0.0087	0.08106	-0.11	0.9143
$g_{4\text{-}C702}$	-0.1738	0.07274	-2.39	0.0182
$g_{4\text{-}C703}$	0.06805	0.07296	0.93	0.3526
$g_{4\text{-}C705}$	0.0647	0.07596	0.85	0.3958
$g_{4\text{-}C707}$	-0.1373	0.06581	-2.09	0.0388
$g_{4\text{-}C708}$	-0.0468	0.06708	-0.70	0.4866
$g_{4\text{-}C709}$	-0.183	0.08305	-2.20	0.0292
$g_{4\text{-}C710}$	0.01454	0.06734	0.22	0.8293
$g_{4\text{-}C712}$	-0.0476	0.07022	-0.68	0.4986
$g_{4\text{-}C713}$	0.1103	0.06836	1.61	0.1088
$g_{4\text{-}C714}$	-0.1892	0.06958	-2.72	0.0074
$g_{4\text{-}C715}$	-0.0606	0.06098	-0.99	0.3222
$g_{4\text{-}C716}$	-0.0818	0.07674	-1.07	0.288
$g_{4\text{-}C717}$	0.1551	0.09515	1.63	0.1053
$g_{4\text{-}C718}$	-0.1512	0.07944	-1.90	0.0591
$g_{4\text{-}C719}$	0.04129	0.1125	0.37	0.7142
$g_{4\text{-}C720}$	-0.0513	0.07709	-0.66	0.5072
$g_{4\text{-}C726}$	0.1439	0.07455	1.93	0.0555
$g_{4\text{-}C728}$	-0.0148	0.1454	-0.10	0.9191
$g_{4\text{-}C729}$	0.198	0.1599	1.24	0.2174
$g_{4\text{-}C730}$	-0.039	0.08117	-0.48	0.6319
$g_{4\text{-}C777}$	0.1966	0.1450	1.36	0.1773
$g_{4\text{-}C130}$	0	.	.	.
Fit statistics				
ω (residual)	0.0184	0.00219	8.40	<.0001
R^2	0.6157			

3.7 Figures

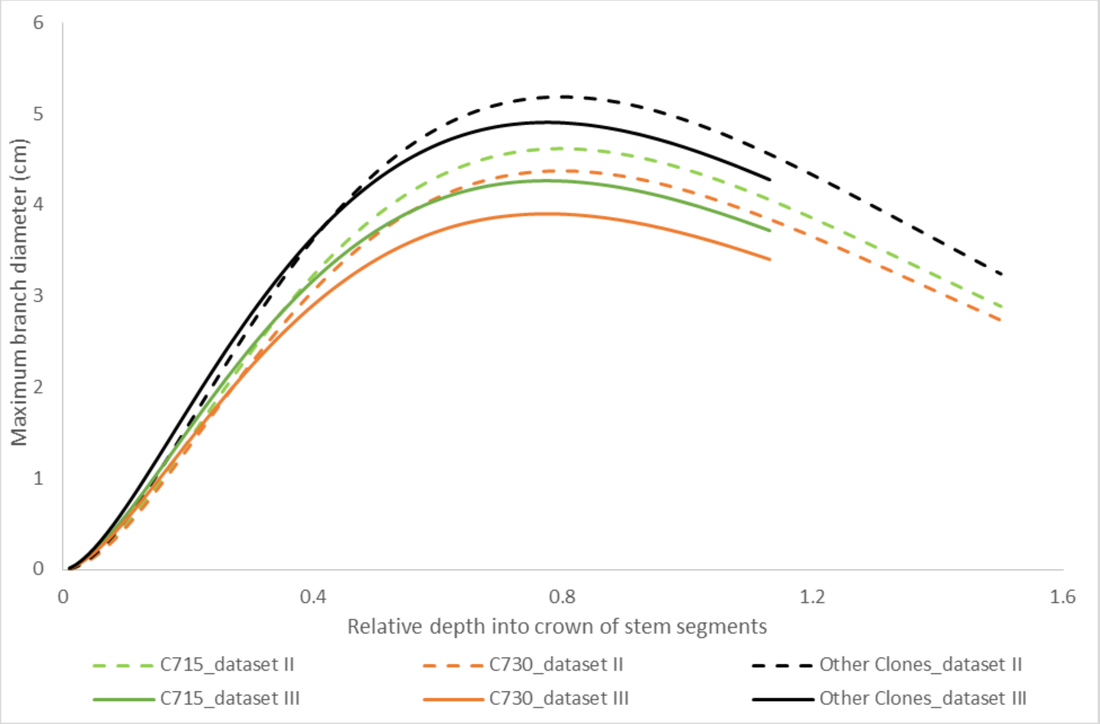

Figure 3-1 Predicted maximum branch diameter in a one-meter stem segment by model [1] for both pruned and unpruned branches (dataset II, dashed lines) and unpruned branches only (dataset III, solid lines), respectively. DBH was held constant at 14.52 cm. 0= crown apex, 1 = crown bottom, >1 = below crown, all referred to the segment center, not the actual branch. Although all unpruned branches were not lower than crown base, the relative depth of the segment center can be lower than crown base.

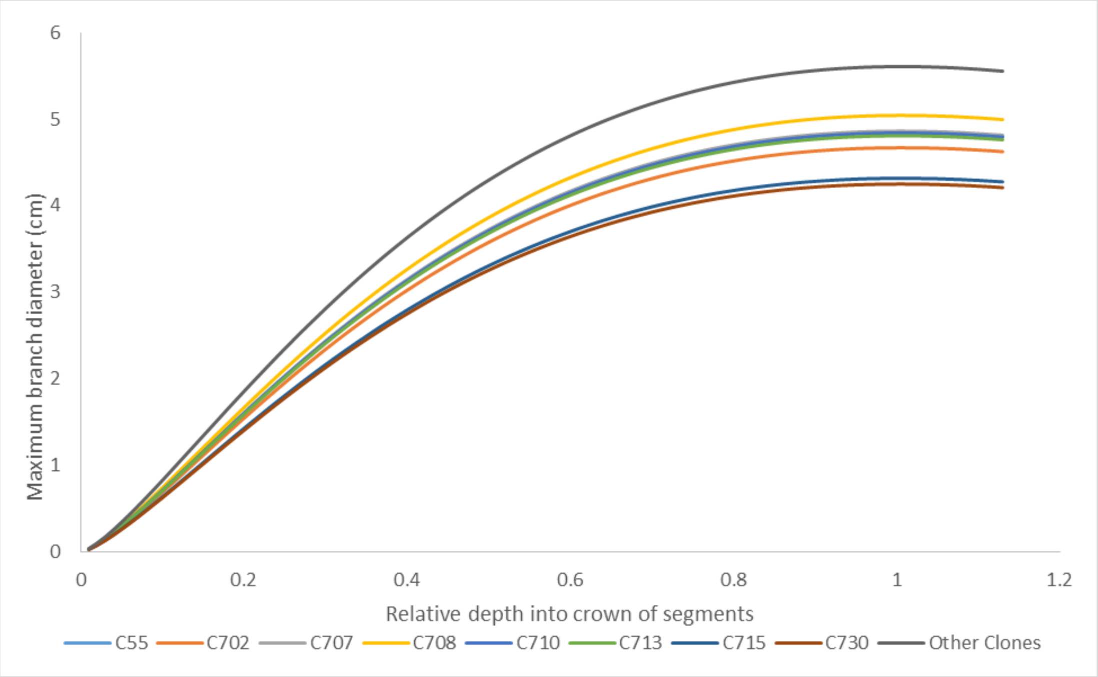

Figure 3-2 Predicted maximum branch diameter in a one-meter stem segment by model [2] for unpruned branches only, dataset III. DBH was held constant at 14.52 cm, and angle = 54.92°, which was the average angle of the 1st branch in a segment. 0= crown apex, 1 = crown bottom, >1 = below crown, all referred to the segment center, not the actual branch. Although all unpruned branches were not lower than crown base, the relative depth of the segment center can be lower than crown base.

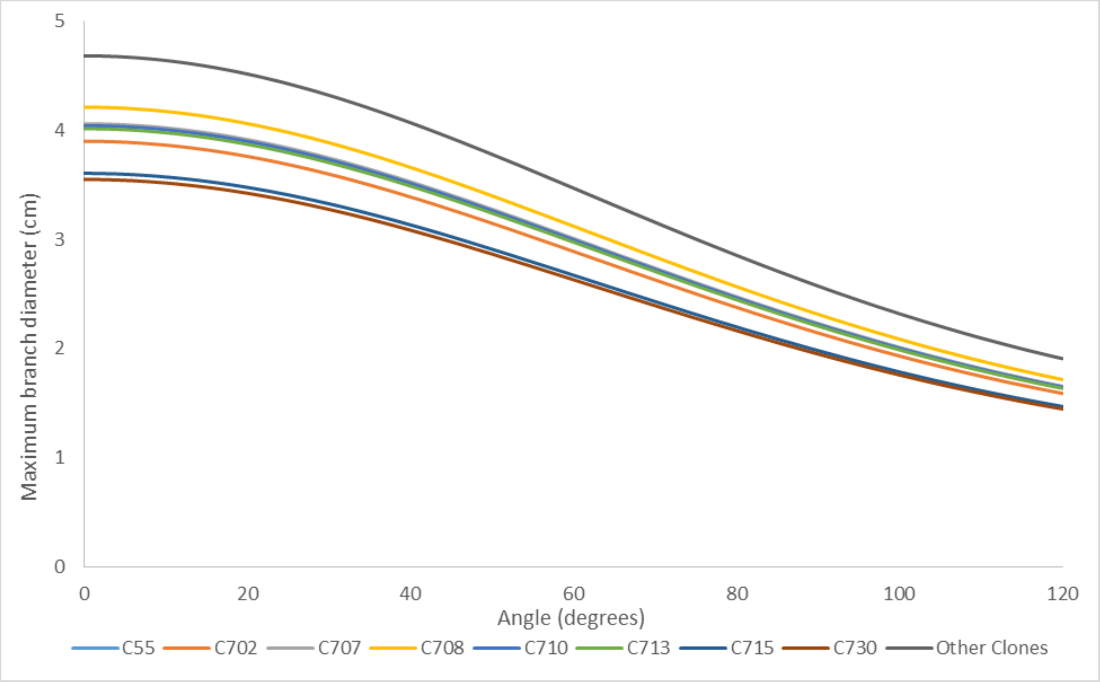

Figure 3-3 Predicted maximum branch diameter in a one-meter stem segment by model [2] for unpruned branches only, dataset III. DBH was held constant at 14.52 cm, and C_RDINC = 0.4.

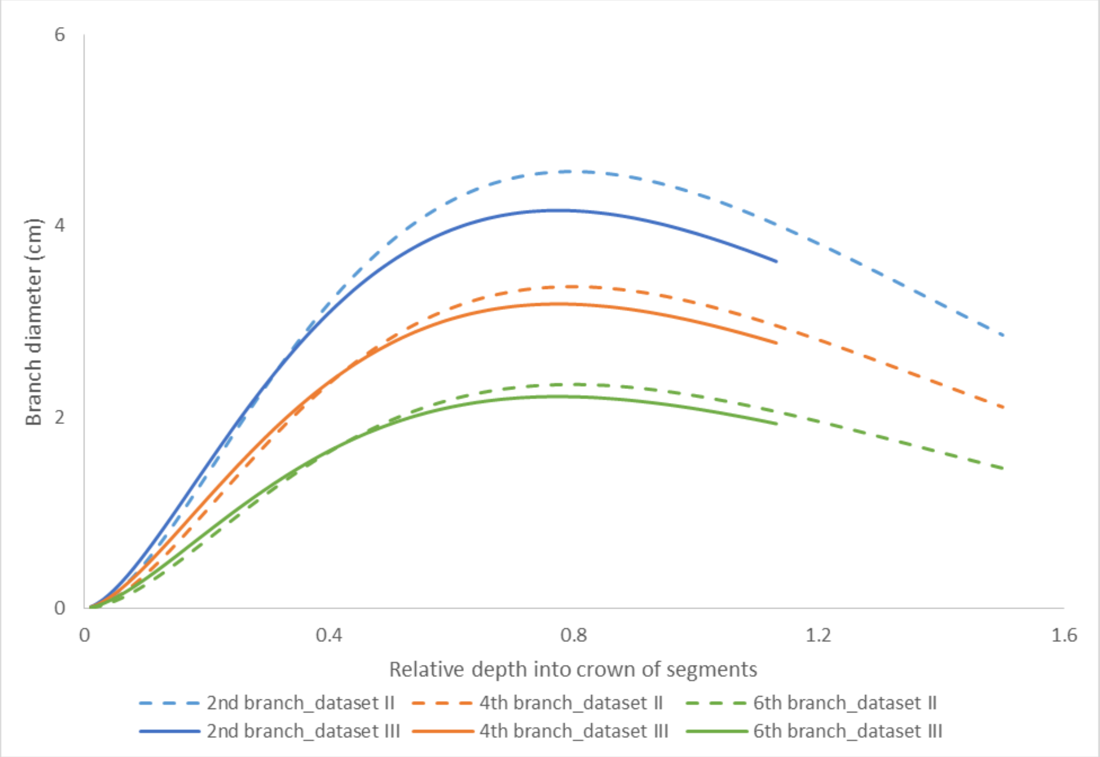

Figure 3-4 Predicted diameter of the 2nd, 4th, and 6th branch in a one-meter stem segment by model [3] for both pruned and unpruned branches (dataset II, dashed lines) and unpruned branches only (dataset III, solid lines), respectively. DBH was held constant at 14.52 cm. 0= crown apex, 1 = crown bottom, >1 = below crown, all referred to the segment center, not the actual branch. Although all unpruned branches were not lower than crown base, the relative depth of the segment center can be lower than crown base. Clonal difference was not counted in this graph due to limited space.

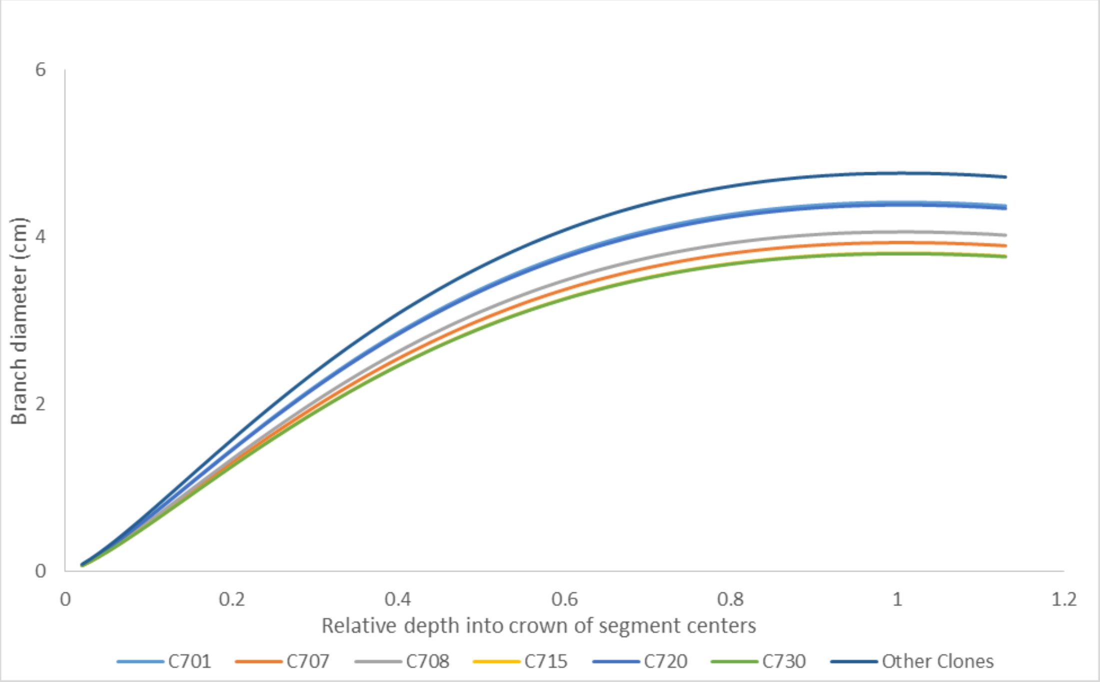

Figure 3-5 Predicted branch diameter of the 2nd branch in a one-meter stem segment by model [4] for unpruned branches only, dataset III. Branch angle for the 2nd branch was set at 58.38°, which was the average angle of the 2nd branch in a segment. 0= crown apex, 1 = crown bottom, all referred to the segment center, not the actual branch. Although all unpruned branches were not lower than crown base, the relative depth of the segment center can be lower than crown base. Maximum branch diameter in a segment used to calculate the 2nd branch diameter in the same segment was predicted from model [2] (DBH was held constant at 14.52 cm, and angle for thickest branch was set at 54.92°, which was the average angle of the thickest branch in a segment).

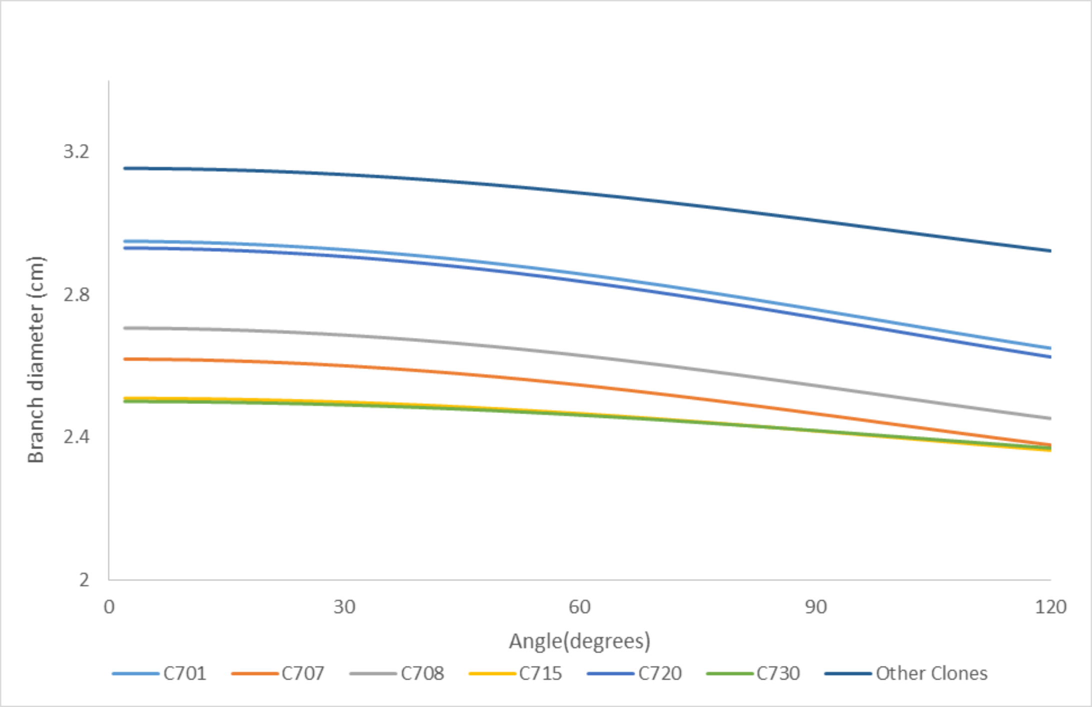

Figure 3-6 Predicted branch diameter of the 2^{nd} branch in a one-meter stem segment by model [4] for unpruned branches only, dataset III. C_RDINC was held constant at 0.4. Maximum branch diameter in a segment used to calculate the 2^{nd} branch diameter in the same segment was predicted from model [2] (DBH was held constant at 14.52 cm, and angle for thickest branch was set at 54.92°, which was the average angle of the thickest branch in a segment).

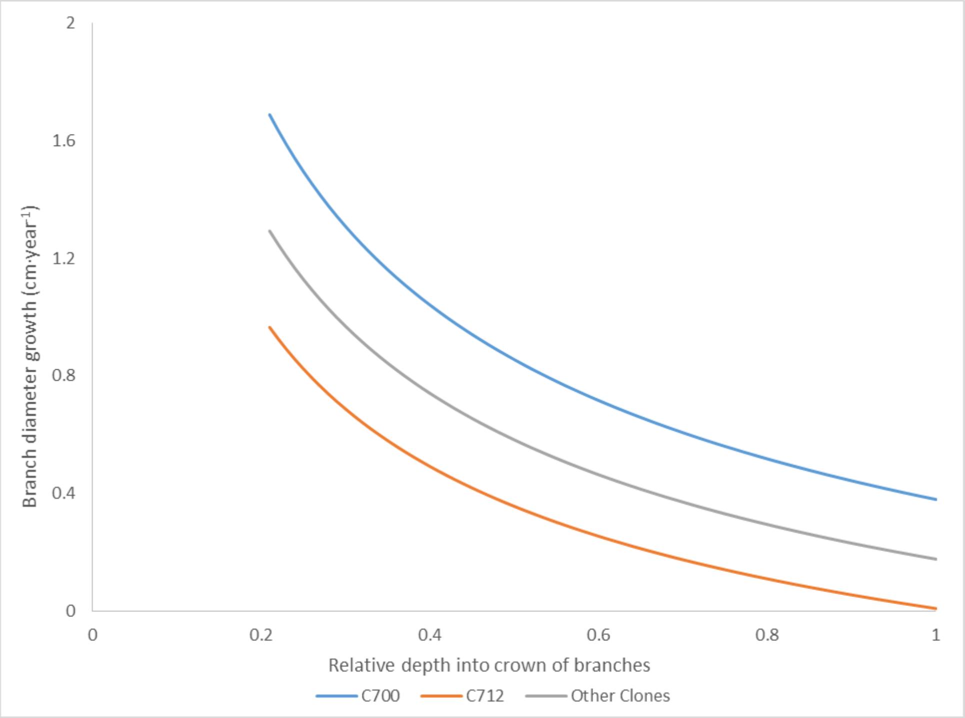

Figure 3-7 Predicted branch radial growth in one year by model [5] for unpruned branches only (dataset III). Initial branch diameter was held constant at 2.54 cm.

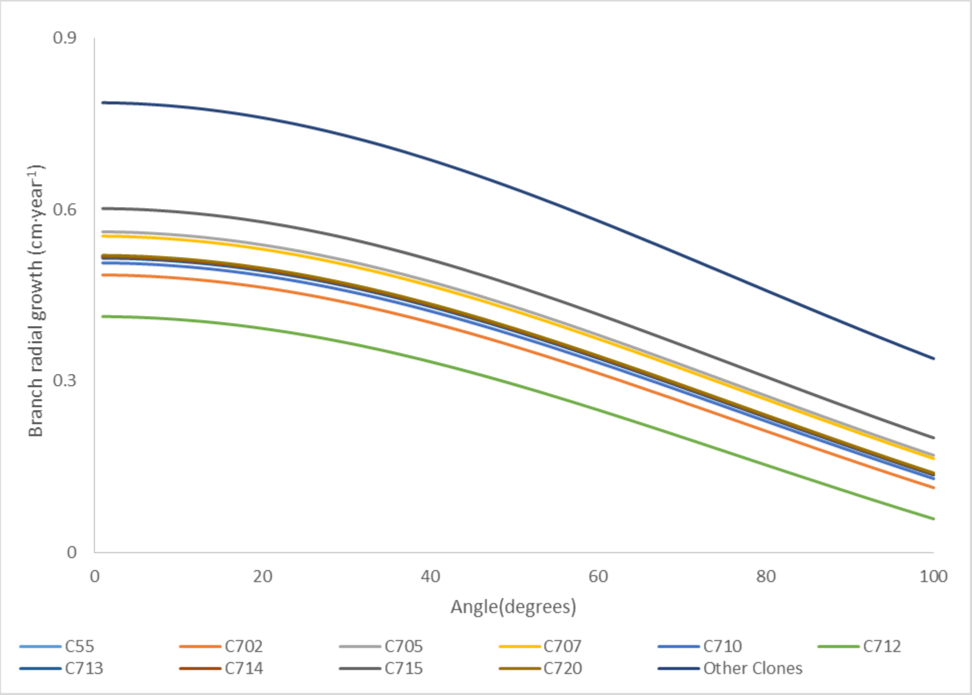

Figure 3-8 Predicted branch radial growth in one year by model [6] for unpruned branches only (dataset III). Initial branch diameter was held constant at 2.54 cm.

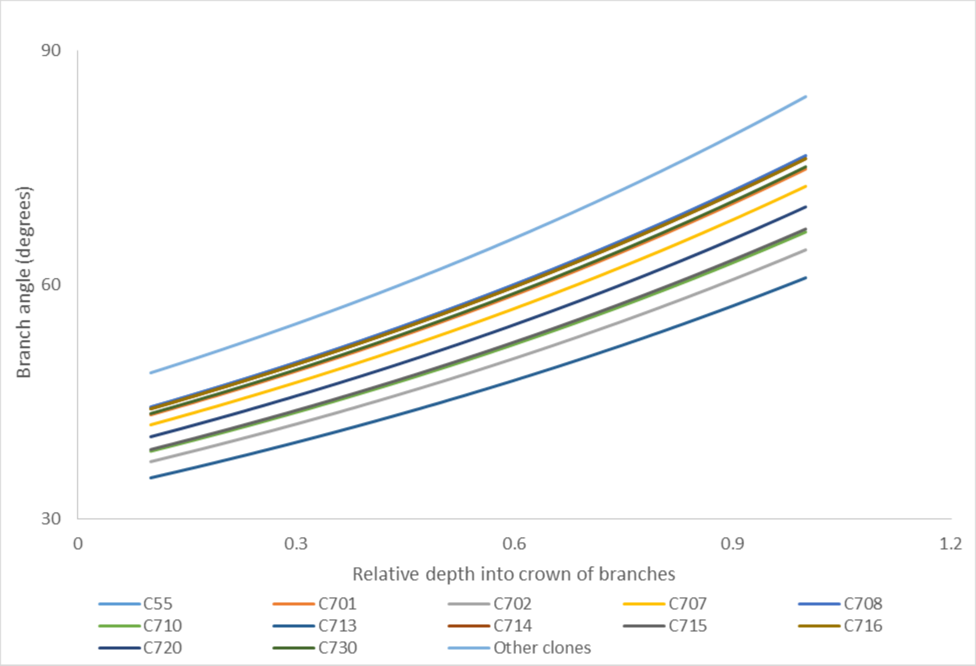

Figure 3-9 Predicted branch angle by model [7] (dataset IV). Branch diameter was held constant at 2.54 cm.

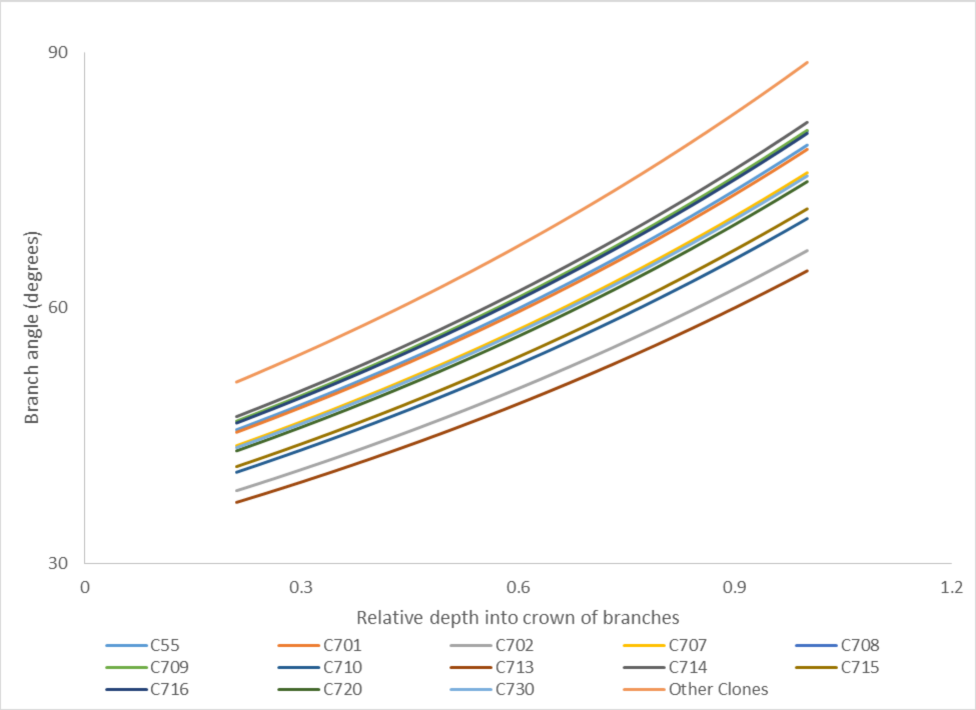

Figure 3-10 Predicted branch angle by model [8] (dataset IV) based on relative depth of branches into crown.

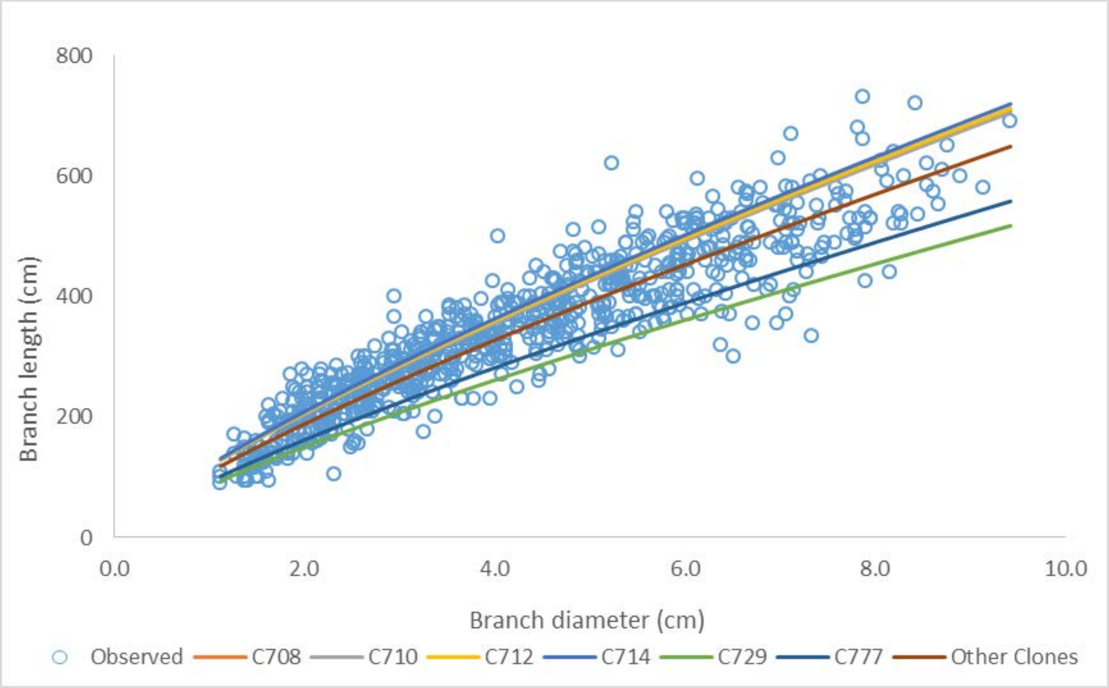

Figure 3-11 Predicted branch length by model [9] based on branch diameter.

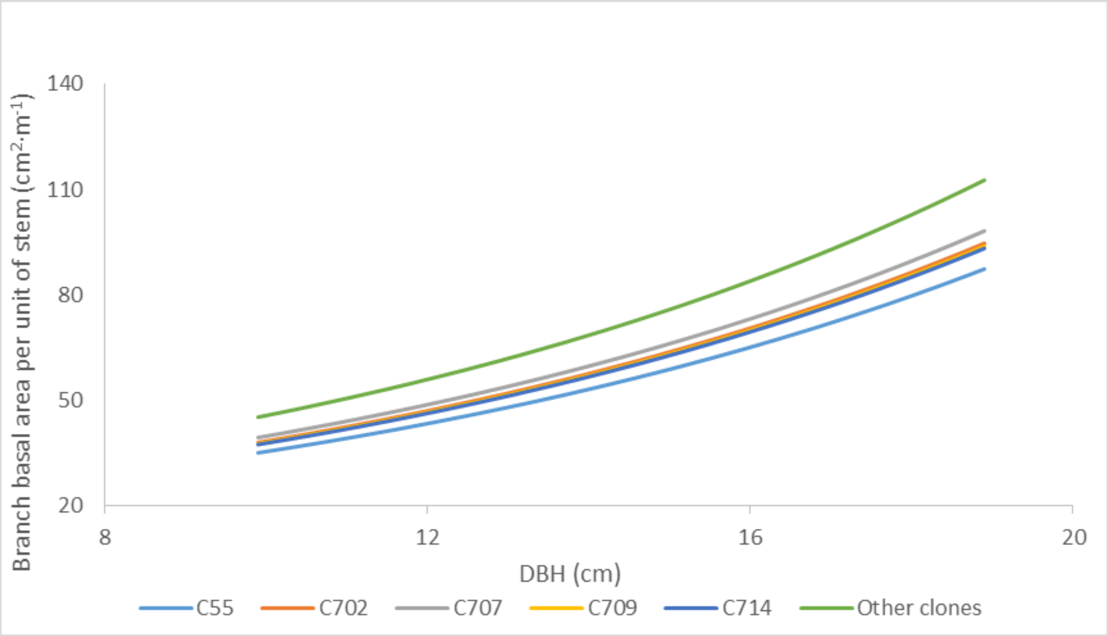

Figure 3-12 Predicted branch basal area per meter of stem based on DBH.

CHAPTER 4. GENETIC VARIATION, REPEATABILITY, AND CORRELATIONS OF VARIOUS TRAITS IN 25 PLANTATION-GROWN BLACK WALNUT CLONES IN INDIANA, USA

4.1 Introduction

Black walnut (*Juglans nigra* L.), native to North America, is a fine hardwood species renowned for its highly valuable timber. Its wood is mainly used for veneer, flooring, furniture, and gunstocks. Although it is mostly grown in natural forests, black walnut plantations have been established in the United States (about 13,800 acres in 2004) in the pursuit of high economic return (Shifley, 2004). Most plantations are seedling plantations; however, some plantations contain grafted and genetically improved black walnut clones. One of the advantages of clonal forestry over seedling plantations is the potential to maximize genetic gain through selection by capturing both non-additive and additive genetic effects (Libby and Rauter, 1984). Clonal forestry has achieved success with tree species such as willow (Tharakan et al., 2005) and loblolly pine (*Pinus taeda* L.) (Stovall et al., 2011) in the United States, but clonal production of black walnut is still in its infancy.

Ideotype breeding, which has been applied to many agronomic crops, some fruit tree crops, and a few conifer species, may be a key to the success of black walnut clonal forestry. Ideotype was proposed as a biological model which has predictable performance and behavior in a defined environment (Donald, 1968). To implement ideotype breeding, numerous traits of interest, including but not limited to traits related to phenology, morphology, and physiology, need to be investigated. Morphology, phenology, physiology, and the interaction between them control the dynamics of plant structure and productivity (Ford, 1992). Thus, to define timber ideotypes or select elite genotypes for tree improvement of a species, it is important to examine the amount of variation in traits that affect yield and quality, and to estimate the heritability and correlations among these traits of interest (Campbell, 1961; Weber et al., 1985; Dunlap and Stettler, 1998). If a trait is proven to be under strong genetic control, then it may be improved via clonal selection and hybridization (Tharakan et al., 2005). In addition, a weak correlation between two traits means they may be genetically independent and may be selected simultaneously (Tharakan et al., 2005). Overall, the estimation of genetic parameters helps improve the efficiency of genotype evaluation and selection in plan breeding programs (Hansche et al., 1972a, 1972b).

The black walnut clones in this study were obtained from both wild populations and breeding programs, so they offered an excellent opportunity for a further selection. It is advantageous to compare different clones growing in one site because the environment and management are homogeneous. For instance, comparisons of crown form traits of different genotypes are only meaningful when they are growing in the same site under the same management, otherwise their form may be significantly altered by differences in height growth (Cannell, 1974).

The objectives of this study were to: 1) assess the amount of variation and clonal repeatability of multiple traits in a black walnut population of 25 clones; 2) investigate the correlations among a list of potential indicator traits (phenological, morphological, and physiological, etc.) and growth and quality traits so that traits correlated to timber production may be identified.

4.2 Materials and methods

4.2.1 Materials

This clone test included 212 trees that belonged to 25 grafted black walnut clones, either selected from wild populations or genetically improved, and some of which were patented (Table 4-1). Some trees were excluded from some analyses because of wind damage that occurred in summer 2009, 2010 and 2011.

4.2.2 Data collection

4.2.2.1 Tree growth

Diameter at breast height (DBH, 1.37m) tree height, and crown radius were measured at the end of each season from 2008 to 2011. DBH of each tree each time was measured twice: North-South and West-East and the average was used for analysis, while crown radius was the average of the four cardinal directions of each tree.

4.2.2.2 Fruit production

The number of fruits each tree produced was tallied visually with two independent observers in October in 2009, 2010, and 2011. In October 2011, three to five trees were randomly selected from each clone. Up to 30 fruits were harvested from each tree, and fruits from the same clone were mixed. Fruits were collected directly from the tree to avoid taking them from neighboring trees or clones. Then 15 to 17 fruits were randomly chosen from each clone for size and weight measurement. After width, length, and height of these fruits were measured, husks were separated from seeds. Both husks and seeds were dried in an oven at 100 °C for three days. Thus, seed dry weight and husk dry weight were determined, and the summed value was the total dry weight of fruit. Fruit size and seed size was calculated using the ellipsoid volume equation, which is V_f or V_s = $4/3\pi abc$, where a, b, and c were the radii in three dimensions of a fruit or seed.

4.2.2.3 Crown architecture

Branch diameter was measured for each branch at its base, branch insertion angle was measured for branches that were equal or larger than 1.27 cm throughout the stem, and those that were smaller than 1.27 cm but still vigorous in upper crown. Although a tree has multiple branches, it is preferred to have one summarized value per trait per tree to quantitatively describe branch attributes (Campbell, 1961). The average insertion angle (AvgAng) and average diameter (AvgBD) of branches of each tree were calculated for analysis. Due to the great contribution of large branches to tree growth, the thickest branch in each one – meter stem segment was singled out, and the average insertion angle (AvgAngMax) and average diameter (AvgBDMax) of these branches of every tree were summarized as well for variation and correlation analysis.

Branch frequency was determined as the number of branches (including pruning scars) per meter of stem, while branch basal area per meter of stem was the accumulated branch basal area per meter of stem. Stem volume was estimated by using the paraboloid equation: $V_{st} = 1/2 * A_b * Ht$ (Husch et al., 2002), where A_b is the cross sectional area at breast height (1.37 m) including bark, and Ht is tree height. Individual branch volume was estimated using the same equation where A_b was the cross sectional area at the base of the branch, and branch length was estimated by the allometric equations developed in chapter 3. Branch volume was summed from each branch to obtain total branch volume of each tree. Branch volume and the percentage of stemwood volume out of aboveground wood volume (stem and branch) were estimated.

Stem straightness, as one important aspect of timber quality, was rated by HTIRC field staff in 2009. The average score of the two raters' was used for data analysis. The standard for stem form evaluation follows Beineke et al (1991) but with a reverse rubric: a rating of 5 indicated the most straight stem, while 1 was the most crooked stem. A similar stem form rubric was published by Hai et al. (2008).

4.2.2.4 Physiology

Specific leaf area (SLA), individual leaf area (ILA), and leaf mass (ILM) were determined in July 2010. Five leaves were randomly selected from lower crown and mid-upper crown of five random trees of each clone, respectively. Collected leaves were stored in a 4°C cooler, then scanned by an Epson scanner in the lab and processed via WinFolia^{TM} (Régent Instruments, Québec, Canada) to determine ILA. Leaves were then oven dried at 65 °C for 72 hours and ILM was weighed. SLA was determined as the ratio of ILA to

ILM. Leaves used for SLA determination were ground and two 2 mg leaf powder was randomly collected for foliar nitrogen and carbon concentration analysis using LECO® Elemental Analysis System; the average was used for data analysis.

Net photosynthetic rate was monitored at the end of July and August 2011. Twelve clones (C55, C130, C701, C708, C710, C712, C714, C715, C717, C720, C726, and C729) that covered the full size range of all clones and also represented a range of crown densities were selected for photosynthesis measurement. Three trees were randomly chosen from each clone, making 36 trees in total. Because the number of trees that can be measured in each day was limited due to the traveling time from one tree to the next in a large plantation and the time for positioning the lift and the LiCOR – 6400, we took three days to measure all the sample trees each month. In each day, we measured one tree from each clone (12 trees in a day), and the sequence of clones in a day was randomized. Three fully expanded and undamaged sun-lit leaves in upper crown of each tree were randomly chosen and their net photosynthesis rate was recorded between 10 AM and 2 PM.

4.2.2.5 Phenology

Foliation dates, the time of the initiation of dormancy break, were monitored every two or three days in April and May in 2009, 2010, and 2011. Leaf flush was rated as five stages: dormant, bud swell, green tip, leaf burst, and leaf expansion (Figure4-1; personal communication, Guillermo Pardillo). The foliation date of a tree was defined as the date that about 50% of the terminal buds in a tree was visually observed to be at stage 3 (leaf burst). The foliation dates were then transformed to Julian days for the convenience of records and analysis. Pistillate flowers of protogynous varieties precede staminate flowers, while protandrous plants start pollen shed before pistillate flowers are visible (Warmund and Coggeshall, 2009).

Flowering dates usually started shortly after leaf flush. Anthesis dates were recorded every three days in May and June in 2010 and 2011 to determine the first pistillate flower bloom date, as stage 2 in Figure 16.8 in Polito (1998), and date of first pollen shed.

4.2.3 Data Analysis

4.2.3.1 Variance components

Variance analysis was conducted in PROC MIXED in SAS 9.3 (SAS Institute, Inc., Cary, NC). Restricted maximum likelihood approach (REML) was used to determine the amount and significance of clonal (genotypic) effect, and the variance components of residual effects. All traits were analyzed following the model below:

$$X_{ij} = \mu + C_i + \varepsilon_{ij} \quad [1]$$

where X_{ij} is the observation on the jth ramet of ith clone, μ is the overall mean, C_i is the random effect of ith clone, and ε_{ij} the residual effect. If the traits were measured in multiple years, or multiple months within one year, or at multiple crown positions, they were still analyzed separately (year by year, month by month, and position by position) without being pooled together in order to get separate estimates of genetic parameters, since genetic parameters such as repeatability may change over time. Another mixed effect model was used to conduct a joint analysis on pooled data from different time and locations together so that the fixed time effects could be estimated:

$$X_{ijk} = \mu + C_i + T_k + C_iT_k + \varepsilon_{ijk} \ [2]$$

Where X_{ijk} is the observation on the jth ramet of ith clone in kth year or day, μ is the overall mean, C_i is the random effect of ith clone, T_k is the fixed time effect of the kth year (age) or day, C_iT_k is the random interaction effect between clone and time (year or day), and ε_{ijk} the residual effect.

For traits measured at different crown positions, a joint analysis was conducted via the following model to estimate location effects:

$$X_{ijl} = \mu + C_i + P_l + \varepsilon_{ijl} \ [3]$$

Where X_{ijl} is the observation on the jth ramet of ith clone in lth location, μ is the overall mean, C_i is the random effect of ith clone, P_l is the fixed effect of the lth crown position, and ε_{ijl} the residual effect.

For phenological events such as foliation dates, first pistillate bloom, and first pollen shed, data were recorded in a way that each clone was considered an experimental unit, i.e., no variation was assumed existing within each clone. Therefore, only variation between clones and years needed to be analyzed. Each trait was tested on the assumptions of normal distribution of residuals and the homogeneity of variance using PROC MIXED and PROC UNIVARIATE. Number of nuts produced in each year (FruitNum2009, FruitNum2010, and FruitNum2011) was logarithmically transformed in order to improve the distribution of the residuals.

4.2.3.2 Genetic parameters estimates

Clonal repeatability R_c^2, usually interpreted as an upper bound for broad sense heritability (Falconer and Mackay, 1996) – the genotypic variance component, was expressed as the percentage of total phenotypic variation out of all random effects (Pliura et al., 2007):

$$R_c^2 = \frac{\sigma_c^2}{(\sigma_c^2 + \sigma_e^2)}$$

Where σ_c^2= clonal variance;

σ_e^2= variance of error (residual variance),

Standard error for clonal repeatability was estimated followed Becker (1984):

$$S.E.(R_c^2) = \sqrt{\frac{2(n-1)(1-R_c^2)^2[1+(k-1)R_c^2]^2}{k^2(n-N)(N-1)}}$$

Where N is the number of clones in this test, n is the number of individual observations, and k is the harmonic mean number of trees per clone.

Genotypic coefficients of variation was estimated using the following equation:

$$CV_G = \frac{100\sqrt{\sigma_c^2}}{\mu}$$

Where μ is the clonal mean for each trait estimated by model [1], and residual coefficients of variation was estimated by using a function similar to that of CV_G:

$$CV_e = \frac{100\sqrt{\sigma_e^2}}{\mu}$$

The phenotypic coefficients of variation was estimated using: $CV_p = CV_G + CV_e$.

Correlations among these traits were calculated via Pearson's product-moment correlation analysis (Beineke et al., 1991; Tharakan et al., 2005), using clonal means. This analysis was done using PROC CORR in SAS. Genotypic correlation coefficients (r_G^2) between two traits were estimated following Becker (1984):

$$r_G = \frac{\sigma_{C(xy)}}{\sqrt{\sigma_{c(x)}^2 \sigma_{c(y)}^2}}$$

Where $\sigma_{c(xy)}$ is the clonal covariance component of trait x and y, $\sigma_{c(x)}^2$ and $\sigma_{c(y)}^2$ are the clonal variance component for trait x and y, respectively.

The clonal identity of each tree was verified by microsatellite markers in 2012, and mislabeled trees were corrected (see chapter 5 for details).

4.3 Results

4.3.1 Clonal variation and repeatability

4.3.1.1 Tree growth

The variation in clone means for size and growth traits was small in magnitude for nearly every trait (Table 4-2), as indicated by CV_p values that ranged from 4.45 to 10.04%. The exception was stem volume, which had a larger dispersal (23 – 24%) as expected because volume was estimated as the product of DBH and tree height. The largest clone had a mean DBH of 14.13 cm in 2009, 16.40 cm in 2010, and 18.10 cm in 2011, and they were 66.04%, 65.49%, and 63.80% higher than the DBH of the smallest clone in these three years, respectively. The tallest clone was 60.61%, 50.62%, and 59.92% taller than the shortest one in 2009, 2010, and 2011, respectively. Compared to DBH and height, crown radius showed a smaller but more variable range of variation; the widest clone was 20.57%, 29.83%, and 58.67% wider than the narrowest clone in 2009, 2010, and 2011, respectively. This large instability of difference in crown radius may be due to differences in pruning practiced every year. As for stem volume, which was estimated based on DBH and tree height, the clone with the highest volume was 346.56%, 314.81%, and 331.62% greater than the clone with the lowest stem volume in 2009, 2010, and 2011, respectively. Clonal mean HD ratio, an indicator of slenderness, ranged from 55.09 to 74.61, 56.44 to 73.59, and 58.41 to 71.71 in 2009, 2010, and 2011, respectively.

Differences among clones were significant ($p<0.01$) for nearly all traits except crown radius ($0.01<p<0.05$ in 2010 and 2011, while $p=0.0679$ in 2009) (Table 4-5). The highest coefficients of genotypic variation (CV_G) were for stem volume, ranging from 0.1947 to 0.2055, while CV_G for DBH, tree height, crown radius, and HD ratio varied between 0.0414 and 0.0840, indicating DBH, tree height, crown radius, and HD ratio had a better fit with model [1] than stem volume, because the lower the CV, the smaller the dispersal of the residuals relative to the predicted value. The clonal repeatability of tree size variables (growth) was stable from 2009 to 2011, albeit with some slight variation (Table 4-5). Moderate repeatability was observed for DBH (0.60±0.11 in 2010), tree height (0.71±0.10 in 2011), estimated stem volume (0.63±0.11 in 2011), and HD ratio (0.55±0.11 in 2010). The repeatability of crown radii was relatively low, with the highest value observed in 2011 (0.27± 0.09). Stem form had a repeatability of 0.47±0.08. Year effect was significant for all growth traits ($p<0.0001$) except HD ratio ($p=0.0863$) (Table

4-7). This indicated that while other size traits change dramatically as trees grow, the slenderness of a black walnut tree remains relatively constant as its size increases.

4.3.1.2 Fruit production

The black walnut clones showed an alternate bearing pattern, with year 2010 being the least productive year, while the previous year (2009) and following year (2011) trees produced significantly more fruit (year effect: $p<0.0001$, Table 4-7). Examples were clones C130, C709, C712, C713, C720, and C730, which produced heavily in 2009 and 2011, but light crops in 2010. By contrast, however, clones C714, C707, and C717, produced fruits more evenly across three years. This may indicate that some clones exhibit less alternate bearing. Clone mean of fruit size ranged from 56.03 to 145.01 cm^3, seed size extended from 10.81 to 24.29 cm^3, fruit dry weight varied from 12.94 to 24.57 g, while seed weight fluctuated between 7.68 and 14.94 g. Overall, number of fruits showed greater variation than the characteristics of fruits and nuts at clone level, as the CV_G for size and dry weight of fruit and seed ranged from 15.54 to 19.9 %, while that for number of fruits fluctuated from 62 to 120%.

Clonal effects were significant for number of fruits produced in all three years and size and dry weight of fruit and seed ($p<0.001$, Table 4-5). Fruit number (log-transformed data) had moderate repeatability across three years, ranging from 0.62±0.11 (2001) to 0.72±0.10 (2009). Characteristics of fruit and seeds were only evaluated in 2011. Dry weight of fruit and seeds presented moderate repeatability (both 0.58±0.08), while estimated size (volume) of fruit and seeds had higher repeatability than dry weight, 0.71±0.08 and 0.75±0.08, respectively. The coefficient of genotypic variation (CV_G) for size and dry weight of both fruits and nuts were similar in magnitude (between 0.1517 and 0.1964).

4.3.1.3 Crown architecture traits

Most crown architecture traits had small variation with a coefficient of genotypic variation CV_G between 0.0634 and 0.1322, but estimated branch volume and stem form had larger variation with a CV_G of 0.1756 and 0.1996, respectively (Table 4-3). At the clone level, the average branch angle (AvgAng) of living branches ranged from 53.21° to 79.56°, while the average angle of the thickest branch in each one-meter segment along the stem (AvgAngMax) varied between 45.12° and 68.00°, indicating the thickest branches tended to have smaller insertion angles than the thinner branches. Average branch diameter (AvgBD) of all living branches of these clones changed from 2.18 to 3.19 cm, while the average diameter (AvgBDMax) of the thickest branch in each one-meter segment along stem extended from 3.33 to 4.83 cm. Branch frequency (number of branches per meter of stem length) ranged from 8.89 to 18.36 m^{-1}, while estimated branch basal area per meter of stem (accumulated branch basal area per meter of stem length) ranged from 54.31 to 94.60 $cm^2 \cdot m^{-1}$. In 2010, the branchiest clone had 286.29% more branch volume than the least branchy one. As for stem volume percentage (out of the aboveground volume of branch and stem), clonal means ranged from 44% to 61%. In the case of stem form, the straightest clone had an average score of 4.5, while the most crooked averaged 1.6. Overall, clone C715, C714, C710, C716, C55, C712, and C730 had excellent (straight) forms, while C719, C726, C728, C717, C705, C709, and C729 were crooked, with C130 being ranked at the intermediate level of stem straightness.

Among the crown architecture traits, average branch diameter of living branches (AvgBD), average diameter of the thickest branches, average angle of thickest branches (AvgBDMax), and branch basal area per meter of stem (BrBasalArea) had low repeatability ranging from 0.24 ± 0.09 to 0.34 ± 0.10 (Table 4-6). Average angle of living branches (AvgAng), average angle of the thickest branches along stem (AvgAngMax), branch frequency, stem volume percentage, and estimated branch volume showed higher repeatabilities than diameter based traits, from 0.39 ± 0.10 up to 0.59 ± 0.11.

3.1.4 Leaf characteristics and photosynthesis

Specific leaf area (SLA) in the lower crown was significantly higher than SLA in upper crown (crown position effect: $p<0.0001$, Table 4-7). Clonal mean SLA in the lower crown ranged from 127.85 to 183.65 $cm^2 \cdot g^{-1}$, while in the upper crown it extended from 99.71

to 147.04 $cm^2 \cdot g^{-1}$. Leaves in upper crown also had significantly higher nitrogen (upper: 2.82±0.05 %, lower: 2.59±0.05 %) and carbon concentration (upper: 48.12±0.29 %, lower: 46.32±0.27 %) than leaves in the lower crown (crown position effect: $p<0.0001$, Table 4-7). Leaves in the upper crown were significantly larger (upper: 452.87±10.74 cm^2, lower: 421.62±11.98 cm^2) and heavier (upper: 3.74±0.13 g, lower: 2.88±0.09 g) than those in the lower crown (crown position effect: $p<0.0007$ for ILA and $p<0.0001$ for ILM, Table 4-7). Net photosynthesis rate ranged from 14.33 to 17.16 mol s^{-1} m^{-2} in July 2011, and 8.64 to 13.99 mol s^{-1} m^{-2} in August of the same year. Although I observed significant differences in all leaf traits between the upper and lower crown, the coefficients of phenotypic variation CV_p at the two crown positions for each leaf trait were quite close to each other (Table 4-5), indicating crown-wide similarity for the degree of variation of the leaf traits.

Net photosynthesis rate had the lowest repeatability among all leaf traits (0.18 ± 0.06 to 0.19 ± 0.06), ILA, ILM, and SLA at different crown positions generally had slightly higher repeatability ranging from 0.22 ± 0.08 to 0.41 ± 0.10, while foliage carbon and nitrogen concentration showed even greater repeatability, varying from 0.37 ± 0.10 to 0.50 ± 0.10 (Table 4-6). In addition, foliar carbon concentration also showed smaller coefficients of genotypic variation CV_G (0.0263 – 0.0271) than that of foliar nitrogen concentration (0.0795 – 0.0813) and other leaf morphological traits (0.0602 – 0.1236).

4.3.1.4 Phenology

Foliation dates varied from year to year, with 2010 being the earliest year (clones leafed out on the 112th day on average) but later in 2009 (122nd day on average) and 2011 (122nd day on average). The earliest leafing clone (C712) was 17 days earlier than the latest clone (C729) in 2009, the range between the earliest (C712) and the latest (C720) was 22 days in 2010, and 20 days (C712 and C729) in 2011(year effect: $p<0.0001$, Table 4-7).

The black walnut clones I observed had two flowering types: protogynous and protandrous. On average, the first pistillate bloom date in 2010 was seven days earlier than in 2011, while the average first pollen shed date in 2010 was 13 days earlier than in 2011 (Table 4-4). In 2010, the clones with earliest pistillate bloom (C55, C705, and C728,) was 22 days earlier than the latest clones (C130, C703, and C730) , while in 2011 the earliest clone (C710) was 14 days earlier than the latest (C700) (year effect: $p<0.0001$, Table 4-7). The clones with earliest pollen shed (C700, C702, C717, and C728 in 2010; C712, C715, and C728 in 2011) were 22 days earlier than the latest clones in both 2010 (C709 and C726) and 2011 (C720) (year effect: $p<0.0001$, Table 4-7).

4.3.2 Correlations among traits

4.3.2.1 Correlations between phenological traits and stem growth and fruit production traits

For individual phenological traits, such as the dates of leaf flush (LFlush) and first pollen shed (MFS), the records in one year were strongly positively correlated with those in recent and subsequent years. An exception to this general rule was the first pistillate bloom date (FFR), which in 2010 was only marginally significantly correlated with FFR in 2011 ($p=0.0666$, Table 4-8). First pollen shed (MFS) dates were positively related to leaf flush dates across the years, and negatively correlated with first pistillate bloom dates (FFR2011 and MFS 2010) (Table 4-8). No obvious correlations were detected between leaf flush dates (LFlush) and first pistillate bloom dates (FFR).

Leaf flush and first pollen shed dates had significant negative correlation with DBH, stem volume and its increment, and stem form, but strong positive correlation with HD ratio across years from 2009 to 2011 (Table 4-9, the correlations between MFS and tree growth traits were significant for MFS2011, not MFS2010). This implies that clones with late flushing and late pollen shed were smaller (grew slower) and had more crooked stems. First pistillate bloom date in 2010 was negatively correlated with HD2010, HD2011, and HD2009, but no other correlations with tree size and growth traits were significant.

Except for the negative correlation between first pistillate bloom dates in 2010 and fruit number produced in 2010, no other phenological events were found significantly correlated with number of fruits produced in any year (Table 4-9). Nevertheless, phenological events had moderate correlations with size and dry weight of fruits and seeds. For instance, leaf flush dates and staminate flowering dates had positive correlation with the size and dry weight of individual fruits, and pollen shed dates were also moderately positively correlated with the size and dry weight of seeds (Table 4-9). The correlations between date of pistillate bloom and size and dry weight of fruits and seeds were insignificant.

As for the correlations between phenological traits and branching pattern, pollen shed dates and leaf flush dates were marginally negatively correlated with branch frequency and branch basal area per meter of stem, and leaf flush date marginally with average branch angle. All other correlations between phenological and crown architecture traits were weak or insignificant.

4.3.2.2 Correlations between physiological traits and stem growth and fruit production traits

Specific leaf area (SLA) in both lower crown and upper crown were positively correlated with foliar nitrogen concentration, while individual leaf mass (ILM) in each position was negatively correlated with foliar nitrogen concentration (although the correlation between ILM and nitrogen concentration in lower crown was marginally significant, p=0.0755, Table 4-10). Foliar nitrogen concentration in both crown positions was also positively correlated with the carbon concentration in both positions (Table 4-10). SLA of upper crown was negatively correlated with DBH and stem volume increment in 2010, while both individual leaf area (ILA) and mass (ILM) in the upper crown were positively correlated with DBH increment in 2010, although the correlation coefficient between ILA and DBH increment was marginal (Table 4-11). Foliar nitrogen concentration did not correlate with tree size traits, however, it was marginally negatively correlated with DBH increment in 2010 (r_G =-0.3722, p=0.067 for upper crown nitrogen; r_G=-0.4835, p=0.0143 for lower crown nitrogen, Table 4-11). No obvious correlations were found between these leaf traits and characteristics of individual fruits and seeds.

Foliar carbon concentration in both the upper and lower canopy was significantly negatively correlated with DBH, tree height, stem volume and its increment, and stem form, but positively correlated with size of individual fruits, dry weight of individual fruits and seeds (Table 4-12). Foliar carbon concentration was also negatively correlated with branch frequency, but positively correlated with angle variables AvgAng and AvgAngMax. No significant correlations between net photosynthesis rate and other traits were found.

4.3.2.3 Correlations between crown architectural traits and stem growth and fruit production traits

Architectural traits were correlated with each other. Branch frequency was negatively correlated with AvgAngMax (r_G=-0.4375, p=0.0287) and AvgAng (r_G =-0.37476, p=0.0649). The branch angle variables AvgAng and AvgAngMax were strongly positively correlated (r_G=0.8889, p<0.0001), and so were the two branch diameter variables AvgBD and AvgBDMax (r_G=0.7989, p<0.0001), indicating any one of them can be used as the whole-tree level variable for branch angle, however, AvgAngMax and AvgBDMax may be more convenient because they require less measurement. Average diameter of the thickest branches (AvgBDMax) was more closely related to branch basal area per meter of stem (r_G=0.6631, p=0.0003) than AvgBD (r_G=0.3970, p=0.0494). Branch angle was negatively correlated to estimated branch volume (for AvgAng, r_G=-0.3878, p=0.0554; for AvgAngMax, r_G=-0.4071, p=0.0434), and negatively correlated with stem form (for AvgAng, r_G=-0.5267, p=0.0068; for AvgAngMax, r_G=-0.5813, p=0.0023), indicating trees with larger angled branches were more inclined to have crooked stems. Branch basal area per meter of stem was negatively correlated with the stem volume percentage - an indicator of a trade-off in carbon allocation between branches and stem.

Architectural traits were also correlated to growth traits. Branch frequency, branch basal area per meter of stem, AvgBD, and AvgBDMax all had positive correlations with DBH, tree height (except branch basal area per meter of stem), and stem volume and its increment, while angle variables AvgAng and AvgAngMax were negatively correlated with aforementioned tree growth traits. Branch basal area per meter of stem, AvgBD, and AvgBDMax also were positively correlated with crown radius. Branch frequency and percentage of stemvood volume were significantly negatively correlated with the size and weight of individual fruits and seeds. The correlations between these crown architectural traits and number of fruits produced each year were not significant.

4.3.2.4 Correlations between fruit production and stem growth traits

Fruit production and characteristics of fruits and seeds were correlated. Number of fruits produced in 2009 was positively correlated with the same trait in 2011, but not correlated with number of fruits in 2010. This pattern in correlation among years was in accordance with the alternate bearing pattern of black walnut, for both 2009 and 2011 had large yields of fruits. The size and dry weight of fruits and seeds (measured in 2011) were both negatively related to the number of fruits in 2009 and 2011, indicating the expected trade-off between number and size of fruit. Fruit size, fruit dry weight, seed size, and seed dry weight (collected in 2011) were strongly positively interrelated, indicating larger, heavier fruits also had larger and heavier seeds.

Fruit production and characteristics of fruits and seeds were correlated with vegetative growth. Number of fruits produced in each year was positively related to tree height, in general, but the correlations between number of fruit and DBH and crown radius were weak and insignificant. The size and dry weight of fruits and seeds were negatively correlated with DBH, tree height (only dry weight of fruits and seeds), and stem volume across the years, and also negatively correlated with stem form. Tree height increment in 2009 was positively correlated with fruit number in 2010, and tree height increment in 2010 had positive correlations with fruit number in 2011 - one year’s stem growth was positively correlated with next year’s fruit production, this phenomena may be correlated with the alternate bearing habit of black walnut, and also it may indicate differences in carbon allocation patterns between heavy and light fruiting years. For the whole three-year period, total number of nuts produced was positively correlated with total stem volume increment in the same three-year period (r_G=0.43895, p=0.0319). The size and weight of fruits and seeds were negatively correlated with stem volume increment in each year, and the total volume increment from 2009 to 2011.

4.4 Discussion

4.4.1 Correlations between phenological events, stem growth, and fruit production

Foliation is an essential annual event of temperate woody plants. The practical implication of foliation timing is significant for two reasons. First, if a woody species started foliation too early, then it is in danger of exposure to early frost, which kills the vegetative and reproductive buds. As a consequence, frost can slow growth and degrade form by damaging terminal buds (Beineke et al., 1991). Second, early foliation may increase growth by elongating growing season. Because black walnut is rather susceptible to frost once buds break (Tryon and True, 1964), and is a highly valuable timber species, usually late flushers have been preferred. Hemery et al. (2005) found that early flushing individuals in Persian walnut (*Juglans regia* L.) had the least height growth increment due to frost injury. The correlation between foliation date and height growth in black walnut was reported to be 0.02 (Beineke, 1975).

My results that early flushing clones in the population of this study tended to have larger size (DBH, estimated stem volume, and its increment, no significant relations with tree height though) appears contradict to the aforementioned literature, but the variance for flushing date is smaller for *J. nigra* than for *J. regia*. When growing under the same climate conditions, *Juglans nigra* L. varieties start foliation about three weeks later than *Juglans regia* L. (Pollegioni et al., 2013). This means the late time window of leaf flush for *Juglans nigra* L. reduces their exposure to frost. On the other hand, it was also reported that early foliating genotypes had higher tree height and larger trunk diameter (higher tree vigor) than later leafing ones (Solar et al., 2001), and this was to some extent in accordance with the findings in this study.

My results also showed that early flushing clones had better stem form, albeit on a marginal significant level, and this was in agreement with the finding that several clones which had relatively early foliation dates exhibited excellent stem form (Beineke, 1975). The correlation between flushing date and stem form that was observed in my study ranged between -0.3379 to -0.3877, while Beineke (1975) reported that there was no correlation between foliation timing and stem form (r_G=-0.03, a study based on 144 ramets that belonged to 27 black walnut clones). However, both results indicate that although clones with early foliation dates may be more likely to suffer frost damage, it does not necessarily lead to poor stem form.

Clones that flushed late and had late pollen shed also tended to produce larger and heavier fruits (Table 4-9). The observed correlation between late leaf flush, late pollen shed, slow growth, and poor stem form, and the strong positive correlation between foliation and pollen shed, may be evidence for the presence of epistasis among these traits, or a linkage block. The positive correlation between leaf flush date and first pollen shed date was also reported by Solar et al. (2001) and Amiri et al. (2010) for *Juglans regia* L. in Slovenia and Iran, respectively.

4.4.2 Correlations among physiological traits, stem growth, and fruit production

Although high SLA has been regarded as an indicator of vigorous growth, SLA in the upper crown was negatively correlated with DBH increment (r_G=-0.3720, p=0.0671) and stem volume increment (r_G =-0.3494, p=0.0869) in 2010 (Table 4-11). More interestingly, the individual leaf mass and area in the upper crown were positively correlated with DBH increment. This was in agreement with my branch leaf area and growth models in Chapters 2 and 3 that showed same sized branches in the upper crown grew more foliage than the ones in the lower crown, and branches in the upper crown grew more in diameter than those in the lower crown. These results indicated that besides more branch leaf area, larger and heavier leaves in upper crown may also be potential indicators for faster growth.

Foliar nitrogen concentration was related to stem productivity in short rotation species such as *Populus spp.* (Stettler et al., 1992). In my study, foliage nitrogen and carbon concentration in both upper and lower crown were negatively correlated with tree growth (Table 4-11 & 4-12), especially foliar carbon concentration, which was strongly negatively correlated with DBH, tree height, and stem volume across three years. These negative correlations may indicate sink dynamics at the particular time of a year when the data was collected, between the end of July and middle of August, a period when fruits become the strongest sink in *J. regia* (Polito et al., 1998). At that time, stem growth is slowing down and eventually stops, as evidenced by DBH and height measurement, so the carbon in leaves is probably for fruit development. This was corroborated by the strong positive correlation between foliar carbon concentration at both crown positions and dry weight of fruits and seeds, and size of fruits (Table 4-12). The negative correlations between foliar carbon concentration and branch frequency, between foliar carbon concentration and stem form, but positive correlations between foliar carbon concentration and branch angle variable AvgAng and AvgAngMax, may indicate a genetic linkage block or the presence of epistasis among these traits.

Clonal effects for net photosynthesis rate were marginal (Table 4-6), and no correlations were found between net photosynthesis and other traits. This was no surprise because photosynthetic rate was found to be poorly related to growth rate in seedlings in a provenance tests of *Pinus contorta* (Sweet and Wareing, 1968) and *Picea sitchensis* (Ludlow and Jarvis, 1971). Actually, even slow – growing inland populations of *Pinus contorta* (Cannell, 1974) and *Pinus sylvestris* (Gordon and Gatherum, 1969) were capable of high rates of photosynthesis.

4.4.3 Correlations among crown architecture, stem growth, and fruit production

Based on the correlations among crown architecture traits (Table 4-13), branch frequency was negatively correlated with branch angle variables. It was also interesting to see the negative correlation between branch angle variables and stem form, meaning black walnut clones that had more horizontal branches tended to have more crooked stems.

Solar et al (2001) reported that branching frequency was positively correlated with trunk diameter and tree height, which was in accordance with the findings in this study, as branch frequency was positively correlated with DBH and other growth traits (Table 4-14). Positve correlations between branch diameter variables (AvgBD and AvgBDMax) and tree growth variables (DBH, tree height, and stem volume) indicate that larger branches usually lead to faster growth. However, as far as branch angle is concerned, it was smaller branch angles that were associated with faster growth (Table 4-14). These results were in agreement with branch attributes models in Chapter 3 that smaller angled branches were linked to larger DBH. It was also reported in previous research that branching habit is related to high production of stemwood in Sitka spruce (*Pinus sitchensis*) (Cannell et al., 1983) and lodgepole pine (*Pinus contorta*) (Thompson, 1985).

Furthermore, large branch diameters, and higher branch basal area per meter of stem led to a wider crown (Table 4-14). These results may be useful when narrow crown ideotype is desired. Narrow crown ideotype may be realized in black walnut breeding programs, since branch angle was negatively correlated with DBH and stem growth, i.e., the smaller the average branch angle, the larger the DBH. Thus, rapid growth and narrow crown may be combined together. High branch frequency, higher percentage of stem wood volume, and straighter stems were all associated with smaller, lighter fruits and seeds, while large branch angle indicated larger and heavier fruits and seeds. This may be of particular importance when large sized fruit is the primary goal.

Previous work showed that heritability of branch angle in Douglas-fir was lower in mature branches (Weiskittel et al., 2007) than young branches (St. Clair, 1994). Heritability of branch angle was moderate in Scots pine (Velling, 1988; Haapanen et al., 1997), but branch diameter was under weak genetic control (Haapanen et al., 1997). The repeatability of average angle of the thickest branches and living branches in my study was 0.59±0.11 and 0.39±0.10, respectively. Weiskittel et al. (2010) reported that the rank in primary branch frequency of five conifer species in Maine was inversely related to their rank in maximum size, suggesting that species with fewer branches may have larger maximum branch sizes. The correlation between branch frequency and maximum branch diameter in my study was weak and insignificant.

4.4.4 Correlations between stem growth and fruit production

Black walnut has an alternate fruit bearing habit, and this was reflected in the number of fruits produced each year in this study. The number of fruits produced in two heavy fruiting years (2009 and 2011) was negatively correlated with the size and weight of individual fruits and seeds, although the correlations were only marginally significant in some cases (Table 4-15). This observation conformed to a trade – off between seed number and size, which is called the Smith – Fretwell model (Smith and Fretwell, 1974). The observation that number of fruits produced each year was positively related to tree height across three years (Table 4-16, r_{G2009}=0.3178, p=0.1216; r_{G2010}=0.4314, p=0.0313; r_{G2011}=0.4076, p=0.0480) was probably because higher trees had more branches (the correlations between branch frequency and tree height: r_{G2010}=0.4162, p=0385; and there was a weak but significant correlation between branch frequency and number of fruits produced at individual tree level: r_{G2011}=0.1678, p=0.0282). A negative correlation between tree height and fruit yield was reported for *Juglans regia* by Forde and McGrannahan (1996). In spite of the alternate fruiting pattern, the number of fruits produced in the three-year period (FruitNum3yr) was positively correlated with stem volume increment (StVolIncre3yr) in the same time period (r_G=0.4390, p=0.0319), indicating a long – term positive correlation between vegetative growth and reproduction. This was also in agreement with previous findings in *Xanthium strumarium* L. (Farris and Lechowicz, 1990) and *Juglans regia* L. (Atefi, 1990). This relationship was also corroborated by the positive correlation between stem volume percentage and number of fruit produced in 2009 and 2011 (Table 4-14, r_{G2009}=0.44067, p=0.0275; r_{G2011}=0.416, p=0.0386). The result that the size and weight of individual fruits and seeds were negatively correlated with DBH, tree height, stem volume and its increment, and the percentage of stem volume, may indicate that the size and weight of fruit and seed can be used as indicators for stem growth.

In studies where resource (water, nutrient, and light) availability was highly managed, species generally conform to a positive relationship between plant growth rate and seed number (Vega et al., 2001; Andrade et al., 2005; Sadras, 2007). The positive relationship between stem growth and fruit number in my study was in agreement with these findings. High quality environments such as open or mesic sites tend to favor species producing smaller seeds than low – light or arid sties (Baker, 1972; Salisbury, 1974; Foster and Janson, 1985; Mazer, 1989). Because my study site was characterized by homogeneous site condition and intensive management (high resource availability), we can conclude that the observed variation in fruit size and mass among clones was largely genetic, as reflected by the high repeatability of size and mass of fruits and seeds in this study. In many plant species, the variation in seed size is generally narrow, and the heritability of seed size and mass are usually high (Sadras, 2007).

4.5 Conclusion

Phenological traits (e.g., leaf flush dates and first appearance of pollen shed), physiological traits (e.g., individual leaf area and mass in upper crown, foliar nitrogen and carbon concentration), crown architecture traits (e.g., AvgAng, AvgAngMax, AvgBD, AvgBDMax, and branch frequency), and fruit production, and size and mass of fruits were all important indicators for timber production and stem form for black walnut ideotypes. The genetic parameters, i.e., clonal repeatability and genetic correlations among different traits, obtained for black walnut was based on the black walnut population in this study, which were previously selected based on size and stem form. These genetic estimates will be useful for continuous breeding program within this population, however, conclusions may need to be constrained within this particular population and not be drawn for other populations, for the genetic parameters of these traits may change when the population changes.

4.6 References

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4.7 Tables

Table 4-1 Origin of the 25 black walnut (*Juglans nigra* L.) clones investigated in this study.

Clone	Mother	Origin[1]	Patented Clone Names
C55	Unknown	Darlington, Indiana	Purdue-1
C130	Unknown	West Lafayette, Indiana	Tippecanoe-1
C715	Tippecanoe-1	West Lafayette, Indiana	Beineke 1
C720	Fayette-1	West Lafayette, Indiana	Beineke 2
C702	BW95	West Lafayette, Indiana	Beineke 3
C703	BW249	South Raub, Indiana	Beineke 4
C707	BW95	South Raub, Indiana	Beineke 5
C710	Purdue-1	South Raub, Indiana	Beineke 6
C714	Purdue-1	South Raub, Indiana	Beineke 7
C705	BW205[a]	West Lafayette, Indiana	Beineke 8
C701	BW41	West Lafayette, Indiana	Beineke 9
C717	BW36	West Lafayette, Indiana	Beineke 10
C718	Purdue-1	--	--
C730	Purdue-1	--	--
C700	Unknown	--	--
C708	Unknown	--	--
C709	Unknown	West Lafayette, Indiana	--
C712	Unknown	--	--
C713	Unknown	--	--
C716	Unknown	--	--
C719	Unknown	--	--
C726	Unknown	--	--
C728	Unknown	--	--
C729	Unknown	--	--
C777	Unknown	--	--

1: Means the places where the selections were found, usually from the progeny test of a previous elite black walnut selection, but some were from wild populations.

a. The maternal grandmother of BW205 was BW97.

Table 4-2 Mean and range in size and growth traits of 25 black walnut *(Juglans nigra* L.*)* clones. Nc: number of clones, Nt: number of trees in total, SE: standard error.

Trait	Nc	Nt	Mean±SE (clone)	Mean±SE (individual tree)	Range (min-max, clone)	Range (min-max, individual tree)	CV_p (%, clone)	CV_p (%, individual tree)	Units
DBH2009	25	172	12.02±0.24	12.42±0.10	8.51-14.13	8.51-16.89	10.04	10.9	cm
DBH2010	25	172	14.19±0.26	14.62±0.10	9.91-16.40	9.91-18.67	9.29	9.25	cm
DBH2011	25	169	15.76±0.28	16.17±0.11	11.05-18.10	11.05-19.94	8.79	8.54	cm
DBH2009Incre	25	172	1.94±0.06	1.98±0.03	1.02-2.43	0.89-3.05	14.69	17.13	cm
DBH2010Incre	25	172	2.18±0.05	2.20±0.03	1.40-2.54	1.27-2.92	10.69	15.05	cm
DBH2011Incre	25	169	1.56±0.04	1.55±0.02	1.14-1.91	0.63-2.29	11.66	17.07	cm
Ht2009	25	172	794.83±13.74	811.57±5.64	584.00-937.94	584-1007.36	8.64	9.12	cm
Ht2010	25	172	928.57±17.21	953.92±6.21	728.98-1098.08	720.73-1132.84	9.27	8.54	cm
Ht2011	24	152	1052.32±18.37	1076±6.66	771.00-1233.15	771-1322.22	8.55	7.63	cm
Ht2009Incre	25	166	125.95±5.01	127.64±4.04	71.97-194.28	10.06-272.8	19.88	40.75	cm
Ht2010Incre	25	169	137.15±6.87	145.74±3.64	54.57-180.89	11.79-265.66	25.04	32.43	cm
Ht2011Incre	24	151	124.61±6.42	122.03±3.55	42.02-173.22	21.89-300.61	25.25	35.7	cm
CR2009	25	172	291.76±2.62	293.47±1.72	258.62-311.81	237.52-351.82	4.49	7.7	cm
CR2010	25	172	273.67±3.71	273.94±2.10	247.86-321.79	198.58-351.66	6.77	10.06	cm
CR2011	25	169	253.92±4.44	255.70±2.4	198.73-315.32	141.96-324.23	8.75	12.23	cm
CR2009Incre	25	172	63.45±2.85	61.63±1.59	36.65-91.29	1.68-111.79	22.44	33.91	cm
CR2010Incre	25	169	64.22±2.93	65.19±1.80	35.51-96.57	6.63-142.65	22.81	35.83	cm
CR2011Incre	25	166	63.61±3.90	64.15±2.15	33.62-115.29	3.43-144.93	30.66	43.19	cm
StVol2009	25	171	46231±2222	49851±980	16605-74151	16605-90354	24	25.7	cm^3
StVol2010	25	171	75144±3577	81025±1430	28091-116525	28091-130779	24	23.08	cm^3
StVol2011	24	152	104561±4835	111949±1964	36962-159359	36962-183441	23	21.63	cm^3
StVol2009Incre	25	171	18588±957	20019±469	5812-32626	2073-40615	26	30.63	cm^3
StVol2010Incre	25	172	28943±1486	31265±604	11487-42374	7198-49632	26	25.34	cm^3
StVol2011Incre	24	152	29669±1292	30710±590	8871-42834	8871-54602	21	23.7	cm^3
HD2009	25	172	66.58±1.03	65.84±0.55	55.09-74.61	49.86-82.77	7.72	10.95	/
HD2010	25	172	65.71±0.94	65.53±0.44	56.44-73.59	51.17-78.02	7.19	8.79	/
HD2011	24	152	67.08±0.61	66.80±0.40	58.41-71.71	51.57-76.21	4.45	7.35	/

Incre: increment; Ht: tree height; CR: crown radius; StVol: stem volume; HD: the ratio of height to DBH.

Table 4-3 Mean and range in nut production and crown architecture traits of 25 black walnut (*Juglans nigra* L.) clones. Nc: number of clones, Nt: number of trees in total, SE: standard error.

Trait	Nc	Nt	Mean±SE (clone)	Mean±SE (individual tree)	Range (min-max, clone)	Range (min-max, individual tree)	CV_p (%, clone)	CV_p (%, individual tree)	Units
Nut production									
FruitNum2009	25	172	153±23	159±9	8-457	7-646	75	77.62	--
FruitNum2010	25	169	75±18	86±9	8-364	1-547	120	134.53	--
FruitNum2011	25	169	222±28	235±13	18-495	2-680	62	69.77	--
FruitSize2011	24	378[1]	76.79±3.12	76.54±0.89	56.03-122.12	36.79-145.01	19.9	22.71	cm^3
SeedSize2011	24	378[1]	16.71±0.63	16.64±0.18	10.81-24.29	8.13-27.30	18.52	20.66	cm^3
FruitDW2011	24	378[1]	18.61±0.59	18.59±0.19	12.94-24.57	8.76-29.45	15.54	19.42	g
SeedDW2011	24	378[1]	11.53±0.39	11.50±0.12	7.68-14.94	5.08-18.43	16.62	20.94	g
Crown architecture									
AvgAng	25	172	65.46±1.13	63.8±0.51	53.21-79.56	47.94-79.56	8.65	10.5	degrees(°)
AvgAngMax	25	168	57.49±1.32	54.94±0.70	45.12-68.00	29.50-73.33	11.5	16.48	degrees(°)
AvgBD	25	172	2.77±0.04	2.79±0.02	2.18-3.19	1.82-3.69	7.88	10.89	cm
AvgBDMax	25	168	4.30±0.07	4.33±0.04	3.33-4.83	2.97-5.65	8.66	12.74	cm
BrFreq	25	172	14.12±0.39	14.56±0.19	8.89-18.36	7.76-20.41	13.69	17.55	m^{-1}
BrBasalArea	25	172	70.47±2.07	71.57±1.09	54.31-94.60	41.68-112.14	14.7	19.99	$cm^2 \cdot m^{-1}$
BrVol2010	25	171	70020±3250	73749±1383	25712-99322	25712-122289	23.21	24.52	cm^3
StVolPercen2010	25	172	0.52±0.01	0.52±0.00	0.44-0.61	0.41-0.64	7.28	9.05	--
StForm2009	25	209	3.37±0.15	3.48±0.07	1.60-4.50	1.00-5.00	21.51	28.31	--

1: number of nuts in total.

Num: number; DW: dry weight; AvgAng: average angle of living branches; AvgBD: average diameter of living branches;
AvgAngMax: average angle of the thickest branches along the stem; AvgBDMax: average diameter of the thickest branches along the stem;
BrFreq: branch frequency; BrBasalArea: branch basal area; BrVol: total branch volume;
StVolPercen: stem volume percentage out of total aboveground wood volume (branch and stem); StForm: stem form.

Table 4-4 Mean and range in Leaf and photosynthesis traits of 25 black walnut *(Juglans nigra* L.) clones.

Traits	Nc	Nt	Mean±SE (clone)	Mean±SE (individual tree)	Range (min-max, clone)	Range (min-max, individual tree)	CV_p (%, clone)	CV_p (%, Individual tree)	Units
Leaf characteristics									
ILAUpper	25	128	452.87±10.74	449.1±7.17	337.16-554.18	259.92-635.19	11.86	18.05	cm^2
ILALower	25	120	421.62±11.98	416.89±7.56	322.40-554.65	193.30-754.65	14.21	19.87	cm^2
ILMUpper	25	128	3.74±0.13	3.69±0.08	2.72-5.56	1.86-5.75	17.69	23.54	g
ILMLower	25	120	2.88±0.09	2.83±0.06	2.19-3.85	1.38-5.01	15.75	22.33	g
SLAUpper	25	125	122.21±2.18	122.42±1.21	99.71-147.04	99.71-164.04	8.92	11.08	$cm^2 \cdot g^{-1}$
SLALower	25	120	148.02±2.25	148.79±1.44	127.85-183.65	111.21-202.72	7.59	10.64	$cm^2 \cdot g^{-1}$
CarbUpper	25	126	48.12±0.29	48.04±0.16	45.52-50.50	43.67-52.24	2.97	3.82	%
CarbLower	25	120	46.32±0.27	46.21±0.16	43.87-48.81	42.17-49.76	2.95	3.75	%
NitrUpper	25	127	2.82±0.05	2.82±0.03	2.47-3.46	2.08-3.68	9.01	11.78	%
NitrLower	25	122	2.59±0.05	2.57±0.03	2.14-3.08	1.57-3.64	9.99	13.34	%
PhotoJuly	12	112[1]	15.89±0.30	15.88±0.19	14.33-17.16	9.43-20.50	6.52	12.58	mol s^{-1} m^{-2}
PhotoAug	12	120[1]	11.88±0.44	11.91±0.26	8.64-13.99	3.41-19.00	12.69	24.30	mol s^{-1} m^{-2}
Phenology[2]									
LFlush2009	24	171	122±1		115-133		4.34		day
LFlush2010	23	169	111±2		100-122		6.80		day
LFlush2011	24	171	124±1		113-132		4.81		day
FFR2010	24	171	129±1		122-144		4.11		day
FFR2011	24	171	136±1		130-144		3.62		day
MFS2010	24	171	127±1		117-139		4.82		day
MFS2011	24	171	140±1		130-152		4.30		day

1: number of leaves. 2: expressed in Julian days.

ILA: individual leaf area; ILM: individual leaf mass; SLA: specific leaf area; Carb: foliar carbon concentration; Nitr: foliar nitrogen concentration; PhotoJuly: net photosynthesis rate in July 2011; PhotoAug: net photosynthesis rate in August 2011; LFlush: date of first leaf flush; FFR: date of first pistillate bloom (timing that female flowers being receptive); MFS: date of first pollen shed (timing that male flowers shedding pollen); Upper: upper crown; Lower: lower crown.

Table 4-5 Analysis of variance for tree growth and nut production traits of 25 black walnut (*Juglans nigra* L.) clones: variance components, Z probability of the random effects, repeatability estimates, and genetic, environmental and phenotypic coefficients of variation from model [1].

Trait	Clone		Random error		Repeatability	CV_G	CV_e	CV_p
	σ^2_c	Pr > Z	σ^2_e	Pr > Z				
Tree growth								
DBH2009	1.0326	0.0026	0.8875	<.0001	0.54±0.11	0.0840	0.0779	0.1618
DBH2010	1.2234	0.0025	0.8214	<.0001	0.60±0.11	0.0775	0.0635	0.1410
DBH2011	1.2844	0.0031	0.8856	<.0001	0.59±0.11	0.0716	0.0594	0.1310
DBH2009Incre	0.03838	0.0102	0.08282	<.0001	0.32±0.09	0.1001	0.1470	0.2471
DBH2010Incre	0.01167	0.0679	0.09804	<.0001	0.11±0.08	0.0492	0.1425	0.1916
DBH2011Incre	0.01794	0.0100	0.05165	<.0001	0.26±0.09	0.0855	0.1451	0.2306
Ht2009	3051.00	0.0038	3017.79	<.0001	0.50±0.10	0.0690	0.0686	0.1376
Ht2010	5941.27	0.0015	2694.15	<.0001	0.69±0.10	0.0826	0.0556	0.1382
Ht2011	6212.04	0.0020	2512.80	<.0001	0.71±0.10	0.0746	0.0474	0.1220
Ht2009Incre	252.95	0.0967	2476.32	<.0001	0.09±0.09	0.1250	0.3911	0.5161
Ht2010Incre	554.06	0.0276	1809.22	<.0001	0.23±0.09	0.1656	0.2993	0.4649
Ht2011Incre	199.23	0.1272	1726.70	<.0001	0.10±0.08	0.1145	0.3371	0.4516
CR2009	52.1204	0.0659	458	<.0001	0.10±0.08	0.0247	0.0732	0.0978
CR2010	178.35	0.0139	590.79	<.0001	0.23±0.09	0.0488	0.0889	0.1377
CR2011	267.95	0.0113	731.70	<.0001	0.27±0.09	0.0645	0.1067	0.1712
CR2009Incre	146.20	0.0053	291.19	<.0001	0.33±0.10	0.1926	0.2718	0.4644
CR2010Incre	96.4388	0.0305	456.90	<.0001	0.17±0.09	0.1525	0.3319	0.4844
CR2011Incre	178.78	0.0173	605.36	<.0001	0.23±0.09	0.2101	0.3866	0.5966
StVol2009	87376570	0.0029	88985640	<.0001	0.50±0.10	0.1983	0.2001	0.3984
Vol2010	2.46E+08	0.0019	1.58E+08	<.0001	0.61±0.11	0.2055	0.1649	0.3705
Vol2011	4.26E+08	0.0022	2.45E+08	<.0001	0.63±0.11	0.1947	0.1476	0.3423

Table 4-5 continued

StVol2009Incre	15444994	0.0039	22895905	<.0001	0.40±0.10	0.2067	0.2517	0.4583
StVol2010Incre	41316796	0.0023	31868139	<.0001	0.56±0.11	0.2180	0.1915	0.4095
StVol2011Incre	23119525	0.0060	31585282	<.0001	0.42±0.10	0.1595	0.1864	0.3458
HD2009	24.7764	0.0011	21.6411	<.0001	0.53±0.11	0.0747	0.0699	0.1446
HD2010	17.5173	0.0019	14.2268	<.0001	0.55±0.11	0.0636	0.0573	0.1209
HD2011	7.7096	0.0030	13.0126	<.0001	0.37±0.10	0.0414	0.0538	0.0951
Nut Production								
FruitNum2009	0.7161	0.0005	0.275	<.0001	0.72±0.10	0.1819	0.1127	0.2946
FruitNum2010	1.1987	0.0005	0.6415	<.0001	0.65±0.11	0.3074	0.2249	0.5324
FruitNum2011	1.1394	0.0009	0.6951	<.0001	0.62±0.11	0.2985	0.2332	0.5317
FruitSize2011	227.36	0.0005	91.5183	<.0001	0.71±0.08	0.1964	0.1246	0.3210
SeedSize2011	9.3662	0.0005	3.0802	<.0001	0.75±0.08	0.1832	0.1050	0.2882
FruitDW2011	7.969	0.0006	5.7087	<.0001	0.58±0.08	0.1517	0.1284	0.2801
SeedDW2011	3.4952	0.0006	2.5601	<.0001	0.58±0.08	0.1622	0.1388	0.3011

Incre: increment; Ht: tree height; CR: crown radius; StVol: stem volume;
HD: the ratio of height to DBH. Num: number; DW: dry weight.

Table 4-6 Analysis of variance of crown architecture and leaf traits of 25 black walnut (Juglans nigra L.) clones: variance components, Z probability of the random effects, repeatability estimates, and coefficients of variation resulted from model [1].

Traits	Clone		Random error		Repeatability	CV_G	CV_e	CV_p
	σ^2_c	Pr > Z	σ^2_e	Pr > Z				
Crown architecture								
AvgAng	26.2437	0.0014	18.5408	<.0001	0.59±0.11	0.0787	0.0661	0.1448
AvgAngMax	31.293	0.0037	49.0887	<.0001	0.39±0.10	0.0988	0.1237	0.2225
AvgBD	0.03355	0.0066	0.06532	<.0001	0.34±0.10	0.0659	0.0920	0.1579
AvgBDMax	0.07476	0.0186	0.2416	<.0001	0.24±0.09	0.0634	0.1141	0.1775
BrFreq	3.5013	0.0009	2.4491	<.0001	0.59±0.11	0.1322	0.1106	0.2428
BrBasalArea	64.4805	0.0071	142.32	<.0001	0.31±0.09	0.1139	0.1692	0.2830
StVolPercen	0.00118	0.0017	0.001091	<.0001	0.52±0.11	0.0661	0.0635	0.1296
BrVol	1.56E+08	0.0049	1.91E+08	<.0001	0.45±0.10	0.1756	0.1946	0.3702
StForm2009	0.4568	0.0014	0.5211	<.0001	0.47±0.08	0.1996	0.2132	0.4128
leaf traits								
SLAUpper	80.0793	0.0107	174.94	<.0001	0.31±0.09	0.0602	0.0890	0.1493
SLAUpper	79.8947	0.0055	113.43	<.0001	0.41±0.10	0.0729	0.0869	0.1598
ILALower	2493.36	0.0078	4520.72	<.0001	0.36±0.10	0.1189	0.1600	0.2789
ILAUpper	1480.94	0.0269	5209.13	<.0001	0.22±0.08	0.0855	0.1604	0.2459
ILMLower	0.1117	0.0199	0.2989	<.0001	0.27±0.09	0.1171	0.1916	0.3087
ILMUpper	0.2090	0.0194	0.5689	<.0001	0.27±0.09	0.1236	0.2040	0.3276
CarbLower	1.4769	0.0030	1.6301	<.0001	0.48±0.10	0.0263	0.0276	0.0538
CarbUpper	1.7330	0.0020	1.7016	<.0001	0.50±0.10	0.0274	0.0271	0.0545
NitrLower	0.04428	0.0073	0.07618	<.0001	0.37±0.10	0.0813	0.1066	0.1879
NitrUpper	0.05044	0.0032	0.06284	<.0001	0.45±0.10	0.0795	0.0887	0.1682
PhotoJuly	0.7204	0.0590	3.3216	<.0001	0.18±0.06	0.0534	0.1147	0.1681
PhotoAug	1.621	0.0492	6.8543	<.0001	0.19±0.06	0.1071	0.2202	0.3273

AvgAng: average angle of living branches; AvgBD: average diameter of living branches; AvgAngMax: average angle of the thickest branches along the stem; AvgBDMax: average diameter of the thickest branches along the stem; BrFreq: branch frequency; BrBasalArea: branch basal area; BrVol: total branch volume; StVolPercen: stem volume percentage out of total aboveground wood volume (branch and stem); StForm: stem form; Upper: upper crown; Lower: lower crown; ILA: individual leaf area; ILM: individual leaf mass; SLA: specific leaf area; Carb: foliar carbon concentration; Nitr: foliar nitrogen concentration; PhotoJuly: net photosynthesis rate in July 2011; PhotoAug: net photosynthesis rate in August 2011.

Table 4-7 Analysis of variance components of traits of black walnut (*Juglans nigra* L.) clones measured in multiple years or at multiple crown positions from joint analysis model [2] or [3]: F-test and probability of fixed effects, and variance components of random effects.

Traits	Fixed effects		Random effects							
	Year (Age)		Clone		Clone*Year		Random error		AR(1)	
	F	P	σ^2_c	Pr > Z	σ^2_{cy}	Pr > Z	σ^2_e	Pr > Z	ρ	Pr > Z
DBH	4274.51	<.0001	1.1403	0.0028	0.008288	0.0095	0.89	<.0001	0.957	<.0001
Ht	676.36	<.0001	4689.82	0.0019	314.15	0.0061	2809	<.0001	0.6347	<.0001
CR	46.58	<.0001	58.1346	0.0969	104.22	0.0019	594.27	<.0001	0.3422	<.0001
StVol	643.77	<.0001	2.16E+08	0.0031	27074507	0.0001	1.78E+08	<.0001	0.9094	<.0001
HD	2.64	0.0863	13.7491	0.0019	2.2373	0.0042	16.949	<.0001	0.6321	<.0001
FruitNum	18.8	<.0001	0.1999	0.0814	0.6477	<.0001	0.4649	<.0001	-0.0451	0.3937
LFlush	201.26	<.0001					35.5491	<.0001	0.7894	<.0001
FFR	41.16	<.0001					26.1368	<.0001	0.3796	0.0335
MFS	190.58	<.0001					36.9819	<.0001	0.7011	<.0001
	Day		Clone		Clone*Day		Random error			
	F	P	σ^2_c	Pr > Z	σ^2_{cy}	Pr > Z	σ^2_e	Pr > Z		
PhotoJuly	5.3	0.013	0.484	0.1759	1.3668	0.0097	1.7651	<.0001		
PhotoAug	1.1	0.3498	0.5367	0.3231	4.5371	0.0041	3.6046	<.0001		
	Crown position		Clone				Random error			
	F	P	σ^2_c	Pr > Z			σ^2_e	Pr > Z		
SLA	207.5	<.0001	100.78	0.0022			181.84	<.0001		
ILA	11.86	0.0007	1334.11	0.0099			5514.24	<.0001		
ILM	96.8	<.0001	0.1231	0.0117			0.4792	<.0001		
Carb	106.3	<.0001	1.6791	0.0011			2.0535	<.0001		
Nitr	55.24	<.0001	0.0514	0.0014			0.06641	<.0001		

DBH: diameter at breast height; Ht: tree height; CR: crown radius; StVol: stem volume; HD: ratio of height to DBH; FruitNum: number of fruits; LFlush: date of first leaf flush; FFR: date of first pistillate bloom (timing that female flowers being receptive); MFS: date of first pollen shed (timing that male flowers shedding pollen); ILA: individual leaf area; ILM: individual leaf mass; SLA: specific leaf area; Carb: foliar carbon concentration; Nitr: foliar nitrogen concentration; PhotoJuly: net photosynthesis rate in July 2011; PhotoAug: net photosynthesis rate in August 2011; AR(1): autoregression variance structure

Table 4-8 Genotypic correlations among phenological traits of black walnut (*Juglans nigra* L.) clones.

	LFlush2009	LFlush2010	LFlush2011	FFR2010	FFR2011	MFS2010	MFS2011
LFlush2009	1	0.8621	0.83224	0.00616	-0.00639	0.44718	0.73426
		<.0001	*<.0001*	*ns*	*ns*	*0.0285*	*<.0001*
LFlush2010		1	0.85392	0.01699	-0.1168	0.62458	0.78624
			<.0001	*ns*	*ns*	*0.0014*	*<.0001*
LFlush2011			1	-0.05136	0.11124	0.37889	0.75268
				ns	*ns*	*0.0679*	*<.0001*
FFR2010				1	0.38047	0.00425	-0.14999
					0.0666	*ns*	*ns*
FFR2011					1	-0.61112	-0.34718
						0.0015	*0.0965*
MFS2010						1	0.70117
							0.0001
MFS2011							1

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10.

LFlush: date of first leaf flush;

FFR: date of first pistillate bloom (when female flowers were receptive);

MFS: date of first pollen shed (when male flowers shed pollen).

Table 4-9 Genotypic correlations among phenological traits and other traits of black walnut (*Juglans nigra* L.) clones.

	DBH 2009	DBH 2010	DBH 2011	HD 2009	HD 2010	HD 2011	StVol 2009	StVol 2010	StVol 2011	StVol2009 Incre	StVol2010 Incre	StVol2011 Incre	StForm 2009
LFlush2009	-0.57336	-0.54234	-0.53467	0.3802	0.45218	0.45998	-0.50668	-0.42609	-0.41917	-0.4956	-0.27326	-0.39587	-0.33471
	0.0034	*0.0062*	*0.0071*	*0.0669*	*0.0265*	*0.0237*	*0.0115*	*0.0379*	*0.0415*	*0.0138*	*ns*	*0.0555*	*ns*
LFlush2010	-0.4984	-0.42849	-0.42694	0.37106	0.50443	0.51899	-0.43786	-0.31756	-0.31412	-0.40143	-0.11656	-0.3312	-0.33787
	0.0155	*0.0414*	*0.0422*	*0.0813*	*0.0141*	*0.0112*	*0.0367*	*ns*	*ns*	*0.0576*	*ns*	*ns*	*ns*
LFlush2011	-0.59979	-0.54275	-0.52458	0.53234	0.52142	0.50027	-0.5199	-0.43052	-0.43358	-0.47285	-0.2661	-0.42946	-0.38767
	0.0019	*0.0061*	*0.0085*	*0.0074*	*0.009*	*0.0128*	*0.0092*	*0.0357*	*0.0343*	*0.0196*	*ns*	*0.0362*	*0.0612*
FFR2010	0.23674	0.2183	0.21134	-0.6035	-0.45335	-0.60877	0.04474	0.06774	0.05074	-0.02555	0.10848	0.04967	0.1341
	ns	*ns*	*ns*	*0.0018*	*0.0261*	*0.0016*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
FFR2011	0.13983	0.13029	0.1414	-0.1983	-0.18038	-0.33071	0.10675	0.09552	0.12728	0.13499	0.07445	0.13048	0.19787
	ns	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
MFS2010	-0.2371	-0.21011	-0.21024	0.24711	0.30781	0.3603	-0.19367	-0.13808	-0.15471	-0.22718	-0.04419	-0.18535	-0.30493
	ns	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
MFS2011	-0.56539	-0.5324	-0.53301	0.46214	0.51899	0.52179	-0.49084	-0.41427	-0.43291	-0.50555	-0.27044	-0.44685	-0.45504
	0.004	*0.0074*	*0.0073*	*0.023*	*0.0094*	*0.0089*	*0.0149*	*0.0442*	*0.0346*	*0.0117*	*0.2012*	*0.0286*	*0.0255*

Table 4-9 continued

	FruitNum 2009	FruitNum 2010	FruitNum 2011	FruitDW	FruitSize	SeedDW	SeedSize	BrFreq	BrBasalArea	AvgAng
LFlush2009	-0.0675	-0.26708	0.19836	0.38943	0.36034	0.26376	0.12823	-0.2817	-0.39417	0.27405
	ns	*ns*	*ns*	*0.06*	*0.0837*	*ns*	*ns*	*ns*	*0.0567*	*ns*
LFlush2010	-0.17035	-0.04262	0.22314	0.38248	0.39523	0.30019	0.28242	-0.17888	-0.25955	0.16813
	ns	*ns*	*ns*	*0.0717*	*0.062*	*ns*	*ns*	*ns*	*ns*	*ns*
LFlush2011	-0.22676	-0.12279	0.14248	0.39445	0.45967	0.29987	0.29048	-0.24415	-0.48846	0.39221
	ns	*ns*	*ns*	*0.0565*	*0.0238*	*ns*	*ns*	*ns*	*0.0154*	*0.058*
FFR2010	0.00753	-0.52183	0.20079	-0.04183	-0.11247	-0.17453	-0.26693	0.19985	0.26323	-0.16523
	ns	*0.0089*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
FFR2011	-0.08158	-0.23297	0.17149	-0.11956	-0.22387	-0.27689	-0.37354	0.14037	0.03981	0.15017
	ns	*ns*	*ns*	*ns*	*ns*	*ns*	*0.0722*	*ns*	*ns*	*ns*
MFS2010	0.05191	0.09146	0.08236	0.41253	0.53123	0.39266	0.42787	-0.36506	-0.00101	0.0188
	ns	*ns*	*ns*	*0.0451*	*0.0076*	*0.0577*	*0.037*	*0.0794*	*ns*	*ns*
MFS2011	-0.21622	0.01763	-0.031	0.42401	0.61398	0.36311	0.43505	-0.40994	-0.46044	0.21799
	ns	*ns*	*ns*	*0.0389*	*0.0014*	*0.0812*	*0.0336*	*0.0466*	*0.0236*	*ns*

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10.

DBH: diameter at breast height; HD: ratio of tree height to DBH; StVol: stem volume; Incre: increment; StForm: stem form;

LFlush: date of first leaf flush; FFR: date of first pistillate bloom (when female flowers were receptive); MFS: date of first pollen shed (when male flowers shed pollen);

FruitNum: fruit number; DW: dry weight; BrFreq: branch frequency; BrBasalArea: branch basal area per meter of stem; MFS: date of first pollen shed (timing that male flowers shedding pollen; AvgAng: average angle of living branches.

Table 4-10 Genotypic correlations among leaf traits of black walnut (*Juglans nigra* L.) clones.

	SLAUpper	SLALower	ILAUpper	ILALower	ILM Upper	ILM Lower	Nitr Upper	Nitr Lower	Carb Upper	Carb Lower
SLAUpper	1	0.76422	-0.38531	0.04307	-0.76213	-0.32794	0.39077	0.55061	0.13426	0.2411
		<.0001	*0.0572*	*ns*	*<.0001*	*ns*	*0.0534*	*0.0043*	*ns*	*ns*
SLALower		1	-0.07427	0.07262	-0.46733	-0.40517	0.40383	0.48376	0.10502	0.13021
			ns	*ns*	*0.0185*	*0.0445*	*0.0453*	*0.0143*	*ns*	*ns*
ILAUpper			1	0.33737	0.86065	0.36194	-0.2382	-0.35676	-0.05479	-0.08216
				0.0991	*<.0001*	*0.0754*	*ns*	*0.08*	*ns*	*ns*
ILALower				1	0.26693	0.87884	-0.17147	-0.1488	0.10971	0.17978
					ns	*<.0001*	*ns*	*ns*	*ns*	*ns*
ILMUpper					1	0.48242	-0.43506	-0.56737	-0.13055	-0.16072
						0.0146	*0.0297*	*0.0031*	*ns*	*ns*
ILMLower						1	-0.34599	-0.36183	0.04519	0.12549
							0.0902	*0.0755*	*ns*	*ns*
NitrUpper							1	0.85703	0.54597	0.58074
								<.0001	*0.0048*	*0.0023*
NitrLower								1	0.37483	0.51986
									0.0649	*0.0077*
CarbUpper									1	0.7916
										<.0001
CarbLower										1

First row: Pearson correlation coefficients; second row: p-values. ns: insignificant, p>0.10.
Upper: upper crown; Lower: lower crown; ILA: individual leaf area; ILM: individual leaf mass; SLA: specific leaf area;
Carb: foliar carbon concentration; Nitr: foliar nitrogen concentration;
PhotoJuly: net photosynthesis rate in July 2011; PhotoAug: net photosynthesis rate in August 2011.

Table 4-11 Genotypic correlations among leaf traits and other traits of black walnut (*Juglans nigra* L.) clones.

	DBH2010 Incre	Ht2010 Incre	CR2011 Incre	StVol2010 Incre
SLAUpper	-0.37196	-0.27223	-0.63023	-0.34942
	0.0671	*ns*	*0.0007*	*0.0869*
SLALower	-0.43738	-0.12582	-0.42665	-0.2817
	0.0288	*ns*	*0.0334*	*ns*
ILAUpper	0.38468	-0.00546	0.42523	0.21852
	0.0576	*ns*	*0.0341*	*ns*
ILALower	-0.13075	-0.27419	0.05777	-0.25029
	ns	*ns*	*ns*	*ns*
ILMUpper	0.45349	0.0729	0.61934	0.31673
	0.0228	*ns*	*0.001*	*ns*
ILMLower	0.10008	-0.20064	0.28993	-0.09779
	ns	*ns*	*ns*	*ns*
NitrUpper	-0.37213	0.04351	-0.33279	-0.23691
	0.067	*ns*	*ns*	*ns*
NitrLower	-0.48348	-0.16144	-0.56671	-0.38799
	0.0143	*ns*	*0.0031*	*0.0553*

First row: Pearson correlation coefficients;
second row: p-values. *ns*: insignificant, p>0.10.
Upper: upper crown; Lower: lower crown.
ILA: individual leaf area; ILM: individual leaf mass;
SLA: specific leaf area; Nitr: foliar nitrogen concentration;
DBH: diameter at breast height;
Ht: tree height; CR; crown radius;
StVol: stem volume; Incre: increment.

Table 4-12 Genotypic correlations between foliar carbon concentration and other traits of black walnut (*Juglans nigra* L.) clones.

	DBH 2009	DBH 2010	DBH 2011	Ht 2009	Ht 2010	Ht 2011	CR 2009	CR 2010	CR 2011	StVol 2009	StVol 2010	StVol 2011
CarbUpper	-0.63484	-0.64221	-0.61862	-0.58601	-0.65521	-0.64287	-0.3139	-0.10775	-0.40428	-0.67117	-0.68971	-0.68834
	0.0007	*0.0005*	*0.001*	*0.0021*	*0.0004*	*0.0007*	*ns*	*ns*	*0.045*	*0.0002*	*0.0001*	*0.0002*
CarbLower	-0.41214	-0.44705	-0.43087	-0.40232	-0.53783	-0.51574	-0.2772	0.07063	-0.22174	-0.478	-0.54072	-0.55836
	0.0406	*0.0251*	*0.0315*	*0.0462*	*0.0056*	*0.0099*	*ns*	*ns*	*ns*	*0.0157*	*0.0053*	*0.0046*

	DBH2010 Incre	Ht2010 Incre	StVol 2010Incre	FruitDW	FruitSize	SeedDW	SeedSize	BrFreq	AvgAng	AvgAngMax	AvgBDMax	StForm 2009
CarbUpper	-0.34743	-0.42729	-0.66067	0.53437	0.43659	0.38957	0.2571	-0.55473	0.70356	0.7556	-0.34169	-0.63145
	0.0888	*0.0331*	*0.0003*	*0.0071*	*0.0329*	*0.0599*	*ns*	*0.004*	*<.0001*	*<.0001*	*0.0946*	*0.0007*
CarbLower	-0.3963	-0.45412	-0.58976	0.53288	0.42051	0.46632	0.32177	-0.43474	0.53974	0.61391	-0.16666	-0.47108
	0.0499	*0.0226*	*0.0019*	*0.0073*	*0.0407*	*0.0216*	*ns*	*0.0299*	*0.0054*	*0.0011*	*ns*	*0.0175*

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10.

Upper: upper crown; Lower: lower crown; Carb: foliar carbon concentration; DBH: diameter at breast height; Ht: tree height; CR: crown radii; StVol: stem volume; Incre: increment; DW: dry weight; BrFreq: branch frequency; AvgAng: average angle of living branches; AvgAngMax: average angle of the thickest branches in each one meter segment along the stem; AvgBDMax: average diameter of the thickest branches in each segment along the stem; StForm: stem form.

Table 4-13 Genotypic correlations among crown architectural traits of black walnut (*Juglans nigra* L.) clones.

	BrFreq	BrBasalArea	AvgAng	AvgBD	AvgAngMax	AvgBDMax	BrVol 2010	StVolPercen2010	StForm 2009
BrFreq	1	0.20786	-0.37476	-0.06784	-0.4375	0.12749	0.34423	0.3359	0.35248
		ns	*0.0649*	*ns*	*0.0287*	*ns*	*0.092*	*ns*	*0.084*
BrBasalArea		1	-0.27803	0.39697	-0.19473	0.6631	0.77605	-0.49321	0.24321
			ns	*0.0494*	*ns*	*0.0003*	*<.0001*	*0.0122*	*ns*
AvgAng			1	0.0476	0.88885	-0.02603	-0.38778	-0.14967	-0.52668
				ns	*<.0001*	*ns*	*0.0554*	*ns*	*0.0068*
AvgBD				1	0.01091	0.79889	0.55544	-0.15036	0.1682
					ns	*<.0001*	*0.0039*	*ns*	*ns*
AvgAngMax					1	-0.00993	-0.40713	-0.22501	-0.58129
						ns	*0.0434*	*0.2795*	*0.0023*
AvgBDMax						1	0.62289	-0.14377	0.11256
							0.0009	*ns*	*ns*
BrVol2010							1	-0.31721	0.5041
								ns	*0.0102*
StVolPercen2010								1	0.37779
									0.0626
StForm2009									1

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10.

BrFreq: branch frequency; BrBasalArea: branch basal area per meter of stem; AvgAng: average angle of living branches; AvgBD: average diameter of living branches; AvgAngMax: average angle of thickest branches per one meter segment along the stem; AvgBDMax: average diameter of the thickest branches along the stem; BrVol: total branch volume; StVolPercen: percentage of stem volume (out of total above ground wood volume); StForm: stem form.

Table 4-14 Genotypic correlations between crown architectural traits and other traits of black walnut (*Juglans nigra* L.) clones.

	DBH 2009	DBH 2010	DBH 2011	Ht 2009	Ht 2010	Ht 2011	CR 2009	CR 2010	CR 2011	Vol 2009	Vol 2010	Vol 2011
BrFreq	0.51492	0.51566	0.49501	0.30811	0.41622	0.36759	0.11967	-0.03533	0.33355	0.49462	0.51911	0.46975
	0.0084	*0.0083*	*0.0119*	*ns*	*0.0385*	*0.0772*	*ns*	*ns*	*ns*	*0.012*	*0.0078*	*0.0206*
BrBasalArea	0.56806	0.58535	0.59104	0.11307	0.11548	0.30242	0.691	0.65851	0.57634	0.45139	0.441	0.50088
	0.0031	*0.0021*	*0.0019*	*ns*	*ns*	*ns*	*0.0001*	*0.0003*	*0.0026*	*0.0235*	*0.0273*	*0.0127*
AvgAng	-0.5341	-0.53745	-0.51988	-0.40027	-0.39984	-0.46174	-0.42521	-0.1145	-0.17975	-0.4866	-0.47339	-0.48964
	0.006	*0.0056*	*0.0077*	*0.0474*	*0.0477*	*0.0231*	*0.0341*	*ns*	*ns*	*0.0136*	*0.0168*	*0.0152*
AvgBD	0.40665	0.45316	0.46965	0.45399	0.41717	0.46064	0.40046	0.43071	0.25756	0.46851	0.48489	0.50837
	0.0437	*0.0229*	*0.0178*	*0.0226*	*0.038*	*0.0235*	*0.0473*	*0.0316*	*ns*	*0.0182*	*0.014*	*0.0112*
AvgAngMax	-0.52804	-0.51782	-0.48924	-0.44264	-0.53228	-0.50227	-0.23102	-0.06119	-0.18927	-0.5256	-0.53849	-0.52505
	0.0067	*0.008*	*0.0131*	*0.0267*	*0.0062*	*0.0124*	*ns*	*ns*	*ns*	*0.007*	*0.0055*	*0.0084*
AvgBDMax	0.51343	0.53514	0.54704	0.35894	0.37599	0.46998	0.45724	0.46334	0.5128	0.51512	0.52404	0.55092
	0.0087	*0.0058*	*0.0047*	*0.0781*	*0.064*	*0.0205*	*0.0216*	*0.0197*	*0.0088*	*0.0084*	*0.0072*	*0.0053*
StForm2009	0.72881	0.73783	0.74375	0.64659	0.66651	0.71691	0.35968	0.13798	0.22987	0.75346	0.75477	0.75768
	<.0001	*<.0001*	*<.0001*	*0.0005*	*0.0003*	*<.0001*	*0.0774*	*ns*	*ns*	*<.0001*	*<.0001*	*<.0001*

Table 4-14 continued

	DBH2009 Incre	DBH2010 Incre	DBH2011 Incre	StVol 2009Incre	StVol 2010Incre	StVol 2011Incre	FruitNum2009	FruitNum2010	FruitNum2011	FruitDW	FruitSize	SeedDW	SeedSize
BrFreq	0.22681	0.25208	0.02361	0.46213	0.51498	0.24448	0.12458	0.12784	0.30933	-0.57147	-0.57154	-0.49294	-0.45825
	ns	*ns*	*ns*	*0.02*	*0.0084*	*ns*	*ns*	*ns*	*ns*	*0.0035*	*0.0035*	*0.0144*	*0.0243*
BrBasalArea	0.44986	0.37149	0.22031	0.46566	0.39115	0.55407	-0.18685	-0.19417	-0.09805	-0.04396	-0.14013	0.03037	-0.08371
	0.0241	*0.0675*	*ns*	*0.019*	*0.0532*	*0.005*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
AvgAng	-0.25201	-0.27609	-0.0428	-0.39807	-0.41811	-0.37721	-0.17131	0.00923	0.00041	0.39447	0.33158	0.32106	0.23205
	ns	*ns*	*ns*	*0.0487*	*0.0375*	*0.0692*	*ns*	*ns*	*ns*	*0.0565*	*ns*	*ns*	*ns*
AvgBD	0.41389	0.4594	0.28754	0.50469	0.46626	0.5139	-0.1006	0.27358	0.07534	-0.09491	-0.08497	0.04614	-0.01864
	0.0397	*0.0209*	*ns*	*0.0101*	*0.0188*	*0.0102*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
AvgAngMax	-0.19284	-0.19626	0.05069	-0.42596	-0.51747	-0.31176	-0.14519	-0.00893	-0.13526	0.40071	0.24316	0.33922	0.22127
	ns	*ns*	*ns*	*0.0337*	*0.0081*	*ns*	*ns*	*ns*	*ns*	*0.0523*	*ns*	*ns*	*ns*
AvgBDMax	0.37642	0.37021	0.28711	0.51467	0.48976	0.56624	-0.04995	0.13966	0.11848	-0.24709	-0.19695	-0.0828	-0.07527
	0.0637	*0.0685*	*ns*	*0.0085*	*0.013*	*0.0039*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
BrVol2010	0.6098	0.58939	0.38146	0.7337	0.74682	0.75656	-0.01627	0.03022	0.11467	-0.24453	-0.11874	-0.12854	-0.13268
	0.0012	*0.0019*	*0.0599*	*<.0001*	*<.0001*	*<.0001*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
StVolPercen2010	-0.09089	-0.11458	-0.11272	0.26888	0.32562	0.19417	0.44067	0.31042	0.416	-0.66111	-0.52724	-0.66866	-0.50062
	ns	*ns*	*ns*	*ns*	*ns*	*ns*	*0.0275*	*ns*	*0.0386*	*0.0004*	*0.0081*	*0.0004*	*0.0127*
StForm2009	0.55569	0.40203	0.27147	0.76575	0.69664	0.66597	0.15085	0.05032	0.10696	-0.52709	-0.3295	-0.48612	-0.34863
	0.0039	*0.0463*	*ns*	*<.0001*	*0.0001*	*0.0004*	*ns*	*ns*	*ns*	*0.0081*	*ns*	*0.016*	*0.095*

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10. BrFreq: branch frequency; BrBasalArea: branch basal area per meter of stem; AvgAng: average angle of living branches; AvgBD: average diameter of living branches; AvgAngMax: average angle of thickest branches along stem; AvgBDMax: average diameter of the thickest branches along the stem; BrVol: total branch volume; StVolPercen: Stem volume percentage out of total aboveground wood volume.

Table 4-15 Genotypic correlations among fruit traits of black walnut (*Juglans nigra* L.) clones.

	FruitNum2009	FruitNum2010	FruitNum2011	FruitDW	FruitSize	SeedDW	SeedSize
FruitNum2009	1	0.05374	0.67509	-0.44445	-0.40498	-0.41042	-0.33583
		ns	*0.0002*	*0.0296*	*0.0496*	*0.0464*	*0.1086*
FruitNum2010		1	0.03227	-0.16909	-0.14148	-0.08079	0.02445
			ns	*ns*	*ns*	*ns*	*ns*
FruitNum2011			1	-0.40501	-0.33736	-0.35814	-0.28008
				0.0496	*0.1069*	*0.0857*	*ns*
FruitDW				1	0.8338	0.92994	0.70876
					<.0001	*<.0001*	*0.0001*
FruitSize					1	0.80013	0.8148
						<.0001	*<.0001*
SeedDW						1	0.83623
							<.0001
SeedSize							1

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10.

FruitNum: fruit number; DW: dry weight.

Table 4-16 Genotypic correlations between fruit traits and other traits of black walnut (*Juglans nigra* L.) clones.

	DBH2009	DBH2010	DBH2011	Ht2009	Ht2010	Ht2011	HD2009	HD2010	HD2011	StVol 2009	StVol 2010	StVol 2011	StForm 2009
FruitNum2009	0.24436	0.21548	0.21429	0.31781	0.34444	0.3875	0.02304	0.14994	0.23332	0.27545	0.26882	0.30664	0.20486
	ns	*ns*	*ns*	*0.1216*	*0.0918*	*0.0614*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
FruitNum2010	0.10974	0.11068	0.10534	0.50258	0.43141	0.36058	0.39653	0.39407	0.35762	0.2684	0.24462	0.23946	0.11204
	ns	*ns*	*ns*	*0.0105*	*0.0313*	*0.0835*	*0.0497*	*0.0513*	*0.0862*	*ns*	*ns*	*ns*	*ns*
FruitNum2011	0.29242	0.30363	0.27535	0.20615	0.40689	0.40761	-0.17068	0.11824	0.10902	0.28408	0.36823	0.38444	0.1634
	ns	*ns*	*ns*	*ns*	*0.0435*	*0.048*	*ns*	*ns*	*ns*	*0.1687*	*0.0701*	*0.0636*	*0.4351*
NutDWeight	-0.59356	-0.59109	-0.59817	-0.49237	-0.58139	-0.60401	0.234	0.05309	0.04908	-0.5967	-0.61443	-0.61625	-0.52919
	0.0022	*0.0024*	*0.002*	*0.0145*	*0.0029*	*0.0018*	*ns*	*ns*	*ns*	*0.0021*	*0.0014*	*0.0013*	*0.0078*
NutSize	-0.47384	-0.4631	-0.4692	-0.26552	-0.30603	-0.3517	0.31991	0.22605	0.26055	-0.44534	-0.43495	-0.45301	-0.34215
	0.0193	*0.0227*	*0.0207*	*ns*	*ns*	*0.0919*	*ns*	*ns*	*ns*	*0.0292*	*0.0337*	*0.0262*	*0.1017*
SeedDWeight	-0.51657	-0.4944	-0.50008	-0.38454	-0.4752	-0.48543	0.25155	0.0522	0.06925	-0.52917	-0.52903	-0.53073	-0.46916
	0.0098	*0.0141*	*0.0128*	*0.0635*	*0.0189*	*0.0162*	*ns*	*ns*	*ns*	*0.0078*	*0.0079*	*0.0076*	*0.0207*
SeedSize	-0.45713	-0.43251	-0.459	-0.25082	-0.32304	-0.34087	0.31424	0.15672	0.25134	-0.45962	-0.44852	-0.46926	-0.33029
	0.0247	*0.0348*	*0.0241*	*ns*	*ns*	*0.1031*	*ns*	*ns*	*ns*	*0.0238*	*0.0279*	*0.0207*	*0.115*

Table 4-16 continued

	Ht2009 Incre	Ht2010 Incre	Ht2011 Incre	CR2009 Incre	CR2010 Incre	CR2011 Incre	StVol2009 Incre	StVol2010 Incre	StVol2011Incre	StVol Incre3yr	FruitNum3yr
FruitNum2009	0.23255	0.16046	0.12538	-0.16701	-0.40082	-0.1705	0.1156	0.23516	0.29802	0.29068	0.84614
	ns	*ns*	*ns*	*ns*	*0.0471*	*ns*	*ns*	*ns*	*ns*	*ns*	*<.0001*
FruitNum2010	0.62941	0.07088	-0.20703	-0.37379	-0.08523	-0.15166	0.29961	0.18473	0.10006	0.17006	0.36728
	0.0007	*ns*	*ns*	*0.0657*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*0.0775*
FruitNum2011	0.0108	0.50252	0.03034	-0.00586	-0.38592	0.24004	0.11122	0.46089	0.29732	0.42812	0.8573
	ns	*0.0105*	*ns*	*0.9778*	*0.0567*	*ns*	*ns*	*0.0204*	*ns*	*0.0369*	*<.0001*
FruitNum3yr	0.36806	0.369	0.00776	-0.19467	-0.36909	0.16577	0.261	0.45994	0.35157	0.43895	1
	0.0768	*0.076*	*ns*	*0.362*	*0.0759*	*ns*	*ns*	*0.0237*	*0.0921*	*0.0319*	
FruitDW	-0.13641	-0.43699	-0.12229	0.50811	0.18802	-0.1422	-0.53202	-0.58736	-0.54038	-0.5991	-0.4865
	ns	*0.0327*	*ns*	*0.0112*	*ns*	*ns*	*0.0075*	*0.0025*	*0.0064*	*0.002*	*0.0159*
FruitSize	-0.21983	-0.22912	-0.15693	0.45103	0.17416	0.03903	-0.40675	-0.38313	-0.43088	-0.4274	-0.42194
	ns	*ns*	*ns*	*0.027*	*ns*	*ns*	*0.0486*	*0.0646*	*0.0356*	*0.0372*	*0.04*
SeedDW	-0.08335	-0.40734	-0.07284	0.48708	0.2242	-0.12	-0.48613	-0.48396	-0.45366	-0.4963	-0.41631
	ns	*0.0482*	*ns*	*0.0158*	*ns*	*ns*	*0.016*	*0.0166*	*0.026*	*0.0136*	*0.043*
SeedSizeume	-0.16054	-0.2988	-0.09893	0.33431	0.08721	0.05226	-0.43334	-0.39511	-0.47188	-0.44621	-0.31196
	ns	*ns*	*ns*	*ns*	*ns*	*ns*	*0.0344*	*0.056*	*0.0199*	*0.0288*	*0.1378*
StVolIncre3yr	0.3154	0.5861	0.33323	-0.18743	0.02649	0.21068	0.8285	0.95639	0.93896	1	0.43895
	ns	*0.0026*	*ns*	*ns*	*ns*	*ns*	*<.0001*	*<.0001*	*<.0001*		*0.0319*

First row: Pearson correlation coefficients; second row: p-values. *ns*: insignificant, p>0.10. FruitNum: fruit number; DW: dry weight; DBH: diameter at breast height; Ht: tree height; HD: ratio of tree height to DBH; StForm: stem form; Incre: increment; CR: crown radius. 3yr: within three years from 2009 to 2011.

4.8 Figures

Figure 4-1 Leaf flush stages of black walnut (*Juglans nigra* L.)

1. Dormant; 2. Bud swell; 3. Green tip; 4. Leaf burst; 5. Leaf expansion (photo credit: Guillermo Pardillo)

CHAPTER 5. CULTIVAR IDENTIFICATION AND GENETIC RELATEDNESS AMONG 25 BLACK WALNUT (*JUGLANS NIGRA* L.) CLONES BASED ON MICROSATELLITE MARKERS

5.1 Introduction

Black walnut is a highly valuable timber species that is planted widely in the eastern USA. The genetic improvement program of black walnut at Purdue University was initiated in 1967, and a clone bank of numerous black walnut genotypes was established (Beineke, 1983, 1989). This clone bank contained genotypes from various parts of Indiana and other U.S. states.

Accurate and fast cultivar identification is particularly important for vegetatively propagated commercial species for the purpose of improving the efficiency of breeding and protection of property rights (Nicese et al., 1998). Numerous molecular techniques have been developed to verify cultivar identification, conduct parentage analysis, and evaluate genetic correlation among walnut cultivars (Dangl et al., 2005). These techniques include isozymes (Arulsekar et al., 1985; Solar et al., 1994), restriction fragment – length polymorphism (RFLP) (Fjellstrom and Parfitt, 1994), randomly amplified polymorphic DNA (RAPD) (Nicese et al., 1998), and microsatellite (simple sequence repeats, SSR) markers (Woeste et al., 2002). Microsatellite markers developed by Woeste et al.(2002) have been widely used in genetics studies of walnut (*Juglans* spp.) (Dangl et al., 2005; Zhao et al., 2013; Parks et al., 2014). These molecular techniques will help genetically characterize commercial plant species with higher accuracy than traditional methods that rely on the evaluation of phenological and morphological traits that are usually time consuming and subject to large errors due to the environmental effects (Weising et al., 1994; Nicese et al., 1998).

The goals of this study were to 1) use microsatellite markers to verify the clonal identities of 212 black walnut trees that belonged to 25 clones; 2) examine the genetic relatedness of 25 black walnut clones; and 3) determine the level of correspondence between genotypic and phenotypic clusters of 25 black walnut clonal selections.

5.2 Materials and Methods

5.2.1 Materials

Twenty – five clones planted in a plantation in West Point, IN, were from the Purdue University Black Walnut Improvement Program and a commercial company. Five to ten trees were randomly chosen from each clone, and there were 212 trees in total. See Chapter 4 for more details about these clones.

5.2.2 Genomic DNA extraction

DNA extraction followed the procotol described in Zhao et al. (2011). Fresh leaf samples were collected from each tree, put in plastic bags, and then placed in a cooler in the field. Then leaves were stored at 4 °C in a refrigerator. The leaf sample (about 100 mg) was cut into small pieces and then put into a screw-cap tube with a ceramic bead. CTAB buffer containing 2- mercaptoethanol (2%) was heated in a hybridization oven to 65 °C for 10 minutes. One mL of CTAB buffer was then added into the DNA extraction tube containing the sample. Tubes were placed in a FastPrep tissue grinder (BioSavant®), shaken three times at speed setting of 4.0 for 30 seconds each time to grind the leaf samples. Tubes were then incubated in hybridization oven at 50 °C for 30 minutes.

Tubes were centrifuged 15 minutes at 14000 RPM, and supernatant (600 – 700 μL) was extracted and transferred to a 1.5 mL Eppendorf centrifuge tube with 350 μL of phenol: chloroform: isoamyl alcohol (25: 24: 1). Tubes were centrifuged 5 minutes at 14000 RPM, and then supernatant was transferred to a new centrifuge tube with 400 μL of chloroform. Then tubes were shaken thoroughly and centrifuged at 14000 RPM for 5 minutes. The chloroform extraction was then repeated. Supernatant (about 500 μL) was transferred to a new tube, and 250 μL of 50% sodium acetate (3M) and 750 μL of 4 °C isopropanol were added to the tube, mixed briefly, then put into -20 °C freezer 10 minutes, and centrifuged 30 minutes at 4 °C at 14000 RPM for DNA precipitation.

After discarding the supernatant, DNA pellets were washed with 400 μL of 70% ethanol and centrifuged at 14000 RPM for 3 minutes. DNA pellets were washed twice. Ethanol was discarded and tubes (with DNA pellets) were air dried. Then DNA was re-suspended with 100 μL of TE buffer (pH= 8.0). Quality of DNA was assessed using 2% agarose gel, and the concentration of DNA was quantified by a Nanodrop® – 800 spectrophotometer (Thermo Scientific, Wilmington, Delaware).

5.2.3 PCR amplification

Twelve pairs of primers (Integrated DNA Technologies®, Table 5-1) from Woeste et al. (2002) were selected to fingerprint these 25 black walnut clones. Genomic DNA was diluted to 50 – 100 ng·μL^{-1}. Polymerase chain reactions were performed in a volume of 15 μL in 96-well plates, containing 1.5 uL of 2 mM dNTPs (GeneMate), 1.5 μL of 1 mg·mL^{-1} bovine serum albumin (BSA), 1.5 μL of 1× *Taq* buffer, 1.5 μL of 1 mM MgCl2, 1.5 μL of 10 μM reverse primer, 0.3 μL of 10 μM forward primer, 1.5 μL of 10 μM M13 tag with FAM or HEX fluorescent (Schuelke, 2000), 0.5 μL of 5 units·μL^{-1} *Taq* polymerase, 1 μL of genomic DNA, and 4 μL of nanopure water. The thermal cycle procedure for all primers was 3 minutes at 94 °C, 35 cycles of 45 seconds at 94 °C, 1 minute at 55 °C, and 45 seconds at 72 °C, then ending with one cycle of 5 minutes at 72 °C. Size multiplexing, which combines different markers with non-overlapping size ranges (Dangl et al., 2005), was used with color multiplexing (FAM and HEX).

PCR products were diluted using nano pure water to 1/20 of its original concentration. One μL of diluted PCR product with 14 μL of formamide: rox (67: 3) added mixed, the DNA was denatured by heating at 95 °C for 5 minutes, snap cooled, and then submitted to Purdue Genomic Center for analysis with an ABI 3700 sequencer (Applied BioSystems).

5.2.4 Data analysis

Allele peaks were marked using GeneMapper v3.7.1 (Applied BioSystems), with a few samples from genotype Purdue 1 as positive controls in each plate. Errors with 2 bp difference in allele size were allowed when binning and labeling the allele peaks. A pair wise genetic distance (Ds) matrix was generated using GenAlEx 6.41 (Peakall and Smouse, 2006), following Nei (1978). Then A cluster dendrogram based on the pair wise genetic distance was prepared by NTSYSpc 2.0 (Rohlf, 1997) using neighbor – joining tree method. Two dendrograms were constructed using PROC Cluster and PROC Tree in SAS 9.3 (SAS Inc., Carey, North Carolina), following the average linkage method (Sokal and Michener, 1958), with one of them based on the crown architecture traits, and the other one based on tree size and form traits. The crown architecture traits were clonal means of each tree's average branch angle, branch frequency, branch diameter, and branch basal area per meter of stem; the tree size and from traits included clonal mean of DBH (diameter at breast height, 1.37m), tree height, crown radii, the ratio of tree height to DBH (HD ratio), and stem form. See chapter 4 for detailed information of the measurement of these traits.

5.3 Results and discussion

5.3.1 Success and failure of the twelve microsatellite markers

The visualization of allele peaks at loci WAG06, WAG24, WAG69, and WAG90 was not successful. Among them, WAG06, WAG24, and WAG90 had multiple (more than three) allele peaks; thus it was difficult to make allele calls. Touchdown PCR may be tried for WAG24, WAG69, and WAG90 and see if two clear allele peaks can be obtained. WAG69 is known to contain a null allele, so allele size was hard to determine. Thus only eight markers were left for analysis. WAG32, WAG27, WAG86, WAG89, and WAG97 were more polymorphic than WAG72 and WAG76 based on their number of alleles observed in these 25 clones (Table 5-3).

5.3.2 Cultivar identification

Several trees were found to be wrongly labeled based on the allele sizes (Table 5-2) at the eight loci. BD111 was labeled as C55 (Purdue 1), and BM111 was marked as C703, however, their genotypes matched that of clone C707. AS115 was labeled as C728, but its genotype did not match other trees of C728 nor any other clones. AY138 and AZ130 were both recorded as C716, but their genotypes were different from other trees in C716. It was seen from the allele sizes that AY138 and AZ130 shared the same genotype, so they were temporarily named C777, a clone that was not in the original list. Trees of C704 were found identical to C715. These results were in accordance with the phenological observations recorded for each clone from 2009 and 2010 (see Chapter 4). Thus there were still 25 genotypes in total and the mislabeled trees mentioned above were corrected before further analysis.

5.3.3 Genetic relatedness among 25 black walnut clones

A genetic dengrogram can summarize microsatellite data as well as reveal the genetic relationships among tested cultivars (Dangl et al., 2001). It is known that C55 (Purdue-1) was the mother of C710, C714, C718, and C730; C130 (Tippecanoe-1) was the mother of C715. All these relationships were correctly revealed by the genetic distance dendrogram (Figure 5-1), which was built on the genetic distance matrix (Table 5-4). According to previous breeding records, C702 and C707 shared one mother – BW95, which was not among the clones in this study. They were not grouped closely, however, like the half siblings of C55 mentioned above. It may be because they inherited different alleles from their mother at some of the eight loci or it may be that at least one of them is incorrectly assigned as an offspring of BW95. The genotype of BW95 will need to be compared with both C702 and C707 to obtain more information. C55 and C702 were also closely related – they shared one allele at all eight loci (Table 5-2), indicating C55 may be the sire of C702, considering C702's mother was known to be BW95 as mentioned above. C705 and C728 shared one allele at each locus, indicating close consanguinity.

5.3.4 Genetic relatedness and phenotypic relatedness

The crown architecture dendrogram (Figure 5-2) revealed some relatedness among clones. C705 and C728 were closely related (Ds=6, Table 5-4) and they also had similar crown architecture traits. C702 and C707 were half siblings and they were grouped in one crown architecture cluster at a distance of 0.52. Half siblings C718, C710, and C714 were close to each other, with C718 and C710 more closely clustered. C55, as the mother of C730, and possible father to C702, was located near C730 and C702 in the crown architecture dendrogram as well. C716 was near C714, C718, and C710, as it was in the genetics dendrogram. It was surprising that C715, as an offspring to C130, was far from C130 in these three branch attributes as revealed by Figure5-2. The separation of these clones in the dendrogram makes sense, however, because C715 had significantly larger branch frequency and smaller branch angle than its mother C130 (see chapter 3 and 4).

The tree size and form dendrogram was constructed based on the DBH, tree height, crown radii, and stem form that measured between 2009 and 2011. Although C715 and C130 were unlike each other in branch characteristics as shown in the crown architecture dendrogram, they were grouped in one cluster in this dendrogram, indicating C715 inherited size and form from its mother but not the branch structure. C702 and its half sibling C707 were clustered closely, C718 was close to its mother C55, and C702 was near its potential father C55 too. C710 was grouped closely to its mother C55, albeit a little further than the distance between its half sibling C718 and their mother C55. Among all the half siblings, C714 was furthest from its mother C55, because C714 was significantly larger than C55 in DBH, tree height, and crown radii than C55. C716 clustered close to C710, C718, and C55, as it did in the genetics dendrogram. Again, C728 and C705, two clones that were closely related, were not far apart in this tree size and form dendrogram.

The genetic dendrogram showed that these eight molecular markers had the ability to distinguish genetically related clones from less related ones. The comparison between the three dendrograms revealed that crown architecture traits and tree size and form traits were able to group genetically related clones together, but not as well as the genetic dendrogram which was based on microsatellite markers. This makes sense because growth is a process of deviation – amplifying (Stage, 1987) and thus phenotypic traits cannot be as stable as molecular markers. Because the clones were in a plantation with homogenous soil and management regime, the crown architecture and tree size and form traits were able to group genetically related clones together because the effect of environmental factors was reduced to the minimum.

By adding more microsatellite markers and more black walnut clones involved in the genetic improvement program, more genetic relations among these clones may be revealed.

5.4 References

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5.5 Tables

Table 5-1 Characteristics of 12 microsatellite markers used to genotype 25 black walnut (*Juglans nigra* L.) clones

	Microsatellite Loci	Primer Sequence (5' - 3')	Allele Size Range
1	WAG 06	F: CCATGAAACTTCATGCGTTG	134-172
		R: CATCCCAAGCGAAGGTTG	
2	WAG 32	F: CTCGGTAAGCCACACCAATT	163-217
		R: ACGGGCAGTGTATGCATGTA	
3	WAG 72	F: AAACCACCTAAAACCCTGCA	135-159
		R: ACCCATCCATGATCTTCCAA	
4	WAG 27	F: AACCCTACAACGCCTTGATG	199-245
		R: TGCTCAGGCTCCACTTCC	
5	WAG 69	F: TTAGTTAGCAAACCCACCCG	164-188
		R: AGATGCACAGACCAACCCTC	
6	WAG 82	F: TGCCGACACTCCTCACTTC	140-234
		R: CGTGATGTACGACGGCTG	
7	WAG 76	F: AGGGCACTCCCTTATGAGGT	228-254
		R: CAGTCTCATTCCCTTTTTCC	
8	WAG 90	F: CTTGTAATCGCCCTCTGCTC	142-178
		R: TACCTGCAACCCGTTACACA	
9	WAG 24	F: TCCCCCTGAAATCTTCTCCT	222-248
		R: TTCTCGTGGTGCTTGTTGAG	
10	WAG 86	F: ATGCCTCATCTCCATTCTGG	208-250
		R: TGAGTGGCAATCACAAGGAA	

Table 5-1 continued

11	WAG 89	F: ACCCATCTTTCACGTGTGTG	179-233
		R: TGCCTAATTAGCAATTTCCA	
12	WAG 97	F: GGAGAGGAAAGGAATCCAAA	149-189
		R: TTGAACAAAAGGCCGTTTTC	

Note: Sequence of M13 tag: AGTAAAACGACGGCCAGT; F: forward; R: reverse.

Table 5-2 Allele sizes (in base pairs) at eight microsatellite loci for 25 black walnut (*Juglans nigra* L.) clones

Clone	WAG32		WAG86		WAG72		WAG82*		WAG27		WAG89		WAG76		WAG97	
C130	183	185	222	222	146	146	172	182	217	227	199	209	230	238	171	189
C55	169	191	222	240	146	146	182	190	225	229	197	197	232	236	155	161
C700	181	181	220	232	144	144	168	178	223	227	209	211	232	236	163	169
C701	179	189	216	226	146	146	194	196	221	227	185	219	230	236	155	161
C702	189	191	228	240	146	146	162	190	225	229	191	197	232	236	159	161
C703	171	171	222	236	144	146	184	196	221	225	189	197	236	236	155	173
C705	181	187	216	238	146	148	178	182	213	213	201	213	232	232	157	161
C707	181	181	222	224	146	148	190	196	221	233	209	211	232	236	155	169
C708	187	195	232	238	146	146	178	180	221	221	211	217	232	238	159	161
C709	177	199	212	232	144	144	.	.	219	221	189	209	232	234	163	171
C710	181	191	214	240	146	152	170	184	221	229	197	209	230	236	161	173
C712	179	183	214	222	146	146	176	194	241	241	195	207	230	236	161	161
C713	183	193	216	224	144	144	194	200	211	219	191	209	236	236	157	159
C714	169	173	234	240	146	146	176	182	221	229	187	197	232	232	155	161
C715	181	183	222	230	146	146	182	194	211	217	199	209	232	238	161	189
C716	169	169	222	222	146	146	182	206	223	225	197	201	230	236	155	173
C717	169	181	222	230	146	158	178	200	221	221	187	187	230	236	167	173
C718	171	191	220	222	146	146	168	182	223	229	197	207	232	234	155	163
C719	183	214	222	250	146	156	.	.	211	241	187	199	234	234	163	167
C720	175	207	214	238	146	146	166	180	211	223	201	215	230	232	153	155
C726	179	189	214	216	146	154	.	.	219	219	199	211	230	236	159	167
C728	181	181	216	228	146	146	178	194	213	213	197	213	232	232	161	173
C729	183	197	214	222	144	150	168	188	225	225	205	205	232	236	161	169
C730	169	187	216	222	146	152	182	190	221	229	197	209	232	236	155	175
C777	181	212	220	236	144	152	162	178	211	225	169	191	232	232	133	149

*C709, C719, and C726 were not successfully amplified by primer WAG82, therefore their allele sizes were missing.

Table 5-3 Frequencies of obverserved alleles at eight microsatellite loci based on 25 black walnut (*Juglans nigra* L.) clones (number of alleles observed for each loci was in parenthesis under locus name)

Locus	Allele size (base pair)	Frequency	Locus	Allele size (base pair)	Frequency
WAG32	169	0.120	WAG89	169	0.020
(19)	171	0.060	(17)	185	0.020
	173	0.020		187	0.080
	175	0.020		189	0.040
	177	0.020		191	0.060
	179	0.060		195	0.020
	181	0.220		197	0.200
	183	0.120		199	0.080
	185	0.020		201	0.060
	187	0.060		205	0.040
	189	0.060		207	0.040
	191	0.080		209	0.160
	193	0.020		211	0.080
	195	0.020		213	0.040
	197	0.020		215	0.020
	199	0.020		217	0.020
	207	0.020		219	0.020
	212	0.020	WAG76	230	0.160
	214	0.020	(5)	232	0.380
WAG86	212	0.020		234	0.080
(15)	214	0.100		236	0.320
	216	0.120		238	0.060
	220	0.060	WAG97	133	0.020
	222	0.280	(14)	149	0.020
	224	0.040		153	0.020
	226	0.020		155	0.180
	228	0.040		157	0.040
	230	0.040		159	0.080
	232	0.060		161	0.240
	234	0.020		163	0.080
	236	0.040		167	0.060
	238	0.060		169	0.060
	240	0.080		171	0.040
	250	0.020		173	0.100
WAG72	144	0.180		175	0.020
(8)	146	0.640		189	0.040
	148	0.040	WAG82	162	0.045
	150	0.020	(16)	166	0.023
	152	0.060		168	0.068
	154	0.020		170	0.023
	156	0.020		172	0.023
	158	0.020		176	0.045
WAG27	211	0.100		178	0.136

Table 5-3 continued

(11)	213	0.080	180	0.045
	217	0.040	182	0.182
	219	0.080	184	0.045
	221	0.220	188	0.023
	223	0.080	190	0.091
	225	0.140	194	0.114
	227	0.060	196	0.068
	229	0.120	200	0.045
	233	0.020	206	0.023
	241	0.060		

Table 5-4 . Pair wise genetic distance among 25 black walnut (*Juglans nigra* L.) clones based on the allele information at eight microsatellite loci, calculated by GenAlEx 6.41.

C130	C55	C700	C701	C702	C703	C705	C707	C708	C709	C710	C712	C713	C714	C715	C716	C717	C718	C719	C720	C726	C728	C729	C730	C777	
0																									C130
13	0																								C55
18	18	0																							C700
13	12	17	0																						C701
15	5	17	11	0																					C702
16	11	16	12	13	0																				C703
17	14	15	15	14	19	0																			C705
14	12	10	12	13	12	13	0																		C707
15	14	16	12	12	16	12	13	0																	C708
18	19	12	18	18	16	18	16	16	0																C709
14	9	14	11	9	11	15	11	13	16	0															C710
13	13	20	10	13	16	17	16	15	21	12	0														C712
18	18	13	15	15	14	18	15	19	14	15	17	0													C713
15	6	18	12	9	15	12	13	11	17	11	14	20	0												C714
6	11	15	12	12	16	12	11	12	17	12	11	15	11	0											C715
11	7	19	13	13	11	17	14	17	21	13	14	19	12	13	0										C716
15	15	16	13	16	13	17	12	13	18	11	16	17	13	14	12	0									C717
12	7	14	13	10	12	14	13	14	16	12	14	19	9	11	10	16	0								C718
14	17	19	17	17	18	19	17	18	13	17	15	18	17	13	17	15	13	0							C719
14	13	17	12	13	16	13	14	12	18	13	14	18	12	12	12	16	11	16	0						C720
16	17	18	12	14	17	18	16	16	14	14	15	14	18	16	17	16	17	13	15	0					C726
18	13	15	14	12	18	6	13	14	20	13	16	20	12	11	17	16	14	20	15	19	0				C728
17	14	14	17	14	14	17	15	18	17	15	15	15	17	15	16	18	16	18	17	18	19	0			C729
12	6	15	11	10	11	12	9	12	15	9	15	14	8	11	9	12	9	16	13	15	14	15	0		C730
19	16	11	18	13	16	13	14	16	15	15	20	15	15	14	19	17	15	18	15	19	14	14	14	0	C777

5.6 Figures

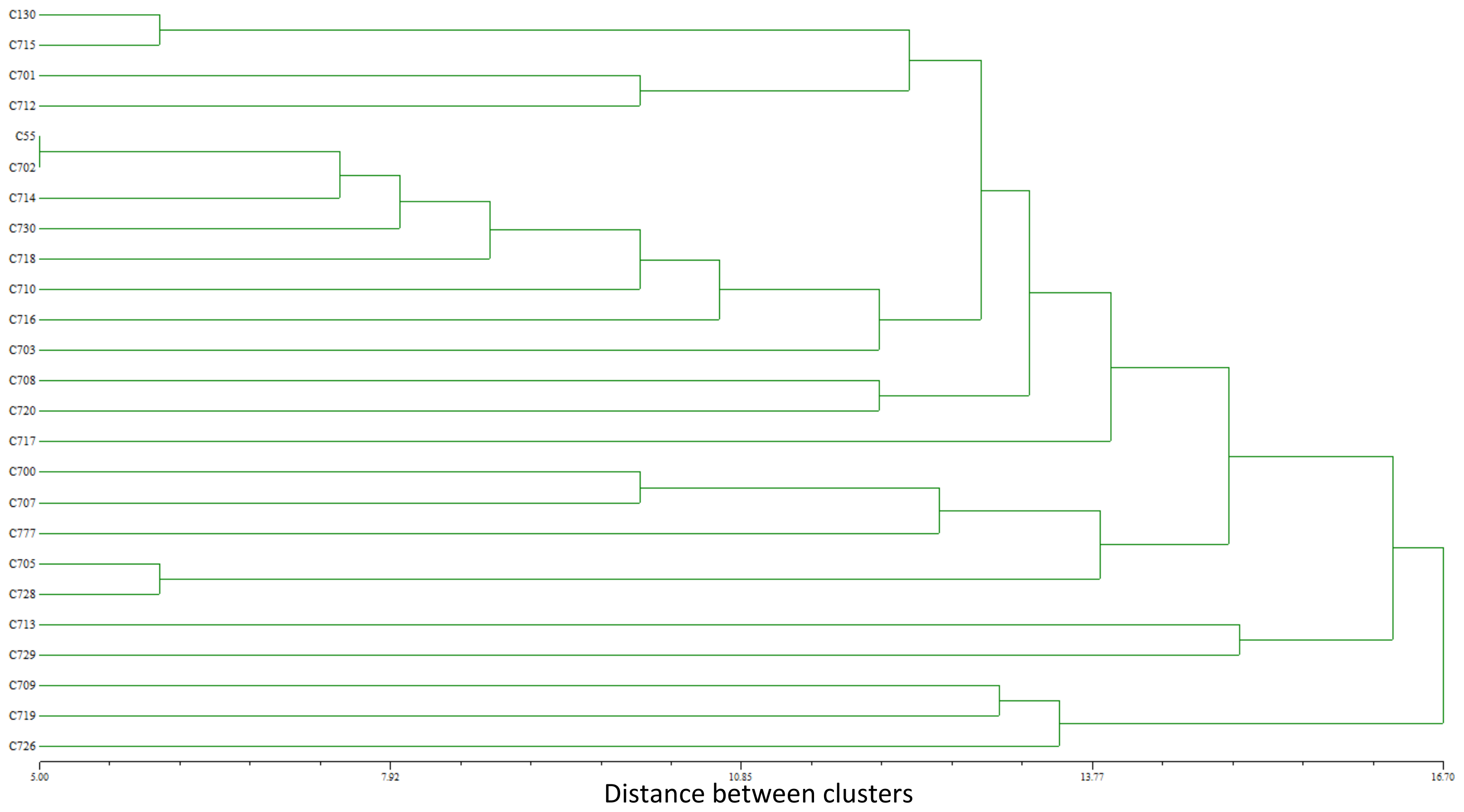

Figure 5-1 Dendrogram generated using cluster analysis based on the proportion of shared alleles among 25 black walnut (*Juglans nigra* L.) genotypes by NTSYSpc 2.0

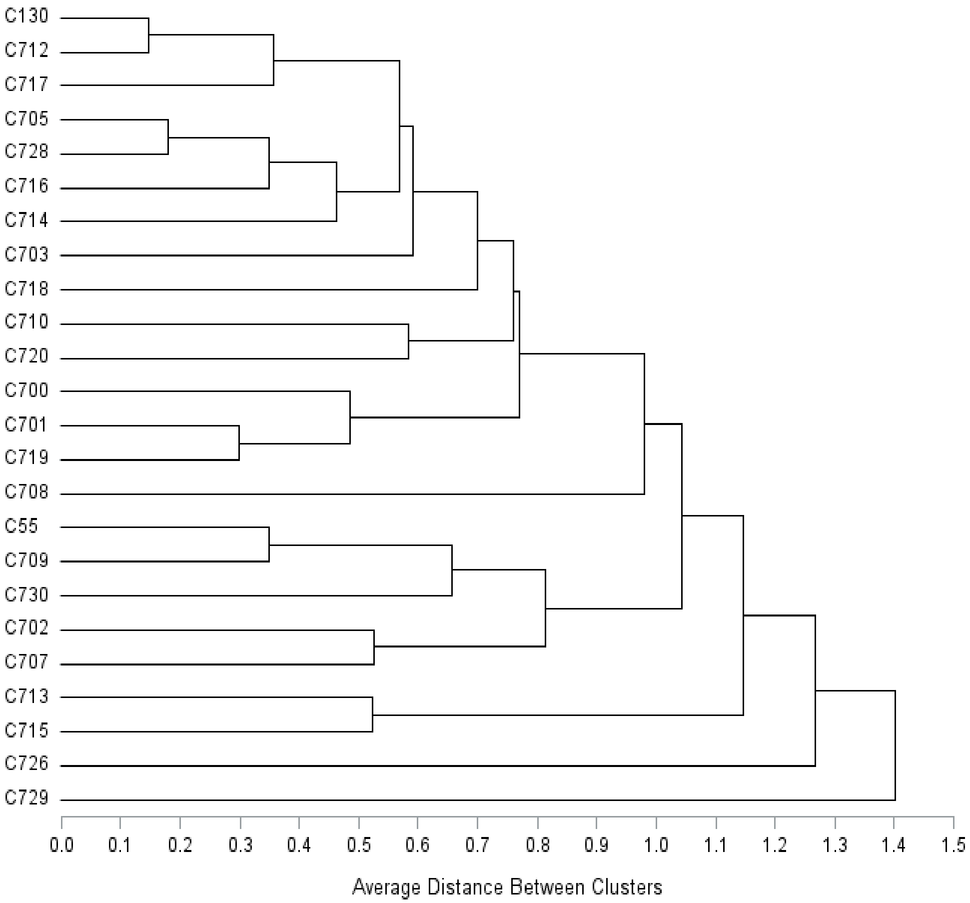

Figure 5-2 Dendrogram generated using cluster analysis based on crown architectural traits of 25 black walnut (*Juglans nigra* L.) genotypes

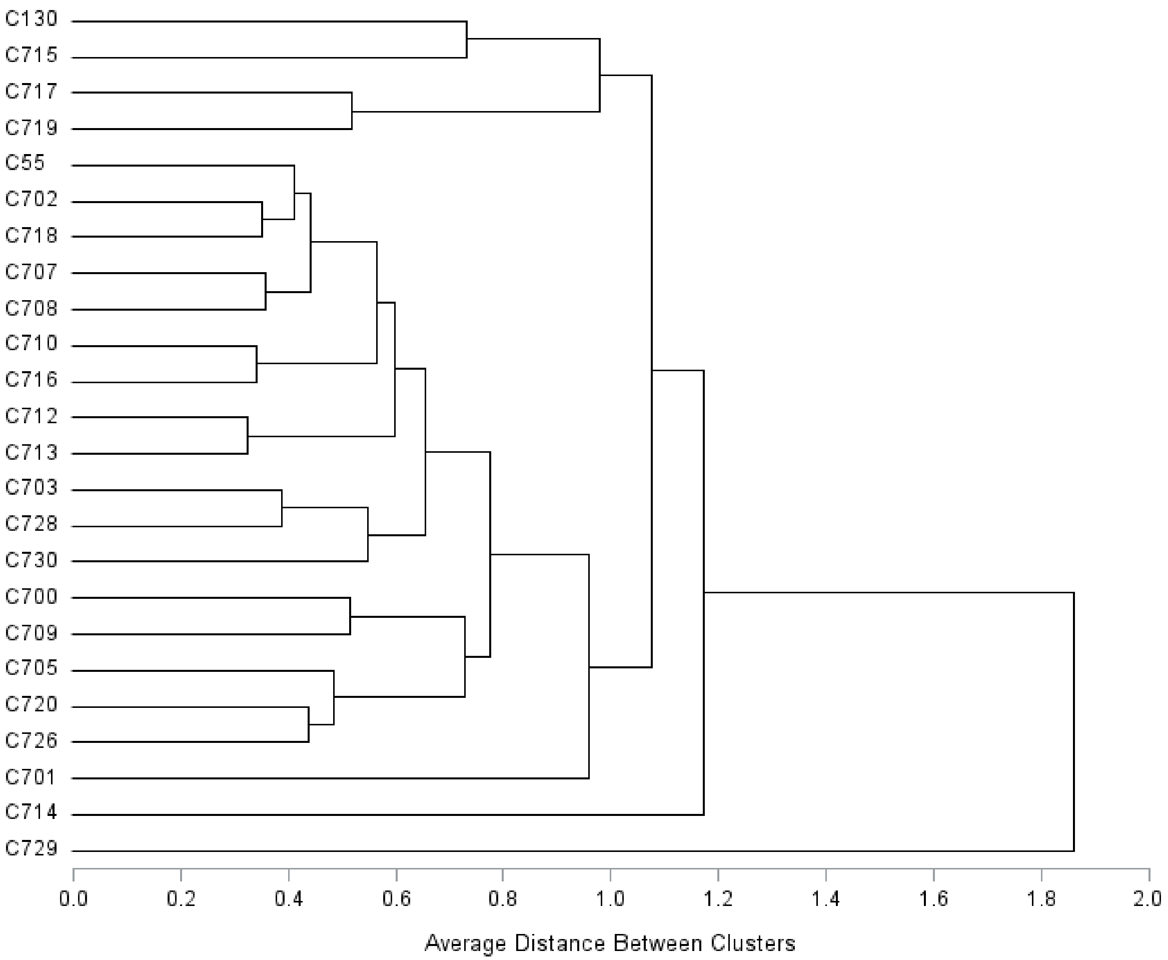

Figure 5-3 Dendrogram generated using cluster analysis based on tree size and form traits of 25 black walnut (*Juglans nigra* L.) genotype

CHAPTER 6. SUMMARY, CONCLUSIONS, AND FUTURE DIRECTIONS

Timber has been a major product for black walnut grown in Central Hardwood Region in the USA, and it can be produced more efficiently if the best crown ideotype of a timber species is known to us. To define crown ideoypes for black walnut grown in intensively managed timber plantations, the following investigations were conducted on 25 genetically improved black walnut clones:

6.1 Foliage area and mass models at both branch- and tree- level, and stem growth efficiency

Foliage area and mass models were developed at branch-level first, as a way to estimate foliage area and mass at tree-level by the branch summation method, so that growth efficiency of different clones could be analyzed. Tree-level foliage models were then developed for these black walnut clones. The results showed that within the black walnut population in this study, stem volume increment increased as total leaf area of a tree (TLA) increased, however, growth efficiency declined as total leaf area (TLA), leaf area index (LAI) and foliage density index (FDI) increased. Genotypic effect was significant as evidenced by the results that some clones had both high stem volume increment (absolute growth) and high growth efficiency (C714), some clones had growth efficiency but moderate stem volume growth (C55), and some other clones were low in both stem volume increment and growth efficiency (C717 etc.). The high growth efficiency of some clones was also reflected in their branch-level and tree-level foliage area and mass models, i.e., they used less amount of foliage to sustain larger branches, larger stem diameter, and wider crown than those clones with low growth efficiency. The implications from the results are: 1) although more foliage leads to higher stem growth in general for this population, it is the right amount of foliage that matters, because excessive foliage may create more mutual shading, thus lowering the growth efficiency; and 2) the branch- and tree-level models of the high-efficiency clones indicate these clones may have had crown architecture (leaf arrangement and branch arrangement) that enabled better light penetration and light use efficiency than the low-efficiency clones. Therefore, foliage area and mass models and growth efficiency, i.e., how effectively each clone utilizes its foliage, will be of great importance in defining crown ideotypes for black walnut.

The foliage models also indicated that branch diameter is the strongest predictor for branch-level foliage area and mass, and likewise, DBH is the strongest predictor for tree-level leaf area. Adding branch position variables or an angle variable improved the precision of branch-level models, and adding crown radius increased the prediction power of tree-level models.

6.2 Branch attributes models and carbon allocation between branches and stem

Branch attributes are related to both tree growth and quality. The following branch attributes were modeled to quantitatively characterize the crown architecture of the 25 black walnut clones: 1) maximum branch diameter in a segment along the stem; 2) relative branch diameter in a segment along the stem; 3) one-year radial growth of branches; 4) branch insertion angle; 5) first – order branch length; 6) branch frequency; and 7) density of branch basal area.

Genotypic effects were significant as reflected in the clonal coefficients in the branch attributes models. The results showed that, for instance, some clones tended to have high branch frequency, while the accumulated branch basal area per unit of stem length was low. Because branch frequency is positively correlated with stem growth, then the result mentioned above means that those clones may be the ideal that tend to produce high stem volume with relatively low bole defects. Similarly to the aforementioned correlation between total tree leaf area and stem volume increment, stem volume increased as total branch volume increased. The ratio of stem volume to total branch volume, being regarded as a carbon allocation ratio, however, decreased as branch volume increased. Nevertheless, some clones have both high branch volume and relatively high carbon allocation ratio. This means that although these clones had large branch volume, there had been more carbon allocated to the stem, and therefore, they are more efficient than other clones with lower carbon allocation ratios. Based on these branch attributes and carbon allocation ratios, clone C55 (Purdue 1) was the most efficient clone, and its offspring C714 was the most productive clone with a relative high efficiency. These branch characteristics models and the carbon allocation pattern they revealed are also essential in determining crown ideotypes for black walnut.

As for the models, branch and segment position within a crown were major predictors for branch characteristics, while branch angle also influenced branch allometry. DBH was the most useful tree-level predictor for branch attributes. These models can be used to assess black walnut wood quality as well as build a simulation system for intensively managed black walnut in clonal forestry in Central Hardwoods Region.

6.3 Variation in and heritability of various traits and the phenotypic correlations among them

The population of the black walnut clones in this study varied greatly for a number of traits in phenology, morphology, physiology. Among these traits, the following had medium to high repeatabilities (broad sensed heritability): specific leaf area, leaf area and mass of individual leaves, foliar nitrogen and carbon concentration, DBH, tree height, HD ratio (tree height: DBH), percentage of stem volume out of total above ground volume, stem form, number of fruits produced, size and weight of fruits and seeds, average branch angle, branch frequency, leaf flush dates, pistillate bloom dates, and pollen shed dates. Correlations among these traits were revealed, and some traits were found to be correlated to timber production, fruit production, and size of fruits and seeds. Important implications from these correlations are: 1) Leaf area (ILA) and mass (ILM) of individual leaves in the upper crown may be better indicators for tree vigor than specific leaf area (SLA); 2) foliar carbon concentration in both upper and lower crown in second half of July and early August can be used as indicators for stem growth and dry weight and size of fruits; 3) phenological events leaf flush dates and first pollen shed dates were strongly interrelated to each other, indicating some evidence for the presence of epistasis among these traits, or a linkage block. Meanwhile, these traits may be indicators for crown architecture, stem growth, and fruit production because the strong correlation among them; 4) crown architecture traits such as branch frequency, average branch diameter, and average branch angle were strongly correlated with stem growth and fruit production; and 5) the long – term correlation between stem growth and reproduction tended to be positive, however, the size and weight of individual fruits and seeds were negatively correlated with stem size and growth, indicating size of fruits and seeds are potential indicators for stem growth.

Overall, the heritability of and correlations among important traits are important information for defining black walnut ideotypes for both timber and fruit production. Future black walnut programs may focus on improving the traits that had both high heritability and strong correlation with growth and nut production. Quantitative trait loci (QTL) mapping may be used to study the genetic basis of correlations among traits at a greater depth.

6.4 Molecular characterization, genetic relatedness, and phenotypic relatedness

Microsatellite markers were useful in fingerprinting cultivars and determine genetic relatedness among them. A few mislabeled trees were verified because they showed different allele sizes on eight loci. In addition to verifying known pedigrees, some other closely related clones were revealed by the eight markers: clone C55 may be the sire of C702, and C705 and C728 are closely related. A genetic dendrogram constructed based on the eight markers was able to distinguish genetically related clones from less related ones. Crown architecture traits and tree size and form traits were also able to group genetically related clones together. By adding more microsatellite markers and more black walnut clones involved in the genetic improvement program, more genetic relations among these clones may be revealed. Knowing the molecular characteristics and genetic relatedness will be of great aid for black walnut breeding program in the future.

6.5 Does proposed timber ideotype for black walnut in Chapter 1 work?

Based on the investigations on foliage models, crown architecture pattern, and the broad sense heritability of some traits, and the genotypic correlations between these traits and growth or quality, the proposed black walnut ideotype in chapter 1 needs to be revised. The hypothesize traits that need to be revised are listed below:

1. The hypothesis that less fruit production would lead to more timber growth is wrong, since it has been proven that for the population of black walnut in this study, vegetative growth and fruit production (number of fruits produced both in each year and in a three-year period) was positively correlated. Correspondently, those clones that produced large number of fruits should also have had more pistillate flowers, high rate of being pollinated and low fruit abortion rate to ensure a high number of nuts at harvest. Size and dry weight of fruits and seeds were not proposed for a component of the timber ideotype, but they were found to be negatively correlated with stem growth, thus making them good predictors for timber ideotype.

2. Early leaf flush was correlated to faster growth, and does not necessirly cause bad form. Therefore, early leaf flush should be one trait of the timber production ideotype for black walnut, rather than late leaf flush. Meanwhile, pollen shed date was found to be positively correlated with leaf flush, therefore, early pollen shed may function in the same way as early leaf flush date does – an indicator of good stem growth for black walnut.

3. High photosynthetic rate (measured in end of July and August in 2011) did not have significant and consistant correlations with stem growth, probably due to the insignificant difference (a=0.05) in photosynthetic rate among clones, thus it may be not

an essential component of the timber ideotype of black walnut. High specific leaf area (SLA, measured in late July and early August in 2010 when leaves were fully expanded) was also expected to be an ideotype component for timber production, however, SLA in both lower and upper crown was found to be negatively correlated with stem growth. Thus, proposed “high SLA” may need to be revised to intermediate or low SLA. On the other hand, individual leaf area and mass in the upper crown was positively correlated with stem growth, and should be added to the timber ideotype for black walnut. As for total leaf area, although more total leaf area leads to faster stem growth, there were deviations from the regression line between total leaf area and stem growth, the characteristics of fast growing but with intermediate amount of leaf area (high growth efficiency) is ideal for timber production.

4. Foliar nitrogen concentration in both upper and lower crown (measured in late July and early August in 2011) was negatively correlated to stem growth, therefore, the proposed “intermediate to high foliar nitrogen concentration” should be revised to “intermediate to low foliar nitrogen concentration” with a condition that it is measured in late July and early August. Meanwhile, foliar carbon concentration in both lower and upper crown (measured in late July and early August in 2011) was negatively correlated with stem growth, thus “intermediate to low foliar carbon concentration” should be added to the timber ideotype for black walnut as well.

5. Branch frequency, average branch diameter, branch basal area per meter of stem length were all positively correlated with stem growth, however, because fewer number of knots, fewer area of knots are desirable traits for black walnut timber products such as veneer, a deviation from the regression lines between these traits and stem growth should be sought to meet such a balance, i.e., intermediate degree of branch frequency, branch diameter, and branch basal area per unit of stem length should be the ideotype component to insure both fast stem growth and decent product quality.

6. Angle of individual branches was negatively correlated with individual branch radial growth, and average angle of all living branches was negatively correlated with stem growth, thus smaller angle at both individual branch level and tree level are desirable characteristics for fast growing black walnut; however, with the concern that acute angle may reduce wood quality by disturbing larger volume of wood than flat angle, and the risk that branches with acute angle and similar size to the stem diameter where the branch attaches to may jepordize the stem form in the long run, the proposed ideotype component of “intermediate to large average branch angle” may be advised to “intermediate to small average branch angle” to achieve a balance between growth and quality, if acutely angled branches can be pruned in an intensive management regime.

7. Crown width was positively correlated with stem growth. However, balance may be sought via future breeding programs on the attributes combination of intermediate crown width and fast stem growth, and whole stand productivity may be improved on these intermediate or narrow crown types.

Based on the broad sensed heritability of and correlations of various traits, a crown ideotype for timber production with both verbal description and numeric range of the specific characteristics was presented in Table 6-1. Based on the strong correlations between a variety of traits and size and dry weight of fruits and seeds, a nut production ideotype for black walnut was presented in Table 6-2. Developing a nut production ideotype was not in the plan of this dissertation at the beginning, and the trees were not managed in the way of culturing fruit crops, thus, the nut ideotype proposed here may only suit well for landowners who want to benefit mainly from timber production but can still make some profit from nut production of these timber trees. This proposed nut ideotype may need to be revised in real fruit tree plantations. More characteristics of seeds need to be examined, such as kernel weight, kernel percentage, and the correlations between kernel weight and that of the whole seed and whole fruit, etc.

6.6 Future directions

Although crown ideotypes were proposed, there were still correlations that are important, but could not be investigated in this study. These issues need to be discussed and potential projects need to be conducted in the future to make additional determinations.

6.6.1 Establish correlations between early traits and final yields and quality

In forest tree improvement programs, early selection of traits that are highly related to economic yield is essential for success (Dickmann et al., 1994). For instance, height of seedlings was regarded as a common selection criterion among many of the traits. However, the correlations between height of seedlings and final yield of bolewood were reported to be inconsistent, sometimes even contradictory. This correlation was poor in some pine species (Zobel and Talbert, 1984), but strong with half-sibs of a number of conifer families (Greenwood and Volkaert, 1992). Also it was reported that increasing stand density had no effect on the height increment of Norway spruce [*Picea abies* (L.) Karst.] (Mäkinen and Hein, 2006), and increased space did not influence the height growth of Sitka spruce [*Picea sitchensis* (Bong.) Carr.] after 15 years of a re-spacing treatment in Scotland (Deans and Milne, 1999), indicating height growth rate was a highly heritable trait for Norway spruce and had little interaction with the environment (stand density). Most traits related to tree form are highly heritable, however, they are usually polygenic and require longer breeding cycles to establish (Dickmann et al., 1994).

Correlations between growth traits (diameter and growth) of juvenile and mature black walnut from progeny test were investigated by (McKeand et al., 1979; Rink, 1984; Beineke, 1989; Rink and Kung, 1995). Overall, these scientists found that family selection for diameter and height growth, which are regarded as highly heritable, can begin at age 8, while within-family selection can start after age 12. However, the correlation of growth traits in one year was more closely related to adjacent years (Rink, 1984). Clonal rankings of many traits changed during the course of rotation and tradeoffs exist for early selection, and thus a cost-benefit analysis may be needed to find the balancing point of time when selection can optimize both prediction accuracy and cost of selection (Tharakan et al., 2005). It would be necessary and beneficial to revisit the plantation to measure the growth and quality of these black walnut trees, and determine the relation between early growth/quality traits and the same traits at different ages.

6.6.2 Further stem and wood quality evaluation for black walnut

Wood quality is quite important for black walnut because its major product is veneer. However, because these trees cannot be destructively harvested, none of the following wood quality characteristics which require destructive sampling were evaluated: wood specific gravity, wood density, sapwood area ratio, and heartwood ratio. A series of parameters were examined to determine the bole quality of 35-year-old plantation grown black walnut, and they were: number of faces with frost cracks, stem sweep (deviation of the stem from the center vertical line in the butt log), grade defects (oversized knots, stem galls, stem cankers, lesions, suppressed bud clusters, adventitious bud clusters, bud distortions, and epicormic branches) in both butt and upper logs, height to the lowest branch, height to the first grade defect, and defects caused by branches in both butt and upper logs (Bohanek and Groninger, 2003). These traits mentioned above will need to be evaluated at harvest. Also, their relations with growth traits need to be established.

6.6.3 Compromise between growth and wood quality

Landowners were concerned with if fast grown trees will compromise on wood quality at various aspects of the end products (Lenny Farlee, personal communication). Bey (1968) reported that fast grown trees produced equal or better wood for operations such as planning, shaping, and turning. Englerth (1966) indicated that fast growing wood was tougher and denser (i.e. a higher specific gravity). Rink (1987) and Woeste (2002) reported that heartwood area, as one important measure of black walnut wood quality, was positively correlated with total tree height and diameter, meaning that wood quality may not be compromised by faster growth. Dark heartwood color, which is more desirable, tend to be related to slower growth (Rink, 1987). Plantation grown black walnut trees had wider growth rings and consequently wider latewood zones, thus, the vessel area in cross-section was reduced and poorer wood texture was produced, as opposed to the more uniform wood texture, which is favored by industry (Phelps and Workman, 1992). These issues may affect the value of fast growing clones.

6.6.4 Trying out denser plantings in the future

It may be valuable to define crown ideotypes for black walnut planted at higher densities than the trees in this study. The current density promotes large branches and thus requires a large work load of pruning. Denser spacing promotes natural pruning (Kurtz et al., 1984), reduced branch growth in walnut (Van Sambeek, 1989) and other commercial species, such as Douglas-fir (Maguire et al., 1991) and loblolly pine (Peterson et al., 1997). Although higher density plantings will require a thinning regimen which increases costs, planting black walnut trees in higher densities will help reduce the pruning load tremendously before the trees get a desirable length (6 to 8 m, or even more) of clear stem.

Higher densities reduced the number of branches per whorl and branch diameter in Norway spruce (Mäkinen and Hein, 2006). It was also reported that 35-year-old densely planted black walnut (2.7 × 2.7 m) had 31% fewer branch defects, 18% fewer grade defects in the upper log, 18% longer defect-free (grade defect) bole, and 20% longer branch-free bole in the butt log than black walnut that planted in a lower density (4 × 4 m) (Bohanek and Groninger, 2003).

6.6.5 The role of root stocks in black walnut ideotypes

Ideal characteristics of the rootstocks for black walnut ideotypes was beyond the scope of this study, mainly because destructive sampling of the trees were not permitted. Both scion and rootstock impact morphological, physiological characteristics, and growth (Dickmann et al., 1994), although the influence from rootstock is not expected to be heritable. In addition, rootstock can be changed to fit a particular culture regime when needed. Utilizing ground radar to characterize the morphological features of rootstocks or dig root systems to systematically measure their root structure, volume, and biomass at harvest time may be warranted.

6.6.6 Alternative plantation management for black walnut

Black walnut is well suited for a multi-cropping management system owing to its short growing season and sparse foliage. Black walnut imposes light shade on intercrops and it had deep roots that leave a shallow zone for intercrops to develop their roots (Kurtz et al., 1984). Different multi-cropping systems have been explored: timber and nuts; timber, nuts, and wheat; timber, nuts, winter wheat, soybean, and grazing (Kurtz et al., 1984). Trials where black walnut (*Juglans nigra* L.) or common walnut (*Juglans regia* L.) were planted together with nitrogen fixing species such as *Elaeagnus umbellata* in Europe and the USA had demonstrated impressive growth improvement (Finn, 1953; Campbell and Dawson, 1989; Buresti and Frattegiani, 1994; Buresti, 1995). This regime may become another option for landowners in Indiana.

6.7 References

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6.8 Tables

Table 6-1 A crown ideotype for black walnut (*Juglans nigra* L.) grown for stemwood production in a low density plantation, irrigated, and with an intensive silvicultural system

	Traits[1]	Range
Growth	Rapid height and diameter growth	15.8 – 18.1 cm of DBH by end of age nine; 10.8 – 12.3 m of height by end of age nine; 1.9 – 2.3 cm·year^{-1} of DBH growth and 1.4 – 1.8 m ·year^{-1} of height growth on average from age seven to nine
	Intermediate to wide crown	68 – 100 cm in crown radii growth on average between age seven and nine; crown radii kept between 2.7 – 3.2 m yearly by pruning between age seven and nine;
	Intermediate to high number of nuts, but Small sized nuts	225-438 fruits produced yearly on average between age seven to nine; Fruit size: 56-78 cm^3; Seed size: 10.8 – 15.3 cm^3;
	High growth efficiency (ratio of stem volume increment to total leaf area)	0.85 - 1.12 dm^3· m^2 at age eight
Phenology	Early leaf flushing but high survival after frost damage	Warm spring: 100 to 107 Julian day Cold spring: 114 to 121 Julian day
	Early pollen shedding	Warm spring: 117 to 124 Julian day Cold spring: 130 to 137 Juian day
Physiology	Low to intermediate specific leaf area	Upper crown: 99.7 -123.4 cm^2·g^{-1}; lower crown: 127.9 - 155.8 cm^2·g^{-1} in late July and early August.
	High individual leaf area and mass in upper crown	482 – 554 cm^2 · leaf^{-1} on average at full expansion; 4.6 – 5.6 g· leaf^{-1} on average at full expansion;
	Intermediate to low foliar carbon concentration	Upper crown: 45.5 - 48.0 %; lower crown: 43.8 - 46.3 % in late July and early August.
	Intermediate to low foliar nitrogen concentration	Upper crown: 2.47- 3.0 %; lower crown: 2.14 – 2.6 % in late July and early August.
Morphology and Allometry[2]	Intermediate to high branch frequency	13.6 - 18.4 m^{-1} at age eight; but lower branch frequency than the intercept of the reference clone as reflected from the branch frequency model

Table 6-1 continued

	Intermediate to high average branch diameter	2.69 - 3.19 cm at age eight; but smaller branch diameter than the reference clone when given a fixed tree – level dimension, such as DBH as reflected from the branch diameter model
	Intermediate to high branch basal area per m^{-1} stem	74.5 - 94.6 $cm^2 \cdot m^{-1}$ at age eight; but smaller branch basal area m^{-1} than the reference clone when given a fixed tree – level dimension, such as DBH, as reflected from from the branch basal area model
	Intermediate to small average branch angle	53- 66° at age eight;
	Intermediate to large total leaf area	125 – 168 m^2; but smaller total leaf area and mass than population average when relative to a given tree – level dimension, such as DBH or crown radius as reflected from the tree leaf area and mass models; and smaller leaf area and mass than population average when relative to a given branch diameter as reflected from the branch leaf area and mass models
	High portion of biomass (estimated volume) allocation to stem relative that to branches	55 – 61%
Stem form[3]	Straight stem	3.3 - 4.5

1. Intermediate to high: upper 50% of the range of clone mean of a characteristics; intermediate to low: lower 50% of the range; rapid/high: upper one third of the range; slow/small: lower one third of the range.
2. Morphology and Allometry: balance between fast growth and good wood quality, and towards a sparse/intermediate but efficient crown ideotype
3. a rubric of 1 to 5, with 1 being the most crooked, 5 being the most straight.

Table 6-2 A crown ideotype for black walnut (*Juglans nigra* L.) grown for nuts in a low density plantation, irrigated, and with an intensive silvicultural system

	Traits[1]	Range
Nut production and stem growth	Intermediate number of nuts	154-296 fruits produced yearly on average between age seven to nine;
	Intermediate to large sized nuts	Fruit size: 89-122 cm^3; Seed size: 17.6 – 24.3 cm^3;
	Slow height and diameter growth	11.1 - 13.4 cm of DBH by end of age nine; 7.7 – 9.3 m of height by end of age nine; 1.2 – 1.6 $cm \cdot year^{-1}$ of DBH growth and 0.6 – 1.0 $m \cdot year^{-1}$ of height growth on average from age seven to nine
Phenology	Late leaf flushing	Warm spring: 115 to 122 Julian day Cold spring: 125 to 132 Julian day
	Late pollen shedding	Warm spring: 132 to 139 Julian day Cold spring: 145 to 152 Juian day
Physiology	Intermediate to high foliar carbon concentration	Upper crown: 48.0 - 50.5%; lower crown: 46.3 - 48.8% in late July and early August.
Morphology	Intermediate to low branch frequency	8.9 - 13.6m^{-1} at age eight
	Intermediate to large average branch angle	66 - 80°
	Low portion of biomass (estimated volume) allocation to stem	44 - 55 %
Stem form[2]	Crooked stem	1 - 3

1. Intermediate: middle third quantile, from 33.3 to 66.6% of the clonal mean; Intermediate to large: upper 50% of the range of clone mean of a characteristics; Intermediate to low: lower 50% of the range; High: upper one third of the range; Slow/small: lower one third of the range.
2. a rubric of 1 to 5, with 1 being the most crooked, 5 being the most straight.

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- **Kejia Pang**, Michael Saunders, Charles Michler. Modeling branch characteristics of widely spaced black walnut (*Juglans nigra* L.) clones under an intensive management regime in Indiana, USA
- **Kejia Pang**, Keith Woeste, Charles Michler. Genotypic variation of phenonogical, physiological, and morphological traits and their repeatability estimates of 25 black walnut clones in Indiana, USA
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Presentations:

- **Kejia Pang**. Charaterization of black walnut (*Juglans nigra* L.) crown ideotypes. 2010 Summer Meeting Indiana Chapter of the Society of American Foresters. Sep 2010. West Lafayette, IN.
- **Kejia Pang** and Charles Michler. Advancing to a black walnut (*Juglans nigra* L.) ideotype. 2011 Forestry and Natural Resources Department Research Symposium. Apr 2011. Purdue University, West Lafayette, IN.
- **Kejia Pang** and Charles Michler**.** Growth Differences of Black Walnut (*Juglans nigra* L.) Crown Ideotypes. Center for Advanced Forestry Annual Meeting. June 2011. Seattle, WA.
- **Kejia Pang**, Kayla Leach, Lijie Zhao, and Charles Michler. Architectural Characteristics of Black Walnut (*Juglans nigra* L.) Crown Ideotypes. . Nov 2011. 2011 ESE-IGP Symposium, West Lafayette, IN.
- **Kejia Pang**, Kayla Leach, and Charles Michler. Defining Crown Ideotypes for Intensively Managed Black Walnut (*Juglans nigra* L.). Feb 2012. Sigma XI Graduate student research poster competition, West Lafayette, IN.
- **Kejia Pang**, Kayla Leach, and Charles Michler. Characterizing Crown Architecture for Black Walnut (*Juglans nigra* L.) Ideotypes in North Central Indiana. Mar 2012. 127th Annual Indiana Academy of Science Meeting, West Lafayette, IN.
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- **Kejia Pang**, Michael Saunders, and Charles Michler. Leaf mass and area models for even-aged black walnut (*Juglans nigra* L.) under an intensive culture regime in Indiana, USA. North American Forest Ecology Worshop. June 2013. Bloomington, IN.
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- Creating the Engaged Classroom: Discussion Techniques
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Community Engagement:

Fall 2010 organized the graduate and undergraduate research poster competition session for the 2010 ESE-IGP symposium, Purdue University

Fall 2009 – Spring 2011 FNR graduate student council member, helped organizing a variety of student activities; assistant editor for the departmental graduate annual magazine *Compass*

Sports:

National Aerobics Standard (China), Rank 6, 2007
Purdue 2nd Annual Half Marathon, Oct 19, 2013, Finisher (2:25:59.9)
Enjoy hiking, running, swimming, and a variety of workouts